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Aquaculture 189 (2000) 293–305

Aquaculture

www.elsevier.nl/locate/aqua-online

Effect of consecutive 9- or 12-month photothermal cycles and handling on sex steroid levels, oocyte development, and reproductive performance in female striped trumpeter *Latris lineata* (Latrididae)

D.T. Morehead [a,*], A.J. Ritar [a], N.W. Pankhurst [b]

[a] *Marine Research Laboratories and CRC for Aquaculture, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, GPO Box 252C, Hobart, Tasmania 7001, Australia*

[b] *School of Aquaculture, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Locked Bag 1-370, Launceston, Tasmania 7250, Australia*

Received 22 October 1997; accepted 8 March 2000

Abstract

Duplicate groups of sexually mature striped trumpeter *Latris lineata* were maintained for two seasons on either a 12-month cycle of ambient temperature (9–18°C) and photoperiod, or a 9-month compressed temperature and photoperiod cycle. One of the duplicates from each cycle was handled frequently (handled) and blood and ovarian samples taken monthly from females until the start of gonadal recrudescence, and then fortnightly until ovulations had ceased. Fish from the other group were not handled (non-handled), except near the end of their spawning seasons to determine which fish had ovulated. Naturally spawned eggs were collected daily from the tanks and hand-stripping was conducted fortnightly in the handled fish during the respective spawning seasons. The 12-month group started spawning in September in both years, whereas the compressed cycle advanced spawning by 1 and 4 months during consecutive seasons, i.e. August 1995 and May 1996. For all handled fish, oocytes developed to late cortical alveoli/early vitellogenic stage, but on average, only 64% of fish continued development through to ovulation. The duration of spawning averaged 45 days for the 9-month and 64 days for the 12-month cycle. The mean volume of eggs produced for each day of production was higher for the handled than the non-handled fish, but there was no difference between cycles (9- and 12-month). Eggs from fish on the 9-month cycle were significantly smaller than from fish on the 12-month cycle. Plasma levels of testosterone (T) and 17β-oestradiol (E_2) in fish from both the 9- and 12-month cycles were at or near their lowest levels at first sampling (< 0.3 and 0.5 ng ml^{-1}, respectively) and

* Corresponding author.

PII: S0044-8486(00)00371-9

remained low except for elevations during the 3–4 month period of oocyte maturation and ovulation, when levels peaked at 1.3 and 6.3 ng ml^{-1}, respectively.

Keywords: Teleost; Oocyte development; Plasma steroids; Spawning; Photoperiod; Temperature

1. Introduction

For most temperate water or higher latitude fish, spawning is an annual event controlled by endogenous (including endocrine) and exogenous (including photoperiod and temperature) cues (Lam, 1983; Sumpter, 1990). In fish culture, the artificial advancement or delay of spawning is a valuable technique for broodstock management (Zanuy et al., 1986), and temperature and photoperiod have been used successfully to alter the time of spawning in a number of teleosts (reviewed by Bye, 1990). Some studies, especially in salmonids, have employed a constant daylength and/or temperature followed by an abrupt change in daylength and/or temperature to stimulate advances or delays in gametogenesis (e.g. Carrillo et al., 1991; Davies et al., 1991). Other studies have examined compressing or extending natural photoperiod and temperature (photothermal) cycles to entrain fish to spawn at different times of the year (e.g. Blythe et al., 1994a; Norberg et al., 1995).

The present study examined the use of a compressed photothermal cycle to advance the time of spawning in striped trumpeter, *Latris lineata* (order Perciformes). Striped trumpeter occur in the temperate waters of Australia and New Zealand (Last et al., 1983) and form a small commercial fishery in Tasmania (< 100 ton $year^{-1}$). In the waters off south-east Tasmania, wild mature striped trumpeter spawn between August and October (late winter to spring). Our earlier work, using a synthetic luteinizing hormone releasing hormone analogue (LHRHa: des-Gly^{10}, [D-Ala^{6}]-LH-RH ethylamide) to induce ovulation, suggested that striped trumpeter are multiple spawners with group synchronous oocyte development, and that batches of pelagic eggs are released every 3–4 days during the spawning season (Morehead et al., 1998). Despite our ability to produce a regular supply of eggs during the spawning season, larviculture is still restricted to a 2-month period each year. This study aimed to (a) further our knowledge of reproduction in striped trumpeter; (b) acclimate wild broodstock to captive conditions; and (c) phase-shift the spawning period to allow out-of-season egg production. Sampling regimes were designed to correlate endocrine changes with stage in oocyte development for fish on both the compressed and normal photothermal cycles, and to assess the effect of handling stress by comparing reproductive performance between frequently and infrequently handled stocks.

Plasma levels of testosterone (T) and 17β-oestradiol (E_2) were measured as they are known to regulate oocyte development in a number of teleosts (Pankhurst and Carragher, 1991) and are produced by striped trumpeter in significant quantities after treatment with LHRHa (Morehead et al., 1998). Generally, E_2 reaches a peak in fish undergoing vitellogenesis while T is elevated during vitellogenesis and also the early stages of final oocyte maturation (FOM) (Fostier et al., 1983).

2. Materials and methods

2.1. Fish capture and husbandry

Sexually mature striped trumpeter (81 females and 88 males) were caught by drop-lining off the north-east (40°46′S, 148°42′E), north-west (41°15′S, 144°30′E) and south-east coasts of Tasmania (43°32′S, 148°02′E) at depths of up to 100 m between April and September 1994. All fish were tagged intramuscularly with numbered tags, and sex was determined by insertion of a biopsy catheter into the gonopore upon arrival at the laboratory. In December 1994, 68 females and 40 males were selected from this group for this experiment, with just over half of the females ($n = 36$) having been used in the experiment reported in Morehead et al. (1998) during October 1994. Fish were divided into four groups, each of 17 females and 10 males (mean $\pm$ SE body weight, 2.8 ± 0.1 kg, $n = 108$), and were held indoors in circular (25 000 l) fiberglass tanks. Chopped squid and pilchards were fed to the broodstock from the onset of oocyte development until the completion of spawning, and commercial salmon pellets (Gibson's, Hobart, Tasmania) were fed to the fish for the remainder of the year. Initial broodstock numbers were high to compensate for possible mortality, but as there were no mortalities during the first spawning season, broodstock numbers were reduced to 10 females and 8 males per tank.

2.2. Treatment protocols

Two photothermal cycles were employed; a 12-month cycle with flow-through water at ambient temperature and a 9-month compressed cycle with semi-recirculated water maintained using heat–chill pumps. To assess the effect of sampling on reproductive performance, each cycle involved two groups of fish; one group was frequently handled for sampling, whereas the other underwent minimal handling. Local minimum (9.0°C) and maximum (18.0°C) water temperatures were applied to the 9-month cycle with adjustments to temperature made at fortnightly intervals (Fig. 1). Daylengths (sunrise/sunset) were obtained from the Australian Bureau of Meteorology and simulated photoperiods, also adjusted at fortnightly intervals, were applied to both the 9- and 12-month cycles. A micro-computer turned the lights (incandescent, $\sim$100 lx at the tank surface) on and off and a 30-min fade in and fade out period simulated the natural sunrise and sunset. The photothermal regimes were calculated from 1 January 1995 (Day 1), but the fish were not exposed to these regimes until 24 January 1995. Sampling concluded after the 12-month photothermal group had undergone two complete spawning seasons (12 December 1996).

2.3. Sampling procedures

The frequently handled fish (hereafter referred to as 'handled') were sampled each month until oocyte development began and then every 2 weeks until ovulations ceased, at which point monthly sampling resumed. Fish from the infrequently handled group (hereafter referred to as 'non-handled') were sampled near the end of each spawning

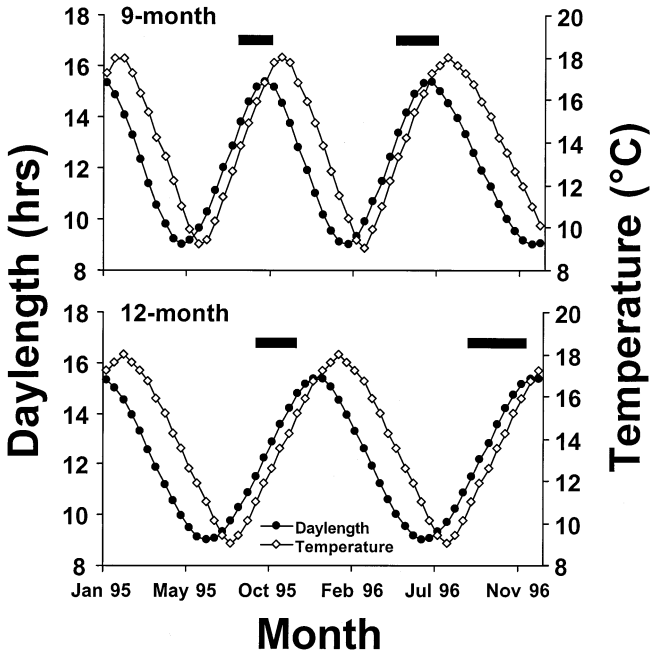

Fig. 1. Daylength and temperature values for 9- and 12-month photothermal cycles. Horizontal bars indicate the spawning season of fish held on each regime.

season to determine which fish had undergone FOM; indicated by the presence of hydrated oocytes or remnant coalesced oil drops within the ovary.

2.3.1. Blood sampling

At each sample time, all fish were netted from the holding tank and placed in 500 l temporary holding bins before being anaesthetised in a 0.02% 2-phenoxyethanol (Sigma) water bath and then sampled. Blood samples (3 ml) were obtained from the duct of Cúvier using 5 ml syringes and 21 G needles heparinized by aspirating a solution of 500 U heparin and 5 mg methiolate ml^{-1} in saline. Blood was centrifuged at 3000 rpm (14 480 g) for 5 min and the plasma was removed and stored at $-18°C$. Plasma levels of T, and E_2 were measured in duplicate by RIA using the reagents and protocol given in Pankhurst and Conroy (1987) and Pankhurst and Carragher (1992), respectively. Detection limits were 0.21 ng ml^{-1} plasma for T and 0.31 ng ml^{-1} for E_2. Interassay variability was measured using a pooled standard giving %CVs of 15% ($n = 14$) and 10% ($n = 14$) for T and E_2, respectively. Extraction efficiency, calculated as recovery of ^{3}H-labelled steroid extracted with plasma, was on average 76% ($n = 14$) for T and 52% ($n = 14$) for E_2. Assay values were corrected accordingly.

2.3.2. Ovarian samples

Ovarian condition was determined by inserting a catheter (''Endometrial biopsy''-Laboratoire CCD 60, Paris) through the gonopore and midway into the ovary to collect about 0.5 ml of ovarian tissue. Ovarian samples were placed in a Petri dish, reduced to a

single layer by dispersing individual oocytes in a saline solution and the size of the largest intact oocyte from each fish was recorded ($n = 1$). Five stages of oocyte development have been defined according to size and status of the germinal vesicle: primary (< 226 μm), cortical alveoli (226–465 μm), vitellogenic (466–727 μm), maturing (728–1032 μm) or hydrated (> 1032 μm) (Morehead et al., 1998). Collectively, maturing and hydrated stages cover the period of FOM.

2.3.3. Egg production (ovulations)

A conical mesh egg collector (500 μm) on the side of the tank collected circulating buoyant eggs into a temporary holding container. In addition, both the handled and non-handled fish were manually hand-stripped at each sample time. The daily volume of eggs produced by each group of fish was recorded (ml). During 1996, the diameter of 10 eggs was measured on the day of collection from 76 separate egg batches ($n = 15$, 17, 24 and 20 for the 9- and 12-month, handled and non-handled fish respectively), using a dissecting microscope attached to a Sony video camera (DXC 151AP) and a Macintosh computer running NIH Image 1.53b. Total counts from 10 measured aliquots (0.5 ml each) of eggs (diameter $= 1249 \pm 4$ μm) collected from the egg collector on a single occasion showed there were 700 ± 6 eggs ml^{-1}. Fertilisation was estimated by assessing the percentage of eggs that had undergone initial cell-division after manual fertilisation (hand-stripped), or that were at some later stage in embryonic development (naturally spawned). However, due to logistical constraints, hatch and larval survival rates were not routinely recorded.

2.4. Statistical analysis

Student's *t*-tests were used to assess for differences in spawning duration, total egg production, and the number of days that eggs were produced between each cycle (9- and 12-month) and handling group (handled and non-handled) ($P = 0.05$). Daily egg production data and egg size data were assessed by two-way ANOVA with 'cycle' and 'handling' as fixed factors ($P = 0.05$). Egg production data had homogenous variance, but despite square-root transformation, conditions for normality were not met in some instances. Egg size data met ANOVA assumptions. Steroid data were $\text{Log}(X + 1)$ transformed, but did not meet ANOVA assumptions of normality or homogenous variance. To reduce type II errors (Underwood, 1981), differences in steroid concentrations at different sample times were examined at an alpha level of 0.01 using a Dunnett's test (Steel and Torrie, 1960) with the control being the initial sample, while steroid data during oocyte development were examined using ANOVA followed by a Tukey test (Steel and Torrie, 1960) at an alpha level of $P = 0.001$.

3. Results

3.1. Oocyte development

The handled fish from both the 9- and 12-month photothermal cycles contained only primary oocytes (largest were 175 ± 7 μm, $n = 17$ and 173 ± 5 μm, $n = 15$, respec-

tively) at the time of first oocyte sampling (April 1995), and attained cortical alveoli oocytes soon after the winter solstice of the regime on which they were held; when daylength was increasing, but while temperatures were at their minimum (Fig. 1). During the first season, 9 of 17 fish from the 9-month and 10 of 15 fish from the 12-month cycle underwent FOM and ovulation, whereas the remaining fish on the 9- and 12-month cycles attained mean maximum oocyte diameters of only 414 ± 37 and 489 ± 18 μm, respectively (Fig. 2). During the second season, 5 of 10 fish on the 9-month cycle and all 10 fish on the 12-month cycle underwent FOM and ovulation, while the remaining fish on the 9-month cycle attained a mean maximum oocyte diameter of only 357 ± 93 μm. In those fish that went on to ovulate, two further

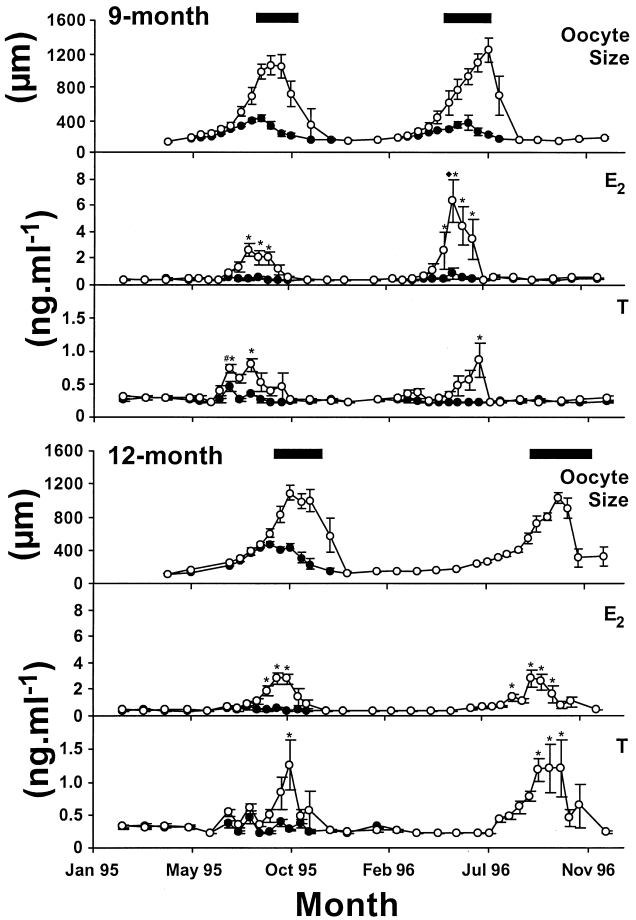

Fig. 2. Oocyte size (μm), and plasma E_2 and T concentrations in striped trumpeter held on consecutive 9- and 12-month photothermal cycles. Data divided into non-ovulating (filled symbols) and ovulating (clear symbols) fish. Horizontal bars indicate the spawning season. '*' and '♦' indicate steroid levels in the ovulating and non-ovulating fish, respectively, that are different from initial levels (Dunnett's, $P < 0.01$). Data are presented as mean ± SE.

clutches of oocytes (cortical alveoli stage and vitellogenic) were present as the first clutch was maturing. A peak in mean largest oocyte diameters occurred earlier in the ovulating fish held on the 9-month cycle during both the 1995 (1 month) and 1996 (4 months) spawning seasons.

3.2. Egg production

Unassisted spawning occurred in each of the four tanks during 1995 and 1996, however, in each year there were fish that either ovulated during consecutive seasons, failed to ovulate at all or went from being non-ovulators to ovulators ($n = 5$) and vice versa ($n = 2$). The duration of the spawning season differed significantly between cycles ($P < 0.05$) and was proportional to the length of the cycle to which the fish were exposed (45 ± 9 and 64 ± 11 days, for the 9- and 12-month cycles, respectively; mean $\pm$ SD, $n = 4$), but not between handling groups ($P > 0.05$), despite the non-handled fish having a shorter season at each spawn than their handled counterparts ($81 \pm 2\%$, $n = 4$).

The number of days that eggs were produced differed between cycles, with fish on the 9-month cycle producing eggs on fewer days (22 ± 1 and 36 ± 4, for 9- and 12-month cycles, respectively; mean $\pm$ SD, $n = 4$; $P < 0.05$), but there was no difference between handling groups ($P > 0.05$). Total egg production did not differ between cycles or handling groups ($P > 0.05$; Table 1). However, the mean volume of eggs produced for each day of egg production differed between handling groups, with the handled fish producing more eggs per day (193 ± 30 and 112 ± 34 ml, for 9- and 12-month cycles respectively; mean $\pm$ SD, $n = 4$; $P < 0.05$), but there was no difference between cycles ($P > 0.05$).

Photothermal cycle had a significant effect on egg size, with the fish on the 9-month cycle having smaller eggs than their counterparts on the 12-month cycle (1214 ± 6 and

Table 1
Ovulatory performance of handled and non-handled female striped trumpeter exposed to consecutive 9- and 12-month photothermal cycles
na = Data not available.

Spawning Season	Cycle	Group	No. of fish per tank (No. ovulating)	Spawning duration	No. of days eggs produced	Total eggs produced (ml)	Mean vol. of eggs per day ($\pm$SD)	% Fertilised	Mean egg size (μm $\pm$ SE)
	9-month	Handled	17 (9)	45	22	4790	218 ± 198	14	na
1995		Non-handled	17 (8)	34	20	2491	125 ± 100	3	na
	12-month	Handled	15 (10)	60	37	7287	197 ± 159	32	na
		Non-handled	16 (9)	52	34	2135	63 ± 78	14	na
	9-month	Handled	10 (5)	55	22	4507	205 ± 126	3	1209 ± 8
1996		Non-handled	10 (7)	45	23	2699	117 ± 113	15	1219 ± 8
	12-month	Handled	10 (10)	79	41	5824	150 ± 122	44	1235 ± 7
		Non-handled	10 (7)	63	33	4945	142 ± 171	33	1245 ± 7

1240 ± 5, respectively, mean ± SE; $P < 0.05$), however, handling had no significant effect ($P > 0.05$; Table 1). The percentage of eggs fertilised from individual batches, both naturally spawned and hand-stripped, ranged from 0% to > 90%, with mean rates during a season ranging from 3–44% (Table 1).

3.3. Seasonal steroid levels

Plasma levels of T and E_2 in both the 9- and 12-month cycles were at or near their lowest levels at first sample and there was no difference ($P < 0.05$) in levels between the 9- and 12-month cycles, or between the potential ovulating and non-ovulating fish (Fig. 2). Plasma T and E_2 levels remained low (< 0.3 and 0.5 ng ml^{-1}, respectively) except for elevations during the 3–4 month period of oocyte development and ovulation. The first significant increase in T, when compared to initial levels at the time of first sampling, occurred in both the ovulating and non-ovulating fish held on the 9-month cycle in July (0.7 and 0.5 ng ml^{-1}, respectively; $P < 0.01$) and this was followed, in the ovulating fish only, by a significant increase in E_2 in August (2.6 ng ml^{-1}; $P < 0.01$). In contrast, only the ovulating fish held on the 12-month cycle underwent a significant increase in T (1.3 ng ml^{-1}, October; $P < 0.01$) and this was preceded by a significant increase in E_2 (1.8 ng ml^{-1}, September; $P < 0.01$). During the second spawning season, both the ovulating and non-ovulating fish held on the 9-month cycle underwent significant increases in E_2 in May (2.6 and 0.9 ng ml^{-1}, respectively; $P < 0.01$), however, only the ovulating fish underwent a significant increase in T (0.9 ng ml^{-1}, June; $P < 0.01$). All of the fish held on the 12-month cycle ovulated during the second

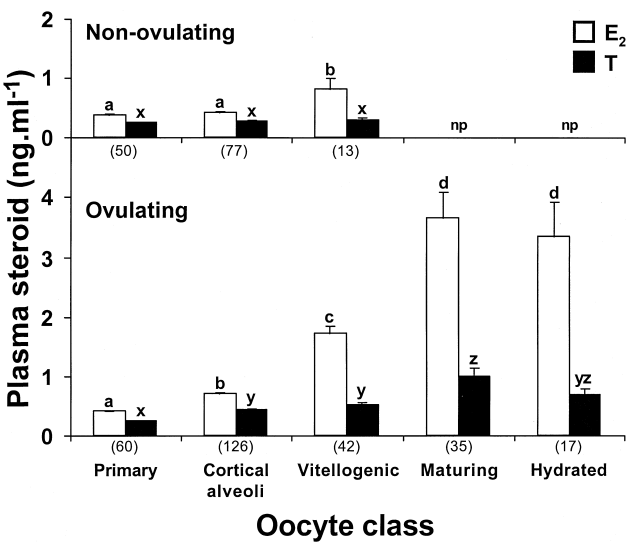

Fig. 3. Mean plasma levels of E_2 and T in the handled non-ovulating and ovulating fish (9- and 12-month cycles combined) in relation to stage in oocyte development prior to ovulation. Different letters indicate significantly different values for each steroid (Tukey, $P < 0.001$). (#) = number of samples. np = not present. Data are presented as mean ± SE.

season and the first significant increase in the level of E_2 (1.4 ng ml^{-1}; $P < 0.01$) and T (1.2 ng ml^{-1}; $P < 0.01$) occurred in August and September, respectively. Generally, increases in T and E_2 occurred at or around the same time, for each cycle and at each spawning season. The highest mean plasma levels of T and E_2 obtained from the ovulating fish during this study were 1.3 (12-month cycle, first season) and 6.3 ng ml^{-1} (9-month cycle, second season), respectively.

3.4. Steroid levels in relation to oocyte stage

Within the fish that did not subsequently ovulate, plasma T and E_2 levels were low when only primary oocytes or primary and cortical alveoli oocytes were present (0.3 and 0.4 ng ml^{-1}, respectively; Fig. 3). However, when vitellogenic oocytes were also present, there was a significant increase in E_2 (0.8 ng ml^{-1}; $P < 0.001$). Similarly, in the fish which subsequently ovulated, levels of T and E_2 were low when only primary oocytes were present (0.2 and 0.4 ng ml^{-1}, respectively), but there was a significant increase in both steroids when cortical alveoli oocytes were present (0.4 and 0.7 ng ml^{-1}, respectively; $P < 0.001$). Levels of E_2 increased further (1.7 ng ml^{-1}; $P < 0.001$) when vitellogenic oocytes were present, but T levels showed no increase. A further significant increase in the levels of E_2 (3.7 ng ml^{-1}; $P < 0.001$) and a significant increase in T (1.0 ng ml^{-1}; $P < 0.001$) occurred when maturing oocytes were present, however, these levels remained unchanged when hydrated oocytes were also present.

4. Discussion

Oocyte development in the fish on the 9-month cycle began earlier than in fish on the 12-month cycle, and the time taken for these oocytes to hydrate was reduced. This suggests that photothermal cues affect not only the time for the initiation of oocyte development but also the rate at which oocytes develop. A similar situation was found in the sea bass, *Dicentrarchus labrax*, with the rate of maturation being increased in fish exposed to compressed photoperiod cycles (Carrillo et al., 1991). Blythe et al. (1994a) suggested that temperature may regulate the process of oocyte development by controlling metabolism. As such, a faster rate of temperature increase in the compressed cycle fish may have resulted in a faster rate of oocyte development.

Gonadal recrudescence began as the temperature was decreasing and when daylength was at a minimum, whereas FOM and ovulation occurred as both the temperature and daylength were increasing; similar to the situation reported for the dab, *Limanda limanda* (Bye, 1990) and the blue cod, *Parapercis colias* (Pankhurst and Conroy, 1987). Data from fish on the 12-month cycle suggest that female striped trumpeter naturally have an oocyte development period (from cortical alveoli to hydrated stage) of approximately 3 months (June–August) and a spawning period of approximately 2 to 2.5 months (September to early November), followed by a dormant period of 6.5 to 7 months (December–May).

The duration of spawning was proportional to the length of the cycle to which the fish were exposed, however, had this experiment started 3 months earlier, in October

1994 rather than in January 1995, the compressed cycle fish would have received a full 9, rather than 6, months exposure to the 9-month cycle during the first season. This may have resulted in these fish spawning 6, rather than 4, months earlier than those on ambient conditions by the end of the second 9-month cycle. Exposure to a 2-month advanced photoperiod regime mid-cycle in Atlantic halibut, *Hippoglossus hippoglossus* produced a similar response, with no advance during the first season of spawning, but with a 1- and 2-month advancement over the following two seasons (Smith et al., 1991).

Frequent handling of the broodstock in this study resulted in a greater volume of eggs being produced by the handled fish, contrary to a study by Blythe et al. (1994a) which found no difference in reproductive success between striped bass, *Morone saxatilis* which spawned unassisted or were hand-stripped. This may in part be explained by hand-stripping being more effective at collecting eggs than the passive collection method used in the current study. An earlier study on wild striped trumpeter found the stress of capture, confinement and subsequent handling during the spawning season to inhibit the ovarian production of T and E_2 and arrest oocyte development (Morehead, 1998), which is similar to findings in a number of teleosts (reviewed in Pankhurst and Van Der Kraak, 1997). However, despite handling stress being implicated with stimulating final maturation and ovulation in other captive fish (Barton, 1997), this cannot be confirmed from the current study for striped trumpeter.

The production of smaller eggs by striped trumpeter on the compressed cycle is consistent with previous studies on rainbow trout, *Oncorhynchus mykiss* (Davies and Bromage, 1991; Bon et al., 1995) and striped bass (Blythe et al., 1994b). In contrast, striped bass hybrids (*Morone* hybrids) exposed to 6- and 9-month phase-shifted cycles did not exhibit any difference in egg size when compared to control fish on a 12-month cycle (Tate and Helfrich, 1995). However, the fish in that study did not have compressed cycles, but instead had dormant periods during the year removed. This suggests that a lengthy dormant period between spawning and recrudescence is not obligatory, but may be necessary in some species for the replenishment of energy reserves.

On average, only 64% of the fish completed vitellogenesis and underwent ovulation, despite all fish developing cortical alveoli oocytes. Duston and Bromage (1987) and Taranger et al. (1991) suggest that a 'gating mechanism' or 'decision period', based on the stage in development and energy stores of individual fish, could explain why some fish fail to undergo maturation. A reduced food supply has also been shown to retard or inhibit gonadal development (reviewed by Lam, 1983) and Blythe et al. (1994a) suggested that nutritional deficiencies may have resulted in 50% of their striped bass (exposed to a 6-month compressed cycle) not maturing. However, in our study, it was not only those fish on a compressed cycle, but some on a 12-month cycle that failed to spawn. Bromage and Jones (1991) found significant increases in egg production could be obtained by optimising feeding regimes in rainbow trout and this may also be the case for striped trumpeter.

Production of T, followed by the conversion of T to E_2, indicates the steroidogenic competence of the follicle cells in the ovary, presumably under the influence of increasing GtH secretion. Plasma E_2 levels were highest (in both the 9- and 12-month cycles for each season) from the period of vitellogenesis through to first spawning and then began to decrease during the spawning season. The relatively high levels of E_2

produced as the first clutch of oocytes progressed through vitellogenesis compared to the lower levels during the spawning season, when successive clutches of oocytes were still undergoing vitellogenesis, suggests that lower levels of E_2 are sufficient to stimulate the production of vitellogenin. It is common for E_2 levels in multiple spawning teleosts to decrease during the spawning season while vitellogenesis is still occurring; as seen in catfish, *Heteropneustes fossilis* (Lamba et al., 1983); gilthead seabream, *Sparus aurata* (Kadmon et al., 1985) and red gurnard, *Chelidonichthys kumu* (Clearwater and Pankhurst, 1994).

In contrast to the ovulating fish, the non-ovulating fish in this study underwent no significant increase in T during the cortical alveoli or vitellogenic stage of oocyte growth. However, an increased amount of E_2 was produced by the vitellogenic follicles of the non-ovulating fish. Failure to detect an increase in T in concert with E_2 in the non-ovulating fish, suggests that most of the T produced was being converted to E_2. In contrast, rates of T synthesis in the fish that subsequently ovulated were probably higher, possibly due to the presence of larger follicles, which resulted in excess T being released into the bloodstream. As such, measures of T during gonadal recrudescence in striped trumpeter may be a practical way to assess which broodstock are likely to spawn in a given season. Similarly, Fitzpatrick et al. (1987) found plasma T levels to be the best predictor of the ovulatory response of coho salmon, *Oncorhynchus kisutch* to GnRHa treatment.

In summary, this study increased our knowledge of reproductive processes in striped trumpeter and found photothermal manipulation to be an effective tool for advancing the spawning season and allowing out-of-season larviculture. Our earlier work (Morehead et al., 1998) showed that freshly caught wild striped trumpeter could be induced to ovulate with exogenous hormone treatment. Here, we have shown that wild striped trumpeter will also acclimate to captivity and, despite regular handling, undergo spontaneous cycles of oocyte growth, maturation, and spawning.

Acknowledgements

Thanks are extended to Eddie Freeman for assistance in fish capture and Greg Goodchild and Alan Beech at the Marine Research Laboratories for husbandry and technical assistance. This study was supported by a grant from the Co-operative Research Centre for Aquaculture, an Australian Research Council Infrastructure Grant and operating funds from the Tasmanian Department of Primary Industry and Fisheries.

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