

Although there are similarities in reproductive behavior among several squid species, our observations of *L. pealei* indicate a social structure which is well defined and different from that described for other species with the possible exception of *S. bilineata* and *S. sepioidea*. Since there are relatively few published accounts of in situ copulation and egg-laying activities, it is difficult to know what is normal and what might be altered behavior patterns due to the presence of human observers, submersibles, lights, etc. However, our observations and those of other divers, including two in the same area a week earlier who reported 12-15 pairs of squids in a semicircle (Turco¹), indicate that the social structure associated with egg-laying behavior is not an isolated phenomenon, but a pattern which is recurrent in populations of *L. pealei* which frequent New England coastal waters in the summer.

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SPAWNING AND SEXUAL MATURITY OF GULF MENHADEN, *BREVOORTIA PATRONUS*¹

Earlier studies of egg and larva collections (Turner 1969; Fore 1970; Christmas and Waller²) have shown that Gulf menhaden, *Brevoortia patronus*, which range throughout the northern Gulf of Mexico from Cape Sable, Fla., to Veracruz, Mexico, spawn from about October to March from near shore to about 97 km offshore at depths of from 2 to 111 m. There have been two previous studies to determine the age of spawning, the number of ova produced, and the peak time of ovary maturation (Suttkus and Sundararaj 1961; Combs 1969). Our objectives in the present study were to: 1) estimate the minimum number of maturing ova for specific age-groups and size groups, 2) estimate the percentage of fish that spawn at each age, 3) determine the time of spawning, and 4) determine the frequency of spawning.

Gulf menhaden make annual inshore-offshore movements. The larvae spend 3-5 wk in offshore waters before moving into estuaries where they

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²Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscript, 20 p. Gulf Coast Res. Lab., Ocean Springs, Miss. (NMFS contract no. 03-4-042-24).

¹Anthony Turco, West Main St., North Kingstown, R.I., pers. commun. June 1979.

transform into the adult form (Reintjes 1970). The following autumn the juveniles, ranging in fork length from about 55 to 130 mm FL, migrate from the estuaries to offshore waters (Tagatz and Wilkens 1973), along with all other age-groups that are moving from inshore waters of the gulf at this time. Fish of all age-groups migrate to inshore waters again the following spring.

While in inshore waters, age 1 and older Gulf menhaden are subject to an intensive purse seine fishery that extends from Florida to eastern Texas from about mid-April to early October. The fish are processed into meal, oil, and solubles at plants in Mississippi and Louisiana.

During the purse seine season Gulf menhaden are sexually inactive. Therefore, gonads collected at that time are of no use for fecundity studies. The only source of Gulf menhaden during the spawning season is the offshore groundfish trawl fishery, which takes Gulf menhaden incidentally along with the primary species. Catches are landed at plants in Mississippi and Louisiana and processed as canned pet food (Roithmayr 1965). The number of Gulf menhaden taken varies, but is never large. From October 1976 to February 1977, 241 females (124-257 mm FL) and 516 males (113-240 mm FL) were collected from the groundfish landings. After January, we were able to collect only 4 maturing females in February and none in March or April.

To assure that Atlantic menhaden, *B. tyrannus*, were assigned to the correct year class, June and Reintjes (1959) developed specific criteria for assigning fish to year classes on the basis of annulus formation. These criteria also were adopted when the investigation of Gulf menhaden was begun in 1964. March 1 was designated as an arbitrary date on which all fish of a given year class were advanced 1 yr in age, regardless of whether or not a new annulus had formed. Since all fish used in this study were collected from October to February, an age-1 fish is one that has one annulus, but has completed two growing seasons; an age-2 fish has two annuli but has completed three growing seasons.

All fish were caught in the northern Gulf of Mexico from lat. 28°35' to 30°15' N and from long. 87°45' to 91°28' W. Fork lengths were measured to the nearest millimeter and wet weights to the nearest 0.1 g. Scale samples for aging were taken from the left side of the body along the midline and below the origin of the dorsal fin. Paired gonads were preserved in a 10% buffered Formalin³ solution.

Stages of Sexual Maturity

Preserved gonads were blotted to remove excess moisture and weighed to the nearest 0.01 g. A sample of 0.1 g or less was cut from the central portion of an ovary and examined microscopically to describe morphology of developing ova and to determine the mean diameter of the largest ova present.

Four groups of ova were found in the most advanced ovaries, while only one to three groups were found in less developed ovaries. Immature ova were under 0.20 mm in diameter, translucent, and contained an irregular spherical nucleus. Intermediate ova ranged from 0.20 to 0.35 mm and had a dark or opaque center surrounded by a wide sphere of dull yellowish to brownish speckling. Maturing ova were 0.36 to 0.72 mm, opaque, and had an outer translucent covering or tissue. Ripe ova were similar to maturing ova except they were >0.72 mm.

Three stages of sexual maturity were recognized on the basis of the most advanced group of ova present: immature, intermediate, and maturing. Fish classified as maturing contained either maturing or both maturing and ripe ova. All maturing or ripe ova in a sample were counted and about 100 were selected randomly and measured for diameter.

Age and Size of First Spawning

Gulf menhaden <135 mm can be considered as age-0 fish (Nicholson and Schaaf 1978). All fish <100 mm FL that we examined showed no evidence of maturing ova. Through December, 63% of age-1 fish and 71% of all fish age 2 or older in our samples contained maturing ova. By January all fish age 1 or older contained maturing ova (Table

³Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of female Gulf menhaden sampled from October 1976 to February 1977 by age, month, and stage of sexual maturity (immature or mature).

Month	Age 1		Age 2		Age 3		Age 4
	Imma- ture ¹	Ma- ture	Imma- ture	Ma- ture	Imma- ture	Ma- ture	Ma- ture
Oct.	5	6	3	10			
Nov.	4	15		3			
Dec.	4	1	4	3	1	3	1
Jan.		19		3		2	
Feb.		3		1			

¹Fish with intermediate ova (as the largest ova present) were included in this category.

TABLE 2.—Number of female Gulf menhaden sampled from October 1976 to February 1977 by fork length, month, and stage of sexual maturity (immature or mature).

Fork length (mm)	Oct.		Nov.		Dec.		Jan.	Feb.
	Imma- ture ^a	Ma- ture	Imma- ture	Ma- ture	Imma- ture	Ma- ture	Ma- ture	Ma- ture
120-129	2							
130-139	1							
140-149			1	1				
150-159			2	3	1		1	
160-169	5	1	2	8	1		6	1
170-179	7	15	2	15	1	2	10	2
180-189	6	17		15			2	
190-199	5	20		12	2		2	
200-209	3	14		11	3	1	3	1
210-219	1	3		1		4	1	
220-229		3		1	1	2	2	
230-239		1		4		1	5	
240-249				1		1	1	
250-259							1	

^aFish with intermediate ova (as the largest ova present) were included in this category.

1). For both aged and unaged fish >140 mm that we examined, 73% contained maturing ova in October, 91% in November, 55% in December, and 100% in January and February (Table 2). From this information we concluded that Gulf menhaden spawn for the first time at age 1, after they have completed two seasons of growth, and then continue to spawn each year thereafter.

Time and Frequency of Spawning

Previous studies of egg and larva collections (Turner 1969; Fore 1970; Christmas and Waller footnote 2) and of increases in gonad weights (Suttkus and Sundararaj 1961; Combs 1969) have indicated that spawning begins in October and ends about March. Our data also show that spawning occurs within this time period. For each month we plotted the mean gonad weight as a percentage of body weight for those fish we were able to age (Figure 1). For females the means, which were already high in October, indicating that gonadal development had begun, increased in November and December and then decreased in January and February. Generally, males followed the same pattern as females when both aged and unaged were combined (Figure 2). We can not explain why the relative gonad weights of age-1 females were higher than those of older fish, unless some of the older fish had partially spawned by the time they were collected, thereby decreasing their gonad weight.

The number of times an individual fish will spawn during a season may be inferred from the difference in size between groups of ova. If there is

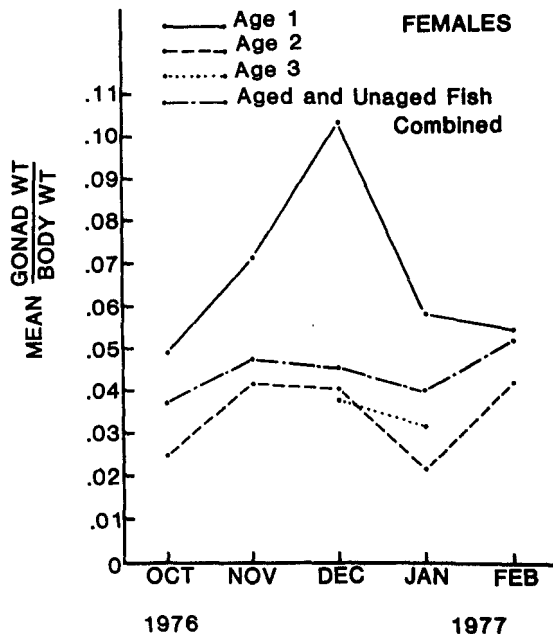


FIGURE 1.—Relation between mean of gonad weight/body weight and month for unaged and different age-groups of female Gulf menhaden.

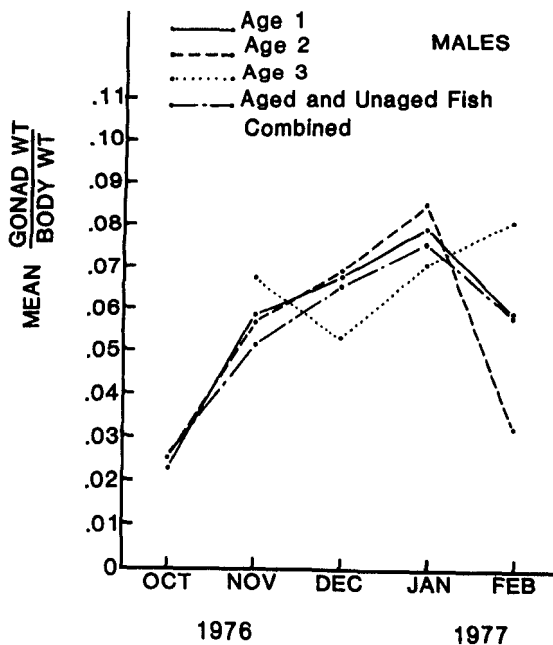


FIGURE 2.—Relation between mean of gonad weight/body weight and month for unaged and different age-groups of male Gulf menhaden.

a large difference in size between immature ova, developing intermediate ova, and maturing ova, the spawning period will be short and definite. If there is only a gradual change in size between these groups of ova, individual fish may spawn several times over an extended period (Hickling and Rutenberg 1936; de Vlaming 1974).

Since there was a gradual change in size between groups of ova, and since the number and diameter of maturing or ripe ova for fish of the same length varied considerably, we inferred that Gulf menhaden were intermittent, or fractional spawners. The number of maturing ova did not change markedly from month to month, or even within the same month. The ripe ova, after being spawned, probably are replaced by a group of the largest maturing ova which in turn are replaced by a group of intermediate ova. Perhaps four or five different groups of ova ripen and are spawned during a single spawning season, although the exact number cannot be estimated.

Higham and Nicholson (1964) stated that, from available evidence, it is impossible to decide conclusively the frequency of spawning of individual Atlantic menhaden but they favored the hypothesis of maturation and fractional spawning of more than one group of ova during the season.

Combs (1969) concluded that *B. patronus* spawns several times from October to February. He found that over a period of months spawnable oocytes occurred together with advanced stages of ova that were potentially spawnable. He described the histological events in the development of Gulf menhaden ova from formation to maturity and found that once the provisional yolk had formed, ova lost all potential to remain in the ovary and had to complete their development prior to spawning or be aborted.

Number of Ova Spawned

Since analysis of variance tests showed no significant difference in the size or number of maturing ova in gram samples from the left and right ovaries, we used either ovary for measurements and counts. (Counts were made of the number of maturing ova in a sample of 0.1 g or less from an ovary.) The number of maturing or ripe ova in each female was estimated by dividing the combined weight of the left and right ovaries by the sample weight and multiplying this number by the number of maturing or ripe ova in the sample.

If fractional spawning occurs, the number of ova

estimated to have been spawned by fish of any given age or size would necessarily be minimal, since some ova probably would have been spawned by the time some ovaries were collected. Fractional spawning also would increase the variability in the number of ova estimated for fish of the same age or size (Bagenal and Braum 1971). Of the 70 maturing females that we could age, 44 were age 1, 20 were age 2, 5 were age 3, and 1 was age 4. The mean number of ova and its standard error for each age-group respectively were $37,100 \pm 3,467$; $47,900 \pm 5,038$; $61,800 \pm 9,486$, and 151,000.

Three relationships that are most useful in explaining and understanding population dynamics of a species are those of fecundity with age, length, and weight. To determine what mathematical models would be most appropriate in describing these relations, we used Statistical Analysis System⁴ to test various statistical regression models. We chose those which had the greater r^2 values and the minimum deviations from the regression line. In the following models F = fecundity, A = age, L = fork length, and W = body weight. For fecundity on age (Figure 3):

⁴Statistical Analysis System; Barr, Goodnight, Sall and Helwig, SAS Institute Inc., P.O. Box 10066, Raleigh, NC 27506.

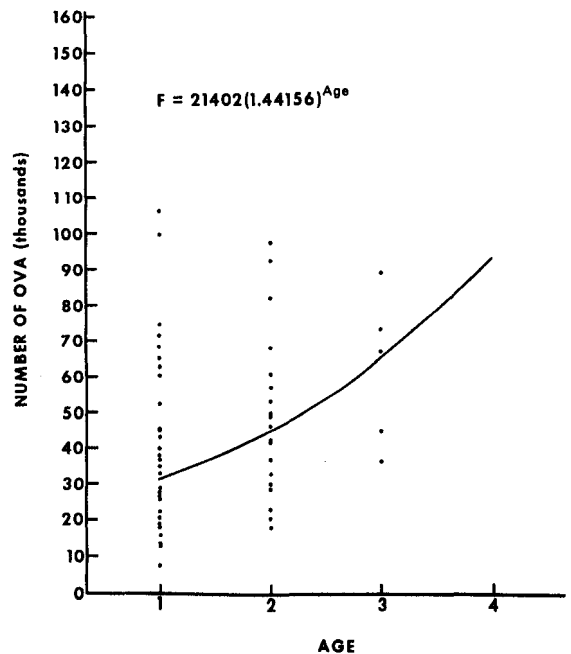


FIGURE 3.—Relation between number of maturing ova and age for Gulf menhaden.

$$\log_e F = 9.9713 + 0.3657(A) \\ (r^2 = 0.1804, s_{y \cdot x} = 0.5466).$$

For fecundity on fork length (Figure 4):

$$\log_e F = -9.8719 + 3.8775(\log_e L) \\ (r^2 = 0.6490, s_{y \cdot x} = 0.3751).$$

For fecundity on weight:

$$F = 12,064.2908 + 374.8848(W) \\ (r^2 = 0.4445, s_{y \cdot x} = 20,427.0752).$$

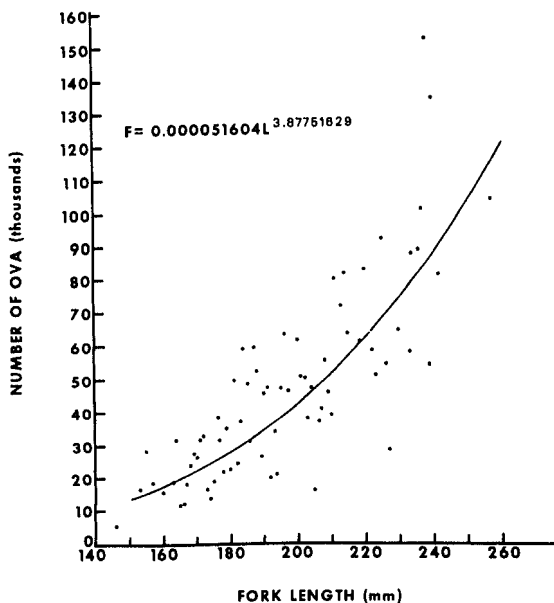


FIGURE 4.—Relation between mean number of maturing ova and fork length for Gulf menhaden.

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FOOD OF THE PACIFIC WHITE-SIDED DOLPHIN, *LAGENORHYNCHUS OBLIQUIDENS*, DALL'S PORPOISE, *PHOCOENOIDES DALLI*, AND NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, OFF CALIFORNIA AND WASHINGTON

Our knowledge of the feeding habits of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, and the Dall's porpoise, *Phocoenoides*