

COURTSHIP AND SPAWNING BEHAVIOR OF THE TAUTOG, *TAUTOGA ONITIS* (PISCES: LABRIDAE), UNDER LABORATORY CONDITIONS¹

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ABSTRACT

Courtship and spawning behavior of the tautog, *Tautoga onitis*, were observed under controlled laboratory conditions. Two separate groups of tautog, consisting of two males and one female, were each studied over an entire spawning season. The larger male of each group was dominant over the other two animals. This dominance was expressed during the spawning season by intensified aggression towards the subordinate male. The dominant male of each group, once reaching seasonal reproductive readiness, was the primary spawning partner of the female. Prior to the onset of spawning, a rapid approach of the dominant, formerly a component of an aggressive chase, functioned as a courtship behavior directed at the female. Each day the female exhibited dynamic and transient shading changes which became maximally developed as the time of each spawning approached in the afternoon. Actual gamete release, which took place each day following 6 to 8 h of courtship, occurred as the dominant male and the female moved upwards in synchrony and spawned near or at the surface. The significance of courtship and spawning in tautog is discussed and compared with reproductive behavior in other labrids.

The tautog, *Tautoga onitis*, a member of the family Labridae, occurs along the coastal regions of North America, ranging from South Carolina to Nova Scotia (Bigelow and Schroeder 1953). As with labrids in general, the fish are found associated with shelter or cover, a habit primarily related to the animals' requiring protection especially during nighttime, when they are quiescent (Olla et al. 1974).

According to previously published accounts, tautog are long-lived, reaching a maximum age of at least 34 yr (Cooper 1965) and becoming sexually mature at 3 to 4 yr of age (Chenoweth 1963; Cooper 1965; Briggs in press). The adults move offshore in the late fall to overwinter, a pattern established in field studies off Rhode Island (Cooper 1966) and off Long Island, N.Y. (Olla et al. 1974; Briggs in press). In contrast to the adults, the young remain inshore, spending the winter in a torpid condition (Olla et al. 1974).

Although a portion of the adult population remains offshore throughout the year in deep water (e.g., sports divers report finding tautog at offshore shipwrecks throughout the year), the remainder of

the population moves inshore in late spring. Peak spawning activity occurs primarily in May and June (Chenoweth 1963; Cooper 1966).

From May through October adults are commonly found, especially in the midportion of their range, wherever there is appropriate cover and food supply. They are frequently seen by divers and are easily disturbed by such intrusions. The fish's reaction to divers may account for the fact that spawning in the natural environment has not been described. Spawning has also not been described under laboratory conditions. Until now the only mention of any components of a possible courtship repertoire has been by Bridges and Fahay (1968). These authors introduced a ripe male and female into a small laboratory aquarium in early June and observed transient changes in the pigmentation pattern of the female, assumed to reflect a reproductive predisposition. However, no actual gamete release was seen.

Courtship and spawning behavior in labrids has been observed in a number of species both under natural and laboratory conditions. Both paired and aggregate spawning occurs within the family. Species which have been observed to be primarily pair spawners include *Crenilabrus melops* (Potts 1974); *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, and *H. radiatus* (Randall and Randall 1963); *Labroides dimidiatus* (Robertson and

¹This work was supported in part by a grant from the U.S. Energy Research and Development Administration, No. E(49-7) 3045.

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Choat 1974); and *L. phthirophagus* (Youngbluth 1968). Pair spawning has also been described in *Cirrhilabrus temminckii* (Moyer and Shepard 1975), although the authors do not discount the possibility that group spawnings may occur as well in this species.

Species in which only group spawnings have been documented include *Thalassoma lucasanum* (Hobson 1965); *T. hardwicki* (Robertson and Choat 1974); and the cunner, *Tautoglabrus adspersus*, a coresident of the tautog (Wicklund 1970).

At least two labrid species have each been shown to possess both modes of gamete release. The bluehead, *Thalassoma bifasciatum*, was first seen to exhibit the dual spawning behavior under natural conditions by Randall and Randall (1963). Robertson and Choat (1974) observed similar behaviors in *T. lunare*. Both *T. bifasciatum* (Reinboth 1967) and *T. lunare* (Choat 1969) are protogynous hermaphrodites, a condition "... in which the individual functions first as a female, and later in life as a male" (Atz 1964). Although protogynous hermaphroditism is rather widespread in labrids (at least 30 species mentioned by Robertson and Choat 1974), until now only the two species mentioned above have been identified as possessing both modes of spawning.

Our aim in this work was to examine and describe the various components comprising courtship and spawning of the tautog. The studies were performed on adults which were held under laboratory conditions in a large aquarium.

MATERIALS AND METHODS

Two studies, spanning the 2-yr period of 1975 and 1976, were conducted on two different groups of adult tautog, with each group consisting of two males and a female. The fish were collected during late summer and early fall at Fire Island, N. Y., at temperatures ranging from 19° to 24°C. Scuba divers, using hand-held nets, were readily able to capture the fish at night when they are normally quiescent. The animals were easily identifiable with respect to their gender by the sexually dimorphic mandible, which is more pronounced in males (Cooper 1967).

The studies were conducted in a 121-kl, elliptically shaped aquarium, 10.6 × 4.5 × 3.0 m, located in a temperature-controlled room in which natural diurnal changes in light intensity were

simulated (Olla et al. 1967). Layers of sand (0.6–0.8 mm) and gravel (2–5 mm), 0.6 m deep, provided a natural substrate for the fish. Beneath the gravel, seawater flowed through a network of pipes on the floor of the aquarium from a series of external filters containing sand, gravel, and oyster shells, and which provided continuous circulation and filtration. Water quality in the aquarium, operated primarily as a semiclosed system, was also maintained by addition of seawater from Sandy Hook Bay. The pH averaged 7.5, salinity averaged 24.0‰, and dissolved oxygen averaged 7.5 ppm.

It had been previously determined that in the natural environment a shelter area is a physical requirement of tautog, particularly during their nighttime quiescence. Shelter was, therefore, provided in the form of a triangular-shaped structure consisting of three clay drainage tiles (30.5 × 60.9 cm) cemented together. The shelter was placed approximately 3 m from one end of the aquarium in proximity to viewing windows. Clumps of live blue mussel, *Mytilus edulis* (5–17 kg), a major component of the tautog's diet (Olla et al. 1974), were introduced periodically to insure a continual food supply which allowed the fish to feed ad libitum. The mussels were placed 4 m from the shelter and constituted a more or less fixed feeding area.

Diurnal changes in light intensity from morning to evening civil twilight were simulated by banks of fluorescent lights mounted on the walls above the aquarium and controlled by a series of timers (Olla et al. 1967). A low level of night illumination, 0.75 lx was provided by incandescent bulbs, programmed to come on before the last row of fluorescent lights was extinguished.

Aquarium Conditions During Animals' Residency

Study 1

One male [51.5 cm TL (total length)] and one female (50.0 cm TL) were introduced into the aquarium on 20 September 1974, with a second male (59.0 cm TL) introduced 7 days later. From this point, the animals were kept in the aquarium for a total of 244 days. The fish were initially held at 19.1°C (+0.8°; -1.6°C) for 50 days. The animals were then the subjects of a long-term study dealing with the effects of temperature on activity and social behavior (Olla in prep.). Beginning at light

onset 51 days after the three fish were placed in the aquarium, the water temperature was increased during a 9-day period (mean rate $0.04^{\circ}\text{C}/\text{h}$) and held for 11 days at 28.7°C ($+0.2^{\circ}$; -0.1°C). The temperature was then decreased over an 8-day period (mean rate $0.05^{\circ}\text{C}/\text{h}$) and held for 165 days from 14 December 1974 to 28 May 1975 at 18.7°C ($+1.1^{\circ}$; -0.8°C).

During the first 10 days of the animals' residency, the photoperiod was decreased from 13.18 h to 12.25 h and then held constant through 22 February 1975. Beginning on 23 February 1975 the light schedule was set to conform with the natural, increasing photoperiod. The interval from 14 December 1974 to 16 January 1975 comprised the baseline nonreproductive period for Study 1. Observations on courtship behavior first began on 11 April 1975.

Study 2

Two males (54.0 cm TL and 55.3 cm TL) and one female (47.0 cm TL) were introduced into the aquarium on 28 August 1975 and kept in the aquarium for a total of 225 days. They were initially held at 21.3°C ($+1.9^{\circ}$; -1.5°C) for 80 days. The animals were then the subjects of a long-term study dealing with the effects of temperature on activity and social behavior (Olla in prep.). Beginning at light onset of the 81st day of the animals' residency, the water temperature was gradually raised over a 9-day period (mean rate $0.04^{\circ}\text{C}/\text{h}$), held for 11 days at 28.7°C ($+0.2^{\circ}$; -0.4°C), decreased during 8 days (mean rate $0.04^{\circ}\text{C}/\text{h}$), and then held for 115 days from 14 December 1975 to 8 April 1976 at 20.2°C ($\pm 0.7^{\circ}\text{C}$).

During the first 22 days of the animals' residency, the photoperiod was decreased from 14.23 h to 12.32 h and then held constant through 2 March 1976. Beginning on 3 March 1976 the light schedule was set to conform with the natural, increasing photoperiod. The interval from 14 December 1975 to 15 January 1976 comprised the baseline nonreproductive period for Study 2. Observations on courtship behavior first began on 29 January 1976.

Observation Schedule

Hourly observations made on the fish during the light period of each study consisted of 15-min readings. During each, the following measures of behavior (described in Results) for each fish were

recorded for 50 counts in sequence at 18-s intervals: 1) number of aggressive interactions between fish and identity of aggressive and submissive individuals, and 2) number of courtship interactions and identity of participants. Qualitative aspects of behavior were also recorded during each reading.

During the nonreproductive period, 12 hourly observations (0700–1800 EST) were made daily in 4-day periods with intervals up to 3 days between periods. A total of 28 observation days (336 h) were made in the nonreproductive period of Study 1 and 20 days (240 h) in Study 2. During the reproductive period 8 hourly observations (0800–1500 EST) were made daily. In Study 1 these were taken in 2-day periods, with intervals up to 5 days between periods, while in Study 2 there were 4-day observation periods with intervals of up to 3 days between each. During the reproductive period a total of 15 observation days (120 h) were made in Study 1, and 13 days (104 h) in Study 2.

To compare differences in aggressive interactions prior to and during spawning, we selected 11 typical days of observations during the nonreproductive and reproductive periods of each study. Data based on the hourly means (0800–1500 EST) from these days are presented in tabular form in the Results.

Once we discovered that gamete release occurred in the afternoon on a daily basis and we had become acquainted with the reproductive repertoire of the animals, we could predict approximately when daily spawnings would occur. Therefore, in addition to the readings mentioned above, we also began to observe the fish at least 60 min and some days up to 150 min prior to and including each spawning. In Study 1 approximately 35 h and in Study 2, 25 h of observations were made prior to spawnings. During 11 typical spawning days, data collected in this fashion enabled us to determine quantitatively: 1) if there were any changes in aggression throughout the day as the spawning time approached, and 2) how close (temporally) to the spawnings, changes in courtship behavior were manifested.

Throughout each study and particularly prior to each spawning, observations were made with the use of a tape recorder. In addition, periodic motion pictures taken throughout the spawning period allowed us to analyze and interpret behavioral components and sequences both in slow motion and at stop frame.

RESULTS

Interactions Prior to Spawning Season

Prior to the onset of spawning in each study, there had developed a clear dominance hierarchy based on size, with the largest fish of each group, a male, being dominant over a smaller male and still smaller female. In turn, the smaller male was dominant over the female. Prior to the reproductive season, the majority of interactions among the three fish consisted of aggressive behavior. During various hours of the day the aggression, initiated particularly by the dominant male, served in part to limit the access of the subordinate male and female to different areas of the tank, such as the feeding area and shelter site (Olla in prep.).

Aggression was manifested at varying levels of intensity with the more intense involving the pursuit of a fleeing subordinate by a dominant, which we termed a chase. Prior to such an encounter a dominant often rapidly approached (swam towards) a subordinate. The subsequent chase could last as long as 30 to 45 s, with the fish swimming the length of the tank and at speeds reaching 100 to 150 cm/s. The most intense but rarest encounter involved a chase accompanied by the dominant biting a subordinate on any area of its body, which we termed nipping.

Aggressive encounters could also be quite subtle, with a subordinate exhibiting a change in its location, either vertically or horizontally, to a new position 0.5 to 1.0 m away, which we termed displacement. The behavior of a dominant causing this response often did not appear to differ from its forward swimming motion. Displacement of a subordinate occurred either as a dominant approached or simply turned towards it, as much as a full tank length away (10.6 m). Then there were instances in which a similar action of a dominant did not elicit any response by a subordinate. This variation in response by a subordinate was due to our not being able to assign an observable cause with regard to the actions of the dominant. We could only infer, through a subordinate's behavior, the generation of an aggressive intention signal by the dominant male.

Aggression by the dominant also caused a subordinate to assume a posture which we interpreted to be submissive, which involved the subordinate tilting its dorsal surface towards the dominant at an angle ranging from 5° to 90°. Frequently, when a subordinate was swimming about the tank and

approaching an area in which the dominant was present, it would show the submissive posture as it bypassed and clearly avoided the dominant. The distance at which this would occur varied, ranging from 1.0 to 3.0 m.

Onset of Reproductive Period and Courtship Behavior

The most obvious manifestation of the approach of reproduction was the change in aggression directed toward the female by the dominant male. Beginning in early April 1975 (Study 1) and in late January 1976 (Study 2), a rapid approach of the male, which had previously represented the initiation of a chase, became functionally transformed into a component of the courtship repertoire. Now when the male approached, when within 5 to 10 cm, he veered off to one side or the other. The female was neither displaced nor showed any change in posture. We defined these acts of the male as rushes to distinguish them from approaches which formerly caused displacements and were aggressive. Rushes were directed at the female whether she was active or resting. At times as the male veered off, the magnitude of the water displacement from the force of the caudal thrusts was great enough to stir the adjacent sand and cause the female to be moved several centimeters. Rushes were observed approximately 2 wk (Study 1) and 7 wk (Study 2) prior to the first spawning.

The female, previously limited in her access to different areas of the tank, now was more mobile and concurrently began to show changes in her behavior towards the dominant. Sometimes immediately after the male's rush, the female followed him at a distance of approximately 0.5 to 1.0 m. The duration of the following behavior was usually short, lasting no more than 2 to 5 s. If the male did not initiate another rush, one of the pair simply swam away.

Another change in the female's behavior towards the dominant male was her resting in areas in which the dominant was resting. While in Study 2 this generally occurred along the walls of the tank or in the feeding area, in Study 1 it often focused around the shelter. On occasion when the dominant male was resting inside the shelter, the female often settled at the base of the structure, or sometimes actually entered and came to rest alongside the male within the same tube or in a different one.

While the female of Study 1 appeared to play a

rather passive role in stimulating the dominant male's attention (except when she simultaneously entered the shelter with him), the female of Study 2 was behaviorally much more conspicuous in attracting the attention of both males, particularly as they fed. On several occasions the female not only ingested mussels from the same small pile on which a male was feeding, but even wrested a clump of mussels from a male's mouth. This behavior was readily tolerated by both males.

In contrast to the termination of aggressive interactions between the dominant male and the female during this early prespawning period, the aggression of the dominant towards the subordinate male began to increase both in frequency and in intensity. In Study 1, aggressive acts by the dominant toward the subordinate rose from an average of 2.4/h during the nonreproductive period to 16.0/h in the week prior to the first spawning. In Study 2 aggressive acts rose from an average of 2.6/h during the nonreproductive period to 6.3/h in the week prior to spawning. Once daily spawning began in both studies, intermale aggression remained consistently high and was significantly greater during the entire reproductive period than during the nonreproductive period ($P \leq 0.05$; end count test; Tukey 1959; Table 1).

The heightened intensity of aggression was reflected by the increased duration of a chase, which commonly lasted as long as 60 to 90 s with the two fish covering anywhere from 1 to 3 circuits around the tank. In both Studies 1 and 2, the other obvious factor reflecting this heightened aggression was that the dominant began nipping and biting the subordinate during chases. As a result, each subordinate male in Studies 1 and 2 bore numerous wounds on all areas of its body.

One further piece of evidence of the increased aggression of the dominant male in each study was that the subordinate male now spent the majority of time confined to either end of the aquarium, sculling in place along the wall between middepth and the surface. These locations appeared to be the ones which elicited least aggression by the dominant male.

Along with behavioral changes, external changes in the appearance of the female were also occurring with the onset of the reproductive period. Enlargement of the gonads increased the girth of the female, resulting in a more rotund appearance. At the same time, we also noted minor changes in the female's pigmentation.

TABLE 1.—Comparison of aggressions by dominant male toward subordinate male *Tautoga onitis* for 11 days during nonreproductive and reproductive (spawning) periods of Studies 1 and 2. Data are presented as a mean of 8 h/day (0800–1500 EST) during nonreproduction and reproduction.

Study 1		Study 2	
No. aggressions per hourly observation per day (\bar{x})	End count	No. aggressions per hourly observation per day (\bar{x})	End count
Nonreproductive period:			
1.5	1-	3.0	-
2.8	-	2.3	-
3.5	-	3.5	-
1.8	-	2.9	-
3.3	-	2.4	-
3.9	-	3.3	-
3.9	-	3.8	-
0.9	-	1.4	-
1.9	-	2.3	-
1.1	-	2.3	-
2.0	-	1.8	-
Reproductive period:			
14.2	2+	10.8	+
22.4	+	10.6	+
10.2	+	10.0	+
9.9	+	7.6	+
8.4	+	12.9	+
10.2	+	14.6	+
7.0	+	12.4	+
8.8	+	20.1	+
3.5	+	23.5	+
3.6	+	26.4	+
7.1	+	26.5	+
Total end count = 18		Total end count = 22	
$P \leq 0.05$		$P \leq 0.05$	

1- = Values for aggression during nonreproduction smaller than smallest reproduction value.
 2+ = Values for aggression during reproduction greater than greatest nonreproduction value.

While prior to this period she was generally a solid dark gray, now there was a mottled white, vertical bar or stripe down the middle of each side of the body, which we termed a "saddle." At this time, the saddle was in an early stage of development (Figure 1a) of what was to be a progression of significant shading changes taking place prior to and during each daily spawning (see below for further explanation). In addition, a pale, grayish-white patch developed in the inter- and supraorbital areas of the female, giving the appearance of eyebrows. The first observations of the female's saddle were made on 11 April 1975 in Study 1 and 29 January 1976 in Study 2.

Unlike the female, the dominant male's appearance prior to and during spawning was altered very little. The only discernible shading changes of the dominant males of both studies were the development of a light gray shading covering the entire head and opercula, and the transient appearance of faint white rays (approximately 2–4 cm long) extending outwards from the orbits of the eyes. Additionally, it appeared that the ventral portion of the maxilla and the entire mandible became a lighter, almost white, shade, with the exception of the dark pores of the mandibular lateral line canals. Otherwise the male's shading re-

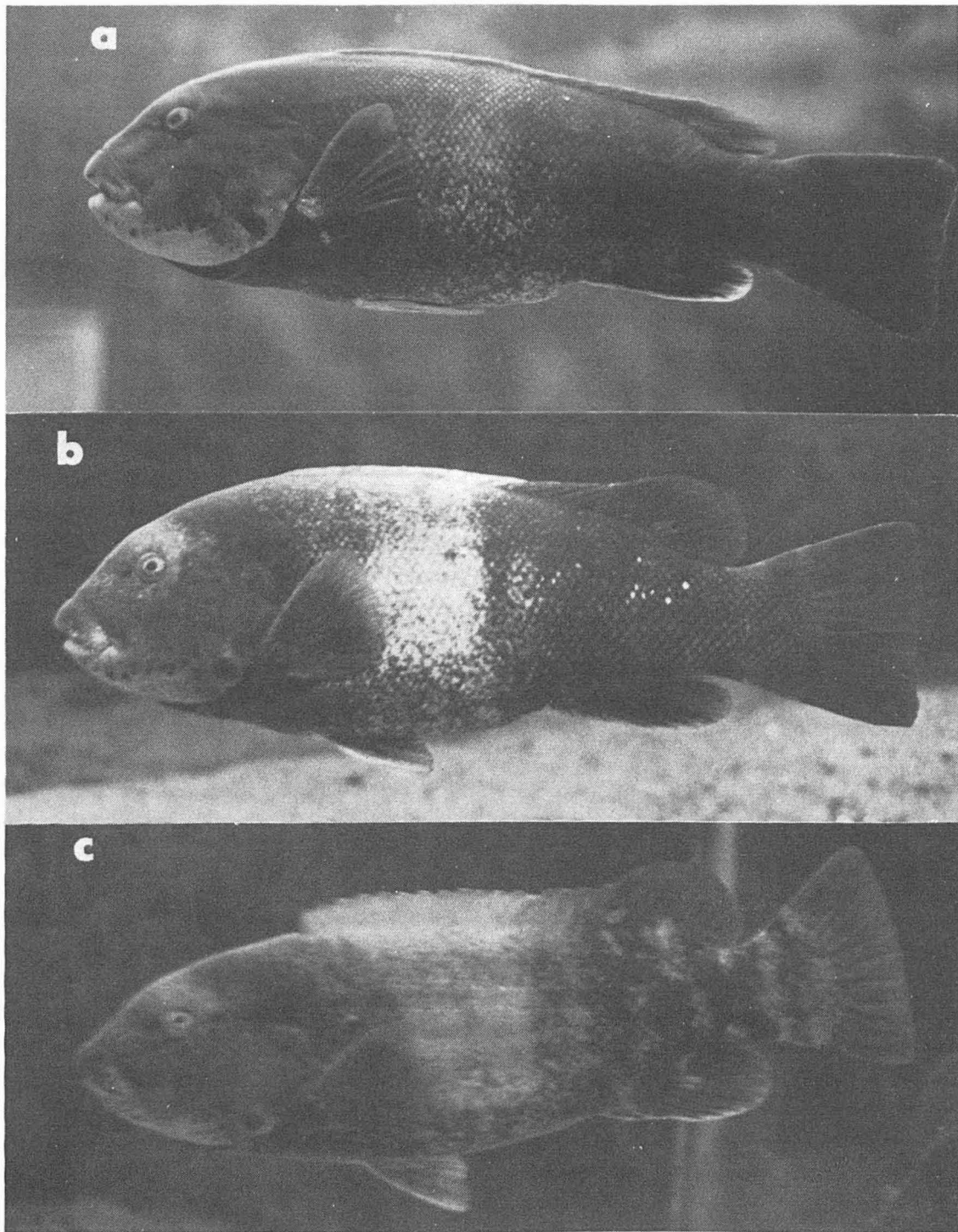


FIGURE 1.—Development of daily shading changes associated with spawning in female *Tautoga onitis*: a) earliest stage of white saddle development; b) increased size of the saddle and first, faint appearance of caudal banding as it occurs in the afternoon; c) final reproductive shading with tail-up posturing exhibited prior to spawning.

mained unchanged, with the trunk being a dark gray. Occasionally in Study 2, we noticed transient shading changes on the dominant male that were most apparent during aggression or courtship. In these cases the length of the male's midsection became a much lighter gray than the darker, dorsal area of its body. This was not a persistent change and lasted perhaps 1 or 2 min.

Development of Pair Formation

On 4 April 1975 in Study 1 (approximately 2 wk prior to the first spawning), it was apparent that there was in progress a transition from nonsexual to sexual (courtship) activities between the dominant male and female. We interpreted this to be the development of pair formation, at least within the context of the social situation and the unnatural laboratory condition.

In this same 2-wk period prior to the first spawning, the dominant's aggression directed at the subordinate male not only persisted but also began to increase and apparently served to inhibit (suppress) the subordinate's motivation to either court the female (i.e., by rushing her) and/or participate eventually in any of the spawning activities as long as the dominant was present. Since our observations in Study 1 began after courtship was under way, we were unable to ascertain the initial responses of the subordinate male toward the female, e.g., whether or not this male had originally shown any receptivity to the female (or vice versa) or attempted to court her.

In contrast to Study 1, the development of pair formation between the dominant male and female in Study 2 was slightly altered at first by the participation of the subordinate male. The dominant male had initiated rushes at the female as early as 29 January 1976 (7 wk prior to the first spawning), but then on 23 February 1976, the subordinate began to rush her periodically. In the 4-wk observation period (23 February–18 March 1976) immediately prior to the first spawning, the rushes by the dominant continued, averaging 8.8/day (range of 3–22/day), and while the rushes by the subordinate also occurred, they were lower in frequency, averaging 1.4/day (range of 0–5/day).

The events during the first and subsequent spawnings of Study 2 offered some preliminary evidence that, while gamete release was not contingent upon an established pair formation, this type of social interaction ultimately prevailed, at

least under laboratory conditions. On the date of the first spawning, 19 March 1976, the female mated not with the dominant, but with the subordinate male. Although the dominant initiated some of the final courtship behavior that normally led to gamete release (see results below), and up to a point, had continued to attack the subordinate, eventually the dominant withdrew from all activities, remained inside the shelter, and did not interfere as the subordinate briefly rushed and then released gametes with the female (details described below). This type of pattern in which the dominant initiated prespawning behavior, but then withdrew and "allowed" the subordinate final access to the female for spawning persisted for 4 days through 22 March 1976.

On 23 March the dominant began taking a more active and sustained role in the final reproductive behavior. Because of this and the fact that his aggression towards the subordinate had been increasing, it appeared that the dominant might be the sole mate of the female. However, just as the dominant and female were about to spawn, the subordinate male rapidly approached the pair and simultaneously released his gametes with theirs. This pattern in which the dominant initiated and completed the spawning activities with the female, but still had not sufficiently inhibited a simultaneous spawning release by the subordinate male persisted for 7 days through 29 March 1976.

It was not until 30 March, 11 days after the first gamete release, that the spawning was completed exclusively by the dominant male and the female. Throughout the remainder of the study, the female mated exclusively with the dominant male.

Daily Reproductive Behavior

All spawnings that were observed during both Studies 1 and 2 occurred between 1330 and 1600 (EST) with the exception of one at 1015 (EST) in Study 1. The first spawning of Study 1 was on 21 April with 36 subsequent spawnings observed (1–3/day), and in Study 2 the first spawning occurred on 19 March 1976 with 22 subsequent spawnings (1–2/day).

Throughout the morning of a typical day when spawning was to occur, the dominant male was generally active, swimming about the tank, feeding, and intermittently rushing the female. Aggression towards the subordinate male usually oc-

curred right up until and after each spawning. The subordinate male continued to be restricted in its movements by the heightened aggression directed towards it and remained almost exclusively at either end of the tank, usually in midwater. The female, besides showing a minimal change in shading (i.e., early saddling, Figure 1a), as well as an occasional responsiveness to the dominant, also engaged in activities not directly related to spawning, such as feeding, swimming (with no apparent interactions with the other animals), and resting.

While the female either briefly followed after and/or rested near the dominant or exhibited no response to the rushes prior to this period, as the morning progressed she responded with progressive shading changes of varying magnitude. For example, within several seconds after a vigorous rush by the dominant male, the saddle oftentimes increased in depth and width. On some occasions the saddle took on a pale yellowish hue. The anterior half of the dorsal fin became a mottled white, ending at the same posterior border as the saddle. In addition, faint, white vertical stripes became evident on the caudal areas of the body, originating at the posterior edge of the saddle and extending just past the caudal peduncle (Figure 1b), similar to that described by Bridges and Fahay (1968). The pattern could vary, with these stripes modified into a kind of checkerboard. Along with this shading, the female often erected her dorsal fin very briefly (1–2 s) immediately following a rush.

Unless spawning was imminent, i.e., occurring within 15 to 30 min, these shading changes in the morning were retrogressive. A particular pattern might not last for more than 10 to 20 s or, at the longest, several minutes, followed by fading, with only a thin saddle persisting.

During the afternoon as the time of spawning approached (30–60 min prior to spawning), the dominant male became more responsive to the female, as evidenced by the increased intensity of the rushes. As these continued the female began to erect the dorsal fin for progressively longer periods, anywhere from 5 to 15 s. During fin erection the total area of white spanning the saddle and the dorsal fin was now maximized and, we believe, served to increase the female's conspicuousness.

In this same period she began to swim at times only with the pectorals and also intermittently began to flex the caudal fin upward. When caudal flexion first began, it usually followed a rush and

was accomplished by a series of small lifts in which the female raised the caudal fin progressively higher.

The responsiveness of both the male and female was at its peak for the 15 min prior to spawning. While the number of rushes during each of the 15-min hourly observations throughout the day averaged 1.2 (Study 1) and 3.3 (Study 2), the number of rushes in this 15-min period preceding a spawning increased to an average of 6.4 (Study 1) and 9.4 (Study 2). Aggression by the dominant towards the subordinate male was not significantly different between morning and afternoon for Study 1 ($P > 0.05$), but increased significantly in the afternoon of Study 2 ($P \leq 0.05$; sign test; Dixon and Mood 1946; Table 2).

During the 15-min period prior to spawning, the saddle of the female was almost maximally developed, appearing whiter than it had been earlier in the day, and extending fully down the abdomen. The caudal checkerboard or striped pattern was now much more clearly defined. In addition the vent began to dilate.

The behavior of the female also began to change. She was now more active, and often swam by using only the pectoral fins. When the male moved rapidly towards her in a rush, she often erected the dorsal fin and flexed the caudal fin before the male had reached her rather than afterwards. The duration of the upward caudal flexion continued to increase. Accompanying the caudal flexion was the forward tilting of the body at about a 20° to 30° angle, serving to expose maximally the dilated vent.

TABLE 2.—Sign test comparing mean number of aggressions per hourly observation by dominant male towards the subordinate male *Tautoga onitis* during the morning (0800–1100 EST) and the afternoon (1200–1500 EST) on 11 spawning days of Studies 1 and 2.

Date	Study 1			Sign test	Date	Study 2			Sign test
	0800–1100	1200–1500				1976	0800–1100	1200–1500	
4/28	17.0	11.5	–		3/24	10.2	11.2	+	
4/29	24.2	20.5	–		3/25	8.0	13.2	+	
4/30	4.5	16.0	+		3/29	5.8	14.2	+	
5/1	8.8	11.0	+		3/30	6.8	8.5	+	
5/2	7.5	9.2	+		3/31	9.2	16.5	+	
5/5	7.2	13.2	+		4/1	12.5	16.8	+	
5/6	8.2	5.8	–		4/2	8.2	16.5	+	
5/12	9.8	7.8	–		4/5	14.5	25.8	+	
5/13	4.0	3.0	–		4/6	15.5	31.5	+	
5/19	2.5	4.8	+		4/7	21.2	31.5	+	
5/20	3.8	10.5	+		4/8	16.0	37.0	+	
No. of +				6					11
No. of –				5					0
Difference				1					11
P				>0.05					≤0.05

Beginning anywhere from 2 to 5 min before spawning, the female began swimming back and forth along the length of the tank close to the sand using only the pectoral fins, a behavior we defined as a run. A run was usually accompanied by a full and constant erection of the dorsal fin and the final shading development in which all of the white areas of her body (i.e., the saddle, caudal stripes or white portions of the checkerboard pattern, the "eyebrows," and the anterior half of the dorsal fin) were almost totally blanched, sometimes colored with a yellowish hue. Then, as a run was either beginning or in progress, the caudal fin was rigidly flexed upward one final time (Figure 1c), exposing the maximally dilated vent, while at the same time the head was tilted downward. The female's swimming in this position seemed awkward, resulting in her moving with a characteristic wobble or wiggle. The female made one or two runs alone which apparently served to heighten the attention of the dominant male, for he would break off other activities (e.g., chasing the subordinate male, swimming randomly about the tank) to usually rush her first and then to follow her (Figure 2a).

As the female continued on the runs, the male tended to swim more in a parallel alignment with her. Eventually he swam just slightly behind with

his head moving closer to the female's operculum or midsection, 30 to 40 cm away from her (Figure 2b). Then suddenly, while increasing her speed by changing from pectoral swimming to caudal thrusts, the female swam rapidly toward the surface, with the male immediately accelerating in a similar manner to keep pace with her (Figure 2c). The angle of their ascent was anywhere from 40° to 70°. When the fish were less than a meter from the surface and while still swimming rapidly, they turned their bodies so that their ventral areas faced toward each other. On those occasions when the fish's movements were perfectly coordinated, the pectorals of the male appeared to be embracing the female (Figure 2d). With the animals in contact, they arched their bodies into U-shapes and released gametes either before reaching the surface or as they broke the surface (Figure 2e). Then the pair separated and swam downwards (Figure 2f), with the female coming to rest on the sand where the male usually rushed her 2 or 3 times within 5 to 10 s following the spawning. After a spawning, the female's shading usually regressed to just a thin saddle within a few minutes.

The spawning as we have described it appeared to comprise the prevalent mode of gamete release. However, there occurred slight variations in the

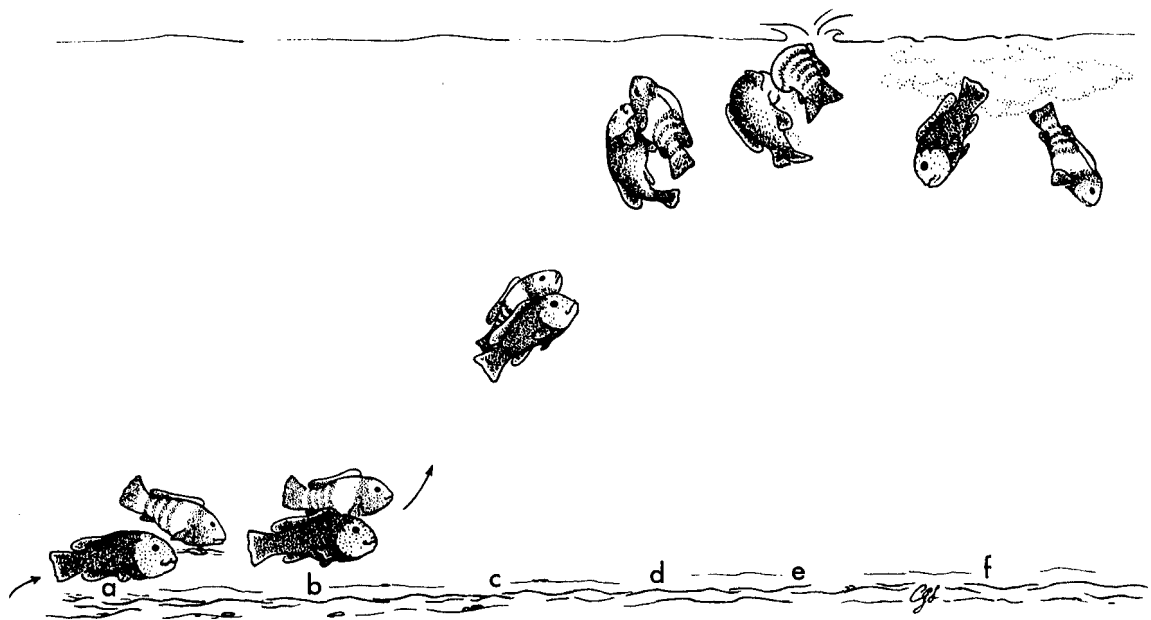


FIGURE 2.—Final sequence of behaviors leading to spawning in *Tautoga onitis*: a) male approaches female; b) they swim parallel with female slightly ahead; c) male and female move upwards in the water column; d) the pair orient to each other in a ventral-to-ventral alignment; e) with bodies flexed the pair release gametes as they break the water surface; f) the fish separate and move downwards.

behavior which still resulted in gamete release. For example, as the female was moving to the surface, rather than orienting the ventral area of her body toward the male, she bent her body into the U-shape with the result that her dorsal side faced the ventral side of the male. Gamete release still occurred as the fish flexed their bodies into U-shapes. The origin of this variation was usually due to the fact that while moving upward the female was swimming too rapidly to assume the proper alignment for the ventral-to-ventral release with the male.

A critical factor for maximizing fertilization was the breaking of the water surface at the time of release. As the fish moved upwards, churned the water, and swam downwards again, currents were created which mixed the "cloud" of gametes together. From visual observations and motion picture analysis, this occurred whether there was ventral-to-ventral or ventral-to-dorsal alignment of the pair. We would assume, however, that the most efficient method for fertilization involved the ventral-to-ventral alignment.

While runs were always performed prior to spawning, on some days there were as few as 2 runs prior to a spawning, while on other days there were as many as 11. Similarly, the duration of a series of runs varied from 30 to 180 s.

Runs were not always performed in succession. Particularly in Study 1, many times after completing one run, the pair began circling around each other in midwater. In some cases they followed each other, head to tail, along the perimeter of an imaginary circle. In other cases, as the male swam around the female, she either remained sculling in a fixed position or pivoted about her vertical axis, obviously orienting to the moving male. The total number of separate circling bouts during a run sequence ranged from 2 to 10 with a duration of each ranging from 2 to 40 s.

Occasionally at the end of a run, the pair began to swim upwards, as if to spawn. Typically, at the onset of this, the female began the transition from pectoral swimming to caudal thrusts. Moving rapidly upwards with the male alongside, the female broke away from him short of the surface and swam downwards to the sand without releasing gametes. This behavior sometimes did not occur at all while in other cases it occurred as many as six times prior to a spawning.

The continuity or fluidity of the run sequences appeared to be a critical factor serving to synchronize the fish for final release of gametes. Lack

of mutual stimulatory behaviors or even slightly inappropriate behavior by one of the mates during a run, in general, were sufficient causes for a temporary breakoff of the entire sequence. During a breakoff the female's shading often regressed somewhat and she came to rest on the sand or even returned to the shelter for a few seconds.

One of the specific causes for these breakoffs was due to the fact that the dominant male, instead of maintaining his attention toward the female, chased or displaced the subordinate male which had either (actively) moved too close to the pair or (passively) happened to be in areas where the pre-spawning behavior was being carried out.

Other reasons for the breakoffs were inappropriate stimuli initiated usually by the male during the run sequence. In Study 1, if the male contacted the female during a run along the sand or as she ascended to spawn rather than at the apex of the pathway, the female often turned away from the male. Conversely, premature contact behavior by the male in Study 2 was an appropriate stimulus to his mate and in fact was frequently exhibited during the run sequence as well as during spawning.

Other cases in which the female initiated a breakoff from a run occurred if the male assumed an atypical position relative to hers. In Study 1, the female usually swam between the wall and the male and slightly ahead of him. Occasionally if the male assumed the position closest to the wall during a run (i.e., the female was now closer to the center of the tank) or if the male swam ahead of her, the female broke away. Since the male sometimes "corrected" his position relative to hers and hence the female did not break away, it appeared that each animal had become conditioned to a rather stereotyped set of behavioral patterns and positions which facilitated bringing the spawning to completion.

Reproductive Behavior of the Subordinate Male

In both studies each subordinate male had achieved gonadal maturation and was able to complete spawning with the female under a limited set of conditions. In each case, the reproductive behavior occurred only when the subordinate was not behaviorally inhibited by the dominant male. In Study 1, the first spawning by the subordinate male and the female occurred later in the spawning season, on the very day (29 May 1975)

that the dominant male was dying (unknown causes). This latter animal was obviously in a weakened condition and did not participate or interfere with the reproductive activities during his last day of survival. In Study 2, as described above, the subordinate male initiated courtship and spawning with the female at the onset of the reproductive season and continued until the aggression by the dominant literally suppressed all of his normal behavior.

The behavior exhibited by each subordinate male immediately prior to and during spawning was essentially comparable to that of the dominant, except that it was less stereotyped. Sometimes during a run the subordinate male weaved from one side of the female to the other; and in other cases he actually swam ahead of her on the first and second runs. Gradually as the male came to align himself more with her position, the male initiated flank contact, and positioned his body slightly above hers.

In both studies, once this continuous contact by the subordinate male was maintained, the runs, as discrete behavioral patterns, were no longer discernible. Generally the pair swam in a meandering, zig-zag pattern in midwater, and eventually circled approximately 0.5 to 1.0 m below the surface. During this behavior, it always appeared that the male was herding the female. Generally, because the pair was now so close to the surface, the final movement upwards covered only a short distance.

The subordinate male of Study 1 was last observed to spawn with the female on 25 July 1975, comprising an estimated total of 57 spawning days for this pair. Conversely, the subordinate male of Study 2 completed only 4 days of exclusive paired spawning with the female before the dominant male took an active role in the reproductive activities.

DISCUSSION

It is well known that light and temperature play a role via the neuroendocrine system in both initiating and synchronizing reproduction in fish (see review and discussion by de Vlaming 1974). However, spawning occurred in the laboratory even though the fish previously had been exposed to an unnatural photoperiod and temperature. Temperatures were, in fact, at high, stressful levels. It is possible that the endocrinological events as-

sociated with gonadal recrudescence may have been initiated 8 to 10 mo or more before the fish were captured. The photoperiod in the laboratory was eventually lengthened and regulated to keep pace of the natural changes beginning 16 days (Study 2) to 56 days (Study 1) before the first spawning. Temperatures of 18° to 20°C, well within levels at which eggs have been found in nature (Perlmutter 1939; Williams 1967), were maintained 93 days (Study 2) to 126 days (Study 1) prior to the onset of spawning.

Previously published field observations indicate that tautog spawn sometime between May and June in the waters of New York (Olla et al. 1974; Briggs in press) and Rhode Island (Chenoweth 1963; Cooper 1966), with June being the principal spawning month in Massachusetts waters (Kuntz and Radcliffe 1917; Bigelow and Schroeder 1953). These spawning dates are supported by data based on collections of eggs and larvae from Sandy Hook Bay estuary (Croker 1965) and are further extended through mid-August based on similar collections from Long Island Sound (Wheatland 1956; Richards 1959).

That the fish spawned earlier in the laboratory than they would have in nature supports the supposition that the final synchrony may depend on proximal environmental cues. While the gonadal recrudescence may have been initiated by events occurring in nature prior to capture, final synchronization may have been caused by the changes in temperature and the advancing photoperiod. Because the study was not designed to examine such questions, assignable causes of the spawning occurrence must be conjectural. Nevertheless, whatever the causative environmental events, the animals did achieve reproductive synchrony.

To date there are no specific descriptions of spawning behavior in the tautog. In a laboratory study on tautog in June 1967, Bridges and Fahay (1968) reported that during a 10-day period, a ripe female and male both underwent a shading change between 1500 and 1630 and exhibited behavior which the authors described as possible courtship. Our observations concur with these authors with respect to the daily afternoon shading alteration of the female. However, their descriptions of the behavior suggested aggressive interactions between the two animals and thus the male's shading more likely reflected an animal involved in aggression rather than courtship. The female and male's behavior further suggest that

either the animals were not in complete reproductive synchrony or the confines of the aquarium may have produced behavioral artifacts.

In our studies, pair spawning, with the dominant male tautog being the exclusive partner of the female, was the prevalent mode of reproductive activity. However, in Study 2 when spawning began, the female spawned first with the subordinate male, then both males, and finally only with the dominant. This transition period, we surmise, may have been caused by either or both of the following: 1) due to the small difference in size (1.3 cm) between the males, dominance may not have been sufficiently defined initially to inhibit the subordinate, and 2) the final phase of seasonal reproductive readiness of the dominant was slightly behind that of the subordinate. Once the dominant reached an appropriate level of sexual maturation, pair spawning involving only the dominant male and the female occurred exclusively for the remainder of the study.

Pair spawning again proved to be the mode of gamete release in our laboratory facility when a single male was in the presence of two gravid females (Olla and Samet unpubl. data). In July 1976 these two females (approximately 48 and 58 cm) were introduced into the aquarium where the dominant male from Study 2 was still residing. During intermittent observations of the fish, pair spawning occurred five times with the smaller female, although both females were rushed and exhibited a high degree of attention towards the male.

While we have never seen tautog spawning under natural conditions, it is reasonable to assume from our observations that pair spawning may play a leading role in the reproductive repertoire of this species. However, we reserve judgment as to whether this is the only pattern of gamete release, especially because of the occurrence in Labridae of both paired and aggregate spawnings within a single species, e.g., *Thalassoma bifasciatum* (Randall and Randall 1963) and *T. lunare* (Robertson and Choat 1974), both of which are protogynous hermaphrodites (Reinboth 1967 and Choat 1969, respectively).

Another factor contributing to our reserve in assigning only one pattern of reproduction to tautog is that during recent preliminary field studies, Olla and Bejda (in prep.) found sexually mature young tautog, both males and females, which were of a much smaller size and younger age than has previously been reported

(Chenoweth 1963; Cooper 1966; Briggs in press). In addition, these young fish did not show sexual dimorphism of the mandible (Cooper 1967), a characteristic trait which was conspicuous in the subjects used in our studies. One explanation for the absence of the mandibular dimorphism in these young fish might be that this trait occurs in older, larger fish. Although we do not now know yet whether the young animals participate in spawning, the other possibility is that these fish may represent a different sexual stage than that of the older fish of our study. It is even possible, as remote as it seems, that hermaphroditism may be present. The question is raised here because we know nothing of the behavior or gonadal development of these young fish and because hermaphroditism, in the form of protogeny, has been found in a number of labrids (e.g., 30 species according to Robertson and Choat 1974).

While it appeared that pair formation did take place within the laboratory, whether or not a true pair bonding between mates occurs in nature is still unanswered. It is possible that in their natural environment, other male tautog in the vicinity of a pair could conceivably participate at the moment of spawning. However, in these circumstances it is also quite possible that the extreme aggression of a dominant, courting male would cause other subordinate males to remain sexually passive or to move away and seek a female partner elsewhere. The hypothesis that within a given locale a dominance hierarchy among males determines which male becomes sexually active is supported by a field experiment on *Thalassoma bifasciatum* by Reinboth (1973). Additionally, it is quite possible in a natural environment that a female might spawn each day with a different male.

On the other hand, if true pair formation solely between one male and a female is possible, the selective advantage here is obvious, inasmuch as 1) it would not be necessary for an animal to expend energy finding a mate each day, and 2) to sustain its dominance (and pairing with a female) the male must continue to be a highly successful competitor. When the motivation to spawn wanes, males capable of becoming sufficiently dominant over others would have priority to act as mates.

Of all the sensory stimuli that could potentially come into play during tautog courtship, visual cues arising from the female appeared to be the most conspicuous. First, the swollen, gravid abdomen of the female, which as Youngbluth (1968)

studying the cleaning wrasse, *Labroides phthiophagus*, and Potts (1974) studying the corksiding wrasse, *Crenilabrus melops*, suggested, may have served as one of the first important visual cues to the male. In addition, the development of the female tautog's saddle, even in its most rudimentary state 2 to 7 wk before the first spawning of each study could have played an important role in identifying the reproductive state of the female. More specifically, the daily transient changes in the saddling would have served to identify the readiness of the female to spawn right up to the moment of spawning.

The existence and development of reproductive shading patterns in the female tautog is in distinct contrast with the situation found in other labrids in which the conspicuous or bright appearance, when present, is usually found in males (see Roede 1972, for review and discussion). Substantiation of the female tautog's spawning pattern was made during an observation with scuba at approximately 1500 (EST) on 26 May 1976 near the Fire Island Coast Guard Station. An adult, gravid female (approximately 45–50 cm) with a well-developed saddle was observed swimming in mid-water along with a dark gray male (A. D. Martin pers. commun.). (Turbidity and the fact that the pair moved away from the diver prevented any further observations.)

Another major difference between tautog and other labrids regarding coloring or shading is that the shading change of the female was a dynamic, transient process each day. This kind of shading change in tautog falls within the category of physiological color changes discussed by Roede (1972), which reflect rapid alterations in shading and which are also reversible processes. Conversely, the descriptions of color patterns in other labrids all appear to reflect morphological color changes, which develop only gradually within each individual and particularly within discrete life phases or stages.

In concert with these shading changes were actions of the female that apparently served to enhance or facilitate the male's perception of these visual stimuli. For example, the final sustained erection of the female's dorsal fin further enlarged the white area of the saddle. Lifting of the female's caudal fin, occurring when the saddle and caudal pattern were maximally developed, was manifested in the final moment before spawning. This lift, coupled with the female's swimming near the male in such a fashion as to expose the dilating

vent, provided another stimulus towards which the male could orient.

Visual shading cues arising from the dominant male appeared to be minimal except perhaps for the lightening of its face and lips. These features may have provided a stimulus to the female indicating the male's motivation to court and spawn, particularly during rushes directed at the female's head. The stimulus value of the male's white lips during courtship displays in *Crenilabrus melops* has also been suggested by Potts (1974).

The obvious visual cues of the male, arising from its rapid approach during a rush, were quite likely a primary source of stimulation to the female. It is also possible that there was a secondary, lateral-line stimulation, created by the force of the water currents as the male rushed by and which may have enhanced the overall response of the female. Other potential stimuli arising from either of the mates may have been chemosensory in origin. We have no basis at this point to conjecture whether or not the animals released and/or perceived any chemical products (i.e., pheromones), which may have functioned to facilitate reproduction.

An important indicator of the approaching onset of the reproductive season was the change in behavior of the dominant male towards the female. It gradually ceased being aggressive to the female, initiated courtship rushes, and permitted her unrestricted access to any area of the tank. This behavioral transition from aggressive to courtship activities is very similar to that observed in *Crenilabrus melops* (Potts 1974). In this species, which pair spawn at a nest site, the nesting male is aggressive to both males and females at the onset of the reproductive period. Eventually, however, instead of approaching a female to chase or bite her, the male performs an exaggerated courtship, swimming around the female which apparently stimulates her to approach the male and his nest.

As with many other species, each of the courtship activities of the tautog seem to serve one major purpose, which was the gradual excitation and synchronization of the partners prior to the spawning each day. In the extended period before the very first spawning of the season, the dominant male appeared to assume the more physically active role in the early courtship, primarily by rushing the female. While the female did occasionally follow after or rest near him, she did not perform any obvious (ritualized) activities. Nevertheless, even the slight shading changes in

her saddle during a rush may have functioned as a type of response, communicating to the male her receptivity and possibly her altering physiological state.

Once the first and subsequent daily spawnings began, it appeared that the female now set the tempo for synchronizing the events leading to spawning. The first "signal" that spawning was imminent occurred when the female's caudal stripe or checkerboard pattern was consistently maintained, followed by a further broadening and blanching of her saddle. Then, once her pectoral swimming, the tail lift, and head-down behaviors were sustained, the female initiated the final courtship behavior (i.e., runs). Even though the male synchronized his movements with hers, the pace and completion of the runs and upward spawning motion were contingent on the female's actions.

The separate behavioral components of the courtship and spawning repertoire in the tautog reflect both similarities and differences when compared with other labrid groups. In the cleaning wrasse, *Labroides phthirophagus*, pair formation and courtship precede spawning by at least a week or more (Youngbluth 1968). During this time the male repeatedly performs rapid approaches ("passes") towards the side of the female which she tolerates; however, the male's action in this case is generally also accompanied by a body quivering. In some species the only vigorous approaches by males toward females are described as chases, such as in the four *Halichoeres* species observed by Randall and Randall (1963); the cunner, *Tautoglabrus adspersus* (Wicklund 1970); *Thalassoma bifasciatum* (Randall and Randall 1963); and *T. lunare* (Robertson and Choat 1974). In *Cirrhilabrus temminckii* the male performs a single rushing action similar to the tautog, but this only occurs immediately prior to the upward darting for gamete release (Moyer and Shepard 1975).

In many of the species described above, the males also perform ritualized swimming patterns or displays to attract the females. These have been described as circling, looping, fluttering, dancing, or simply courtship swimming. The responses of females among the various species can vary from a simple approach such as in *T. bifasciatum* (Reinboth 1973) to an over, reciprocal response such as "sigmoid posturing" and "dancing" as in *L. phthirophagus* (Youngbluth 1968), or a lateral approach to the male in which the swollen flank and

genital papilla are presented as in *Crenilabrus melops* (Potts 1974).

With the exception of *C. melops* which spawn on the sand in a nest, all of the other species mentioned above and tautog share a common mode of swimming or darting rapidly upwards to spawn. Body bending (only by the male of a pair) in *T. bifasciatum* has been observed by Reinboth (1973) as well as the brief alignment of the pair's genital openings.

ACKNOWLEDGMENTS

We thank Anne L. Studholme, Allen J. Bejda, and A. Dale Martin for their valuable assistance throughout all phases of the study. Illustrations of the spawning act, taken from motion picture films, were expertly done by Carol Gene Schleifer. We also thank Myron Silverman for his assistance in photographing the fish.

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