Aquaculture Reports 43 (2025) 102964

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

Effects of hormonal treatments on spawning latency and egg production of captive silver trevally *(Pseudocaranx georgianus)*

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ARTICLE INFO

Keywords:
Induced spawning
Silver trevally
Human chorionic gonadotropin (hCG)
Gonadotropin-releasing hormone agonist (GnRHa)
Egg quality
Aquaculture

ABSTRACT

Controlling reproduction is a vital step in aquaculture to ensure the production of high-quality fertilized eggs in adequate quantities. The silver trevally *(Pseudocaranx georgianus)* is a candidate for the diversification and expansion of the New Zealand aquaculture sector, but initial research showed that it fails to spawn spontaneously in captivity. Therefore, we induced spawning in wild-caught, captivity-acclimated broodstock using an agonist of gonadotropin-releasing hormone (GnRHa) in slow-release implants or an injection of human chorionic gonadotropin (hCG). The GnRHa implants at a dose of 83–152 μg kg^{-1} body weight (BW) for females and 58–167 μg kg^{-1} BW for males induced spawning with latency times of 2 days post-administration. The hCG injection at a dose of 600 IU kg^{-1} BW for both males and females induced spawning with latency times of 8 days post-administration. Total egg production was comparable between GnRHa (~ 2.8 million eggs kg^{-1} BW) and hCG treatments (~ 3.5 million eggs kg^{-1} BW) with egg quality being variable and having a high percentage non-fertilized and dead eggs (66–84 %). On average, egg diameter and total body length of newly-hatched larvae were significantly larger from GnRHa-treated fish compared to those from hCG-treated fish ($P = 0.0121$ and $P < 0.0001$, respectively), while the average oil globule diameter of newly-hatched larvae was significantly smaller from GnRHa-treated fish compared to those from hCG-treated fish ($P = 0.0062$). Both hormonal treatments demonstrated "proof-of concept" in silver trevally by spawning adequate numbers of eggs, but optimization of the treatment is necessary (dose, administration time, etc.), to achieve better egg viability and fertilization success.

1. Introduction

In Aotearoa-New Zealand, there is a desire to diversify aquaculture production with new species, because until now production has been restricted to only three species, *i.e.* Chinook salmon (*Oncorhynchus tshawytscha*), Pacific oyster (*Crassostrea gigas*) and the green-lipped mussel (*Perna canaliculus*) (Symonds et al., 2018, 2019). As a result, new finfish breeding programs have been initiated in recent years, most notably one on the Australasian snapper (*Chrysophrys auratus*) (Ashton et al., 2019a,b; Catanach et al., 2019; Moran et al., 2023; Samuels et al., 2024; Wellenreuther et al., 2019), the wreckfish/hāpuku *(Polyprion oxygeneios)* (Symonds et al., 2014; Wylie et al., 2018, 2019; Camara et al., 2024), the yellowtail kingfish *(Seriola lalandi)* (Poortenaar et al., 2001; Symonds et al., 2014) and more recently on the silver trevally *(Pseudocaranx georgianus)* (Valenza-Troubat et al., 2022a).

The silver trevally is a member of the family Carangidae, known as "araara" by the indigenous Māori people of New Zealand and is a close relative of 'striped jack' or 'white trevally' *(Pseudocaranx dentex)* [formerly known as *Caranx delicatissimus*, Döderlein, 1884] cultured in Japan and Europe (Corriero et al., 2021a). Globally, several other

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https://doi.org/10.1016/j.aqrep.2025.102964
Received 3 December 2024; Received in revised form 15 June 2025; Accepted 2 July 2025
Available online 14 July 2025

species within the family Carangidae are also of significant aquaculture interest due to their high value and growth potential, and exceptional fillet quality (Corriero et al., 2021a). For example, the yellowtail kingfish supports commercial and recreational fisheries worldwide (Poortenaar et al., 2001), and detailed culture protocols have been developed to support aquaculture production (Moran et al., 2007; Symonds et al., 2014; Setiawan et al., 2016).

The first step in the establishment of an aquaculture species is the acclimatisation of captured wild fish broodstock with the aim of maturing reproductively in aquaculture facilities and producing fertilized eggs for larval rearing and fingerling production. Following this, the F_1-generation (F_1) fish must be reared to reproductive maturity and spawning of fertilized eggs, thus completing or 'closing' the life cycle in captivity and enabling the implementation of selective breeding to create elite lines with desired rearing and market traits (Gjedrem et al., 2012; Gjedrem and Robinson, 2014). However, unpredictable and irregular spawning, or the total absence of oocyte maturation is often faced in a wide variety of species when either wild-sourced broodstock or when F_1 breeders are reared in captivity (Mylonas and Zohar, 2000). These reproductive dysfunctions are a major bottleneck in production at a commercial scale and selective breeding progresses. Reproductive dysfunctions are particularly common in female fish, where broodstock that have completed vitellogenesis fail to undergo oocyte maturation, ovulation and spawning. This failure can be caused either because fish synthesize and store the gonadotropin hormone luteinizing hormone (Lh) in the pituitary during vitellogenesis, but do not release it when the appropriate environmental spawning conditions arrive (Mylonas et al., 1997a, 1998). Alternatively, the amount of released Lh into the bloodstream is low and insufficient to accomplish oocyte maturation, ovulation and spawning (Fakriadis et al., 2024). Ultimately, achieving controlled reproduction of high-quality fertilized eggs is a foundation for the establishment of new aquaculture species and any successful breeding program, and is a research objective of high priority.

As a measure to alleviate these reproductive bottlenecks in a large number of fishes, the administration of reproductive hormones has been used to induce oocyte maturation, ovulation and spawning (Zohar and Mylonas, 2001). To date, a variety of different hormones have been developed and administered successfully (Mylonas et al., 2010). One of the most promising therapies are synthetic agonists of gonadotropin-releasing hormone (GnRHa) (Hsueh and Jones, 1981; Sherwood and Adams, 2005), which mimic the actions of the native GnRH peptides from the hypothalamus that are targeting the pituitary gland to induce Lh synthesis/secretion. To date, GnRHa has been used widely on both marine species (*e.g.* Almendras et al., 1988, Amezawa et al., 2018, Wylie et al., 2019) and freshwater species (*e.g.* Taranger et al., 2003, Svinger et al., 2013, Yasmin et al., 2024), although successful application in some freshwater species - such as those of the family Cyprinidae - often requiring the concomitant administration of a dopamine antagonist (Peter et al., 1988; Akbari Nargesi et al., 2024). In marine fish, it has been shown that a dopamine inhibition of GnRHa stimulation of Lh synthesis/release in not very relevant, therefore GnRHa is usually used alone in spawning induction protocols. Another commonly used hormone is human chorionic gonadotropin (hCG), an Lh-like human hormone that acts directly at the level of the gonad (Mylonas et al., 2010). This hormone has been used successfully to induce spawning in rabbitfish (*Siganus guttatus*) (Ayson, 1991), milkfish *(Chanos chanos)* (Marte et al., 1988) and common sole *(Solea solea L.)* (Ramos, 1986). Within the last decade, the administration of recombinant proteins has become increasingly popular as therapies to promote reproductive processes and ameliorate reproductive dysfunctions in many species including Senegalese sole *(Solea senegalensis)* (Chauvigné et al. 2017), carp *(Cyprinus carpio)* (Aizen et al., 2017), anguillid eels (Nguyen et al., 2020; Jéhannet et al., 2023; Suzuki et al., 2024), yellowtail kingfish (Sanchis-Benlloch et al., 2017), flathead grey mullet *(Mugil cephalus)* (Ramos-Judéz et al., 2021), goldfish *(Carassius auratus)* (Mohammadzadeh et al., 2021) and greater amberjack (Seriola dumerili) (Lancerotto et al., 2025).

Similarly, in males, the same endocrine pathways can be manipulated with these hormones to enhance spermiation and increase milt volumes and/or quality (Mylonas et al., 1997b, 2010; Zohar and Mylonas, 2001; Lokman et al., 2016; Ramos-Júdez et al., 2022; Ventriglia et al., 2024). The ability to enhance spermiation has significant utility for the enhancement of fertilization success in regular broodstock management procedures. They are of increased importance for developing species-specific cryopreservation protocols for sperm from elite breeders in commercial aquaculture, and also for threatened species (Wylie et al., 2025), due to the significant increase in milt volume that they usually stimulate.

In Japan, striped jack - a congener of the silver trevally- is spawned routinely in captivity by the manipulation of broodstock tank water temperatures alone (Vassallo-Agius et al., 1998, 1999, 2001c; Watanabe et al., 1998) or in combination with hCG treatment (Vassallo-Agius et al., 2001a, 2001b). In Portugal, wild-caught captivity-acclimated broodstock of the same species have been observed to spawn spontaneously under ambient conditions (Nogueira et al., 2018) and after administration of GnRHa implants (Roo et al., 2012). However, research on wild-caught captivity-acclimated silver trevally broodstock has shown that they repeatedly reach advanced stages of vitellogenesis and spermatogenesis, but fail to complete oocyte maturation and spawning reliably when maintained under ambient photoperiod and water temperature conditions in Aotearoa-New Zealand (Valenza-Troubat et al., 2022a).

The objective of the present study was to develop broodstock management and spawning induction methods for wild-caught silver trevally to support fertilized egg production for further larval rearing and fingerling production. Based on previous research on striped jack (Vassallo-Agius et al., 2001b, 2001c; Roo et al., 2012), we tested experimentally if spawning could be induced in wild-caught captivity-acclimated broodstock using slow-release implants of a salmon GnRHa (target dose of 100 μg kg^{-1} body weight (BW)) or a single injection of hCG (target dose of 600 IU kg^{-1} BW), being the hormones used most commonly in marine fish induced spawning protocols. We evaluated the two hormones based on spawning kinetics in terms of latency and spawning duration, egg production and fertilization success.

2. Materials and methods

2.1. Broodstock origin and maintenance

Two broodstock cohorts were used. The first cohort was caught in 2012 as previously described by Valenza-Troubat et al. (2022a) and denoted as F_0 2012 broodstock. In brief, wild fish were captured initially during two net tows in February 2012 in the North Taranaki Bight. The live fish arrived at the Wakefield Key Finfish Facility (previously managed by The New Zealand Institute for Plant and Food Research Limited-in Nelson, Aotearoa-New Zealand) two days later, where they were acclimated to a single 4400 L tank. In 2014, the remaining broodstock (n = 19) were relocated to the Nelson Research Centre Finfish Facility, which is currently operated by The New Zealand Institute for Bioeconomy Science Limited (trading as Plant & Food Research) in Nelson, Aotearoa-New Zealand (41.2544° Longitude, 173.2812° Latitude).The second cohort was caught in 2018 (denoted as F_0 2018 broodstock) between May and August using baited hook and line in Tasman Bay (n = 44 individuals captured; 41 individuals were successfully acclimated to captivity to form a broodstock population; mean BW 2.5 ± 0.1 kg; mean fork length 54.2 ± 0.64 cm).

Initially, broodstock cohorts were maintained in separate 13,000 L tanks under ambient flow-through water temperature and photoperiod conditions (Fig. 1). Reproductively advanced F_0 2012 broodstock were used for the initial trial (Trial 1 in 2018). Thereafter, both the F_0 2012 and F_0 2018 broodstock cohorts were pooled together to form a single F_0 broodstock population for breeding attempts in subsequent seasons (*i.e.*

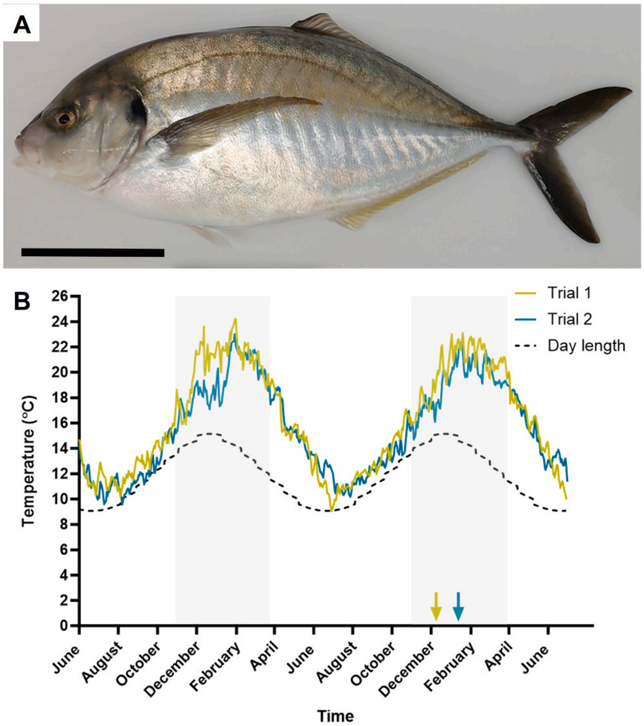

Fig. 1. A wild-caught captivity-acclimated (F_0) silver trevally broodstock (Carangidae: *Pseudocaranx georgianus*) from the breeding program at The New Zealand Institute for Plant and Food Research Ltd in Nelson, New Zealand (A; magnification bar = 15 cm). Ambient day length (▪) and temperature conditions under which wild-caught captivity-acclimated broodstock were maintained for Trial 1 (2018) and Trial 2 (2021) (B). The yellow solid line denotes ambient water temperatures from June 2017 to June 2019 ( ) while the green line denotes ambient water temperatures from June 2019 to June 2021 ( ). The shaded areas indicate the predicted spawning period for silver trevally (Rowling and Raines, 2000). The yellow arrowhead on the X-axis indicates the time of GnRHa implantation (GnRHa; Ovaplant®) in 2018 while the green arrowhead indicates the time of human chorionic gonadotropin (hCG; Chorulon®) injection in 2021.

for Trial 2 in 2021).

The Nelson Research Centre Finfish Facility receives ambient seawater from a sub-surface aquifer (underground bore), which is then filtered. The diet of both broodstock cohorts consisted of daily hand feeding till apparent satiation of formulated pellet feed (Ridley Corporation Limited), supplemented with squid *(Nototodarus spp),* and an in-house mixed seafood diet enriched with vitamins and minerals (Vitamin A, B1, B12, D, K, B9, B2, B6, B5, E, H, B3, Zinc, Iodine, Selenium and Inositol, Image Holdings Ltd, New Zealand) at regular intervals. Broodstock diet was supplemented with oil (NutraBood®, Nutrakol) for approximately one month prior to spawning for Trial 1 but not for Trial 2. Stocking densities of all tanks for both trials were maintained below 25 kg m^3. All broodstock were tagged with passive integrated transponder tags (GPT12, Biomark®) for identification. F_0 2012 broodstock were left to spawn spontaneously without the administration of hormonal therapies until 17 December 2018 (no spontaneous spawning was observed three years prior to this; broodstock were induced to spawn in 2015 with 600 IU kg^{-1} hCG; however, egg production data were not reported by Valenza-Troubat et al., 2022a). All animal handling and manipulations were approved and conducted in accordance with the guidelines of the Nelson Marlborough Institute of Technology Animal Ethics Committee (Approvals: AEC2018-PFR-02 and AEC2020-PFR-01).

2.2. Experimental trials to induce spawning

Two hormone therapies were tested: the first with slow-release implants containing GnRHa (Ovaplant®, Syndel, USA) in December 2018 (Trial 1) and the second, with an injection of hCG (Chorulon®, MSD Animal Health, New Zealand) in January 2021 (Trial 2). Prior to hormone induction, the sex, BW, and reproductive status (i.e., the developmental stage of gonads) of each individual broodstock was assessed as describe below.

2.2.1. Trial 1 (2018): induced spawning using GnRHa

A mixed-sex broodstock was maintained indoors in a single 13,000 L tank. For the duration of the predicted spawning season, the tank's effluent drain was fitted with an external passive egg collector (from 28 October 2018 to 28 February 2019), which was checked twice daily (between 8 and 9 am and between 3 and 5 pm). On 17 December 2018, when ambient water temperatures were 21.5 °C and spontaneous spawning was not evident, fish (n = 12; Table 1) were food-deprived for 48 h and sedated in the tank (20–30 ppm Aqui-S; Aqui-S New Zealand Ltd, Lower Hutt, New Zealand). Subsequently, a gonadal biopsy was taken by inserting a glass cannula (Natelson tube, 3 mm outside diameter) connected to a plastic tubing into the gonopore and applying gentle aspiration by syringe. Ovarian biopsies were placed in chilled Ringer's solution (180 mM NaCl; 4 mM KCl; 1.5 mM $CaCl_2$; 1.2 mM $MgSO_4$; 3 mM NaH_2PO_4; 12.5 $NaHCO_3$ – pH 7.5), examined under a light compound microscope (Model BX50; Olympus, Tokyo, Japan) and photographed with a digital camera (Nikon DS-Ri2). Using the method adapted from Mylonas et al. (2013), the diameters of the most advanced oocytes (n = 10) were then measured with NIS-Elements D Version 5.01 software (Nikon, Tokyo, Japan) to the nearest µm. The remaining portion of ovarian tissue was fixed in a solution of 4 % formaldehyde

Table 1
Wild silver trevally *(Pseudocaranx georgianus)* broodstock data (body weight, oocyte size, hormone type and dose) at the time of hormone administration on 17 December 2018 (Trial 1) and 12 January 2021 (Trial 2).

Trial 1 2018: induced spawning using GnRHa implants

Fish	Body weight (kg)	Mean oocyte diameter (µm ± SE)	Maximum oocyte diameter (µm)	Achieved GnRHa dose (µg kg^{-1})
♀1	3.3	470 ± 5.0	491	152
♀2	4.6	520 ± 4.7	535	109
♀3	4.6	514 ± 8.0	562	109
♀4	5.3	514 ± 9.6	578	94
♀5	3	486 ± 3.4	497	83
♂1	3	-	-	167
♂2	3.7	-	-	135
♂3	3.7	-	-	135
♂4	4.3	-	-	116
♂5	5.1	-	-	98
♂6	3.6	-	-	69
♂7	4.3	-	-	58
	♀$\bar{x}$ = 4.2	$\bar{x}$ = 501 ± 9.8		

Trial 2 2021: induced spawning using hCG injections

Fish	Body weight (kg)	Mean oocyte diameter (µm ± SE)	Maximum oocyte diameter (µm)	hCG dose (IU kg^{-1})
♀1	2.3	490 ± 5.1	513	600
♀2	3.3	476 ± 11.1	521	600
♀3	4.3	492 ± 5.8	524	600
♀4	4.5	515 ± 9.0	540	600
♀5	4.4	504 ± 6.9	537	600
♀6	4.6	496 ± 5.0	526	600
♂1	3.0	-	-	600
♂2	4.2	-	-	600
♂3	4.3	-	-	600
♂4	4.5	-	-	600
	♀$\bar{x}$ = 3.9	$\bar{x}$ = 496 ± 5.4		

and 1 % glutaraldehyde for histological processing (Section 2.3). Due to the firm muscular surrounding of the abdominal cavity, as observed in other carangids (Mylonas et al., 2004), milt samples could not be expressed by applying abdominal pressure and were instead collected using the glass cannula, as described above for the collection of ovarian biopsies. Sperm motility was subjectively screened from each male as motile or not after activation with seawater under a light compound microscope; this was not quantified.

Since the optimal dose of GnRHa for trevally was unknown, females in advanced stages of oogenesis (mean oocyte diameter ≥ 400 µm; Section 2.3) were administered a target dose of ~ 100 µg kg^{-1} BW (achieved dose range: 83–152 µg kg^{-1} BW; Table 1). To achieve this dose, female fish received up to two 250 µg Ovaplant® implants containing GnRHa; one on each side of the dorsal muscle. Due to the limited availability of remaining implants, some males received two implants while others received one implant. Thus, resulting in a dose range of 58–167 µg kg^{-1} BW (Table 1). Immediately afterwards, fish were placed in a new 13,000 L tank with the same ambient environmental conditions as described above. The broodstock tank was monitored for the presence of eggs over the following five weeks, and upon spawning, eggs were retrieved from the external passive egg collector by a measuring jug and bucket and assessed (Section 2.4). At the completion of the study, five weeks after the administration of GnRHa, an attempt was made to collect a second gonad biopsy (as described above) to re-assess the reproductive status of broodstock.

2.2.2. *Trial 2 (2021): induced spawning using hCG*

Mixed-sex broodstock were maintained as described for Trial 1, and fish for this trial were selected on 12 January 2021 from the single F_0 broodstock population formed after Trial 1. When ambient water temperatures reached 22.5 °C, the reproductive status of the broodstock was confirmed by gonopore cannulation and inspection of the gonadal biopsy as described above. Selected broodstock (n = 10; Table 1) received an intramuscular (IM) injection of hCG in the dorsal muscle at a target dose of 600 IU kg^{-1} BW. Fish were then returned to the same 13,000 L broodstock tank that also contained non-treated fish (due to the limited availability of tanks), and the tank was fitted with an external passive egg collector that was monitored for spawning as described below (Section 2.4).

2.3. *Gonadal histology*

Biopsies of gonadal tissue collected during both trials were fixed in a solution of 4 % formaldehyde and 1 % glutaraldehyde and then dehydrated through an ethanol series before being embedded in methacrylate resin according to the Technovit 7100 processing protocol (Kulzer, Wehrheim, Germany). Histological sections were cut to a thickness of 3 µm on a HM355S rotary microtome (Epredia, MI, United States) and stained in 1.3 % methylene blue and 0.2 % azure II prior to being counterstained in 2 % basic fuchsin. Sections were examined under a light compound microscope (Model IX83; Olympus Optical Co. Ltd., Tokyo, Japan) and photographed with a colour digital camera (DP74, Olympus Optical Co. Ltd., Tokyo, Japan). Female reproductive status was classed as described by Murai et al. (1985b) for striped jack where oocyte diameters of approximately 400 µm were defined as late vitellogenic.

2.4. *Egg production and quality*

For both trials, eggs were collected for assessment and incubation when spawning events were detected. The total volume, floating (buoyant) and sinking fractions were estimated in a measuring cylinder or jug before the weight of each fraction was estimated to the nearest gram (g) using an electronic balance. In brief, the buoyant fraction of eggs was strained in a container with a fine mesh base to enable the water to drain. Thereafter, the base of the mesh container was gently dried with a paper towel to remove excess water before being weighed. The same process was followed to calculate the weight of the sinking fraction. To establish the number of eggs per gram for each spawning season, 0.1 g of eggs was weighed in triplicate and the number of eggs per 0.1 g was counted. There were an estimated 2476 and 3074 trevally eggs per 1 g in 2018 and 2021, respectively. Sinking fractions of eggs from each spawn were discarded prior to incubation and excluded from further sampling. For egg production metrics, multiple spawns per day were pooled to estimate daily relative fecundity (eggs per kg^{-1} of mean female BW).

From the buoyant eggs, the fertilization percentage, defined as the number of fertilized eggs among 100–200 randomly selected eggs, was determined under a Nikon SMZ-18 microscope and photographed with a digital camera (Nikon DS-Ri2). Using NIS-Elements D Version 5.01 Software (Nikon, Tokyo, Japan), diameters of 20 floating eggs selected at random were measured from all spawns from GnRHa-treated fish (n = 8) and three out of the four spawns from hCG-treated fish.

Where possible, hatching success (as percentage of buoyant eggs) was estimated after 2 days of incubation in 450-L incubator tanks at 18.8–22.5 °C in Trial 1, and 20.6–24.1 °C in Trial 2 before rearing in the hatchery. A sample of newly hatched larvae was euthanised with an overdose of Aqui-S® and photographed with a Nikon SMZ-18 stereoscope fitted with a digital camera (Nikon DS-Ri2) to estimate larval total body length (TL), yolk sac area and oil globule diameter.

2.5. *Statistical analysis*

To evaluate potential differences in oocyte diameters, the data were first checked for normality (Shapiro–Wilk test) and equal variance. The data conformed to this and were subsequently analysed using a two-tailed unpaired *t*-test to test for differences in mean oocyte diameters between GnRHa- and hCG-treated fish. To avoid pseudo-replication, diameters of the most advanced oocytes (n = 10; mean ± SE; Table 1) for each hormone treatment were obtained as the mean value from each GnRHa-treated female (n = 5) and hCG-treated female (n = 6).

Differences in egg diameter between GnRHa- and hCG-treated fish were examined by a two-tailed non-parametric Mann–Whitney *U* test as data did not follow a normal distribution (even after log transformation). To avoid pseudo-replication, egg diameters (n = 20; mean ± SE) for each hormone treatment were obtained as the mean value from each spawning event of the GnRHa-treated fish (n = 8) and three out of the four spawning events from the hCG-treated fish.

To examine differences in the TL, yolk sac area and oil globule diameter of newly hatched larvae from GnRHa- and hCG-treated fish, the data were first evaluated to assess normality (Shapiro–Wilk test). All data were normally distributed, and then a two-tailed unpaired *t*-test with Welch's correction was used to assess potential differences. It should be noted that measurements were only collected from the first spawn of each trial. Analyses comparing mean oocyte diameter, egg diameter, larval TL, yolk sac area and oil globule diameter were performed using GraphPad Prism version 10 for Windows (GraphPad Software, California, USA), and all numerical data are presented as means ± SE. Differences between mean values were regarded as significant when $P < 0.05$.

3. Results

3.1. *Reproductive status and hormone administration*

3.1.1. *Trial 1 (2018): induced spawning using GnRHa*

At the time of hormone administration, biopsies revealed that the broodstock population consisted of seven males and five females. All five females had large vitellogenic oocytes (Fig. 2) with mean oocyte diameters ranging between 470 and 520 µm among fish (Table 1). Maximum oocyte diameters among fish ranged from 491 to 578 µm. Milt could not be expressed from males following the application of gentle,

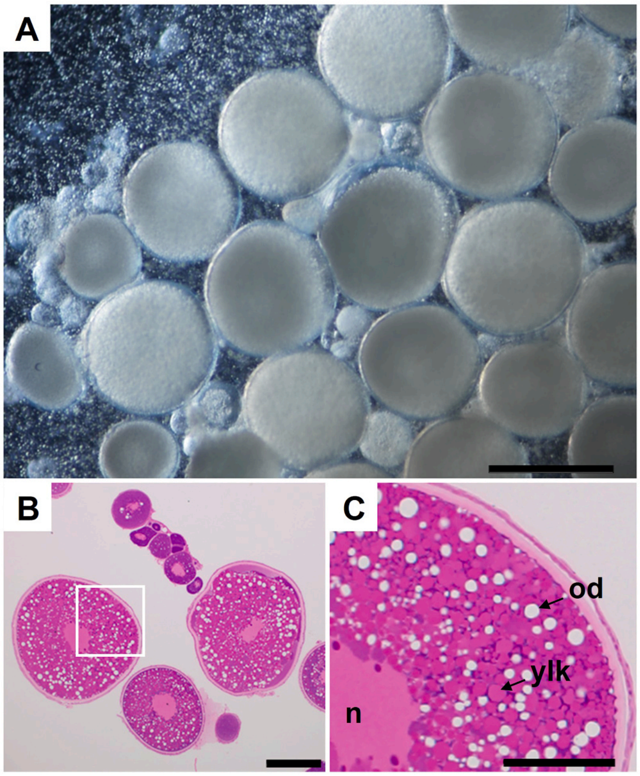

Fig. 2. Microphotographs of representative wet mounts preparations (A; magnification bar = 500 µm) and histological sections (B–C; magnification bars = 200 and 100 µm respectively) of ovarian biopsies from silver trevally *(Pseudocaranx georgianus)* exhibiting late vitellogenic oocytes at the time of hormone treatment with GnRHa implants (Ovaplant®) in 2018. The white box represents the area at higher magnification in the adjacent image. Abbreviations: n = nucleus; ylk = yolk platelet; od = oil droplets.

bilateral abdominal pressure; however, milt samples could be obtained with ease by cannulation with no apparent contamination with faeces, blood, or urine. Upon activation with filtered seawater and subjective observation under the microscope, sperm motility was observed to be vigorous. At five weeks post-GnRHa administration, no free-flowing milt was observed from the gonopore of males when assessed for spermiation but could be collected by cannulation. Of the five females, two still exhibited some late vitellogenic oocytes (Fig. 3), while the gonopore was closed in the remaining three females and these fish could not be biopsied.

3.1.2. Trial 2 (2021): induced spawning using hCG

As observed in Trial 1 at the time of hormone administration, biopsies revealed that all females in Trial 2 had large vitellogenic oocytes with mean diameters ranging between 476 and 515 µm among females (Table 1). No significant difference in mean oocyte diameters was detected from ovarian biopsies at the time of hormone treatment between GnRHa-treated and hCG-treated females (Table 2; two-tailed unpaired *t*-test; *t*-statistic = 0.4998, $P = 0.6292$, d.f. = 9). Maximum oocyte diameters among fish ranged between 476 and 515 µm. Upon activation with filtered sea water and subjective observation under the microscope, motility of sperm collected by cannulation was vigorous, as observed also in Trial 1.

Table 2
Cumulative spawning parameters of wild-caught captivity-acclimated silver trevally *(Pseudocaranx georgianus)* broodstock after induction of spawning with an agonist of gonadotropin-releasing hormone (GnRHa) (Trial 1; Year 2018) and human chorionic gonadotropin (hCG) (Trial 2; Year 2021).

	GnRHa	hCG	*P*
Ovarian biopsy			
Mean oocyte diameter (µm) (mean ± SE)	501 ± 9.8	496 ± 5.4	0.6292
Spawning			
Spawning length (days)	6	3	
Number of spawning events	8	4	
Total number of spawned eggs	12,004,787	13,789,196	
Total relative fecundity (eggs kg^{-1} mean BW)	2,858,283	3,535,691	
Percentage of buoyant eggs	16 %	34 %	
Fertilization success of buoyant eggs (%) (mean ± SE)	60 % (60.1 ± 8.7)	83 % (83.1 ± 8.4)	
Hatching success of buoyant eggs (%) (mean ± SE)	15 % (14.8 ± 4.3)	76 % (76.3 ± 2.4)	
Eggs			
Egg diameter (mean ± SE, mm)	0.9 ± 0.007	0.8 ± 0.05	**0.0121**
Newly-hatched larvae			
Total body length (mean ± SE, mm)	2.6 ± 0.06	2.2 ± 0.03	**< 0.0001**
Yolk sac area (mean ± SE, µm^2)	304.42 ± 21	352.3 ± 7.9	0.0693
Oil globule diameter (mean ± SE, µm)	205.7 ± 3.07	227.6 ± 6.07	**0.0062**

All numerical data are presented as means ± SE. Differences between mean values were regarded as significant when $P < 0.05$ (bold font). Data were analysed using a two-tailed unpaired t-test to test for differences in mean oocyte diameters between GnRHa- and hCG-treated fish. Differences in egg diameter between GnRHa- and hCG-treated fish were examined by a two-tailed non-parametric Mann–Whitney *U* test while differences in the body length, yolk sac area and oil globule diameter of newly hatched larvae from GnRHa- and hCG-treated fish were tested with a two-tailed unpaired t-test with Welch's correction.

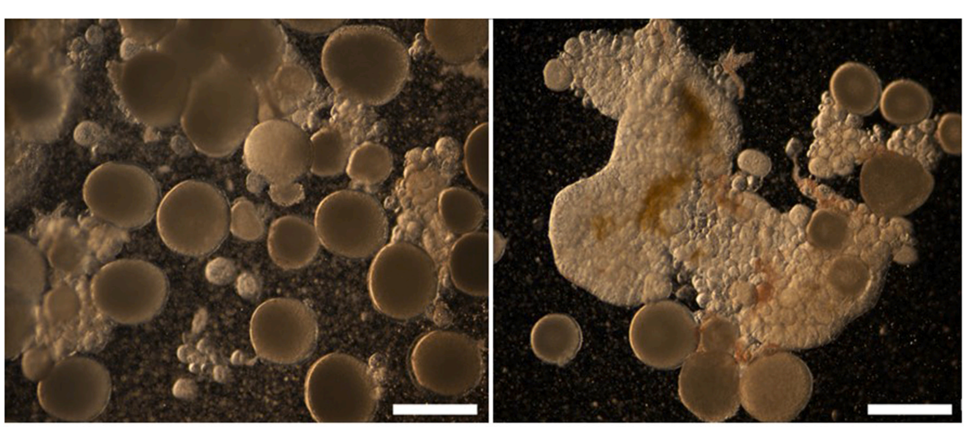

Fig. 3. Microphotographs of wet mounts preparations of ovarian biopsies from silver trevally *(Pseudocaranx georgianus)* exhibiting late vitellogenic oocytes five weeks after hormone treatment with GnRHa implants (Ovaplant®) in 2018. Magnification bar = 500 µm.

3.2. Egg production and quality

3.2.1. Trial 1 (2018): induced spawning using GnRHa

During the induced spawning trial in December 2018, eggs were first detected in the egg collector of the tank at approximately 44 h post-administration (7:30 a.m.). Egg production occurred daily with a total of eight spawning events observed and up to two spawning events per day until 7 days post-implantation; multiple spawns per day were pooled to estimate daily relative fecundity (Fig. 4**A**). Estimates of fertilization and hatching success of the buoyant eggs were variable and ranged between 29 % and 95 % and 3–27 %, respectively. The estimated total number of eggs released over the spawning period was 12,004,787 eggs (2,858,283 eggs kg^{-1}; Supplementary Fig. 1) with average fertilization and hatching percentages of buoyant eggs being 60 % (60.1 ± 8.7) and 15 % (14.8 ± 4.3), respectively (Table 2).

The average size of spawned eggs was 0.9 ± 0.007 mm in diameter with a range of 0.8–1.0 mm (Table 2). Hatching of larvae occurred at 1–2 days post-fertilization when eggs were incubated at 18.8–22.5 °C. Newly hatched larvae (n = 12) were 2.6 ± 0.06 mm in length, with a yolk sac area of 304.42 ± 21 μm^2, and an oil globule diameter of 205.7 ± 3.07 μm (Fig. 5).

3.2.2. Trial 2 (2021): induced spawning using hCG

During the induced spawning trial with hCG in January 2021, eggs were first detected in the egg collector at 8 days post-injection of hCG (9:00 a.m.). Egg production occurred daily and was highest on the first day. A total of four spawning events were observed until 10 days post-injection – with two different spawns being observed on day 10; multiple spawns per day were pooled to estimate daily relative fecundity (Fig. 4**B**). Estimates of fertilization and hatching success of the buoyant eggs ranged from 74 % to 100 % and 73 % to 81 %, respectively. The estimated total number of eggs released over the spawning period was 13,789,196 eggs (3,535,691 eggs per kg^{-1}; Supplementary Fig. 1) with average fertilization and hatching percentages of buoyant eggs being 83 % (83.1 ± 8.4) and 76 % (76.3 ± 2.4), respectively.

In 2021, the average spawned egg size was 0.8 ± 0.05 mm in diameter with a range of 0.6–0.9 mm in diameter. A Mann-Whitney *U* test revealed that on average the egg diameters were significantly smaller from the hCG-treated fish ($Md = 0.796$, $n = 3$) compared to egg diameters of GnRHa-treated fish ($Md = 0.906$, $n = 8$), $U = 0$, $P = 0.0121$ (Table 2).

When eggs were incubated at temperatures between 20.6 and 24.1 °C, hatching of larvae occurred at 1–2 days post-fertilization. Newly hatched larvae (n = 10) were 2.2 ± 0.03 mm in length, with an oil globule of 227.6 ± 6.07 μm in diameter. The mean TL of newly hatched larvae from hCG-treated fish was significantly smaller than that of larvae from GnRHa-treated fish (Fig. 5; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 6.99, $P < 0.0001$, d.f. = 15.23). On the contrary, mean oil globule diameters were significantly larger in newly hatched larvae from hCG-treated fish when compared to larvae from GnRHa-treated fish (Fig. 5; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 3.240, $P = 0.0062$, d.f. = 13.54). There was no significant difference in average yolk sac diameters of newly hatched larvae from GnRHa-treated and hCG-treated fish (Fig. 5; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 1.969, $P = 0.069$, d.f. = 13.87).

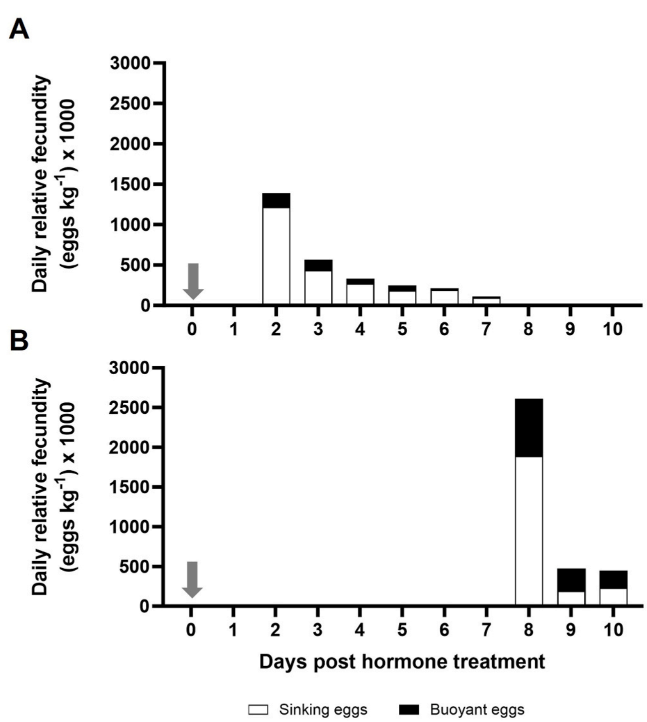

Fig. 4. Spawning performance of silver trevally *(Pseudocaranx georgianus)* treated with (A) GnRHa implants (Ovaplant®) at a target dose of 100 μg kg^{-1} BW (females) and 50–100 μg kg^{-1} BW (males) in 2018 and (B) human chorionic gonadotropin (hCG; Chorulon®) at a target dose of 600 IU kg^{-1} BW in 2021. Total number of buoyant and sinking (unviable) eggs are plotted as daily relative fecundity (eggs kg^{-1} mean female BW) for both trials. For data collected in 2018, multiple spawns on days 4 and 5 were pooled for each day; mean BW of females was 4.2 kg (n = 5). For data collected in 2021, multiple spawns on day 10 were pooled for that day; mean BW of females was 3.9 kg (n = 6). Grey arrows indicate time zero when fish were administered hormone treatments.

4. Discussion

The sustainability of aquaculture and the implementation of selective breeding programmes depends in part on the ability to control reproduction in captivity, and the production of adequate numbers of high-quality eggs from many individuals. This study highlights the existence of reproductive dysfunctions in wild-caught captivity-acclimated silver trevally and demonstrated that under ambient conditions a) fish readily complete vitellogenesis between late spring and summer (December–January) and b) reproductive dysfunctions occur during the later phase of the reproductive cycle, impacting oocyte maturation and spawning.

To date, it is unclear as to why this dysfunction exists in silver trevally, although it is likely a result of an unspecified chronic stressor or lack of an undetermined environmental cue (Zohar and Mylonas, 2001; Mylonas et al., 2010; Migaud et al., 2013). Such stressors for silver trevally could include inappropriate rearing conditions, such as tank size and/or depth and confinement, disturbance from routine husbandry practices, such as tank cleaning, and suboptimal water quality and lighting conditions. The endocrine cause behind the failure of oocyte maturation and spawning in other fish species is often the lack of Lh release from the pituitary during the onset of the natural spawning period (Rosenfeld et al., 2012; Fakriadis et al., 2024; Mylonas et al., 2010, 1998). In agreement with previous studies, we found that the administration of sustained-release implants containing GnRHa or an injection of hCG induced spawning in silver trevally. In our study, the reproductive outputs from both treatments were broadly comparable, and overall, the resulting egg quality was poor. These results highlight potential limitations of the treatments in this species and suggest future research directions, particularly in the context of findings from other carangid species that may be relevant to this teleost family.

4.1. Evaluating treatment success in terms of latency, spawning duration, and egg production

At the time of hormone administration, the mean oocyte diameters of females were comparable between GnRHa- and hCG-treated fish, however, latency times (i.e. duration of spawning and the number of

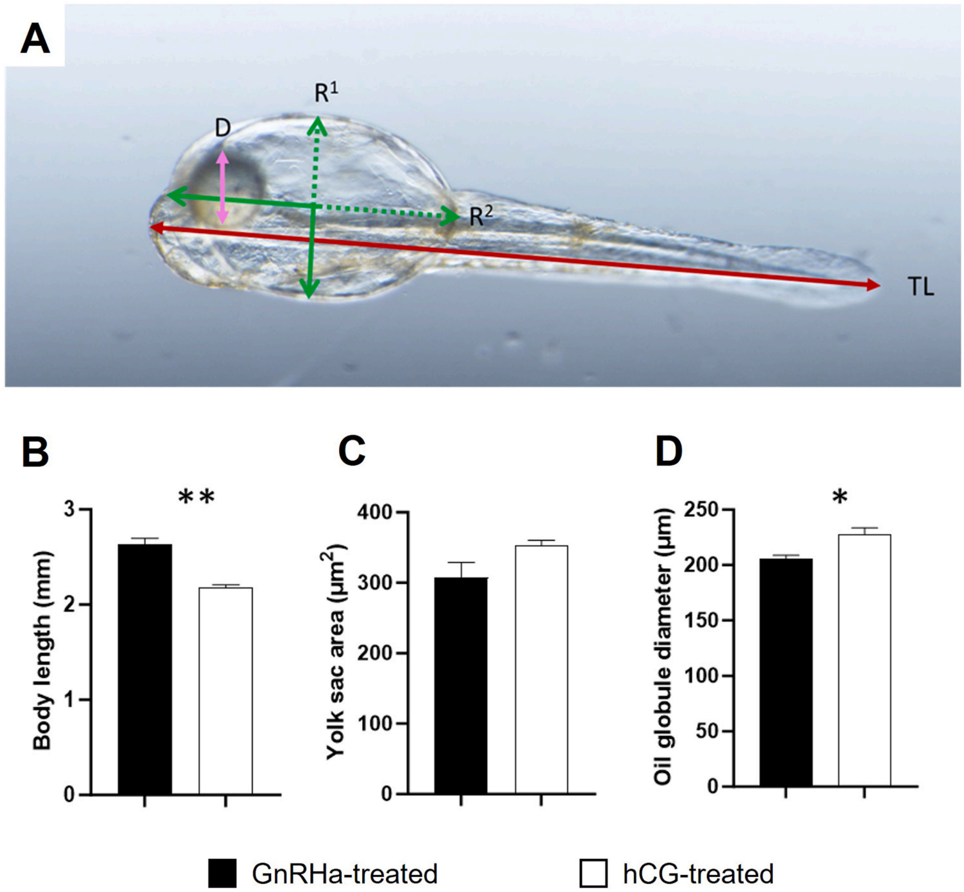

Fig. 5. Body morphometrics of silver trevally *(Pseudocaranx georgianus)* larvae collected at the time of hatching (A). Body length (B), yolk sac area (C) and oil globule diameter (D). Closed bars represent larvae body morphometrics collected from GnRHa-treated fish in 2018 while open bars represent larvae body morphometrics collected from hCG-treated fish in 2021. Abbreviations: D = oil globule diameter; R^1 = yolk sac radius 1; R^2 = yolk sac radius 2; TL = total body length. The data represent means ± SE. Significant differences between hormone treatments are denoted by $^{**}P < 0.05$, $^{***}P < 0.01$, $^{****}P < 0.0001$.

spawning events) differed between the two trials. Oocyte diameters and the associated large quantities of yolk observed in late vitellogenic oocytes of silver trevally in this study are comparable to those described previously for captive striped jack by Murai et al. (1985b). In wild silver trevally off the coast of New South Wales in Australia, Rowling and Raines (2000) observed that in some females, the ovaries contained mainly oocytes of 400 μm in diameter, along with a small number of hydrating oocytes with diameters exceeding 500 μm. This suggests that the reproductive status of female silver trevally at the time of hormone administration was appropriate in both trials, with most individuals having completed or nearly completed vitellogenesis. However, the duration that females remain in the post-vitellogenic stage before the onset of atresia remains unknown for this species.

Total relative fecundity between GnRHa- and hCG-treated fish was comparable with egg production being highest on the first day that spawning was detected in both hormone treatments and declining as days post-administration progressed. However, latency times differed between silver trevally treated with GnRHa and hCG, despite the two broodstock tanks' comparable mean oocyte diameters and water temperatures. Reports on the induced spawning of species from the genus *Pseudocaranx* using GnRHa are limited to Roo et al. (2012). In contrast, several studies exist on the induced spawning of striped jack using hCG (Vassallo-Agius et al., 2001a, 2001b). While latency time and pattern of egg production after successful spawning induction of striped jack using GnRHa implants (dose: 20 μg kg^{-1} BW) were not reported by Roo et al. (2012), 98 % of the estimated 4 million eggs produced were buoyant, with fertilization and hatching success of 98 % and 53 %, respectively.

In studies where striped jack were induced to spawn with hCG (dose: 600 IU kg^{-1}), broodstock started spawning at ~ 36–48 h post-injection when maintained at water temperatures of 22.0 °C (Vassallo-Agius et al., 2001a, Vassallo-Agius et al., 2001b). When manipulation of broodstock tank water temperatures is used alone to induce spawning of striped jack broodstock (i.e., using a single-step temperature increase to 22 °C), spawning can be observed within 24 h of reaching the target temperature (Watanabe et al., 1998). Given the notion that Lh preparations like hCG are potent and act directly at the level of the gonad (Mylonas et al., 2010), it remains unclear why hCG-treated silver trevally in our study took 8 days to spawn as opposed to the 36–48 h latency time observed in striped jack. The staggered production of eggs from GnRHa-treated fish is a likely reflection of the controlled-release delivery of the implant that promotes a long-term elevation of plasma Lh (Mylonas et al., 2010). Of the two hormone therapies trialled, the short spawning duration observed in hCG-treated fish may be advantageous to streamline hatchery production in which all eggs can be collected over a 3-day period (as opposed to a 6-day period from GnRHa-treated fish), thus producing larvae that belong to a similar age group and size-class for downstream rearing and refinement of on-growing protocols (see below). Refinement and future use of hormone therapies is also likely to be advantageous for synchronizing and enhancing the parental contributions and thus diversity of offspring for downstream genomic selection, during in-tank mass-spawning events (also see below).

4.2. *Egg viability, fertilization and hatching success*

Buoyant eggs from GnRHa-treated fish had average fertilization and hatching success of 60 % and 15 %, respectively, while those from hCG-treated fish had success of 83 % and 76 %. While the percentage of buoyant eggs as well as fertilization and hatching success appeared higher from fish treated with hCG, the overall quality of eggs from both hormone treatments was poor as evident by a high proportion (66–84 %) of sinking (unviable) eggs. This underscores the necessity to enhance our understanding of and improve gamete quality in this species prior to induction.

Although the factors that affect egg quality are still not very well known in fish, they are thought to include age and broodstock nutrition (Brooks et al., 1997; Bobe and Labbé 2010; Migaud et al., 2013), egg size (Stuart et al., 2020), and intrinsic properties or 'molecular cargo' of the egg and sperm themselves (Bobe and Labbé 2010; Migaud et al., 2013; Lubzens et al., 2017; Reading et al., 2018). Other factors related to husbandry (e.g., captivity-induced stress, water temperature, photoperiod, tank size, stocking density) and social interactions, such as sex ratios, dominance hierarchy and pheromones can also influence reproductive success and gamete quality (Bobe and Labbé 2010; Mylonas et al., 2010; Migaud et al., 2013; Alix et al., 2020). In terms of artificially induced maturation and spawning, the reproductive status of broodstock at the time of hormone administration, as well as the type and dose of the hormone administered have been shown to exert an influence (Zohar and Mylonas, 2001; Mylonas et al., 2010; Jerez et al., 2012). Of the latter, the exact stage of the ovaries at the time of hormone administration can have significant consequences on gamete quality (Mylonas et al., 2010). Inducing spawning too early, before vitellogenesis is complete in some females (*i.e.* smaller oocyte diameters), can lead to failed spawning or poor-quality eggs (Gardes et al., 2000). Similarly, inducing spawning too late, when the occurrence of follicular atresia has increased, can also result in poor outcomes, usually expressed as reduced fertilization and hatching success (Carral et al., 2003; Corriero et al., 2021b). Data on mean oocyte diameter of silver trevally indicated that vitellogenesis was completed and the reproductive status was appropriate to induce oocyte maturation in both trials. However, with knowledge gaps regarding their annual reproductive cycle in captivity, the timing of hormone application may have influenced egg quality, with December treatments potentially occurring too early compared to January treatments. Future research should clarify the reproductive cycle of captive silver trevally under ambient conditions to better understand the optimal timing for hormone application and its effects on egg fertilization and hatching success. The administration of hormones at a dose too high can also negatively affect egg quality (Mylonas et al., 1992, 2010). While hCG at a dose of 600 IU kg^{-1} BW appears to be standard practice for spawning induction of striped jack with no other doses reported (Vassallo-Agius et al., 2001a, 2001b), a GnRHa dose of 20 μg kg^{-1} given to broodstock by Roo et al. (2012) was far lower than that received by silver trevally in our study indicating that a lower dose could be examined in the future as a measure to improve egg quality and obtain higher egg fertilization and hatching success.

On average, spawned egg diameter and total body length of newly-hatched larvae were significantly larger from GnRHa-treated fish compared to those from hCG-treated fish, while the average oil globule diameter of newly-hatched larvae was significantly smaller from GnRHa-treated fish compared to those from hCG-treated fish. Without further investigation and replication, it is difficult to conclude whether differences in egg and larvae size can be attributed to the type of hormone used and how this might have affected larval survival in the present study. Interestingly, egg diameter has been identified as a useful predictor of egg quality in California yellowtail *(Seriola dorsalis)*, where spawned egg size decreased as the spawning season progressed and larger eggs typically are found to result in higher quality larvae (Stuart et al., 2020). On the contrary, smaller eggs usually led to higher quality in cultured yellow croaker *(Larimichthys polyactis)*, and using eggs later in the spawning season improved production outcomes (Hwang and Kang, 2025). Overall, the size range of spawned egg size observed in our study (0.6–0.9 mm in diameter), was comparable to that reported in wild silver trevally (range: 0.76–0.86 mm) that were strip-spawned and fertilized *in vitro* by James (1976). Mean egg diameters obtained from spontaneously spawning striped jack held in captivity were also comparable to those of silver trevally and have been reported as 0.953 mm (range: 0.88–1.02 mm) (Murai et al., 1987), 0.969 mm (Nogueira et al., 2018) and 0.950 mm (Honryo et al., 2020).

A likely avenue to improve egg fertilization and hatching success is through the appropriate formulation of specific broodstock diets to ensure that the nutritional requirements of the species are met (Brooks et al., 1997; Bobe and Labbé 2010; Migaud et al., 2013). The nutritional requirements of silver trevally remain largely unexplored, but studies on striped jack reveal that diet composition affects significantly reproductive output. In Japan, broodstock fed a raw fish diet (jack mackerel, squid and shrimp) produced comparable fertilization success (78 % and 80 %) to those fed commercial soft-dry pellets, but with higher egg production and buoyancy of 87 % (Watanabe et al., 1998). Further studies indicated that while the addition of zeaxanthin to dry pellets did not enhance reproductive metrics (Vassallo-Agius et al., 1999), astaxanthin improved broodstock condition and egg production without affecting egg quality (Vassallo-Agius et al., 2001a). Additionally, a mix of fish and squid meal in dry pellets improved egg quality but not production, while a combination of fish, squid, and krill meals had no effect (Vassallo-Agius et al., 2001a). Notably, a study by Nogueira et al. (2018) reported over 10.8 million eggs from striped jack fed a moist pellet diet supplemented with various marine species, achieving over 95 % fertilization success for buoyant eggs. These findings underscore the potential for developing species-specific diets to enhance spawning performance and meet the nutritional needs of silver trevally by drawing on insights from closely related species.

Sperm quality is another important factor affecting fertilization and hatching success of eggs (Bobe and Labbé 2010; Gallego et al., 2013; Mylonas et al., 2017; Marc et al., 2024). While spermiation was not observed from males when light abdominal pressure was applied, sperm samples could be collected with ease by cannulation. This enabled the visual inspection of sperm by light microscopy and showed that sperm were vigorously motile upon activation in seawater. A comprehensive assessment of sperm quality (e.g., using computer-assisted sperm analysis, CASA) and understanding factors that influence this are future research priorities for silver trevally. Such information also provides a foundation for the development of species-specific sperm cryopreservation protocols for the downstream cryobanking of genomic resources (Mylonas et al., 2010, 2017; Wylie et al., 2025).

4.3. Opportunities and challenges associated with the selective breeding and future avenues of research that are critical to achieve controlled reproduction

Our findings indicate that both hormone therapies can address effectively the reproductive dysfunction of silver trevally, facilitating the production of fertilized eggs. Implementing selected-pair matings through in-tank spawning or *in vitro* fertilization from high-performing individuals will enhance selective breeding efforts. Recent multi-omics studies have provided valuable insights into the genetic architecture of growth in silver trevally (Catanach et al., 2021; Valenza-Troubat et al., 2022a, 2022b, 2022c), revealing promising heritability values for growth traits (0.27–0.76) (Valenza-Troubat et al., 2022a) and temperature-modulated growth responses (Valenza-Troubat et al., 2022c); something that has also been reported in otehr finfish aqaucl-ture candidated (Wellenreuther et al., 2019). Additionally, molecular pedigree analyses have shown a bias in parental contribution during mass spawning events (Valenza-Troubat et al., 2022a), a phenomenon observed commonly in other species (Bright et al., 2016; Ashton et al., 2019b; Nousias et al., 2020; Schmidt et al., 2021; Superio et al., 2021). Thus, refining spawning induction protocols with hormone therapies may improve spawning synchronization and offspring diversity for genomic selection.

With the ability to spawn wild-caught captivity-acclimated broodstock on demand, research avenues open to optimize larval rearing protocols for F_1 progeny, understand the effect of nutrition on growth performance in land-based facilities and sea pens, and describe the endocrine control of gametogenesis, spawning and subsequent reproductive output from captive-bred individuals. This will aid in determining age at sexual maturity, estimating generation intervals for selective breeding, and identifying reproductive dysfunctions in F_1 broodstock, which is crucial as such issues can diminish in successive generations (Zohar and Mylonas, 2001; Mylonas et al., 2010) or emerge in captive-bred fish (Morais et al., 2016; Wylie et al., 2019; Fatsini et al., 2020; Lancerotto et al., 2025). Future studies should also examine the effects of conditioning silver trevally broodstock in sea pens during the year, before transferring them to land-based facilities for induced spawning using hormone therapies, or water temperature manipulation, as done routinely in Japan with striped jack (Vassallo-Agius et al., 1998, 1999, 2001c; Watanabe et al., 1998). Spontaneous spawning may also occur in wild-caught, captivity-acclimated silver trevally given sufficient adaptation time, as seen in striped jack broodstock maintained in tanks for extended periods (Murai et al., 1985a; Nogueira et al., 2018). And finally, assessment of egg quality could be improved by developing and employing the use of microtiter well-plates to estimate embryo and larval survival as established for greater amberjack (Fakriadis et al., 2019). The latter will be useful for elucidating the effects of hormone type and dose as well as broodstock diets on gamete quality as outlined above.

4.4. Conclusions

Silver trevally is a promising species for diversifying New Zealand's aquaculture sector, particularly in the warm waters around the North Island and parts of the South Island. Our trials showed that both GnRHa and hCG hormone therapies addressed effectively the reproductive dysfunction of failure to undergo oocyte maturation and spawning, enabling the production of fertilized eggs for larval rearing. Given the higher synchronization of the induced egg production, we prefer the use of hCG in silver trevally. However, future research should focus on optimizing hormone therapies to facilitate spawning on demand and ensure synchronized breeding of selected individuals, but also on understanding the environmental and husbandry conditions necessary for spontaneous spawning and out-of-season production of high-quality eggs. Key research areas include optimizing broodstock diets to enhance gamete and larval quality, and improving larval rearing protocols. Additionally, ongoing implementation of multi-omics approaches in selective breeding to assess the heritability of desirable traits and developing cryobanking for preserving genomic resources from elite breeders are crucial for the long-term sustainability of silver trevally aquaculture.

Author Statement

The work described has not been published previously except in the form of a conference abstract. This article is not under consideration for publication elsewhere.

CRediT authorship contribution statement

Flavio F. Ribeiro: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Warren Fantham:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Matthew J. Wylie:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Morgan E. Puklowski:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Ria Rebstock:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology. **Nicola Shaw:** Writing – review & editing, Visualization, Resources, Methodology. **Abigail Elizur:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Maren Wellenreuther:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization. **Constantinos C. Mylonas:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Keitaro Kato:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Maren Wellenreuther reports financial support was provided by Ministry of Business Innovation and Employment. Maren Wellenreuther reports financial support was provided by Royal Society of New Zealand. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to acknowledge the staff that assisted with the breeding and husbandry operation for the trevally populations in the Nelson Research Centre Finfish Facility. This research was funded by the Royal Society of New Zealand Catalyst Seeding General Contract "Enabling breeding of indigenous aquaculture species by overcoming reproductive dysfunctions" CSG-PAF1803 (to MW and MJW), and through the MBIE Endeavour Program "Accelerated breeding for enhanced seafood production" (#C11X1603) to MW.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2025.102964.

Data availability

Data will be made available on request.

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