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First controlled out of season spawning for California yellowtail (*Seriola dorsalis*)

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A R T I C L E I N F O

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A B S T R A C T

The ability to control egg production and have a consistent supply of high quality eggs is critical to the commercial success of any farmed marine finfish species. Here we describe the first documented controlled spawning of California yellowtail (CYT; *Seriola dorsalis*). The aim for this study was to shift volitional spawning six months ahead of when natural spawning typically occurs for the species using photothermal manipulation. Over the course of one year we tracked spawning for two sibling groups of F1 generation broodstock and recorded relevant metrics for all spawn events (egg production, viability), eggs (egg and oil diameters, hatch rates), and larvae (notochord length at hatch, yolk sac volume, survival to first feeding). The first group was subjected to natural day length and temperature conditions (Natural) and produced eggs from March through October in 2023. The second group had a shifted day length and temperature regime (Controlled) designed to stimulate spawning from October 2022 through April 2023. Egg production for both groups was similar, with the Natural group producing 37 spawns resulting in 25 million eggs (682,086 ± 299,821 eggs spawn^{-1}), and the Controlled group producing 34 spawns resulting in 20 million eggs (604,825 ± 315,412 eggs spawn^{-1}). Egg quality was also similar, with only hatch rate being different between the groups (Natural 48.8 ± 28.9 %; Controlled 75.1 ± 15.5 %). Through the control of temperature and day length, we demonstrated that CYT spawning can occur outside the natural spawning window and that achieving year round egg production is possible. This is an important step forward for commercial production of this high value marine finfish species.

1. Introduction

Eleven marine finfish species have been identified as commercially ready in the United States (Andersen et al., 2021; Drawbridge et al., 2021; Le François et al., 2021; Rotman et al., 2021; Stieglitz et al., 2021; Watanabe et al., 2021; Weirich et al., 2021). One of these commercially ready species is California yellowtail (CYT*, Seriola dorsalis*), which has been cultured by the Hubbs-SeaWorld Research Institute (HSWRI) since 2003 (Rotman et al., 2021). Growth of the aquaculture industry depends on consistent production of juveniles, which can only become a reality with a consistent source of high quality eggs. Having the ability to produce eggs throughout the year offers advantages over seasonal spawning because it facilitates size homogeneity at the time of harvest, when harvesting is done over a 12-month cycle and it allows hatchery infrastructure to be used year-round. Photothermal manipulation is often used in aquaculture to control the reproductive cycle and produce eggs year round (Watanabe et al., 2006; Wang et al., 2010; Stieglitz et al., 2012; Migaud et al., 2018). Multiple commercially ready marine finfish species in the United States, such as black sea bass (*Centropistis striata*), striped bass (*Morone saxatilis*), white seabass (*Atractoscion nobilis*), cobia (*Rachycentron candum*), and red drum (*Sciaenops ocellatus*), utilize photothermal cues to advance sexual maturation and promote out of season spawning (Andersen et al., 2021; Drawbridge et al., 2021; Stieglitz et al., 2012; Howell et al., 2003; Higuchi et al., 2023). To control spawning effectively, it is important to understand whether the reproductive cycle for a given species is driven by short initial cues for temperature or photoperiod or long periods of shifted temperature and photoperiod, and the relative importance of temperature and photoperiod in the manipulation process (Wang et al., 2010; Bromage et al., 2001).

The reproductive biology and physiology of multiple *Seriola* species has been well studied including; *S. dumerili*, *S. quinqueradiata*, *S. lalandi*, and *S. dorsalis* (Benetti et al., 1997; Poortenaar et al., 2001; Mylonas et al., 2004; Jerez et al., 2006; Moran et al., 2007; Stuart and Drawbridge, 2013; Corriero et al., 2021). Of those species both *S. lalandi* and *S. quinqueradiata* have had, their reproductive cycle controlled

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photothermally, and are able to produce eggs indoors as well as out of season (Mushiake et al., 1998; Symonds et al., 2014; Yang et al., 2016). Here we look to determine if CYT can produce eggs when conditioned to spawn six months out of season, and if so, to see if egg production and egg quality will be similar to a natural spawning group.

2. Materials and methods

2.1. Ethical statement

The authors cite compliance with the US National Research Council's 'Guide for the Care and Use of Laboratory Animals', the US Public Health Service's 'Policy on Humane Care and Use of Laboratory Animals', and 'Guide for the Care and Use of Laboratory Animals'. Live animal research was conducted in accordance with the HSWRI IACUC protocol 2014-01.

2.2. Broodstock

Adult fish used for this study were 7 year-old F1 generation broodstock that were produced at HSWRI, San Diego, CA. The broodstock diet for both groups consisted of a frozen fresh fish product (90 % sardines and 10 % squid) that were thawed and injected with vitamins. The vitamin pack consisted of a custom premix (1.5 % of the total diet; Zeigler, Gardners, PA), thiamin (0.02 % of the total diet; Nutrablend, Neosho, MO), vitamin C (0.5 % of the total diet; Nutrablend), lecithin (2.0 % of the total diet; Nutrablend), astaxanthin (1.5 % of the total diet; Aquafauna, Hawthorne, CA), choline chloride (0.08 % of the total diet; Nutrablend), arachidonic acid (0.05 % of the diet; Zeigler), and AlgaMac-3050 (10.0 % of the total diet; Aquafauna). The two fiberglass spawning tanks were 30 m^3 (4.9 m diameter × 1.6 m deep), and covered with 95 % shade cloth. A 500 μm net was placed in a sump on the outside of each spawning tank to collect all of the eggs from the tank effluent, which flowed by gravity into the net. The natural spawning group (Natural) was comprised of two females (16.0 ± 0.1 kg) and six males (15.4 ± 2.4 kg) (Table 1). These fish were supplied sand filtered flow through seawater (5 turnovers per day) and were exposed to natural light (day length ranging from 10.5 to 14.0 h light) and ambient water temperatures ranging from 14 to 23 °C throughout the year (Fig. 1). The controlled spawning group (Controlled) was comprised of two females (11.2 ± 2.3 kg) and five males (12.7 ± 2.2 kg). The Controlled group fish were supplied with temperature controlled recirculating seawater (3 turnovers per day) with a 3-hp pump (Sparus Pump; Pentair Aquatic Ecosystems), and were subjected to water temperatures ranging from 14 to 23 °C (Fig. 2). Filtered seawater was added continuously to the system at an exchange rate of 15 L/min. Fish were subject to natural light from March through September (day length ranging from 12.5 to 14.0 h light), and from September through February (day length ranging from 13.0 to 14.0 h light) were exposed to a combination of natural light and artificial light (dimmable fluorescent daylight light; set to 600 lx) to extend the photoperiod when natural day length was shorter (Fig. 2). Water temperature was controlled with a heat pump (XLHP High Performance Heat/Cool pump; Pentair Aquatic Ecosystems), and maintained from 14 to 23 °C throughout the year (Fig. 2).

Table 1
Broodstock population information for California yellowtail (*Seriola dorsalis*) subjected to natural conditions and controlled conditions.

	Natural	Controlled
Sex ratio (M:F)	3:1	2.5:1
No. of males	6	5
No. of females	2	2
Male biomass (kg)	92.1	63.3
Female biomass (kg)	32.0	25.6
Total density (kg/m^3)	3.9	2.8

2.3. Egg collection and egg quality

Eggs were collected from both broodstock groups as described in Stuart and Drawbridge (Stuart and Drawbridge, 2013). Total egg production was calculated by taking triplicate one milliliter samples and counting the number eggs in each sample. The eggs per milliliter average from those samples was then multiplied by the total number of milliliters collected of floating, neutral, and sinking eggs to estimate the total number of eggs from each spawn event. Percent viability was calculated for each spawn as the ratio of the floating and neutral portions of each spawn versus total eggs produced, multiplied by 100. For each spawning event, the following egg and larval measures were recorded directly or calculated using floating eggs; egg diameter (ED ±0.01 mm), oil diameter (OD ±0.01 mm), percent oil volume (POV ±0.01 %), hatch rate (HR ±0.1 %), survival to first feeding (SFF ±0.1 %), yolk sac volume (YSV ±0.01 mm^3), and notochord length (NL ±0.01 mm) at hatch. To obtain these measures, a digital image was taken of a cluster of eggs from each spawn event at 6.3x magnification using a dissecting scope (SZX9; Olympus Corp., Tokyo, Japan, fitted with a camera MiniVID USB 3.0; LW Scientific, Lawrenceville, GA, USA). Once the digital image was taken, the ED and OD were measured from 20 "qualifying" eggs using image analyses software (ToupView). A qualifying egg was one that was in full view and could be measured. Eggs and oil globules (CYT eggs have a single oil globule) were assumed to be spherical, and volumes were calculated from single measurements of diameter according to the formula for the volume of a sphere (i.e. $V = 4/3\pi r^3$). POV was then calculated for each egg using the corresponding egg and oil volumes, which were then averaged for each spawn event. The average HR was determined by setting up five 1.0 L beakers filled with 800 ml of clean seawater with twenty floating eggs in each beaker. On the day of hatch (0 dph), the number of hatched larvae was counted in each beaker. HR was calculated as the average for all five replicate beakers (totaling 100 eggs) for the spawn event. SFF was conducted by using the same methodology as the one used for calculating hatch rates, except 0-day post hatch (dph) larvae were used instead of eggs. The average percentage of larvae surviving to first feeding (2–3 dph) was used as an index of spawn hardiness. Finally, NL and YSV were measured from pictures taken at 0-dph of 20 larvae per spawn event. YSV was calculated based on the formula used in Blaxter and Hempel (Blaxter and Hempel, 1963), $YSV = \pi/6 * (\text{Yolk Length} * (\text{Yolk Height}^2))$.

2.4. Statistical analyses

The results from this study are summarized using descriptive statistics only because there was no replication between the Natural and Controlled groups.

3. Results

Spawn events in the Natural group were recorded from April through September 2023 (150 aggregate spawn days; Fig. 1), and spawn events in the Controlled group were recorded from October 2022 through April 2023 (170 aggregate spawn days; Fig. 2).

Egg production for both groups was similar, with the Natural group spawning 37 times producing 24,920,966 eggs and the Controlled group producing 34 spawns resulting in 20,564,037 eggs (Table 2). Eggs $spawn^{-1}$ was also similar between the groups (Natural - 673,540 ± 291,002 eggs $spawn^{-1}$; Controlled 604,852 ± 315,412 eggs $spawn^{-1}$) (Table 2). Egg quality was also similar between the groups with regards to viability, OD, and POV (Table 2). However, egg diameters were smaller in the Natural group (Table 2; Fig. 3). For both groups egg diameters decreased as the season progressed (Fig. 3). HR was much lower on average in the Natural group (48.8 ± 28.9 %) when compared to the Controlled group (75.1 ± 15.5 %; Table 2). Using an HR threshold of 70 % (a threshold used by HSWRI for fish production), we found that the Natural group had 14 of the 37 spawn that met this threshold, while the

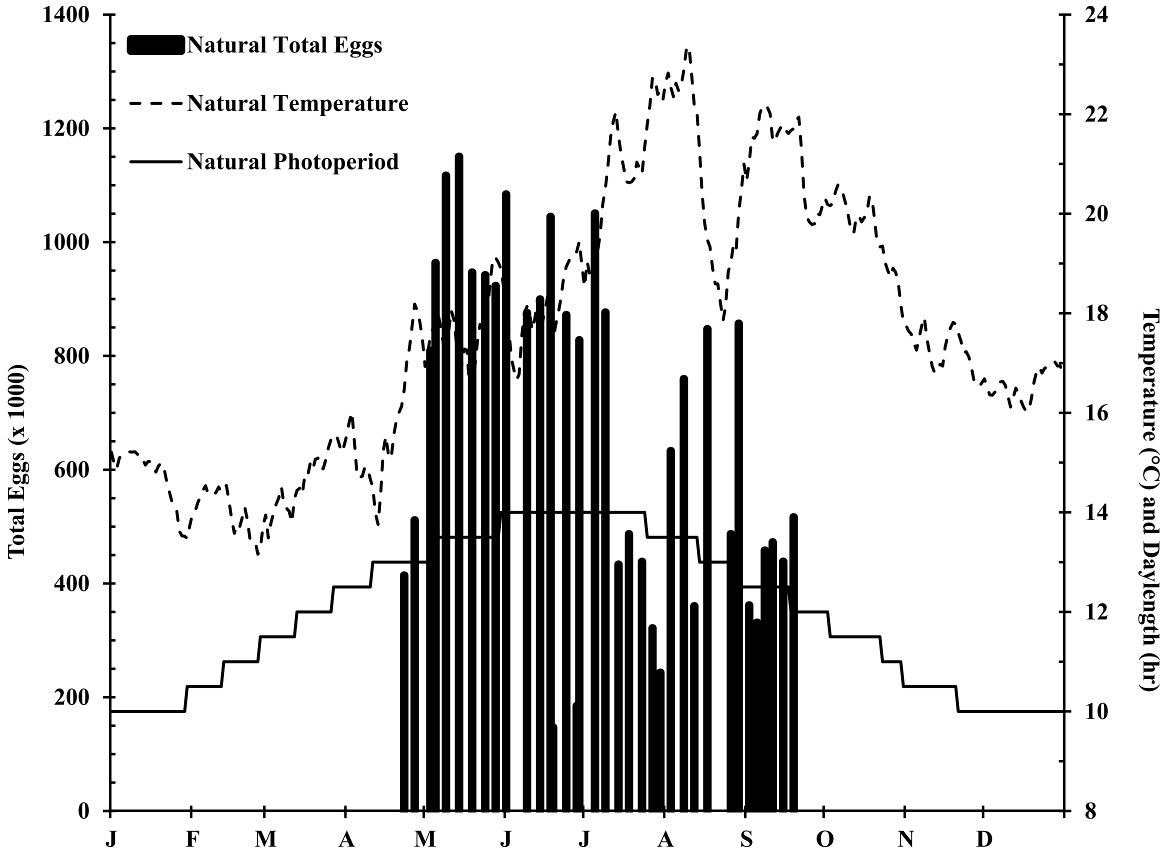

Fig. 1. Spawning profile for California yellowtail (*Seriola dorsalis*) under a natural spawning regime. Black bars represent amount of eggs collected, dotted black line represents water temperature, and the solid black line represents the day length.

Controlled group had 23 of the 34 spawn events (Fig. 4).

4. Discussion

Egg production of marine finfish can be achieved through volitional spawning with and without hormone manipulation and when ideal environmental conditions are met (e.g. temperature and day length). Controlling the temperature and day length is advantageous because fish can be held under consistent environmental conditions in order to advance sexual maturation and promote egg production. This has been demonstrated for multiple marine species whereby photothermal cycles are offset from ambient conditions in order to successfully promote year-round spawning. These species include; Atlantic cod (*Gadus morhua*), cobia (*Rachycentron canadum*), southern flounder (*Paralichthys lethostigma*), red drum (*Sciaenops ocellatus*), white seabass (*Atractoscion nobilis*), and various *Seriola* spp (Drawbridge et al., 2021; Watanabe et al., 2006; Stieglitz et al., 2012; Mushiake et al., 1998; Symonds et al., 2014; Arnold, 1988; Hansen et al., 2001). Year-round spawning offers advantages to hatcheries and growers. The hatchery can maintain a consistent level of production instead of having periods of "down time", which maximizes skilled labor required for successful hatchery production. Downstream growers benefit from being able to stagger crops, and ensure that there is no interruption in providing the product to the market.

The natural spawning season for captive CYT is reported to be from March through October when the water temperatures range from 15 to 23 °C, and day length ranges from 12 to 14 h (Rotman et al., 2021; Stuart and Drawbridge, 2013; Schmidt et al., 2021). In the present study, the spawning season for a group of CYT was shifted by six months from the natural season and yielded a high quantity and quality of eggs from October through April. Being able to control the timing of the spawning season for CYT is a key aspect to commercialization of the species in the United States. Researchers studying other Seriola species such as *S. lalandi* and *S. rivoliana* have shown the ability to control spawning and these species are currently being cultured commercially in many countries including: Australia, Chile, the Netherlands, Germany, Denmark, and the United States (Corriero et al., 2021).

There are two important environmental cues that help drive sexual maturation in marine finfish, these are day length (photoperiod) and temperature. An increase in the duration of the day length has been used in many marine finfish species including bluefin tuna (*Thunnus orientalis*), yellowtail (*S. lalandi*), and greater amberjack (*S. dumerili),* to induce spawn events prior to the natural spawning season (Higuchi et al., 2023; Nyuji et al., 2018). Similarly, temperature manipulation has been shown to control off season spawning for species such as Nassau grouper (*Epinephelus straitus*), cobia, and red drum (Stieglitz et al., 2012; Arnold, 1988; Tucker Jr et al., 1996). In the current study, a combination of increasing both day length and temperature was needed to stimulate egg production for CYT. In both the Natural and Controlled group, egg production was first observed when day length reached 13 h and temperature was above 15 °C. Wang et al. (2010) defined three general functional groups of fish species sharing similar cueing control of reproduction. They described fish species in "Group II" as species that are driven by specific photothermal stimuli, with temperature playing a cueing role and with photoperiod required to induce maturation. Based on the information from this study, we suggest that CYT are also part of this group, however more research should be done in order to manipulate temperature and photoperiod independently, in order to clearly define this relationship.

Egg production documented here was similar to what has been previously reported for CYT (Stuart and Drawbridge, 2013; Schmidt et al., 2021; Stuart et al., 2020). The average eggs spawn^{-1} for both

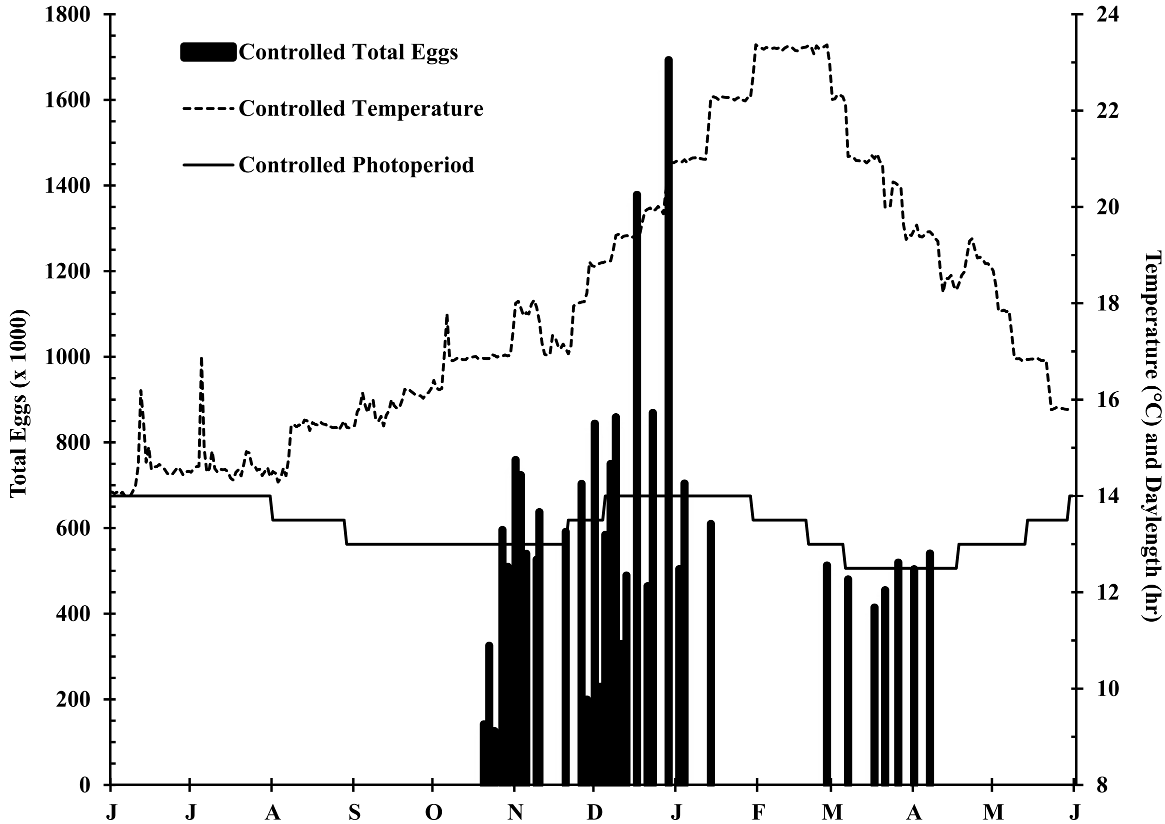

Fig. 2. Spawning profile for California yellowtail (*Seriola dorsalis*) under a controlled spawning regime. Black bars represent amount of eggs collected, dotted black line represents water temperature, and the solid black line represents the day length.

Table 2
Egg production and egg quality metrics (ED – Egg Diameter; OD – Oil Diameter, POV – Percent Oil Volume, YSV – Yolk Sac Volume, NL – Notochord Length, HR – Hatch Rate, SFF – Survival to First Feeding) for both California yellowtail (*Seriola dorsalis*) under a natural spawning cycle and a controlled spawning cycle. Results expressed a mean ± SD.

Parameter	Natural	Controlled
Number of Spawns	37	34
Length of Spawning Season (days)	156	170
Egg Production	24,920,966	20,564,037
Eggs spawn^{-1} (Num)	673,540 ± 291,002	604,825 ± 315,412
Viability (%)	81.1 ± 9.8	80.1 ± 14.2
ED (mm)	1.34 ± 0.04	1.36 ± 0.04
OD (mm)	0.31 ± 0.01	0.31 ± 0.02
POV (%)	1.24 ± 0.13	1.25 ± 0.19
YSV (mm^3)	0.34 ± 0.15	0.35 ± 0.12
NL (mm)	4.09 ± 0.21	4.03 ± 0.21
HR (%)	48.8 ± 28.9	75.1 ± 15.5
SFF (%)	74.1 ± 17.6	61.8 ± 25.8

groups in this study was over 600,000 eggs spawn^{-1} (Natural: 140,000 to 1,690,000 eggs spawn^{-1}; Control 147,000 to 1,180,000 eggs spawn^{-1}), which is within the range of what was reported in 2013 and 2014 (240,000 to 895,000 eggs spawn^{-1}) in wild fish held at HSWRI (Stuart and Drawbridge, 2013; Schmidt et al., 2021). Similarly, F1 CYT broodstock, were previously shown to produce 290,000 to 660,000 eggs spawn^{-1} (Chin et al., 2023). Batch fecundity, as described here, was used even though more than one female may have contributed to a given "batch". A more accurate representation of batch fecundity would use eggs spawned per female or even better eggs spawn^{-1} kg female weight^{-1}, which for CYT ranges from 24,000 to 60,000 eggs spawn^{-1} kg female weight^{-1} (Schmidt et al., 2021; Chin et al., 2023). Based on the previously reported batch fecundity estimates for CYT and the size of female brood fish in this study, we estimate that five spawn events out of thirty-seven (13.5 %) in the Natural group and seven spawn events out of thirty-four (18.9 %) in the Controlled group had two females that contributed eggs to a single spawn event.

Average egg quality values reported here for viability (80–81 %), HR (48–75 %), and SFF (61–77 %) were generally higher than previously reported for this species (Stuart and Drawbridge, 2013; Stuart et al., 2020; Chin et al., 2023). The lowest average HR seen in this study was in the Natural group (48 %), which was much less than the hatch rate of the Controlled group (75.1 %). The variability in HR among spawns was also much higher in the Natural group (SD = ±28.9) than the Controlled group (SD = ±15.5). Both Stuart et al. (2020) and Chin et al. (2023, 2025) showed seasonal variation in hatch rates for CYT but these variations were explained through nutritional deficiencies, specifically in essential fatty acids. In the current study, diet was not a factor since both populations were offered the same feed. Further, one would expect that the Natural group would have an advantage over the manipulated Controlled group if the uptake of nutrients (provided in the same diets) was to be a factor. Another explanation for the difference in hatch rates between treatments could be the variation in egg quality between females in a tank (as indicated by the range of SD) or between tanks independent of a treatment effect. In each group in this study there were multiple females and without the ability to determine individual contribution, it is not possible to determine if poor hatch rates were from eggs of specific female(s). Future work should look to either increase replication, isolate individual females, or conduct parentage analyses to better understand if hatch rates are positively impacted by photothermal control. Another egg quality metric that has been identified as an indicator of quality for marine finfish eggs is egg size (Brooks et al., 1997; Gruenthal et al., 2014). It has been shown that large eggs produced by CYT early in the season have the best quality (Stuart et al., 2020). Here, smaller EDs were observed in the Natural group, but these smaller eggs

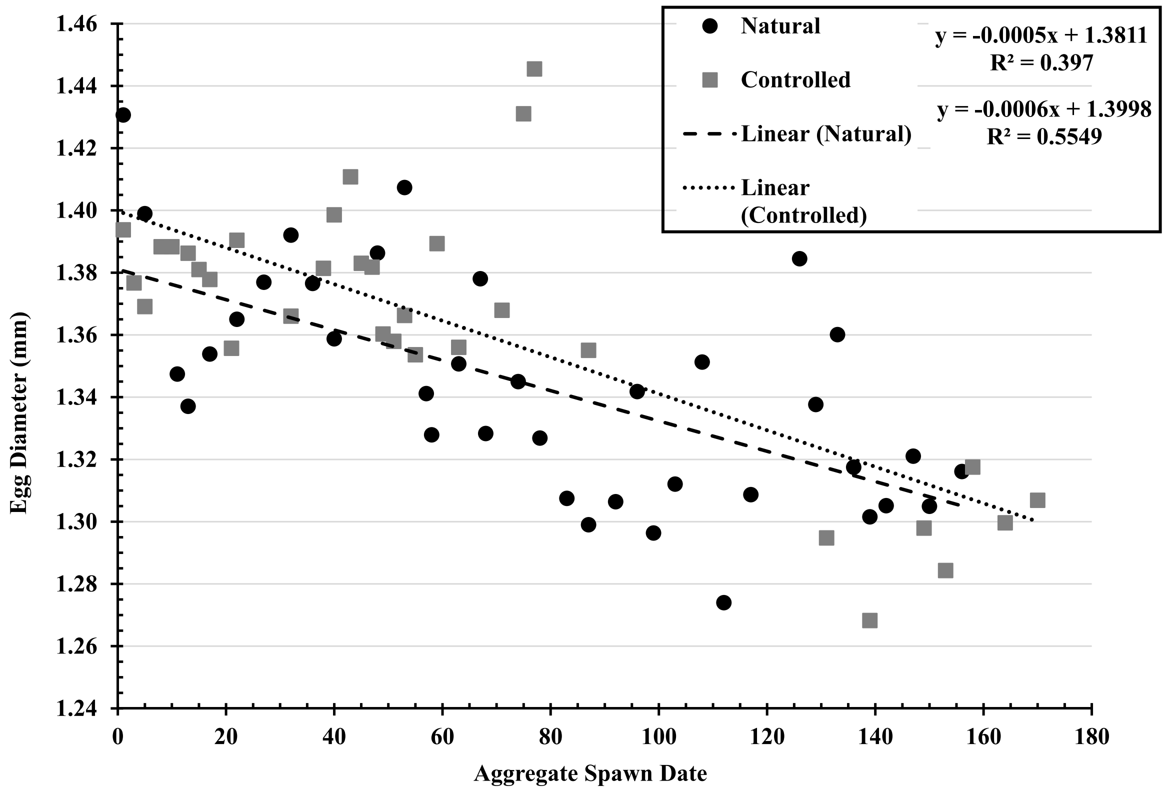

Fig. 3. Egg diameter of California yellowtail (*Seriola dorsalis*) plotted against aggregate spawn date for two spawning populations under a natural and controlled spawning regimes.

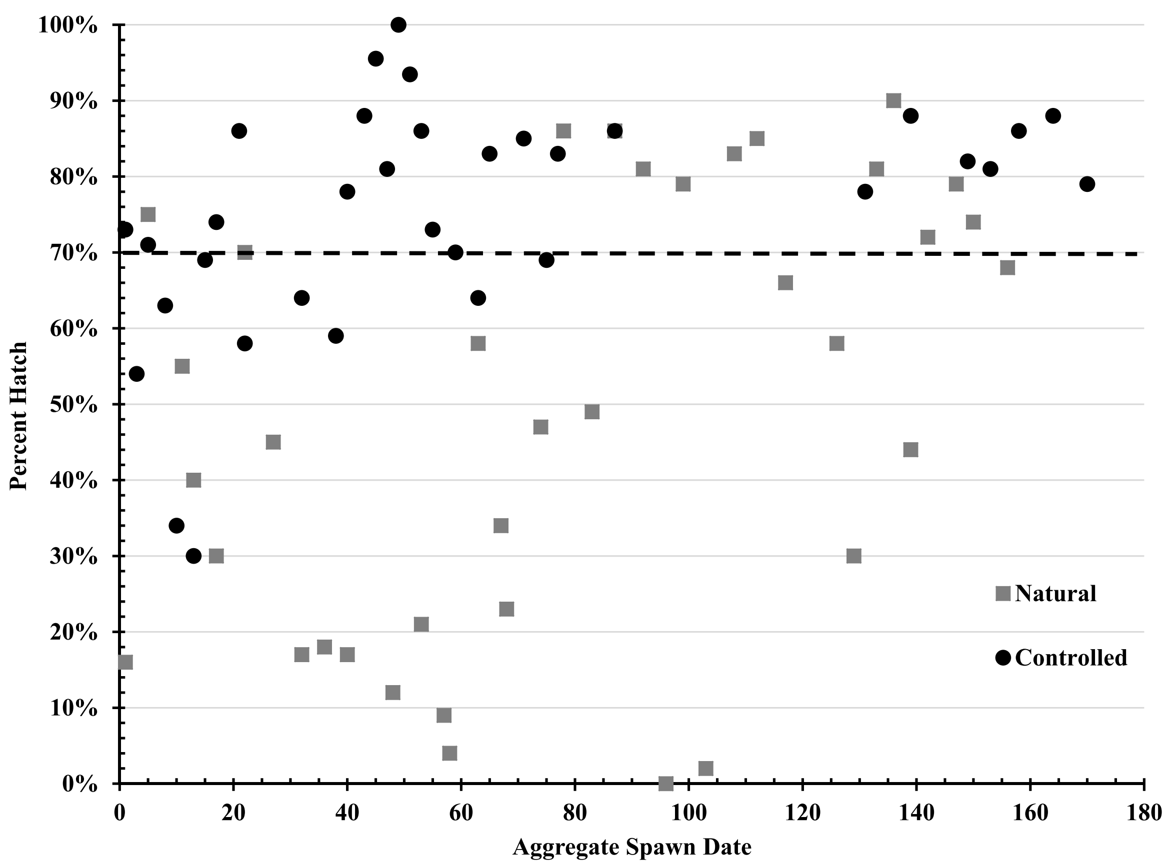

Fig. 4. Hatch rate (%) values from spawn events of California yellowtail (*Seriola dorsalis*) under a natural and controlled spawning regime. The line at 70 % represents the HSWRI target threshold in fish production.

over the course of the year did not appear to have lower overall quality, when compared to the Controlled group. In addition, the smaller ED observed in the Natural group was within the range of what has been reported for both *S. dorsalis* and *S. lalandi*, 1.31–1.50 mm (Moran et al., 2007; Yang et al., 2016; Stuart et al., 2020; Chin et al., 2023).

This study demonstrated that out of season spawning is possible for CYT, through photoperiod and temperature manipulation. Having the ability to control reproduction of this high value aquaculture species and spawn them year-round will be beneficial for the development of the Seriola industry in the United States.

CRediT authorship contribution statement

Drawbridge Mark: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition. **Stuart Kevin R.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Author statement

We the declare that this manuscript is original, has not been published before and is not currently being considered for publication elsewhere. We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us. We understand that the Corresponding Author is the sole contact for the Editorial process. He/she is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs.

Declaration of Competing Interest

The authors 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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Data availability

Data will be made available on request.

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