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Hormonal profiles and reproductive development of hatchery-reared first filial (F1) generation silver trevally (*Pseudocaranx georgianus*, Carangidae)

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ABSTRACT

We examined the annual (maiden) reproductive cycle of hatchery-reared first filial (F1) generation silver trevally *(Pseudocaranx georgianus)* by tracking ovarian development and plasma levels of follicle-stimulating hormone (Fsh), luteinizing hormone (Lh), and estradiol-17β (E2). Our aims were to determine the age at puberty, identify reproductive dysfunctions, and lay the groundwork for manipulating the spawning season. To achieve this, mixed-sex two-year-old fish (n = 424) were maintained in a 13-m^3 tank under ambient conditions. Baseline samples were collected in April 2018, followed by near-monthly sampling (every 4–6 weeks) from July 2018 to April 2019. Puberty occurred at 3 years of age. Fish showed distinct seasonality in their reproductive cycle, with a clear peak in activity during the months of November to December (late spring/early summer). Reproductive development in females was limited, with only 2.7 % out of 113 females sampled achieving late vitellogenesis, and no instances of oocyte maturation or spontaneous spawning were observed. Contrary to increasing plasma E2 content as oogenesis progressed, plasma concentrations of Lh and Fsh remained relatively stable across oogenesis stages. The lack of increased plasma Lh suggests that reproductive dysfunction (absence of spontaneous spawning) may be due to insufficient quantities of Lh being released into the bloodstream to accomplish oocyte maturation, ovulation and spawning.

1. Introduction

Aquaculture, the controlled cultivation of aquatic organisms, has become an indispensable sector in global food production, driven by the rising global demand for seafood and the growing pressures on wild fish populations. As fish stocks in the wild continue to decline because of factors such as overfishing, habitat degradation, and climate change, aquaculture provides a promising solution to meet the increasing needs for protein-rich foods, thus contributing significantly to food security (FAO, 2022). Aquaculture not only offers a means to alleviate the burden on natural marine resources but also serves as a critical economic driver, supporting livelihoods and economic growth in coastal regions worldwide (FAO, 2022).

Among the diverse groups of fish cultivated in aquaculture, the family Carangidae, commonly including but not limited to, amberjacks, trevallies and pompanos, has gained significant attention because of their high market value, rapid growth rates, and adaptability to various farming conditions, as reviewed by Corriero et al. (2021a). Within the Carangidae family, members of the genus *Pseudocaranx* are species with growing significance in aquaculture owing to their rapid growth, high market demand, and excellent meat quality (Corriero et al., 2021a; Kurobe and Kiryu, 2024). In Japan, striped jack or white trevally *(Pseudocaranx dentex)* is a commercially important aquaculture species, with production increasing rapidly since the 1970s (Honryo et al., 2021; Kurobe and Kiryu, 2024). Interest in this species is also emerging in Portugal, with the first report of spontaneously spawning, wild-caught,

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captivity-acclimated broodstock by Nogueira et al. (2018). Meanwhile in Aotearoa-New Zealand (NZ), the silver trevally *(Pseudocaranx georgianus)* (also known as araara by the indigenous Māori people of NZ) has been identified as a potential candidate species to diversify a salmon- and shellfish-dominated aquaculture sector (Camara and Symonds, 2014; Symonds et al., 2019; Valenza-Troubat et al., 2022a).

The successful aquaculture of emerging finfish species hinges on several factors, including optimal environmental conditions, nutrition, and effective breeding strategies. However, one of the most significant challenges in the aquaculture of these species is achieving and subsequently controlling successful reproduction in captivity. To date, advances in the development of silver trevally as an aquaculture species include the assembly of a genome and establishment of muti-omics approaches to understand the genetic architecture and heritability of growth (Valenza-Troubat et al., 2022a; Valenza-Troubat et al., 2022b; Valenza-Troubat et al., 2022c); the development of a molecular sex marker to distinguish the sex of broodstock non-lethally (Catanach et al., 2021); and the development of hormone therapies to induce spawning in wild-caught, captivity-acclimated broodstock (Wylie et al., 2025). With the ability now to produce and rear first-filial (F1) progeny, there is an opportunity to investigate the endocrine control of gametogenesis, age at puberty and spawning capacity of captive-bred individuals, as well as identify reproductive dysfunctions that may impede production and/or selective breeding initiatives.

The brain-pituitary-gonad (BPG) axis is a crucial neuroendocrine pathway that regulates reproductive functions in vertebrates, including fishes. This system orchestrates the communication between the brain, the pituitary gland, and the gonads (ovaries and testes), coordinating the release of hormones that control various aspects of reproduction, such as gametogenesis, sexual maturation, and reproductive behaviour. In response to environmental stimuli, the hypothalamus in the brain releases gonadotropin-releasing hormone (GnRH), which stimulates the pituitary gland to secrete gonadotropins (GTH)—luteinizing hormone (Lh) and follicle-stimulating hormone (Fsh) (Zohar et al., 2010). These hormones then act on the gonads, promoting gametogenesis and the production of sex steroids, which are essential for the development of eggs and sperm (Lubzens et al., 2017). The intricate interplay between these components of the BPG axis is crucial for the timing and success of spawning events, thus making it a focal point for researchers aiming to enhance reproductive success of fishes in captive settings.

Studies on the reproductive biology of wild *Pseudocaranx* species are limited to research from New South Wales, Australia (Rowling and Raines, 2000), and the central North Atlantic (the Azores) (Afonso et al., 2008). In Australia, both sexes can mature at body lengths 10–20 cm, but typically reach sexual maturity at 26–28 cm. Gonadosomatic index (GSI) values had a broad peak for both sexes between September and March, indicating a broad spawning period from spring to autumn – with ripe females most abundant between October and March (Rowling and Raines, 2000). In the North Atlantic, maturity occurs around body lengths of 27.8–30 cm and the spawning season lasts from June to September – evident by the presence of ripe fish during this time (Afonso et al., 2008). Reproduction was closely linked to seawater temperatures with GSI values increasing as spring temperatures increased; spawning commenced round 19°C and ceased when water temperatures reached their peak (Afonso et al., 2008).

By integrating knowledge of reproductive biology, environmental management, and behavioural ecology, effective practices can be developed that promote sustainable production of high-quality gametes from broodstock. Therefore, our aim was to examine ovarian development in F1 silver trevally undergoing their first (maiden) reproductive cycle in captivity when maintained under ambient water temperature and daylength conditions. Our primary goals were to determine the age at puberty for this species in captivity, to track changes in ovarian morphology, and to assess plasma concentrations of Fsh, Lh, and estradiol-17β (E2) in relation to daylength and water temperature to establish a foundation for manipulating the spawning season through photo-thermal interventions and identify any reproductive dysfunction. We discuss these findings in the context of closely related species within the Carangidae family, offering practical guidelines for aquaculture initiatives to inform effective reproductive strategies.

2. Materials and methods

2.1. Experimental fish

Beginning in February 2018, pre-pubertal F1 silver trevally aged two years and three months old (brood year 2015; n = 424; initial mean body weight 309 ± 3 g; initial mean fork length 24.4 ± 0.07 cm) produced at the Nelson Research Centre Finfish Facility of The New Zealand Institute for Bioeconomy Science Limited (formerly, The New Zealand Institute for Plant and Food Research Ltd) in Nelson, NZ (41.2544° Longitude, 173.2812° Latitude), were selected to study their reproductive cycle in captivity. Sporadic sampling of fish from the same population prior to the age of two years old showed no evidence of advancement in gonadal development (unpublished data). All fish were maintained indoors in a single 13-m^3 broodstock tank under ambient photoperiod and temperatures of aerated flow-through water (Fig. 1). Tank water parameters consisted of salinities between 33–35 g/L, oxygen levels near to saturation (90–100 %), a pH of around 8.00 and a flow of 28–35 % turnover per hour. Nitrogen levels were kept below 0.5 mg/L. The tank was fitted with an external passive egg collector as described by Wylie et al. (2025) for the duration of the predicted spawning season (28 October 2018–28 February 2019) of wild-caught captivity-acclimated silver trevally broodstock maintained in the same facility under ambient conditions. Fish were hand-fed daily until satiation on a diet of formulated pellet feed (Ridley Corporation Limited) and supplemented with frozen squid *(Nototodarus spp)*. Animal handling and manipulations were approved and conducted in accordance with the guidelines of the Nelson Marlborough Institute of Technology (NMIT) - Te Pūkenga Animal Ethics Committee (Approvals: AEC2018-PFR-02).

2.2. Sample collection

Baseline samples were collected from euthanised fish in April 2018 (n = 10 females and 10 males) and again 12 weeks later in July (n = 11 females and 4 males). From July onwards, fish were sampled at near-monthly intervals (every 4–6 weeks) through the reproductive cycle until April 2019 (Table 1). As the tank contained both male and female fish, up to 25 fish were sampled per time point until 9–12 females had been collected. Blood plasma and tissue collection for male fish were completed as described for females (outlined below). However, data from males are not described further in this paper.

Fish were starved for two days prior to sampling. At each sampling point, all fish in the tank were lightly sedated with 20–23 ppm Aqui-S® (Aqui-S New Zealand Ltd, Lower Hutt, NZ). Twenty-five fish were netted at random and transferred to a 200-L holding tank. From there, fish were individually subjected to complete sedation and euthanasia by overdose in anaesthetic (40 ppm Aqui-S) prior to dissection.

Blood samples were collected from each fish to estimate circulating concentrations of plasma sex steroids (E2) and gonadotropins (Fsh and Lh). To obtain plasma for E2 measurement, a 2-mL blood sample was collected from the caudal vasculature of each fish using an 18-gauge needle and syringe. Once collected, the blood was transferred to a 2-mL microcentrifuge tube containing 25 μL of 200 mg/mL ethylenediaminetetraacetic acid to prevent clotting, and stored on ice. To obtain plasma for measurement of gonadotropins, a second 2-mL blood sample was collected as described above but using heparinized syringes (heparin 30 iu/mL). Blood was then transferred to a 2-mL microcentrifuge tube containing 5 μL of heparin (45 iu per tube) to prevent clotting, and mixed as described above. Blood plasma was extracted from all blood samples by centrifugation at 10,000 rpm at 4°C for 10 min and then stored in 200-μL aliquots at −80°C until sex steroid

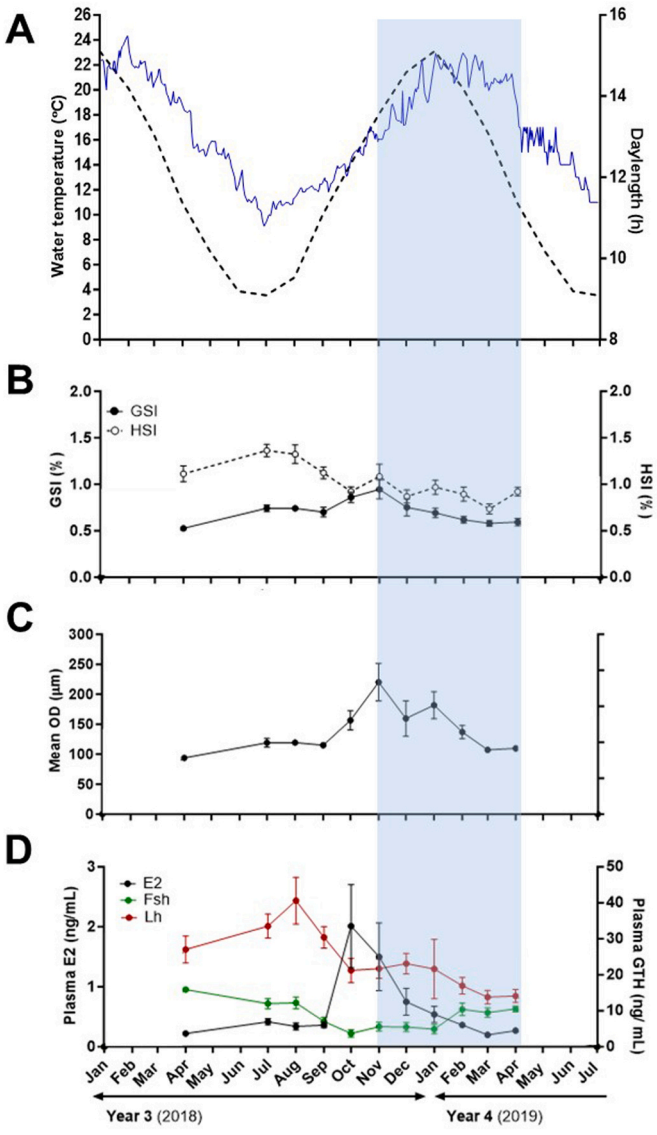

Fig. 1. Ambient day length (▬) and water temperature (▬) conditions under which hatchery-reared first filial (F1) generation silver trevally *(Pseudocaranx georgianus)* were maintained to describe an annual (maiden) reproductive cycle (A). Sampling occurred at near-monthly intervals from April 2018 to April 2019 (n = 9–12 females per sampling point). The shaded area indicates the predicted spawning period for silver trevally (Rowling and Raines, 2000). Annual changes in gonadosomatic index (GSI) and hepatosomatic index (HSI) (B), oocyte diameter (OD) (C), and plasma estradiol-17β hormone (E2), follicle-stimulating hormone (Fsh) and luteinizing hormone (Lh) concentrations (D). Data in B–D are shown as means ± SE.

quantification by radioimmunoassay (RIA) (Section 2.4) and gonadotropin quantification by enzyme-linked immunosorbent assay (ELISA) (Section 2.5).

After blood sampling, gonads and liver were dissected and weighed to enable gonado- and hepatic-somatic indices to be calculated. The GSI was calculated according to the following formula: GSI (%) = (gonadal weight [g]/BW [g]) × 100 %. The hepatosomatic index (HSI) was calculated according to the following formula: HSI (%) = (liver weight [g]/BW [g]) × 100 %.

A fragment of gonadal tissue (ovary and testis) was fixed in a solution of 4 % formaldehyde-1 % glutaraldehyde (Mylonas et al., 2013) for histological processing to confirm the sex of each fish (Section 2.3). A wet mount biopsy was also prepared by placing a fragment of ovary in 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 mM $NaHCO_3$ – pH 7.5) on a microscope slide to determine mean oocyte diameter as described previously by Wylie et al. (2025).

Table 1
Sampling number, date, body weight (BW, g), and fork length (FL, mm) (mean ± SD) of male and female silver trevally *(Pseudocaranx georgianus)* dissected at each time point during the annual reproductive cycle.

Sampling	Date	♀n	♀ BW (g)	♀ FL (mm)	♂n	♂ BW (g)	♂ FL (mm)
1	12/4/18	10	371 ± 52	259 ± 7	10	367 ± 37	261 ± 9
2	5/7/18	11	461 ± 70	272 ± 14	4	406 ± 71	263 ± 13
3	2/8/18	10	462 ± 56	277 ± 11	7	506 ± 82	282 ± 11
4	6/9/18	10	501 ± 53	280 ± 9	4	495 ± 34	280 ± 10
5	11/10/18	10	471 ± 56	279 ± 8	4	462 ± 80	273 ± 16
6	15/11/18	9	548 ± 139	285 ± 20	16	539 ± 82	294 ± 12
7	20/12/18	12	601 ± 118	301 ± 18	5	574 ± 135	294 ± 24
8	17/1/19	10	609 ± 92	305 ± 14	5	638 ± 109	311 ± 12
9	21/2/19	11	626 ± 71	306 ± 13	3	665 ± 98	317 ± 10
10	19/3/19	10	691 ± 73	318 ± 10	8	735 ± 130	328 ± 25
11	17/4/19	10	606 ± 49	299 ± 8	10	690 ± 218	320 ± 24
Total		113			76		

2.3. Gonadal histology

Samples of gonad fixed in a solution of 4 % formaldehyde-1 % glutaraldehyde were 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 as previously detailed by Wylie et al. (2025). The assessment of reproductive stage of females was adapted from Murai et al. (1985a) for striped jack and from Corriero et al. (2021a) for greater amberjack *(Seriola dumerili)* on the basis of the most advanced oocyte stage, the occurrence of post-ovulatory follicles and atretic follicles found within the ovary (Fig. 2). In brief, ovarian development was divided into the five following reproductive stages (Fig. 2; Stages I–V). Stage I: Immature = perinucleolar stage oocytes (PN; oocyte diameters ~70–120 µm), II: Lipid/cortical alveoli stage oocytes (CA; oocyte diameters ~120–200 µm), III: Early vitellogenic oocytes (EV; oocyte diameters ~200–400 µm), IV: Late vitellogenic oocytes (LV; oocyte diameters ~ ≥400 µm), and V: Atretic oocytes (AT).

2.4. Estimation of plasma E2 concentrations by RIA

Concentrations of plasma E2 were estimated by RIA as described by Lokman et al. (1998) with the following alterations. For silver trevally, dispensed plasma volumes in borosilicate glass tubes ranged between 20 and 50 µL, so as a measure to keep extraction volumes constant for the assay, smaller samples were mixed with phosphate buffered saline (PBS; pH 7.5) to obtain a total volume of 100 µL per tube. During the steroid extraction process, plasma proteins were denatured by heating all samples to 95°C for 3 min. After heat-treatment, 1 mL of diethyl ether was added to each sample followed by a brief vortexing (15 s) and freezing on dry ice to retrieve the steroid-containing diethyl ether. The diethyl ether extraction was repeated three times for each sample and the extracts were combined. After evaporation under negative pressure in a vacuum oven at 40°C, dried residuals were reconstituted in PBS containing 1 % bovine serum albumin (PBS-BSA) and assayed.

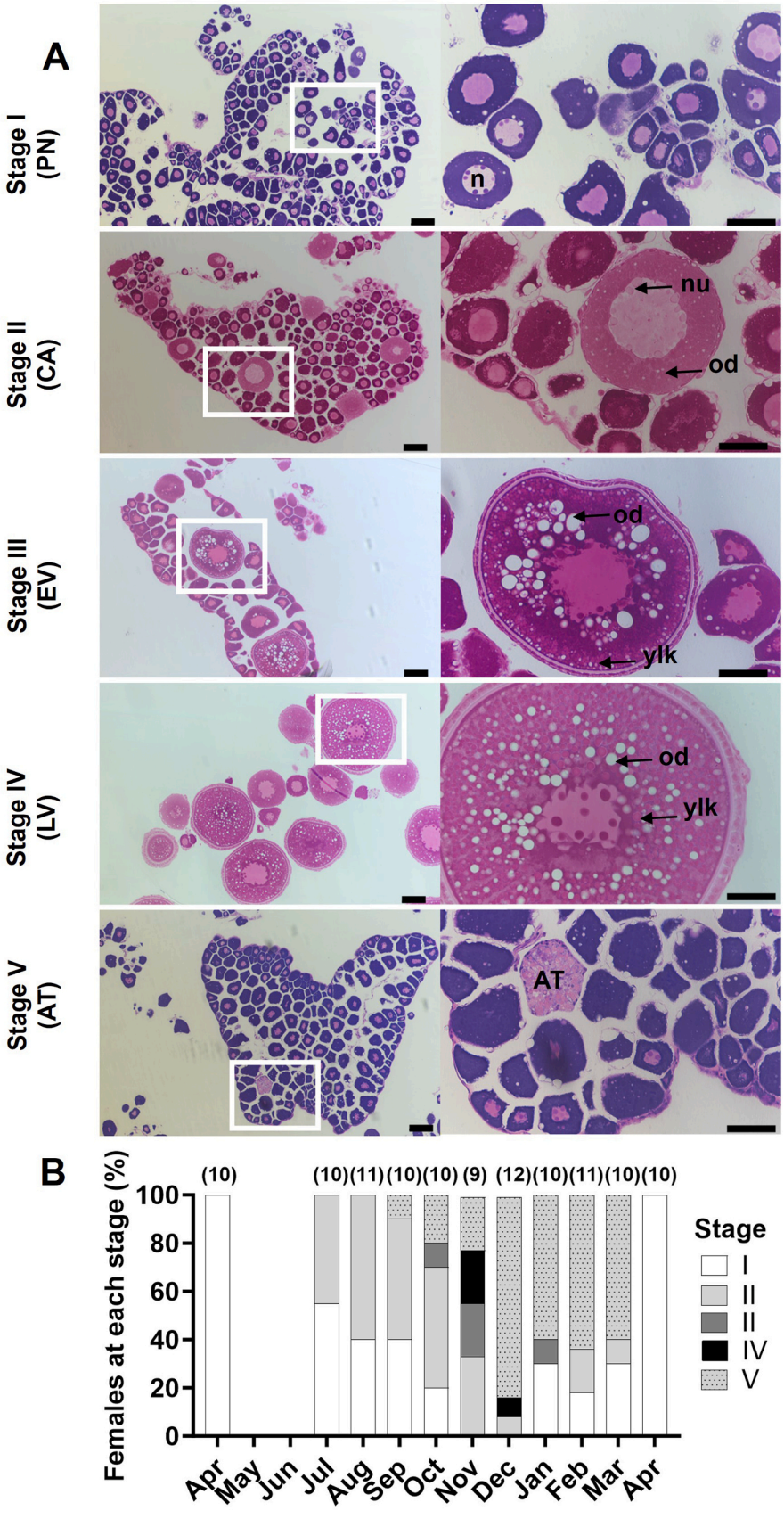

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Fig. 2. Histological micrographs of ovarian tissue from first filial (F1) generation silver trevally *(Pseudocaranx georgianus)* during different stages of oogenesis while maintained in captivity under ambient conditions (A; stages I–V) and the frequency distribution of females at each stage of ovarian development (B). White boxes represent areas at higher magnification in adjacent images (scale bar = 100 μm and 50 μm, respectively). Stage I: Immature – perinucleolar stage oocytes (PN), II: Lipid/cortical alveoli stage oocytes (CA), III: Early vitellogenic oocytes (EV), IV: Late vitellogenic oocytes (LV), and V: Atretic oocytes (AT). For the percentage of females classified into each stage of oogenesis, sample sizes (9–12 fish) are indicated in brackets above each sampling month. Abbreviations: n = nucleus; nu = nucleolus; ylk = yolk platelet; od = oil droplets; AT = atretic oocyte.

Extraction efficiency for E2 using diethyl ether was 95 % (n = 3).

Samples were run in three assays, with an inter-assay coefficient of variation of 25 %. Estradiol-17β antibody (Cat. No. MBS569134) was purchased from MyBioSource (San Diego, USA) and was diluted 1:2000 for the assay and serial dilutions of silver trevally plasma were confirmed to displace labelled E2 in a parallel manner to the standard curve (data not shown). The minimum detection level was estimated at 0.2 ng/mL. Tritiated E_2 (Cat. No. ART1549 [2,4,6,7,6,17–3H]-estradiol-17b, 110 Ci/mmol) was purchased from American Radiolabelled Chemicals Inc. (St Louis, MO, USA).

2.5. Estimation of Fsh and Lh plasma concentrations by ELISA

Prior to transportation and analysis at The Centre for Bioinnovation, University of the Sunshine Coast, Australia, plasma samples (0.2 mL) were freeze-dried (24 h) at The New Zealand Institute for Bioeconomy Science Limited, Nelson, NZ, to minimize degradation and stored at 4°C. Upon arrival at The Centre for Bioinnovation, all plasma samples were rehydrated with 200 μL of PBST-0.1 % BSA and analysed as described below.

Plasma gonadotropins were estimated by competitive ELISA previously developed and detailed for yellowtail kingfish *(Seriola lalandi)* Fsh (Nocillado et al., 2019) and giant grouper *(Epinephelus lanceolatus)* Lh (Dennis et al., 2020). To ensure developed protocols and protein standards could be applied to silver trevally samples, parallel displacement was first confirmed. To do this, silver trevally plasma samples, serially diluted (1:4) in phosphate-buffered saline−0.1 % Tween® 20 (PBST) with 0.1 % BSA, were compared against serially diluted giant grouper plasma (1:4) and recombinant single-chain giant grouper Lh (gg_LH) and yellowtail kingfish Fsh (ytk_FSH) standards. Maximum binding (Bo) and non-specific binding (NSB) reactions were prepared as controls. Briefly, the primary antibody was diluted 1:15,000. The wells of ELISA plates (Nunc Maxisorp) were coated with 100 μL of rgg_LHβ (250 ng/mL) or rytk_FSHβ (10) ng mL^{-1} in 50 mM sodium carbonate (pH 9.6). Standards were diluted 2-fold from 100 ng mL^{-1} down to 50 pg mL^{-1} in the same buffer used for the parallel displacement test. Standards and reconstituted samples were pre-incubated with equal volumes of the primary antibodies.

Intra-assay coefficient of variation was determined from four replicates of a standard of the same concentration on a plate, while inter-assay coefficient of variation was determined from a standard at 25 ng mL^{-1} from duplicate wells in three separate assays. The detection limit was defined as the lowest concentration of standard whose optical density B/Bo ratio was equivalent to 95 %, where B is the optical density of the standard and Bo is the maximum binding optical density. For analysis, data were first logit transformed, that is logit(Bi/Bo) = log9r/(1-r)), where r = Bi/Bo with Bi representing the optical density of each sample or standard and Bo the maximum binding optical density. Following successful parallelism (Supplementary Figure 1), concentration of hormone present in individual silver trevally plasma was determined via back calculation with a four-parameter logistic regression against the standard curve following the protocols outlined in Nocillado et al. (2019) and Dennis et al. (2020) and expressed as ng/mL.

2.6. Statistical analyses

Data are presented as the means ± standard errors of the mean (SE) and are plotted over time (month) to provide insight into temporal changes throughout the reproductive cycle in relation to water temperature and daylength; statistical analyses were not performed on data plotted in this manner. Data were also plotted according to stage of oogenesis to reveal stage-specific changes that may have been masked by the abundance of immature fish and/or fish with atresia at each monthly sampling point. Analyses were performed using GraphPad Prism version 10 for Windows (GraphPad Software, California, USA). Differences between mean values were regarded as significant when $p < 0.05$.

To determine differences in mean body morphometrics (body weight and fork length) between male and female fish over a 12-month period, including the initial and final sampling points, data were first checked for normality (Shapiro–Wilk test) and equal variance. Data meeting these assumptions were analysed using a two-tailed unpaired *t*-test, while those not meeting equal variance were analysed with Welch's correction.

To evaluate potential differences in physiological responses (plasma Fsh, Lh and E2 concentrations, mean oocyte diameter and GSI) at different stages of oogenesis (stages I–V; Fig. 2), data were first checked for normality (Shapiro–Wilk test) and homogeneity of variance (Brown-Forsythe test). Plasma Fsh concentrations during different stages of oogenesis met the assumptions of normality and homogeneity of variance and were subjected to a one-way ANOVA followed by Tukey's multiple comparison test. Meanwhile, data for oocyte dimeter, GSI and plasma E2 and Lh concentration data did not follow a normal distribution (even after log transformation) and were analysed by a Kruskal-Wallis H test (a nonparametric alternative variance test) followed by a Dunn's multiple comparisons test.

3. Results

3.1. Changes in body growth

Over a 12-month period, both female and male fish experienced significant increases in body weight and fork length. Specifically, the body weight of female fish rose from 371 ± 52 g to over 600 g (Table 1; two-tailed unpaired *t*-test; *t*-statistic = 10.37, $p < 0.0001$, d.f. = 18), while male fish increased from 367 ± 37 g to 690 ± 218 g (Table 1; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 4.618, $p = 0.0011$, d.f. = 9.505). In terms of fork length, female fish grew significantly from 259 ± 7 mm to approximately 300 mm (Table 1; two-tailed unpaired *t*-test; *t*-statistic = 11.65, $p < 0.0001$, d.f. = 18), and male fish from 261 ± 9 mm to 320 ± 24 mm (Table 1; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 7.334, $p < 0.0001$, d.f. = 11.52). Statistical analysis revealed no significant differences in body weights between female and male fish at either the initial (Table 1; two-tailed unpaired *t*-test; *t*-statistic = 0.2322, $p = 0.8190$, d.f. = 18) or final (Table 1; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 1.187, $p = 0.263$, d.f. = 9.919) sampling points. Similarly, there were no significant differences in fork lengths of male and female fish at the initial sampling (Table 1; two-tailed unpaired *t*-test; *t*-statistic = 0.4595, $p = 0.6514$, d.f. = 18). However, at the final sampling point, male fish exhibited a significantly larger fork length than female fish (Table 1; two-tailed unpaired *t*-test with Welch's correction; *t*-statistic = 2.739, $p = 0.0196$, d.f. = 10.81).

3.2. Changes in reproductive development

While males were not the focal point of this study, a number of males (n = 10) with well-developed testes containing free-flowing sperm were dissected (Supplementary Figure 2) between November and February. For females, the percentage of fish to reach the advanced stages of reproductive development in captivity at the age of three years was very low and no spontaneous spawning was observed during the predicted spawning season when an external passive egg collector was fitted to the broodstock tank. Specifically, only three (2.7 %) of all females sampled in the study (n = 113; Table 1) had achieved late vitellogenesis (oocyte diameters >400 μm; Fig. 2A Stage IV) and there was no evidence of oocyte maturation or post-ovulatory follicles within ovarian histological sections or wet mount biopsies of any fish throughout the entirety of the reproductive cycle.

During the first sampling month (April 2018), 100 % of females were immature and were in the previtellogenic stage of ovarian development (Fig. 2B and Table 2), where the ovary primarily consisted of PN oocytes (mean oocyte diameter of 94 ± 7.8 μm) (Fig. 2A Stage I). Females that were defined as having PN oocytes had mean plasma E2 concentrations of 0.3 ng/mL and a mean GSI of 0.6 % (Fig. 3). From the sampling months of July through to September, when water temperatures increased from 9.5°C to 12.5°C, all females remained in the previtellogenic stage with ovaries containing both PN and CA oocytes, except for 10 % of females sampled in September (Fig. 2B and Table 2), which showed the first evidence of oocyte atresia (Fig. 2A Stage V). It was not until October (spring), that entry into vitellogenesis became obvious in some females (10 %) (Fig. 2B and Table 2), with the formation of yolk globules in the periphery of oocytes observed in histological sections (Fig. 2A Stage III). This transition from previtellogenesis to vitellogenesis and the formation of yolk globules within developing oocytes coincided with significant increases in plasma E2 concentrations (Fig. 3A; Kruskal-Wallis H test, Dunn's Multiple Comparisons test, $p = 0.0005$), mean oocyte diameter (Fig. 3B; Kruskal-Wallis H test, Dunn's Multiple Comparisons test, $p = 0.0003$), and GSI (Fig. 3C; Kruskal-Wallis H test, Dunn's Multiple Comparisons test, $p = 0.0063$) when plotted by oogenesis stage. Specifically, females that were defined as having EV oocytes had mean oocyte diameters of ~ 236 μm, mean plasma E2 concentrations of 2.4 ng/mL and a mean GSI of 0.94 % (Fig. 3).

Females in the stages of late vitellogenesis were not observed until November, with only two fish (22.2 %) sampled during that month reaching this stage (Fig. 2A Stage IV; Fig. 2B and Table 2). At this time, ambient water temperatures had reached 18.8°C. When comparing mean plasma E2 concentrations of immature fish (females with ovaries containing PN oocytes) with fish containing LV oocytes, mean concentrations increased significantly, from 0.3 ng/mL to 3.8 ng/mL (Fig. 3A; Kruskal-Wallis H test, Dunn's Multiple Comparisons test, $p = 0.0026$).

From November to December, the percentage of females with LV oocytes had decreased to 8.3 % (one female only) and such females remained absent from subsequent sampling months (Fig. 2B and Table 2). In the months following December, plasma E2 concentrations as well as mean oocyte diameters and GSI declined in fish until they reached similar values to those observed at the start of the reproductive cycle (Fig. 1). While the onset of oocyte atresia was first observed in some females (10 %) as early as September, occurrence of AT oocytes was highest around the predicted spawning season (83 % of females sampled in December) and remained in ~60 % of females in subsequent months until April 2019, when the ovaries of 100 % of females contained PN oocytes (Fig. 2A and 2B and Table 2). Contrary to plasma E2 concentrations, which generally increased as oogenesis progressed, both plasma Lh and Fsh concentrations remained relatively stable across the stages of oogenesis (Fig. 4A & 4B). The only significant differences observed in plasma gonadotropin concentrations were significantly lower amounts of Fsh in females with ovaries containing AT oocytes compared with females with PN oocytes (Fig. 4A; one-way ANOVA, Tukey's HSD test, $p = 0.0049$); while for Lh, plasma concentrations were significantly lower in females with ovaries containing AT oocytes than in females with ovaries with ovaries containing both PN oocytes (Fig. 4B; non-parametric Kruskal-Wallis H test, Dunn's Multiple Comparisons test, $p = 0.0060$) and CA oocytes (Fig. 4B**;** non-parametric Kruskal-Wallis H test, Dunn's Multiple Comparisons test, $p = 0.003$**)**.

Table 2
Monthly proportion of female silver trevally *(Pseudocaranx georgianus)* at each stage of ovarian development during the annual reproductive cycle. Stage I: Immature – perinucleolar stage oocytes (PN), II: Lipid/cortical alveoli stage oocytes (CA), III: Early vitellogenic oocytes (EV), IV: Late vitellogenic oocytes (LV), and V: Atretic oocytes (AT).

Month	Year	♀n	Stage of ovarian development				
			I - PN	II - CA	III - EV	IV - LV	V - AT
April	2018	10	100 %	0 %	0 %	0 %	0 %
May	2018	0	-	-	-	-	-
June	2018	0	-	-	-	-	-
July	2018	11	55 %	45 %	0 %	0 %	0 %
August	2018	10	40 %	60 %	0 %	0 %	0 %
September	2018	10	40 %	50 %	0 %	0 %	10 %
October	2018	10	20 %	50 %	10 %	0 %	20 %
November	2018	9	0 %	33 %	22 %	22 %	22 %
December	2018	12	0 %	8 %	0 %	8 %	83 %
January	2019	10	30 %	10 %	10 %	0 %	60 %
February	2019	11	18 %	18 %	0 %	0 %	64 %
March	2019	10	30 %	10 %	0 %	0 %	60 %
April	2019	10	100 %	0 %	0 %	0 %	0 %

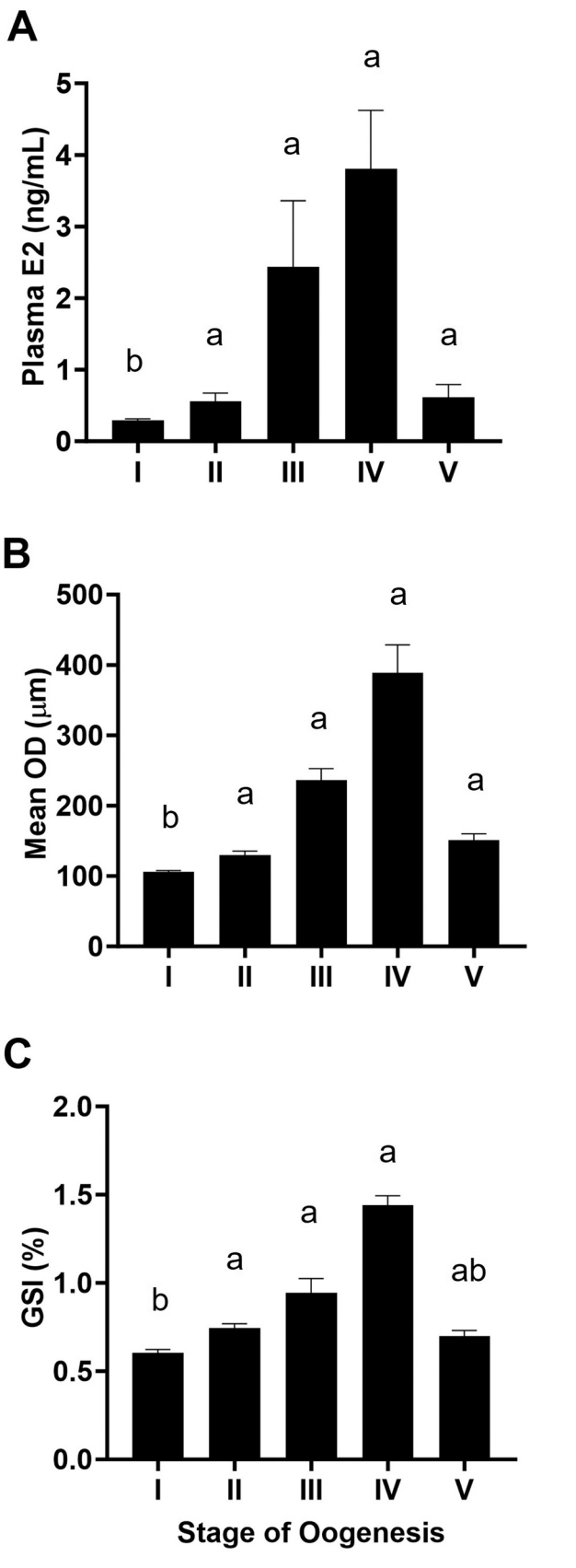
4. Discussion

As fish stocks in the wild continue to decline because of factors such as overfishing, habitat degradation, and climate change, aquaculture offers a promising solution to meet the growing demand for protein-rich foods, thereby playing a crucial role in enhancing food security. As aquaculture practices evolve, gaining a comprehensive understanding of the biology and reproductive mechanisms of emerging candidate species is essential for optimising and sustaining finfish production in captivity. In particular, investigating the molecular and hormonal processes related to the BPG axis can provide valuable insights into managing and manipulating reproduction in aquaculture systems. The silver trevally, identified as a potential aquaculture candidate, could contribute significantly to the diversification of finfish farming in NZ (Valenza-Troubat et al., 2022a). Our current study delineates the annual reproductive cycle of hatchery-reared F1 silver trevally maintained under ambient water temperature and photoperiod conditions. In the following section, we address three major aims: first, to determine the age at puberty in captivity by tracking changes in ovarian morphology and assessing plasma Fsh, Lh, and E2 concentrations; second, to identify potential reproductive dysfunctions and establish a foundation for manipulating the spawning season using photo-thermal adjustments; and third, to contextualize our findings within the broader framework of closely related species in the Carangidae family, providing practical insights for developing effective reproductive strategies in aquaculture.

Our study found that puberty of hatchery-reared F1 silver trevally first occurred at 3 years of age (albeit a low percentage), and fish showed distinct seasonality in their reproductive cycle with entry to, and completion of, vitellogenesis in females occurring around October (spring) and November to December, respectively. Males with well-developed testes containing free-flowing sperm were observed between November and February.

4.1. Factors influencing onset of puberty and sexual maturation

Sexual maturation in captive three-year-old females was not completed, with only 2.7 % of all females sampled achieving late vitellogenesis, and no instances of oocyte maturation or spontaneous



(caption on next column)

Fig. 3. Changes in plasma estradiol-17β (E2) concentrations (A), mean oocyte diameter (OD) (B), and gonadosomatic index (GSI) (C) of first filial (F1) generation silver trevally *(Pseudocaranx georgianus)* during different stages of oogenesis. Based on the most advanced type of oocytes observed in wet mount biopsies, ovarian development was classified into Stage I: Immature – perinucleolar stage oocytes (PN), II: Lipid/cortical alveoli stage oocytes (CA), III: Early vitellogenic oocytes (EV), IV: Late vitellogenic oocytes (LV), and V: Atretic oocytes (AT). The data represent means ± SE. Significant differences are indicated by different letters ($p < 0.05$, non-parametric Kruskal-Wallis H test followed by Dunn's multiple comparison test).

spawning were observed. Taranger et al. (2010) details factors influencing puberty in fish. These factors include, but are not limited to, body size and nutritional status (Chen and Ge, 2013; Sempere et al., 2023), environmental variables such as water temperature (Davis, 2009; Hermelink et al., 2013) and photoperiod (Karlsen et al., 2014; Lundova et al., 2021), as well as genetic factors (Fjelldal et al., 2020; Fraser et al., 2024). Data from wild fisheries off the coast of New South Wales in Australia reported by Rowling and Raines (2000), indicate that both male and female silver trevally can mature at lengths ranging from 10 to 20 cm; however, maturation appears to be progressive for both sexes, with full sexual maturity not attained until they reach a length of 26–28 cm. In wild white trevally sampled in the central North Atlantic, no significant differences were observed between sexes regarding body length at first maturity, which was recorded at 27.8 cm for males and 30 cm for females (Afonso et al., 2008). Furthermore, all individuals were found to be mature when males and females reached body lengths of 33 cm and 36 cm, respectively (Afonso et al., 2008). Given that the mean body length of our females during the final sampling month (April 2019) was close to 30 cm, a plausible explanation for the limited number of females reaching late vitellogenesis may be the small body size of the fish at each sampling point in this study. Females that showed some signs of some advancement in oogenesis before undergoing oocyte atresia may have also been undergoing a 'temporal activation of the BPG axis' or 'dummy run', which can be observed a year before puberty (Okuzawa, 2002). This phenomenon has been documented in an increasing number of cultured fishes undergoing maiden spawning cycles, including pikeperch *(Sander lucioperca)* (Hermelink et al., 2013), European seabass *(Dicentrarchus labrax)* (Espigares et al., 2015) and wreckfish (hāpuku; *Polyprion oxygeneios*) (Wylie et al., 2018). Therefore, as hatchery-reared silver trevally continue to grow and approach four years of age, it is likely that a higher percentage of females will reach late vitellogenesis.

Like the silver trevally sampled in this study, wild stocks of white trevally fished in the central north Atlantic showed a clear seasonality in their reproductive cycle, but with a spawning season spanning from June to September (Afonso et al., 2008). Aggregations of sexually mature adults were observed near offshore reefs when ocean temperatures were approximately 19°C (Afonso et al., 2008). From the same silver trevally wild fisheries data discussed above by Rowling and Raines (2000), a wide spawning period was noted from spring to autumn (September to March), with November to December being the months where highest mean GSI values (~4–6 %) were observed. In hatchery-reared silver trevally, GSI values also peaked around November; however, these values were lower, generally less than 1.5 %. This difference likely reflects variations in the age and size of the sampled individuals between wild and captive populations.

In general, ovarian development of captive silver trevally was slow, with previtellogenic stages being dominant (mean oocyte diameters <200 μm) until October (spring), when vitellogenesis began in 10 % of females. Peak vitellogenesis occurred in November (22.2 % of females with a mean oocyte diameter ≥400 μm), coinciding with rising E2 concentrations and an ambient water temperature of 18.8°C. However, by December (summer), oocyte atresia was prevalent (83 % of females), and reproductive parameters declined thereafter. The development of oocytes in silver trevally is similar to that observed in striped jack (Murai

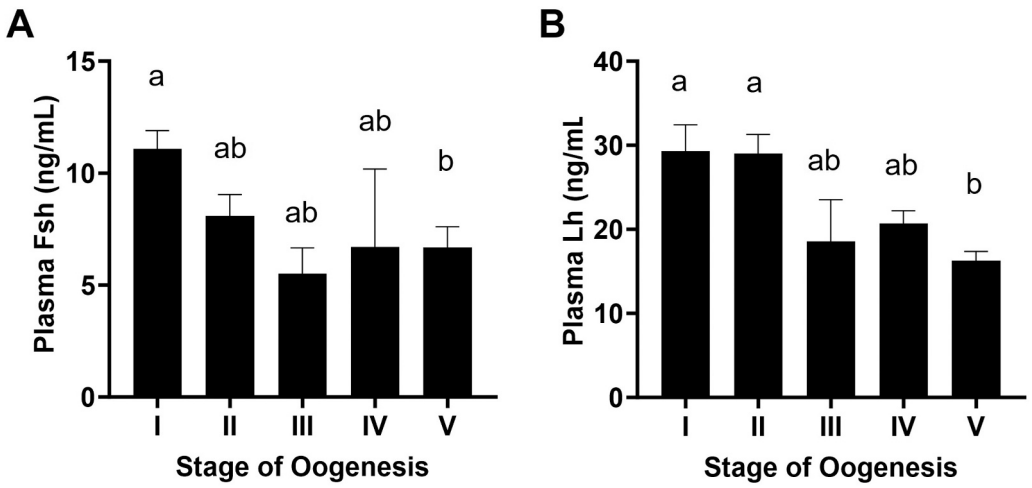


Fig. 4. Changes in plasma follicle-stimulating hormone (Fsh; A) and luteinizing hormone (Lh; B) concentrations of first filial (F1) generation silver trevally *(Pseudocaranx georgianus)* during different stages of oogenesis. Based on the most advanced type of oocytes observed in wet mount biopsies, ovarian development was classified into Stage I: Immature – perinucleolar stage oocytes (PN), II: Lipid/cortical alveoli stage oocytes (CA), III: Early vitellogenic oocytes (EV), IV: Late vitellogenic oocytes (LV), and V: Atretic oocytes (AT). The data represent means ± SE. Significant differences are indicated by different letters ($p < 0.05$, non-parametric Kruskal-Wallis H test followed by Dunn's multiple comparison test for plasma Lh values; $p < 0.05$, one-way ANOVA followed by Tukey's HSD test for plasma Fsh values).

et al., 1985a) and generally follows the same pattern seen in the genus *Seriola*. However, silver trevally's oocytes reach slightly smaller diameters at the end of vitellogenesis compared to these species (Poortenaar et al., 2001; Shiraishi et al., 2010; Zupa et al., 2017; Corriero et al., 2021a). Additionally, a peak in plasma E2 concentrations during vitellogenesis is consistent with patterns observed in other carangid species, such as yellowtail kingfish (Poortenaar et al., 2001) and greater amberjack (Mandich et al., 2004; Nyuji et al., 2016; Zupa et al., 2017; Aoki et al., 2020; Fakriadis et al., 2024). The increase in plasma E2 as oogenesis advances to late vitellogenesis likely reflects the liver's production of vitellogenin, a yolk precursor protein that is transported via the vascular system to developing oocytes (Patiño and Sullivan, 2002; Lubzens et al., 2017). Conversely, insufficient E2 levels can hinder this process, leading to reabsorption of the oocytes. Environmental stressors and rearing conditions—such as suboptimal water temperatures (Wylie et al., 2018), confinement (Coward et al., 1998), and nutritional stress (Yamamoto et al., 2011)—have been shown to lower E2 levels, resulting in arrested vitellogenesis and oocyte atresia.

Unlike plasma E2 concentrations, which increased from 0.3 ng/mL to 3.8 ng/mL as oogenesis progressed to late vitellogenesis, both Lh and Fsh plasma concentrations remained relatively stable across the different stages of oogenesis, except for lower amounts in fish with oocyte atresia compared with those with previtellogenic oocytes. Given the critical role of Lh in oocyte maturation and spawning (Mylonas and Zohar, 2000), the lack of increased plasma Lh concentrations as oogenesis progressed in captive silver trevally may be reflective of a reproductive dysfunction in hatchery-reared fish (discussed below).

4.2. Reproductive dysfunction and challenges in captivity

No instances of oocyte maturation or spontaneous spawning were observed in this study. Atresia of vitellogenic oocytes, along with irregular, asynchronous, or absent spontaneous spawning, are common reproductive dysfunctions in captive settings (Mylonas and Zohar, 2000; Mylonas et al., 2010; Corriero et al., 2021b). These issues significantly impair reproductive success and can hinder the efficiency and sustainability of breeding programmes. Identifying these dysfunctions is crucial for understanding reproductive health and establishing a foundation for manipulating the spawning season through photo-thermal adjustments (Mylonas and Zohar, 2000; Zohar and Mylonas, 2001; Mylonas et al., 2010). Such reproductive dysfunctions are well documented within the Carangidae family and are often due to insufficient quantities of Lh being released into the bloodstream to accomplish oocyte maturation, ovulation and spawning (Nyuji et al., 2019; Corriero et al., 2021a; Fakriadis et al., 2024). While there are some reports of broodstock from the genus *Pseudocaranx* spontaneously spawning in captivity (e.g., Murai et al., 1985b; Nogueira et al., 2018), human chorionic gonadotropin (hCG) administration at a dose of 600 IU kg^{-1} , combined with broodstock tank water temperature manipulations (Vassallo-Agius et al., 2001a, b), or water temperature manipulation alone (Vassallo-Agius et al., 1998; Watanabe et al., 1998; Vassallo-Agius et al., 1999), has been used routinely to synchronise and overcome failure of oocyte maturation and spawning of striped jacks. Furthermore, wild-caught captivity-acclimated silver trevally broodstock maintained under similar ambient photoperiod and temperature conditions as F1 trevally of this study, readily complete vitellogenesis between late spring and summer but fail to spawn spontaneously (Wylie et al., 2025). Thus, indicating that environmental cues provided in captivity are sufficient to support progression gametogenesis in silver trevally until the later phase of the reproductive cycle where reproductive dysfunction impacts oocyte maturation and spawning. The latter reproductive dysfunction in broodstock is overcome by administration of hCG at a dose of 600 IU kg^{-1} or agonists of gonadotropin-releasing hormone (GnRHa) (dose: 83–152 μg kg^{-1} for females and 58–167 μg kg^{-1} for males) (Valenza-Troubat et al., 2022a; Wylie et al., 2025).

While plasma Lh concentrations were not measured in silver trevally after the administration of GnRHa by Wylie et al. (2025), the positive effects of GnRHa administration on the spawning success and concurrent elevation of plasma Lh have been demonstrated in greater amberjack by Nyuji et al. (2019). Thus, given the critical role of Lh in oocyte maturation and spawning (Mylonas and Zohar, 2000; Nagahama and Yamashita, 2008), the lack of significant increases in plasma Lh observed in F1 silver trevally as oogenesis progressed to late vitellogenesis and the successful spawning of wild-caught captivity-acclimated silver trevally broodstock upon administration of GnRHa, it is likely that high rates of atresia and absence of spontaneous spawning may have resulted from the dysfunctional synthesis and/or release of Lh into the bloodstream during the natural spawning period. Comparing plasma Lh concentrations of late vitellogenic silver trevally broodstock prior to and after hormone- or sham-treatment would help to confirm the assumption causing this reproductive dysfunction. An additional explanation for why females reached late vitellogeneses, but did not spontaneously

spawn, could again be related to fish size and nutritional status. Specifically, while fish may have attained a threshold in body growth to initiate oogenesis, the threshold to fully complete vitellogenesis and produce viable gametes may not have been met, as proposed for non-spawning two-year-old European seabass (Sempere et al., 2023).

Taken together, addressing reproductive challenges and improving silver trevally production will require targeted interventions. Future efforts should prioritize the development of hormone therapies to induce spawning in F1 broodstock, alongside the strategic use of photo-thermal manipulations to modify or advance the spawning season. Successfully inducing spawning will enable the closure of the life cycle in captivity, paving the way for selective breeding programmes that produce elite lines with desirable traits (Gjedrem and Robinson, 2014; Samuels et al., 2024). Successful spawning will enable systematic quantification of reproductive output in captive-bred fish (spawning kinetics, egg production and gamete quality), similar to methods developed for greater amberjack (Fakriadis et al., 2019). Manipulating the spawning timing through photo-thermal techniques will ultimately allow for earlier or all-year-round larval production, enabling fingerlings to fully benefit from the warmer summer growing season in sea pens located in temperate climates.

4.3. Photoperiod and temperature manipulation for spawning advancement

To the best of our knowledge, there are no published reports on the effects of phase-shifted photoperiod regimes on the timing of spawning of species within the genus *Pseudocaranx*. However, within the Carangidae family, exposure to a long photoperiod regime is known to induce reproductive development in *Seriola* species. Specifically, a long photoperiod regime (18 L:6D) has been applied to Japanese amberjack or yellowtail *(Seriola quinqueradiata)* to successfully advance ovarian development and achieve spawning several months earlier than the natural spawning season (Mushiake et al., 1998; Hamada and Mushiake, 2006). In greater amberjack, similar long photoperiods applied in autumn and winter have also advanced ovarian development and enabled broodstock to complete vitellogenesis prior to the main spawning season, which extends from later spring to early summer (Hamada and Soyano, 2009; Hashimoto et al., 2016). More recently in a study by Nyuji et al. (2018), exposure of previtellogenic greater amberjack to a long photoperiod regime induced Fsh release into the bloodstream followed by the upregulation in mRNA expression of *fshb* and *lhb* subunit genes in the pituitary. While temperature-control alone does not induce ovarian development (Mushiake et al., 1998), these studies provide evidence that long photoperiod regimes are important for cueing the onset of reproductive development in these carangids. Given that changes in reproductive development of F1 silver trevally in this study aligned with increasing day length and water temperatures, future research should investigate the effects of phase-shifted photo-thermal regimes to advance spawning timing. For instance, once winter conditions in June reach approximately 9°C and a day length of 9 L:15D, artificial conditions mimicking spring or a long photoperiod regime could be applied after a brief period of cool temperatures.

4.4. Conclusions

Our study demonstrated that puberty in hatchery-reared F1 silver trevally first occurs at three years of age. However, reproductive development in captive three-year-old females was limited, with only 2.7 % of all females sampled achieving late vitellogenesis, and no instances of oocyte maturation or spontaneous spawning being observed. The absence of spontaneous spawning indicates a reproductive dysfunction in hatchery-reared fish. Furthermore, the lack of increased plasma Lh concentrations as oogenesis progressed suggests that the observed dysfunction may be due to insufficient Lh release into the bloodstream, preventing oocyte maturation, ovulation, and spawning. To overcome these reproductive challenges and improve silver trevally production, future efforts should focus on developing hormone therapies to induce spawning in F1 broodstock. Additionally, photo-thermal manipulations should be explored to modify or extend the spawning season in captivity, enabling earlier or year-round larval production.

CRediT authorship contribution statement

Kato Keitaro: Writing – review & editing, Supervision, Methodology, Conceptualization. **Abigail Elizur:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Conceptualization. **Maren Wellenreuther:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition. **Wylie Matthew:** Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ria Rebstock:** Writing – review & editing, Writing – original draft, Resources, Methodology, Formal analysis. **Igor Ruza:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Data curation. **Dennis Lachlan:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Formal analysis, Data curation. **Nicola Shaw:** Validation, Resources, Methodology, Data curation. **Josephine Nocillado:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Formal analysis, Data curation. **Pieter Mark:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Maren Wellenruther 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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2025.103303.

Data availability

Data will be made available on request.

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