

MATURATION AND INDUCED SPAWNING OF CAPTIVE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

Pacific mackerel, *Scomber japonicus*, became sexually mature under laboratory conditions and were induced to spawn with hormone injections. Fish caught before the major spawning season became mature under the natural photoperiod and under artificial photoperiods of 4 h light 20 h dark, 8 h light 16 h dark, and 16 h light 8 h dark. Mackerel caught near the end of the spawning season redeveloped their gonads more rapidly at 18°C than at 15°C or ambient temperature. A 16°C-14 h light 10 h dark environment was effective in maintaining mackerel in spawning condition beyond the normal spawning season. Any of three combinations of hormones induced spawning: gonadotropin from ground salmon pituitary followed 24 h later by gonadotropin from pregnant mare serum; human chorionic gonadotropin followed 24 h later by gonadotropin from pregnant mare serum; and salmon pituitary plus human chorionic gonadotropin followed 24 h later by salmon pituitary plus human chorionic gonadotropin plus gonadotropin from pregnant mare serum. The hormones did not induce spawning when used individually. A procedure for routine spawning of Pacific mackerel is described.

Laboratory studies of the biology of pelagic fish larvae are often limited by the uncertainty of collecting eggs at sea. An alternative to collecting eggs at sea is the maturation and spawning of fish in the laboratory. This objective was met for the northern anchovy, *Engraulis mordax* (Leong 1971). Another species whose larvae are under study at the Southwest Fisheries Center is the Pacific mackerel, *Scomber japonicus* Houttuyn, but the eggs are not available off the southern California coast during most of the year. To increase the availability of mackerel eggs for experimental work, I began a study designed to develop procedures for routinely spawning mackerel on demand throughout the year. My approach was to first find a suitable photoperiod-temperature environment which would encourage maturation and to subsequently induce spawning with gonadotropic agents. This report contains observations on the maturation of mackerel under different photoperiod-temperature conditions in the laboratory; results of exploratory tests with hormones to induce spawning; and a description of a procedure currently used to spawn mackerel.

I followed the maturation of mackerel under four photoperiods (4 h light 20 h dark, 8L16D, 16L8D, and ambient day length) and three temperatures (15°C, 18°C, and ambient 12.8° to

19°C). I also examined the effectiveness of a 16°C-14L10D environment for maintaining mackerel in spawning condition after the normal spawning season. The hormones tested for the induction of spawning were gonadotropin from ground salmon pituitary, human chorionic gonadotropin, and gonadotropin from pregnant mare serum. The importance of the photoperiod-temperature environment in regulating maturation in fish and the use of gonadotropins for inducing spawning are well known from the early review of Pickford and Atz (1957), but observations on marine pelagic species are still limited. These are the first observations on the maturation and spawning of a scombrid fish under laboratory conditions.

METHODS

Maturation of Mackerel Under Four Photoperiods

Knaggs and Parrish (1973) examined the ovaries of mackerel from the commercial catch and concluded that *S. japonicus* can spawn from March through October but that the majority spawn from April through August. Kramer (1960), using sea-caught larvae as criteria, concluded that spawning occurs from late April or early May to August.

The fish used in these experiments were caught off the southern California coast by hook and line

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between 1 February and 7 March 1973. The dates of capture were 1 to 2 mo in advance of the major spawning season. The fish ranged from 325 to 340 mm fork length; most fish of this size are capable of spawning (Knaggs and Parrish 1973). During the period of collection, the fish were held under continuous incandescent lighting and a temperature of 19°C. These were arbitrary holding conditions.

On 14 March, 1 wk after the last fish was captured, the mackerel were divided into four groups and placed in three indoor plastic swimming pools (4.6 m in diameter, 1 m water depth) and one outdoor pool (7.3 m in diameter, 1 m water depth). Each of the three indoor pools was enclosed in a separate room lined with black opaque polyethylene film. A 200-W incandescent bulb, 1.2 m above the water surface, illuminated each indoor pool during the artificial day. A timer-controlled rheostat gradually lit and dimmed the bulb over 30 min to avoid startling the fish. The length of day was considered as the time of full illumination. Two 3-W lamps, 1 m above the water surface, burned continuously and provided low-level illumination during the dark period. The light intensity was about 215 lx at the brightest spot on the surface during the day and less than 5.4 lx at night. The outdoor pool was shielded from direct sunlight by an opaque plastic canopy 1.2 m above the water surface but the sides were open and the fish received a natural photoperiod.

Temperature control was achieved with a commercial temperature regulator and mixing valve unit which automatically adjusted the inflow of chilled (10°C) and heated (20°C) seawater to maintain a desired pool temperature. For this series of observations the temperature was set at $19^{\circ} \pm 0.5^{\circ}\text{C}$ for all tanks. I chose this temperature because captive mackerel had spawned at this temperature during a preliminary study. The flow rates were 32 liters/min for the indoor tanks and 50 liters/min for the outdoor tank. Each tank also had a recirculating pump of 250 liters/min capacity.

Each of the experimental groups contained 50 fish. Commencing on 17 March, the three groups of fish in the indoor tanks were maintained on photoperiods of 4L20D, 8L16D, and 16L8D, respectively. The group of fish in the outdoor tank remained under the natural photoperiod where the time between sunrise and sunset was 12 h. Biopsy samples of the gonads were taken prior to the photoperiodic change and again a month later

to note the change in maturation. The biopsies were taken by inserting the tip of a glass pipette (1.2 mm in diameter) through the genital pore of a fish anesthetized in 7 ppm quinaldine and removing a small piece of gonad by mild suction. The technique, a modification of that used by Stevens (1966), did not appear to cause permanent damage to the fish. All ovarian samples were examined with a dissecting microscope and the diameter of the largest eggs measured to the nearest 0.1 mm. No effort was made to categorize the males except to note if milt was obtained. Six females were biopsied at the start of the trial and two from each treatment at the end.

An egg strainer was positioned at the outflow of each tank and inspected daily to detect spontaneous spawning. The strainer, a $1 \times 1 \times 0.2$ m wooden frame with 202- μm mesh netting stretched across the bottom, was partially immersed in a water bath to prevent desiccation of eggs. The mackerel were fed daily with either freshly thawed frozen anchovies or ground squid. Occasionally, Oregon moist chow was mixed in with the ground squid as a supplement. The estimated daily ration was 4% of body weight.

Maturation of Mackerel Under Ambient, 15°C, and 18°C Temperatures

Mackerel judged to be in or near postspawning condition were collected between 23 August and 28 September 1973. The fish ranged from 330 to 370 mm fork length and were kept indoors at 18°C-14L10D during the period of collection. The mackerel were subsequently divided into three groups of 50 fish each and placed in two of the indoor pools and in the outdoor pool already described. Beginning on 3 October, the two groups of indoor fish were kept at 15°C and 18°C, respectively. The fish in the outdoor tank received seawater at ambient temperature (19°C at the outset) which fluctuated with ocean conditions at the intake. The intake was located at the end of the pier at the Scripps Institution of Oceanography, La Jolla. The photoperiods were 14L10D for both indoor groups and natural for the outdoor group. Six females were biopsied at the start of the trial for ova measurements. Several fish from each group were biopsied at various intervals afterwards until March 1974 to observe changes in ovarian development. I attempted to obtain eggs from at least two females per group with every round of sampling.

Test of a 16°C-14L10D Environment for Maintaining Mackerel in Spawning Condition After the Normal Spawning Season

The group of 50 fish that was held outdoors under ambient conditions began to spawn spontaneously at the end of April 1974. On 7 July, while some spawning was still in progress, 25 fish were transferred indoors to a tank with ambient temperature (19°C) seawater and photoperiod of 14L10D. On 8 July, the temperature was lowered to 16°C and the fish were kept at that temperature for 9 mo. Biopsies were taken at the time of transfer and in each succeeding month to determine if at least one female was in spawning condition. During each sampling, fish were catheterized until a female with 0.7-mm diameter eggs was found. Females with eggs of this size are functionally mature, i.e., can be spawned with hormone injections.

Testing of Hormones for Induction of Spawning

The agents tested for the induction of spawning were gonadotropin from ground chinook salmon, *Oncorhynchus tshawytscha*, pituitary (SP), human chorionic gonadotropin (HCG), and gonad-

otropin from pregnant mare serum (PMS). The agents were applied individually and in combination, as indicated in Table 1.

The salmon pituitaries were collected, preserved, and prepared as described by Haydock (1971). The carrier for all injections was saline and the injection volume 0.1 ml. The injections were applied intramuscularly near the base of the dorsal fin with a 24-gauge needle on a 0.5-ml syringe.

The mean weight of the fish was 0.9 kg (range 0.8 to 1.1 kg). Dosages were not adjusted for differences in fish weight, and one male and one female were injected for each treatment. The fish had become sexually mature in the laboratory and were among those used in the photoperiodic experiment. The injection trials were carried out during June through August which is also the time of spawning in nature.

Fish were biopsied beforehand and only males with generous amounts of milt and females with 0.7-mm diameter eggs were injected (preliminary testing indicated that the eggs had to be close to 0.7 mm in diameter before the hormones would stimulate a noticeable response). The injected pair was isolated in a small swimming pool (3 m in diameter, 0.5 m water depth) with water temperature at 17°C and a flow rate of 2.5 liters/min. An egg strainer was placed at the outflow to detect spawning. Biopsies and general observation were

TABLE 1.—Results of tests with gonadotropin from ground salmon pituitary (SP), human chorionic gonadotropin (HCG), and gonadotropin from pregnant mare serum (PMS) for induction of spawning in *Scomber japonicus*.

Hormones and dosages				After 24 h ²					After 40 h					Results of stripping ⁴			
First injection		Second injection ¹		Egg diameter ³ (mm)	Not ovulated	Ovulated	Spawned	Female dead	Female alive	Egg diameter (mm)	Not ovulated	Ovulated	Spawned	Female dead	Female alive	Number eggs	Number live larvae
Hormone	Dosage	Hormone	Dosage														
SP	1 mg	—	—	0.8	X				X	1.1	X			X		<500	<10
SP	5 mg	—	—	0.8	X				X	1.1	X		X			—	—
SP	10 mg	—	—	1.1		X		X								—	—
SP	15 mg	—	—	1.1		X		X					X			<500	<10
SP	25 mg	—	—	0.9	X			X		1.1	X		X			—	—
HCG	12.5 IU	—	—	0.8	X			X		1.1	X			X		<500	<10
HCG	25 IU	—	—	0.8	X			X		1.1	X		X			<500	<10
HCG	50 IU	—	—	0.9	X			X		1.1	X		X			—	—
HCG	125 IU	—	—	1.1		X		X								—	—
HCG	250 IU	—	—	1.1		X		X					X			<500	<10
HCG	500 IU	—	—	1.1		X		X					X			<500	<10
PMS	300 IU	—	—	0.8	X			X		0.8	X			X		—	—
PMS	750 IU	—	—	1.1		X		X						X		<500	<10
PMS	1,000 IU	—	—	0.8	X			X		1.1	X		X			5,000	<10
SP	1 mg	PMS	100 IU	0.9	X			X		1.1			X			50,000	10,000
HCG	12.5 IU	PMS	100 IU	0.8	X			X		1.1			X			30,000	10,000
SP	1 mg	SP	1 mg	0.9	X			X		1.1			X			80,000	30,000
+		+															
HCG	12.5 IU	HCG	12.5 IU														
+		+															
		PMS	200 IU														

¹Second injection given 24 h after first injection.

²Time measured after first injection.

³Egg diameter was 0.7 mm before first injection.

⁴Stripping was attempted on live fish with ovulated eggs. Stripping was attempted even if a fish spawned because the eggs were unfertilized.

taken at 24 and 40 h after injection to note the effects of the hormones. If ovulation or spawning had occurred, stripping was attempted and the eggs fertilized by the dry method (Davis 1961).

RESULTS

Maturation of Mackerel Under Four Photoperiods

The female mackerel caught before the spawning season became mature in the laboratory under the three constant photoperiods (4L20D, 8L16D, and 16L8D) and under ambient light conditions. At the start of the experiment (17 March) the diameter of the largest eggs sampled from the six females ranged from 0.4 to 0.6 mm. Thus, the females were not fully mature but two of the males sampled already had milt and may have been capable of spawning. Recently spawned eggs appeared in the egg strainer of the 16L8D tank on 17 April, 1 mo after the beginning of the experiment. Catheterization of two females from each treatment showed that all treatments contained females with 0.7-mm diameter eggs indicating sexual maturity. None of the treatments appeared to inhibit maturation. The results indicated that female mackerel in prespawning condition will become sexually mature in the laboratory under a wide range of photoperiods at 19°C.

The dates of initial spawning showed no relation to the length of day. Spawning was detected in the 4L20D tank on 25 April and in the outdoor tank on 1 May 1973. In the outdoor tank, the time between sunrise and sunset had lengthened from 12 h at the start of the trial to 13½ h on 1 May. Spawning was never detected in the 8L16D tank although it contained functionally mature males and females.

The mackerel spawned during the dark period but the exact time is not known. Watanabe (1970) stated that mackerel spawn between 2000 and 2400 h in nature. Spawning occurred three or four times a week in the outdoor pool and two or three times a week in the indoor pools from May to mid-June. The frequency of spawning then decreased and was rare by mid-July when observations ended.

Although the fish spawned spontaneously, the predictability of spawning and the viability of eggs were not satisfactory. The number of eggs collected per day was usually less than 3,000, although one collection was over 50,000. The

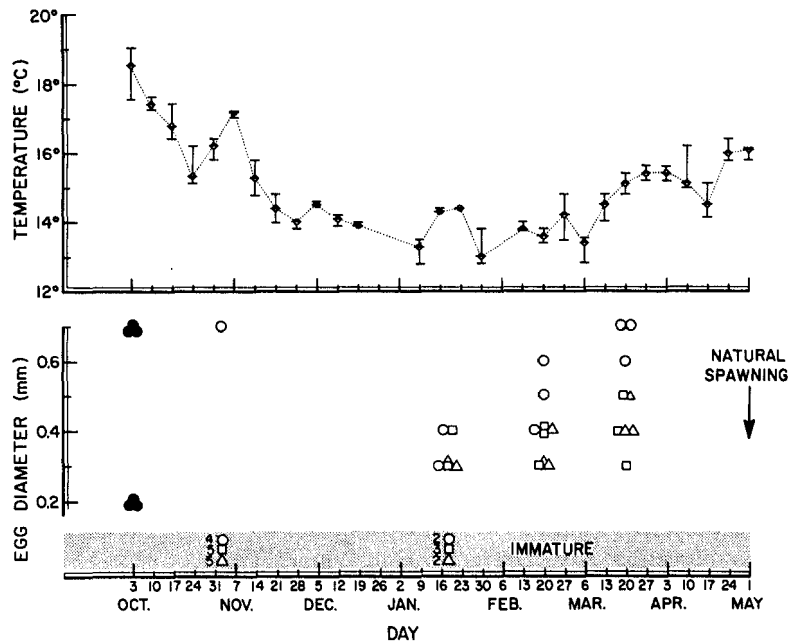
percentage of viable eggs seldom exceeded 10% and was often zero. The spontaneously spawned eggs were translucent and of the proper size, 1.1 mm in diameter, but most were not fertilized.

Observations ended in mid-July because the fish began to feed poorly and started to die. An accompanying symptom of failing health was the malformation of jaws in about half of the fish. Afflicted fish swam with their jaws constantly agape and were unable to bite on food items. The condition may have been partly due to the high water temperature as some fish recovered when transferred to a tank with 15°C seawater. Thus, while the mackerel became fully mature at 19°C a prolonged exposure may be detrimental.

Maturation of Mackerel at Ambient, 15°C, and 18°C Temperatures

Mackerel captured near the end of the spawning season redeveloped their ovaries more rapidly at 18°C than at 15°C or ambient temperature (Figure 1). Three of the females sampled at the start of the trial, 3 October, had eggs 0.7 mm in diameter while three others had eggs 0.2 mm in diameter. This difference in egg size can be expected near the end of the spawning season as some females stop spawning and begin resorption of ovaries earlier than others. In November, one female from the 18°C treatment still had eggs 0.7 mm in diameter but four other fish from that treatment and five from each of the other two treatments could not be sexed because of immaturity of the gonads. Below a certain stage of maturity gonads are too small to remove tissue for biopsy. Biopsies were still difficult to perform in January and samples were obtained from less than half of the fish. The females that did provide samples had eggs measuring 0.3 to 0.4 mm in diameter. Biopsies were more successful in February; the females from the 15°C and ambient temperature groups still had eggs measuring 0.3 to 0.4 mm in diameter but two females from the 18°C group had eggs of 0.5 and 0.6 mm in diameter, respectively. Two of the three females sampled from the 18°C group on 20 March had eggs of 0.7 mm in diameter and one was spawned with hormone injections. The spawning date was about 5½ mo after the start of the trial. On 20 March, the females from the 15°C and ambient temperature groups did not as yet have eggs exceeding 0.5 mm in diameter. Observations ended shortly after for the 15° and 18°C

FIGURE 1.—Development of eggs in female *Scomber japonicus* under three temperature conditions. Upper panel, weekly ambient temperature ranges and medians. Lower panel, diameter of the largest eggs in individual females under 18°C, 15°C, and ambient temperatures. Shaded area, numbers of individuals which could not be sexed due to immaturity. Closed circles represent egg diameters in initial sample, open circles at 18°C, squares at 15°C, and triangles at ambient temperature. Arrow indicates when group under ambient conditions spawned naturally.



groups because of a water system failure and total loss of fish indoors.

The fish in the outdoor tank survived and began to spawn spontaneously on 30 April, nearly 6 wk after the induced spawning. The end of April is also the approximate time that the natural population begins to spawn off the southern California coast (Kramer 1960). The temperatures in the outdoor tank were very similar to the temperatures at Scripps Pier, which can be considered indicative of surface coastal conditions off southern California (Radovich 1961). Thus the mackerel in the outdoor tank should have received temperatures which were like the temperatures found in the southern California spawning grounds and the similar time of initial spawning may be expected. However, it should be pointed out that mackerel in the wild can migrate over long distances (Roedel 1952) and the average temperature cycle they undergo in nature is not precisely known.

The temperature in the outdoor pool at the time of initial spawning was 16°C which is a favorable temperature for mackerel spawning in nature. Kramer (1960), utilizing data from the California Cooperative Oceanic Fisheries Investigations surveys, found mackerel larvae occurring at temperatures (taken at 10 m) ranging from 10.3°C to 26.8°C with more than 68% of all occurrences between 14.0° and 17.9°C. Watanabe (1970), using Japanese data, found early stage mackerel eggs

occurring between temperatures (taken at the surface) of 13° and 23°C with the mode of positive stations between 16° and 19°C.

Test of a 16°C-14L10D Environment for Maintaining Mackerel in Spawning Condition After the Normal Spawning Season

The group of 25 fish that was placed under a 16°C-14L10D environment contained functionally mature individuals at the start of the trial, 7 July. Monthly biopsies indicated that at least one female in the group was sexually mature from July 1974 through March 1975. The months of sampling included December, January, and February when the maturity indices of mackerel are at the lowest levels (Knaggs and Parrish 1973). No more than three females were catheterized in any month before one with 0.7-mm diameter eggs was found. The eggs in the other females ranged from 0.2 to 0.6 mm in diameter. I am not certain if the ripe females remained sexually mature continuously or if they resorbed and subsequently redeveloped their ovaries.

Effectiveness of Hormones for the Induction of Spawning

All injections of ground salmon pituitary (SP) from 1 to 25 mg stimulated hydration and ovula-

tion but the females did not spawn spontaneously nor could they be satisfactorily stripped (Table 1). The females ovulated within 24 h in the 10- and 15-mg trials and between 24 and 40 h in the 1-, 5-, and 25-mg trials. Ovulated eggs were catheterized from live fish in the 1- and 15-mg trials and from dead fish in the 5-, 10-, and 25-mg trials. The live females in the 1- and 15-mg trials were stripped as soon as ovulation was detected but the fish released only small numbers of eggs even with heavy stripping pressure. Attempted fertilization resulted in less than 10 larvae in both trials. The stripped eggs were translucent, measured 1.1 mm in diameter, and appeared normal but nearly all were not viable.

The females that received 5, 10, 15, and 25 mg of SP died within 40 h after injection. The female that received 1 mg was intentionally killed at 72 h for dissection. All of the females including the one that received only 1 mg of SP had severely distended abdomens. Subsequent dissection revealed that the distension was due to extremely enlarged ovaries. The ovaries contained many ovulated eggs which were not extruded and the females were apparently egg bound. I did not see any plugs or clots which impeded the flow of eggs.

All injections of SP, 1 to 25 mg, to male mackerel facilitated the stripping of milt. The milt in the catheter samples before injection was thick and only small amounts could be expressed. The injections of SP brought about a thinning of the milt and made stripping easier. None of the males injected with SP died.

All injections of human chorionic gonadotropin (HCG), 12.5 to 500 IU, stimulated hydration and ovulation but the females could not be easily stripped of eggs. Ovulation occurred within 24 h in the 125-, 250-, and 500-IU trials and between 24 and 40 h in the 12.5-, 25-, and 50-IU trials. None of the females that were alive when ovulation was detected could be stripped of more than 500 eggs. The number of larvae produced was negligible in all trials. All of the females that received 50 or more IU of HCG died within 40 h after injection. The females that received 12.5 or 25 IU of HCG were purposely killed at 72 h. As with SP, all of the females had severely distended abdomens and enlarged ovaries. All dosages of HCG facilitated the stripping of milt without killing the male.

The results of trials with pregnant mare serum (PMS) were variable. In the 1,000-IU trial the eggs increased in size from 0.7 to 0.8 mm in diameter in 24 h and were ovulated by 40 h. More than 5,000

eggs were stripped at 40 h but most of the eggs were cloudy, had collapsed perivitelline membranes, and were apparently overripe. However, a few eggs were viable and a small number hatched following fertilization. In the 750-IU trial, ovulation was detected at 24 h but the eggs already had collapsed perivitelline membranes and were overripe. The eggs in the 300-IU trial grew to 0.8 mm within 24 h but did not show further improvement at 40 h. None of the females injected with PMS had severely distended abdomens and none were dead by 40 h after injection. At all levels tested, PMS made the stripping of milt easier and did not kill the injected male.

The three combinations of hormones tested were all successful in stimulating hydration, ovulation, and spontaneous release of eggs. The first injection, 1 mg SP, of the SP-PMS trial promoted egg growth from 0.7 to 0.9 mm in diameter in 24 h. The second injection of 100 IU PMS 24 h later appeared to stimulate the release of eggs as 50,000 eggs were found in the egg strainer at 40 h. The eggs were translucent, measured 1.1 mm in diameter, and appeared to be of good quality but were unfertilized. However, the female extruded another 50,000 eggs when stripped at 40 h and these were artificially fertilized with milt from the injected male. About half of the eggs showed signs of cleavage and approximately 10,000 larvae hatched. The larvae appeared normal when compared with the larval descriptions of Kramer (1960) and Watanabe (1970). Some of the larvae later developed into juveniles which grew to more than 100 mm total length.

The other two combinations (12.5 IU HCG initially and 100 IU PMS 24 h later; 1 mg SP + 12.5 IU HCG initially and 1 mg SP + 12.5 IU HCG + 200 IU PMS 24 h later) produced similar results. The initial injection produced egg growth to 0.8 or 0.9 mm and spawning occurred after the second injection but the spawned eggs were unfertilized. The fish were then stripped and the eggs artificially fertilized. Many of these hatched and produced thousands of viable larvae. All of the females became bruised from the handling during stripping, and died a few days after spawning.

RECOMMENDED PROCEDURE

A procedure for spawning mackerel has been developed from the foregoing observations and the method has been used since March 1975 to routinely produce viable eggs. The 16°C-14L10D

environment is used to ripen and maintain spawnable stocks of fish in the laboratory and hormone injections are used to induce spawning. I use 1 mg SP + 12.5 IU HCG for the first injection followed by 1 mg SP + 12.5 IU HCG + 200 IU PMS 24 h later to spawn females and a 5-mg SP injection for spawning males. I inject two males to insure an adequate supply of milt. The procedure is essentially the same as described in the Methods section. The egg strainer is checked regularly beginning at 12 h after the second injection to the female and the female is examined whenever eggs are detected. The female is stripped if she releases eggs easily and the eggs are extruded into a dry finger bowl for fertilization. The male is stripped and the milt collected with a spoon held below the genital pore. The milt is washed into the finger bowl with a little seawater and the contents swirled gently for 3 min. The eggs are then placed in an incubation tank for further development and hatching. To date, induction of spawning has been successful 26 times in 36 attempts, each spawning producing 6,000 or more viable eggs, and successful spawning has been induced during every month of the year.

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