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Effect of a long photoperiod on the timing of spawning in the Pacific bluefin tuna, *Thunnus orientalis*

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ABSTRACT

In this study, we examined the effects of a long photoperiod on the reproduction of Pacific bluefin tuna (*Thunnus orientalis*) in a land-based tank. Three-year-old fish were shifted from a short (10.5 L:13.5D) to long (15 L:9D) photoperiod in December. The broodstocks exhibited gonadal development after this photoperiod change and spawned spontaneously the following March, approximately three months earlier than the normal spawning season. Although the results were based on data from a small sample size of fish, the study suggests that a long photoperiod induces the onset of gonadal development in Pacific bluefin tuna, thereby accelerating their spawning time.

1. Introduction

Various environmental factors, such as the photoperiod and water temperature, affect the synchronism of reproduction in fish species that exhibit marked seasonality in breeding activities (Wang et al., 2010). The acute regulation of reproduction by exogenous signals ensures the production of offspring under the most favorable environmental conditions for survival in the wild (Bromage et al., 2001). In fish farms, photothermal programs are commonly used to regulate reproductive cycle and obtain larvae throughout the year (Mañanós et al., 1997; Migaud et al., 2013). A good number of aquaculture fish with uniform size and quality can be supplied to commercial markets throughout the year using large fingerlings from the eggs obtained during either advanced or delayed spawning periods. Therefore, the mechanism by which environmental conditions affect spawning in fish, especially in commercially important aquaculture species, should be investigated for future applications.

Photoperiod manipulation can accelerate or delay spawning in various fish species (Taranger et al., 2010). In the rainbow trout (*Oncorhynchus mykiss*), a long photoperiod early in the year followed by a short photoperiod accelerates spawning, whereas a constant short photoperiod, or a short photoperiod followed by a long photoperiod, delay spawning by up to four months (Bromage et al., 1984). In sea bass (*Dicentrarchus labrax*), exposure to a long photoperiod for the duration of one month in May, June, or July before transitioning a constant short photoperiod regime until the spawning period accelerated the onset of vitellogenesis, advanced ovulation and spawning to December, deviating from their natural spawning time that usually occurs between February and March (Carrillo et al., 1989). In addition, molecular biology studies on the regulation of the brain–pituitary–gonad axis under photoperiod changes have revealed that the pituitary gonadotropin synthesis dynamics is affected by an altered photoperiod (Acharjee et al., 2017; Espigares et al., 2017). In species-specific responses to photoperiod manipulations in fish, the photoperiod is a key factor in modulating gametogenesis and gonadal development by regulating gonadotropin synthesis and release in the pituitary gland, thereby accelerating or delaying spawning.

Recently, we successfully accelerated gonadal development and obtained eggs two months earlier than the normal spawning season in the Pacific bluefin tuna (PBT, *Thunnus orientalis*), by shifting the photothermal conditions by two months, from December (winter solstice condition) to October, from a seasonally changing cycle (Higuchi et al., 2023). Advanced spawning system is a prominent tool for producing large hatchery-reared fingerlings with high survival potential during winter in PBT aquaculture, thereby promoting closed-cycle aquaculture (Higuchi et al., 2018). Previous studies on the sexual maturation of PBT

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reared in sea cages have suggested that broodstocks initiate gonadal development when exposed to a long photoperiod and/or high water temperature (Miyashita et al., 2000; Masuma et al., 2011). In this study, we examined the effects of a long photoperiod regime on the spawning of PBT broodstocks, without the coinciding increase in water temperature at the onset of the photoperiod shift, in order to better understand the reproductive response of PBT to various environmental manipulations. If implementing a long photoperiod regime without seasonally changing in water temperature induces advanced spawning of PBT broodstocks, it may result in significant cost savings in the culture of this species.

2. Materials and methods

2.1. Broodstock management

PBT spawning was induced in a circular land-based tank (diameter: 20 m; depth: 6 m; volume: 1880 m^3) at the Nagasaki Field Station, Fisheries Technology Institute (FTI), Japan Fisheries Research and Education Agency (FRA, Nagasaki, Japan), as previously described by Higuchi et al. (2023). A total of 116 2-year-old PBT raised from fertilized eggs were transported from a sea cage at the Amami Field Station to a land-based tank by a live-fish-transport ship on two separate days (April 16 and July 7, 2018), as previously described by Kadota et al. (2016) and Takashi et al. (2019) (Fig. 1). After stocking, photothermal cycles roughly based on the ambient water temperature and natural day length in sea cages were applied to induce spawning within the normal spawning season, between July 2 and August 7, 2019. Following spawning, a period of high mortality, likely associated with spawning, was observed until early September 2019. In addition, collision-related deaths frequently occurred throughout the project's duration in land-based tanks as with our previous report (Kadota et al., 2016). In the present study, the remaining broodstocks (5 females and 14 males, 3 + years of age) as of October 1, 2019, were utilized for the next part of the experiment and subsequently reared until the end of experiment, April 13, 2020 (Fig. 1). On December 20, 2019 (winter solstice condition), the remaining PBT broodstocks were subjected to a shift from a short (10.5 L:13.5D) to long (15 L:9D) photoperiod, which was maintained until the end of experiment (Fig. 2). Following the shift to the long photoperiod, the water temperature was maintained between 20–22 °C,

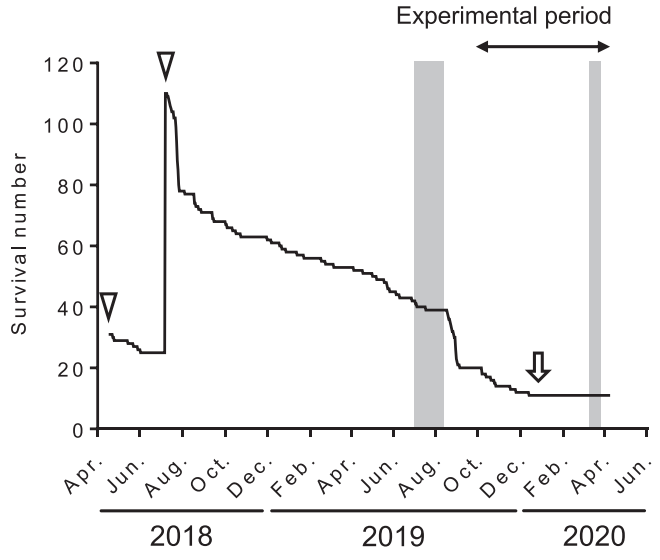

Fig. 1. Number of Pacific bluefin tuna (PBT) that survived from tank stocking to the end of experiment. Arrowheads indicate the transportation and tank stocking of 2-year-old PBT. The arrow shows application of the long photoperiod treatment. Vertical gray bars indicate the spawning periods.

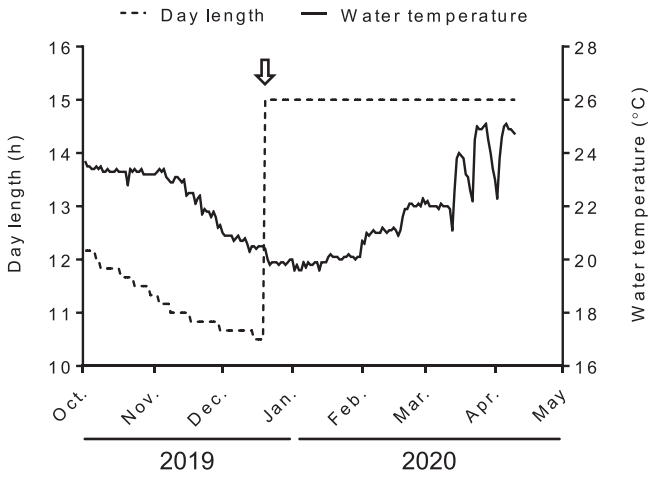

Fig. 2. Photoperiod and water temperature regimes used to induce spawning in the Pacific bluefin tuna in a land-based tank. Broodstocks (2 + years of age) were stocked, and initially kept under photothermal cycles roughly based on the ambient water temperature and natural day length between April 16, 2018 and December 19, 2019, and subsequently shifted from a short to long photoperiod on December 20, 2019 (winter solstice conditions, indicated by the arrow). Dotted and solid lines indicate the day length and water temperature, respectively.

providing conducive condition for the PBT broodstocks to initiate vitellogenesis in sea cages, under the natural photothermal conditions (Higuchi et al., 2021). After observing courting and pairing behaviors (males changing their body color to black with a vertical band pattern and repeatedly chasing one female), the water temperature rapidly increased by approximately 3 °C per day to induce spontaneous spawning (Higuchi et al., 2023). The average fork length (FL) and body weight (BW) of the broodstock, measured using a stereo video camera (AM-100; AQ1 systems, Tasmania, Australia) and built-in software (AM100 analyzer; AQ1 systems) on April 6, 2020 were 123.2 cm and 44.8 kg, respectively. Fish were fed to apparent satiation with a commercial pellet diet (Tuna food, Hayashikane Sangyo, Yamaguchi, Japan) and frozen chub mackerel (*Scomber japonicus*) once a day for five days a week. A premixed vitamin oil supplement (BIO SIENCE, Tokushima, Japan) was provided at 0.25–0.50% of the food weight throughout the experimental period, and astaxanthin oil (Biogenic, Tokyo, Japan) was also provided at 0.5% of the food weight during the spawning season. Ammonia (0.0–0.6 mg/L) content was measured four times per week, and dissolved oxygen (5.21–9.75 mg/L) and salinity (33.1–37.8 g/L) were measured almost daily.

Eggs from spontaneous spawning were collected daily using passive egg collectors fitted to the surface overflow. Buoyant (potentially viable) and non-buoyant (dead) eggs were separated, and the numbers were estimated volumetrically using a 5 mL graduated cylinder. Counting was conducted in triplicate using different cylinders, and the average number was used to estimate the total number of eggs. To evaluate the hatching rates of the eggs, approximately 90 buoyant eggs were incubated in three wells of a 6-well culture plate (30 eggs/well) filled with 5 mL of sterilized seawater containing antibiotics (50 μg/mL streptomycin and 50 U/mL penicillin) at 24 °C until hatching. Normal hatched larvae (with straight bodies) were counted using a light microscope (SZX-7; Olympus, Tokyo, Japan). The normal hatching rate was calculated as follows: (number of normally hatched larvae) × 100/(number of eggs). All the experiments were performed according to the Guidelines for the Care and Use of Live Fish, FTI, FRA.

2.2. Sampling procedure

Some PBT mortality occurred between October 7 and December 14, 2019, before the implementation of the long photoperiod treatment.

Subsequently, all the remaining fish (three females and eight males) at the end of the 2020 spawning period were sampled using a spear gun or conventional fishing gear, and the captured fish were immediately placed on ice. FL and BW were recorded, and the condition factor was calculated using the following formula: (BW, kg)/(FL, cm)^3 × 10^5. Gonads were excised, weighed, and the gonadosomatic index (GSI) was calculated as follows: (gonad weight, kg) × 100/(BW, kg). Small pieces form the mid-region of the gonads were fixed in Bouin's solution and processed for histological analysis.

2.3. Histology

Fixed gonads were dehydrated using a graded ethanol series, embedded in paraffin wax, cut into 5-μm-thick sections, and stained with hematoxylin and eosin. Female maturity was classified according to the most advanced type of oocytes found in the ovaries as follows: ovaries with perinucleolus-stage oocytes (perinucleolus stage), ovaries with oil droplet-stage oocytes (oil droplet stage), and ovaries with oocytes showing a limited number of small eosinophilic yolk globules at the center of the oocyte (early vitellogenesis stage) (Higuchi et al., 2021). According to the methods outlined by Schulz et al. (2010) and Kusakabe et al. (2006), with a few modifications, male maturity was classified according to spermatogenesis stage as follows: immature differentiated testis only containing spermatogonia (immature stage), early-spermatogenesis testis mainly containing spermatogonia and spermatocyte cysts (early-spermatogenesis stage), mid-spermatogenesis testis containing spermatocytes and spermatids as the dominant germ cell types and a small number of spermatozoa (mid-spermatogenesis stage), and late-spermatogenesis testis mainly containing spermatozoa (late-spermatogenesis stage).

3. Results

3.1. Spawning and egg quality

Courting and pairing behaviors were first observed on December 27, 2019. As the number and aggressiveness of chasing males increased in early March, 2020, the water temperature rapidly increased by approximately 3 °C per day on March 12, 21 and April 1, 2020, to induce spawning (Fig. 3A). The first spontaneous spawning of the 4-year-old broodstock was observed three days after the 1st water temperature elevation (Fig. 3A). Spontaneous spawning was also observed the following day, and two consecutive spawning events were observed two days after the 2nd water temperature increase. However, no spawning was observed after the 3rd water temperature increase. The total number of eggs obtained during the spawning period was 1.70 million, and the average number of eggs per batch was 0.43 million. The normal hatching rates of buoyant eggs on March 15, 16, 23, and 24 were 29.1%, 61.9%, 22.4%, and 81.0%, respectively (Fig. 3B).

3.2. Reproductive status of PBT broodstock under a long photoperiod regime

To examine the effects of a long photoperiod on gonadal development, we investigated the GSI and gonadal histology of the PBT broodstocks before the long photoperiod treatment and after spawning (Table 1). The two females and three males that died prior to the long photoperiod treatment exhibited vertebral fractures, a clear indication of collision with the tank wall (Kadota et al., 2016); otherwise, these fish appeared healthy and free from infectious diseases prior to their sudden deaths. Before the long photoperiod treatment, females and males were in the perinucleolus and immature/early/mid-spermatogenesis stages, respectively. Although several vitellogenic oocytes were classified as α-atresia, one female reached the early vitellogenesis stage. Moreover, all the males reached the late-spermatogenesis stage during the spawning period. Notably, the GSI at the end of the spawning period

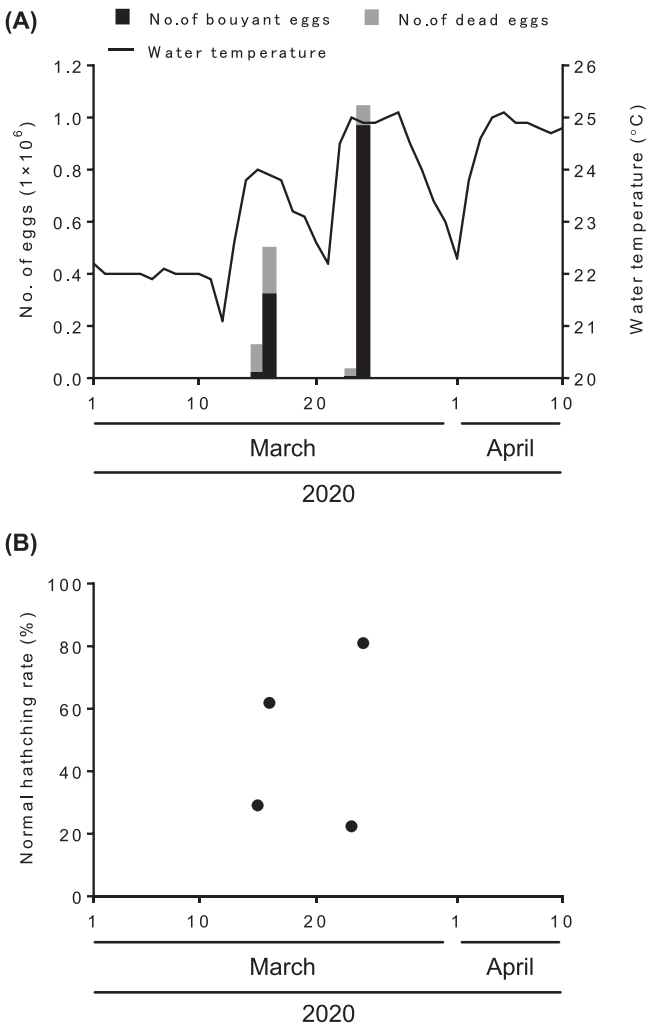

Fig. 3. Water temperature and daily number of eggs (A) and normal hatching rates of buoyant eggs (B) during spawning. Black and gray bars indicate the number of buoyant and dead eggs collected per day, respectively. Black lines indicate the water temperature. Black dots indicates normal hatching rate.

(0.55–0.86, females; 0.71–1.91, males) was higher than that before the photoperiod change (0.23–0.26, females; 0.04–0.21, males).

4. Discussion

In this study, shift from a short (10.5 L:13.5D) to long (15 L:9D) photoperiod induced PBT broodstock spawning in March, approximately three months earlier than the normal spawning season (Masuma et al., 2011; Higuchi et al., 2023). We previously reported that PBT reared in sea cages spawn between late April and October (peaking between June and July) depending on the captive environmental conditions (Higuchi et al., 2021). However, to the best of our knowledge, this is the first study to report evidence of PBT spawning in March, which is completely outside the spawning season. Here, the long photoperiod regime accelerated the timing of spawning in PBT. Generally, the environmental control of fish reproduction is based on gametogenesis and spawning period of fish (Wang et al., 2010). Previous studies on natural gonadal development suggest that in various fish species, such as the common dab (*Limanda limanda*) (Htun-Han, 1978), turbot (*Psetta maxima*) (Imsland et al., 1997), yellowtail (*Seriola quinqueradiata*) (Higuchi et al., 2017), and PBT (Masuma et al., 2011), spawning between spring and summer initiates gonadal recrudescence, undergoing gametogenesis and spawning under an increased

Table 1
Reproductive status of the Pacific bluefin tuna before long photoperiod manipulation (October 1 to December 19, 2019) and after spawning (April 9–13, 2020).

	Date		Fork length (cm)	Body weight (kg)	Condition factor	GSI	Maturity status[a]
Female	Oct. 7, 2019	Dead (collision)	115.3	32.9	2.15	0.23	PN
	Oct. 7, 2019	Dead (collision)	121.7	40.4	2.24	0.26	PN
	Apr. 9, 2020	Sampled	122.4	49.7	2.71	0.86	OD
	Apr. 13, 2020	Sampled	113.0	32.4	2.25	0.85	EVG (with vitellogenic oocytes classfied as α atresia)
	Apr. 13, 2020	Sampled	118.6	37.8	2.27	0.55	OD
Male	Oct. 13, 2019	Dead (collision)	112.5	34.3	2.41	0.21	MSG
	Oct. 25, 2019	Dead	111.5	29.9	2.16	0.10	MSG
	Oct. 27, 2019	Dead (collision)	116.0	37.3	2.39	0.07	ESG
	Nov. 17, 2019	Dead	125.0	41.3	2.11	0.06	ESG
	Nov. 25, 2019	Dead (collision)	115.5	35.9	2.33	0.04	IM
	Dec. 14, 2019	Dead	101.6	24.0	2.29	0.14	MSG
	Apr. 9, 2020	Sampled	115.9	38.4	2.47	1.91	LSG
	Apr. 10, 2020	Sampled	120.9	49.6	2.81	0.71	LSG
	Apr. 10, 2020	Sampled	130.5	58.2	2.62	0.89	LSG
	Apr. 13, 2020	Sampled	115.8	44.7	2.88	1.46	LSG
	Apr. 13, 2020	Sampled	133.5	68.2	2.87	1.00	LSG
	Apr. 13, 2020	Sampled	119.2	48.4	2.86	1.65	LSG
	Apr. 13, 2020	Sampled	123.8	49.5	2.61	1.63	LSG
	Apr. 13, 2020	Sampled	102.2	30.3	2.84	0.94	LSG

Male maturity status is indicated as follows: IM, immature differentiated testis only containing spermatogonia; ESG, early-spermatogenesis testis mainly containing spermatogonia and spermatocyte cysts; MSG, mid-spermatogenesis testis containing spermatocytes and spermatids as the dominant germ cell types and a small number of spermatozoa; LSG, late-spermatogenesis testis mainly containing functional spermatozoa.

[a] Female maturity status is indicated as follows: PN, ovaries with perinucleolus stage oocytes; OD, ovaries with oil droplet stage oocytes; EVG, ovaries with early vitellogenesis stage oocytes.

photoperiod and/or temperature. Moreover, a long photoperiod (18 L:6D) accelerates ovarian development to ovulation in approximately two months in the spring spawner *Seriola* species, yellowtail, and greater amberjack (*Seriola dumerili*) (Mushiake et al., 1998; Nyuji et al., 2018). Furthermore, a shift from a short to long photoperiod stimulates the synthesis and release of pituitary gonadotropins, subsequently inducing ovarian development in greater amberjack (Nyuji et al., 2018). In this study, the PBT broodstock initiated gonadal development after the photoperiod change and progressed to the vitellogenesis or late-spermatogenesis stages at the end of the spawning period. Taken together, our results suggest that a long photoperiod induces the onset of gonadal development, thereby affecting the PBT spawning period. However, further studies are warranted to examine the specific effects of photoperiod regulation on gonadal development, and the synthesis and release of pituitary gonadotropins in PBT.

Here, a shift to a long photoperiod regime in December facilitated the advanced spawning of the PBT broodstocks. This technique requires only three to four months for photothermal control of spawning induction. Previously, we achieved advanced spawning by uniformly shifting the photothermal regime at the end of October, corresponding to the winter solstice conditions (Higuchi et al., 2023). However, this method is disadvantageous because it requires more than six months to induce advanced spawning and involves high environmental control costs, especially water temperature control in a large tank. Therefore, the application of a long photoperiod is a cost-effective method for inducing advanced spawning in PBT broodstocks.

Despite successful advanced spawning induction via photoperiod manipulation, total number of spawning days and number of eggs spawned were quite low in this study. Moreover, gonadal regression was observed in a female that was expected to participate in advanced spawning. The cause for the lower spawning activity and gonadal regression of PBT under long photoperiods remains unknown. Because only three females were used in this study, further studies with larger sample sizes are necessary to determine the characteristics of advanced spawning induced by long photoperiods.

In conclusion, a long photoperiod induced spontaneous spawning approximately three months earlier than the normal spawning season, followed by the initiation of gonadal development in PBT. Moreover, a shift to a long photoperiod regime requires only three to four months to effectively regulate spawning induction, suggesting that this approach could offer a cost-effective way to induce advanced spawning. Therefore, the application of long photoperiod regimes may be a novel technique to induce advanced spawning and produce large hatchery-reared PBT fingerlings with a high survival potential during winter.

Author statement

We confirm that neither the manuscript nor any parts of its content are currently under consideration or published in another journal. No conflict of interest exits in the submission of this paper. All authors have approved the manuscript and agree with its submission to Journal of Aquaculture Reports.

CRediT authorship contribution statement

Mitsuo Nyuji: Writing – review & editing, Investigation. **Takao Hayashida:** Resources. **Kogen Okita:** Resources. **Toshinori Takashi:** Writing – review & editing, Project administration. **Koichiro Gen:** Project administration. **Kentaro Higuchi:** Writing – original draft, Methodology, Investigation, Conceptualization.

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.

Data availability

Data will be made available on request.

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