REPRODUCTIVE BIOLOGY OF WESTERN ATLANTIC BLUEFIN TUNA[1]

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ABSTRACT

Ovaries of bluefin tuna, *Thunnus thynnus*, were collected from the Gulf of Mexico, Florida Straits, Middle Atlantic Bight of the western North Atlantic, and off the northeast coast of the United States. There was relatively little development towards maturity in age 1 through age 7 fish from the Middle Atlantic Bight as evidenced by low gonosomatic index values and histological examination of ovaries. Well-developed ovaries were present in giant bluefin tuna from the Gulf of Mexico and Florida Straits, with heaviest spawning occurring in May. For bluefin tuna measuring 205-269 cm fork length and 156-324 kg round weight, the average number of eggs measuring 0.33 mm in diameter and larger was estimated at 60.3 million, and the average number of eggs measuring 0.47 mm in diameter and larger was estimated at 34.2 million.

Atlantic bluefin tuna, *Thunnus thynnus*, are seasonally distributed over most of the North Atlantic. They are found from Newfoundland to Brazil and from Norway to the Canary Islands (Gibbs and Collette 1967).

In the western Atlantic, a sport fishery for bluefin tuna exists off the east coast of the United States from Maine through North Carolina and along the western Bahamas and the eastern coast of Canada. Also, a substantial commercial bluefin tuna fishery exists in the western Atlantic. There is purse seining along the east coast of the United States from Massachusetts to North Carolina and a handline and harpoon fishery off Massachusetts and Maine. A substantial Japanese longline fishery is present off the east coast of the United States and in the Gulf of Mexico.

In the eastern Atlantic, a sport fishery for bluefin tuna exists around the Canary Islands and a substantial commercial fishery occurs off Europe and North Africa. Purse seining is conducted off the Atlantic coast of Norway and Morocco, the Mediterranean coast of France, the Adriatic coast of Italy and Yugoslavia, in the Tyrrhenian Sea off Italy, and occasionally in the North Sea off Denmark. An important hook-and-line bait fishery occurs in the Bay of Biscay off France and Spain, off Morocco, the Azores, the Canary Islands, the Mediterranean coast of Spain, and occasionally off Turkey. Trap fisheries were present off southern Portugal, southern Spain, and the Straits of Gibraltar, as well as along the Mediterranean coast of Morocco, Tunisia, and Sicily. There is a significant Japanese longline bluefin tuna fishery in the Mediterranean Sea, Bay of Biscay, and off western Europe.

There has been a substantial reduction in the Atlantic-wide catch of bluefin tuna from 38,500 t in 1964 to 12,500 t in 1973 with no large reductions in effort (Miyake et al[3].) A number of studies have been made, and are continuing, to understand the reason for this decline (Parks 1977; Shingu and Hisada 1980; Parrack 1980). Of the various aspects of the dynamics of fish populations, the measure of reproductive potential is of primary importance since it is a basic determinant of productivity. It is used to separate subpopulations, to estimate mortality, and, with ichthyoplankton data, to estimate stock size.

Two major bluefin tuna spawning areas are located in the Atlantic approximately 4,000 mi apart: In the Gulf of Mexico (Richards 1976; Montolio and Juarez 1977; Rivas 1978) and the Florida Straits (Rivas 1954; Baglin 1976) during April, May, and June; and in the Mediterranean Sea during May, June, and July (Frade and Manaças 1933; Rodríguez-Roda 1964). Al-

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[3]Miyake, M. P., A. De Boisset, and S. Manning (compilers). 1974. Int. Comm. Conserv. Atl. Tunas, Stat. Bull. 5. Unnumbered pages.

Manuscript accepted May 1981.
FISHERY BULLETIN: VOL. 80, NO. 1, 1982.

though these two spawning grounds have been well documented, a question remains whether bluefin tuna spawn elsewhere and at other times. Mather[4] believes that some bluefin tuna probably spawn in late spring near the northern edge of the Gulf Stream off the eastern United States. Berrien et al. (1978) have reported collecting bluefin tuna larvae from this area during April and June 1966. These larvae, however, could have drifted to this area from spawning grounds farther south.

In this paper, I describe bluefin tuna ovaries from the Middle Atlantic Bight (the U.S. coastal area between Cape Cod and Cape Hatteras) and examine the possibility that this may be another significant spawning area for bluefin tuna. Also, I make some comparisons of female gonadal development between the known spawning areas.

My literature review on bluefin tuna shows there is a need for additional information on the bluefin tuna's reproductive potential. A wide range in fecundity estimates was found. Frade (1950) reported that an eastern Atlantic 160 kg bluefin tuna produced 18.7 million eggs. Williamson (1962) stated that the ovaries of a 272.4 kg western Atlantic bluefin tuna contained about 1.0 million eggs. Rodríguez-Roda (1967) estimated that off southern Spain a 54 kg fish could produce 5.5 million eggs and a 235 kg bluefin tuna could produce over 30.0 million eggs. Baglin (1976) estimated that a 188.4 kg western Atlantic bluefin tuna could produce 16.7 million eggs and that a 271.5 kg bluefin tuna could produce 31.4 million eggs. Baglin and Rivas (1977) indicated that a 324 kg western Atlantic tuna could produce 57.6 million eggs. I determined the fecundity of bluefin tuna taken from the United States sport fishery in the Florida Straits and Gulf of Mexico and from the Japanese longline fishery in the Gulf of Mexico and compared my findings with previous estimates. I have also examined monthly sex ratios for western Atlantic bluefin tuna.

MATERIALS AND METHODS

Bluefin tuna from the Gulf of Mexico, Florida Straits, Middle Atlantic Bight, and off the northeast coast of the United States were sampled from anglers' catches. Bluefin tuna samples from purse seine catches came from the Middle Atlantic Bight and the northeast coast of the United States. Bluefin tuna were also sampled from the Japanese longline fishery in the Gulf of Mexico and from the New England handgear fishery.

Throughout this paper the classification system of Rivas (1979) was used. Thus, small bluefin tuna are 50-129 cm fork length (FL) and 3-44 kg round weight, medium bluefin tuna are 130-180 cm FL and 45-130 kg round weight, and giant bluefin tuna are >180 cm FL and >130 kg round weight.

Sex data were obtained from 283 small and medium bluefin tuna captured by commercial and sport fishermen off the Middle Atlantic Bight (1974-77). Also, sex data were obtained from 3,429 giant bluefin tuna captured by sport and commercial fishermen in the Gulf of Mexico and along the northeast coast of the United States from North Carolina to Maine, and from fish taken by sport fishermen in the Bahamas (1975-78).

Straight fork length (cm) was measured with calipers and round weight was recorded in pounds and later converted to kilograms. In some instances where either weight or length was unknown, a functional regression (Baglin 1980) was used for estimating the missing measurement.

Small and medium fish were assigned an age based on a length-weight-age conversion table presented by Coan (1976). No ages were assigned to giant fish because of the difficulty experienced in aging them accurately.

Ovaries were examined from 81 small and medium bluefin tuna caught from 1974 through 1977 and from 403 giant bluefin tuna collected during 1965 through 1968 and 1974 through 1978. Ovaries were stored in 10% Formalin[5] and later blotted dry and weighed in grams. The gonosomatic index (GSI) (ovary weight as a percentage of total body weight) was used as a gross indicator of maturity. Only fork length was taken from Japanese longline samples from the Gulf of Mexico for which the GSI was calculated using an estimated body weight from the length-weight relationship of Baglin (1980).

A detailed examination of ovaries from 292

[4]Mather, F. J., III. 1973. The bluefin tuna situation. Proc. 16th Annu. Int. Game Fish. Res. Conf., p. 93-120.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

fish was conducted using histological techniques. Ovaries were sectioned at 8 μ and stained either with haematoxylin and eosin or trichrome stain. The oocytes were grouped into stages according to the classification system of Kraft and Peters (1963) and Smith (1965). From each prepared slide, a measurement was taken of the largest egg diameter. The egg diameters were measured with an ocular micrometer at 30 × magnification, and the orientation of egg diameters was assumed to be random. Stage of maturity was thus based on the histological examinations.

A test was made for heterogeneity of egg size within the ovary. Thin cross sections were taken from the anterior, middle, and posterior parts of one ovary of a mature fish and each section was subdivided into three subsamples, representing the center, midregion, and periphery of the ovary (Otsu and Uchida 1959). Egg diameters from each area were then measured and compared statistically.

Fecundity, defined as the potential number of mature eggs (yolked ova) that could be spawned during one reproductive season, was estimated by using a dry weight method. This consisted of taking samples from the anterior, middle, and posterior parts of each ovary. The eggs from each of these sections and from the remainder of the ovaries were then separated from the ovarian tissue by straining them over a wire screen under running water. The egg samples from each section, in an aqueous solution, were stirred and a subsample from each was pipetted into a beaker. These eggs were stirred and approximately 1-2 g wet weight were taken to be used for the fecundity estimate. The yolked eggs, which were counted and fecundity estimated, were divided into two size categories. Eggs 0.46 mm and larger that were counted were well developed and fully yolked. A second size category for which eggs were counted included smaller eggs (0.32 mm in diameter) that were not in quite as advanced stage of development, but that could possibly undergo further development and be spawned during one reproductive season. The subsample was then weighed to the nearest 0.1 mg, and the weight of the remaining eggs was recorded in grams. Fecundity estimates, rounded to the nearest 0.1 million eggs, were calculated from the relationship $C = (AD/B) + A$, where A is the number of mature ova in the subsample, B is the weight of the ova in the subsample, C is the number of mature ova, and D is the weight of ova from both ovaries minus the weight of the subsample.

RESULTS AND DISCUSSION

Sex Composition

From 1974 through 1977, sex was determined for 283 small and medium bluefin tuna from the Middle Atlantic Bight during June, July, and August (Table 1). No significant difference from an expected 1:1 sex ratio was found. Sampling for the remaining months was inadequate.

From 1975 through 1978, sex was determined for 3,429 giant bluefin tuna from the Gulf of Mexico, March through June; Bahamas, April through June; and from the northeast coast of the United States, July through October (Table 1). The deviation from an expected 1:1 sex ratio was significant for April, May, July, and August. Females were more prevalent than males in spawning aggregations during April and May. Males were more prevalent in feeding schools during July and August. No significant difference from an expected 1:1 sex ratio was found for March, June, September, and October. Sampling during the remaining months was inadequate. These findings suggest that some giant bluefin tuna segregate into distinct areal groups according to the predominating sex and that sex ratios may change with season.

TABLE 1.—Monthly sex ratios for small and medium (1974-77) and giant (1975-78) western Atlantic bluefin tuna.

Size category	Month	Number	Sex ratio males/females
Small and medium	June	204	1.02
	July	35	0.84
	August	44	1.10
Giant	March	66	1.00
	April	292	[1]0.75
	May	356	[1]0.63
	June	106	0.93
	July	800	[1]1.46
	August	1,049	[1]1.74
	September	694	0.93
	October	66	1.13

[1]Significant departure from null hypothesis at 0.05 level (chi-square).

Gonosomatic Index, Gross Morphology, and Size of Ova

The external appearance alone of tuna ovaries is inadequate for gross classification of maturity stage (Buñag 1956). The GSI (also called gonad index, maturity index, gonadosomic or gonadalsomatic index), along with egg diameter measurements, has been a successfully used criterion for selecting specimens for fecundity studies and for determining the spawning periods for various species of fish (Vladykov 1956; Peterson 1961; Erdman, 1968; Mathur and Ramsey 1974; Baglin 1979).

On the basis of the GSI and the gross morphology and size of ova from the preserved ovaries, western Atlantic female bluefin tuna may be assigned to one of the following developmental stages:

I. Immature—Ovaries are thin, hollow tubes; nearly spherical, transparent oocytes range from 0.03 to 0.13 mm in diameter (these eggs were stained with acetocarmine to facilitate measuring). These oocytes were also present during all other developmental stages, and there was no sign of previous spawning. GSI ranges from 0.1 to 0.3.

II. Maturing—Ovaries are flaccid, opaque ova up to about 0.63 mm in diameter. GSI ranges from 0.4 to 1.9.

III. Mature—Ovaries are firm and full of eggs, with many yellow-orange ova up to 0.85 mm in diameter. GSI ranges from 2.0 to 5.3.

IV. Ripe—None of the fish studied were found to be in this developmental stage. However, a few transparent ripe eggs were found in an individual classified as Stage III. The largest of these eggs was 1.16 mm in diameter with an oil droplet 0.30 mm in diameter. This egg corresponds to Stage V of Rodríguez-Roda (1967). A fish would be classified as being ripe only when a substantial number of eggs of this size are present.

V. Spent—Ovaries are flaccid; completely spent fish had a few degenerating eggs up to 0.63 mm in diameter. Fish in this stage taken in the summer and early fall months had ovaries with a large amount of fatty tissue. GSI >0.2 but <2.0.

Size and reproductive data by estimated age and month are presented in Table 2 for 81 small and medium female bluefin tuna from the Middle Atlantic Bight of the western Atlantic and for 15 small and medium eastern Atlantic female bluefin tuna collected by Rodríguez-Roda (1967) and by Cort et al. (1976). Relatively

TABLE 2.—Length, weight, and gonadal data for 81 small and medium female western Atlantic bluefin tuna collected during 1974-77 and for 15 small and medium female eastern Atlantic bluefin collected during 1963 by Rodríguez-Roda (1967) and during 1976 by Cort et al, (1976).

		Fork length (cm)			Round weight (kg)			Ovary weight (g)			Gonosomatic index (%)			
Age	Month	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	Number
							Western Atlantic							
3	June	100	0.59	97-102	19.6	0.57	16.3-23.2	25	3.9	5-52	0.1	0.02	0.03-0.28	12
	July	96		95-100	18.7		16.8-21.8	16		10-23	0.1		0.06-0.14	6
	August	101		98-105	20.7		18.8-22.2	18		8-51	0.1		0.03-0.23	6
4	June	108		107-109	25.4		24.5-26.3	15		10-20	0.1		0.04-0.08	2
	July	121		118-122	34.2		26.8-38.1	76		68-80	0.2		0.21-0.26	3
	August	115		106-124	29.5		19.1-40.9	49		17-94	0.2		0.09-0.26	4
5	June	133	1.42	126-138	44.1	1.18	36.3-49.9	97	9.5	44-148	0.2		0.11-0.33	12
	July	133		126-140	47.2		43.6-50.8	190		149-231	0.4		0.29-0.53	2
	August	129		126-131	41.0		37.9-45.4	69		40-119	0.2		0.11-0.26	4
6	June	150	1.44	142-157	59.1	2.34	45.4-75.4	204	18.5	102-222	0.4	0.03	0.17-0.51	12
	August	150			58.1			126			0.2			1
7	June	163	0.90	157-169	80.2	2.53	65.4-91.7	434	97.9	175-1,605	0.5	0.10	0.17-1.75	14
	July	160		158-165	60.3		53.1-68.1	142		62-211	0.2		0.13-0.31	3
							Eastern Atlantic							
4	July	111			[1]26.2			150			0.6			1
5	May	130			54.0			740			1.4			1
	June	125			[1]37.0			500			1.4			1
	July	126			[1]37.8			450			1.2			1
	August	134			48.0			460			1.0			1
6	June	149			[1]61.7			900			1.5			1
	July	148			[1]61.0			860			1.4			3
	August	152			63.5			470			0.7			2
7	June	171			110.0			1,920			1.9			1
8	May	180			113.0			2,500			2.2			1
	August	185			106.0			660			0.6			2

[1]Round weight estimated using functional regression of Baglin (1980).

little development towards maturity was evident in the age 1 through age 7 western Atlantic fish with the exception of one age 7 fish collected in June with a GSI of 1.75. The eastern Atlantic small and medium fish, on the average, have a larger mean GSI than the western Atlantic small and medium fish. The largest GSI (2.2) calculated from the eastern Atlantic small- and medium-sized bluefin tuna was found for a fish captured during May at an estimated age of 8 yr.

Body and ovary size, by month, for 403 western and 75 eastern Atlantic female giant bluefin tuna are presented in Table 3, with the calculated monthly GSI presented in Figures 1 and 2. The average body and ovary size of the female giant fish from the western Atlantic was larger than that of the eastern Atlantic fish for each month. Well-developed ovaries were present in western Atlantic giant bluefin tuna during April and May. These fish were collected from the Gulf of Mexico longline and sport fishery and from the Florida Straits sport fishery. Ovarian development was minimal during October, as indicated by a low mean GSI,

TABLE 3.—Length, weight, and gonadal data for 403 female giant western Atlantic bluefin tuna collected during 1965-68, 1974-78, and for 75 female giant eastern Atlantic bluefin tuna collected during 1963 by Rodríguez-Roda (1967).

Month	Fork length (cm)			Round weight (kg)			Ovary weight (g)			Number
	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	
				Western Atlantic						
March	237	3.5	199-256	245	10.2	143-307	2,849	448	331-6,810	25
April	242	2.7	190-264	262	8.1	117-335	8,380	564	409-13,166	41
May	240	1.4	205-269	244	4.8	156-324	7,708	475	900-14,960	73
June	246	1.7	213-270	262	5.8	159-351	5,023	341	950-13,600	68
July	254	1.0	218-272	295	3.3	205-375	1,927	89	600-7,000	96
August	257	1.3	224-282	320	4.4	213-424	2,857	158	600-6,250	79
Sept.	256	3.1	235-269	330	7.5	297-374	2,770	533	750-6,500	11
Oct.	242	3.8	212-257	308	16.8	186-370	1,137	71	700-1,400	10
				Eastern Atlantic						
May	211	1.8	200-225	190	4.2	155-219	2,758	318	1,540-6,820	17
June	213	2.6	204-230	189	5.9	167-235	3,148	403	1,780-6,280	12
July	214	2.3	189-244	169	5.8	130-263	1,493	117	700-3,580	30
August	207	2.2	197-232	149	5.6	125-226	1,112	85	840-1,980	16

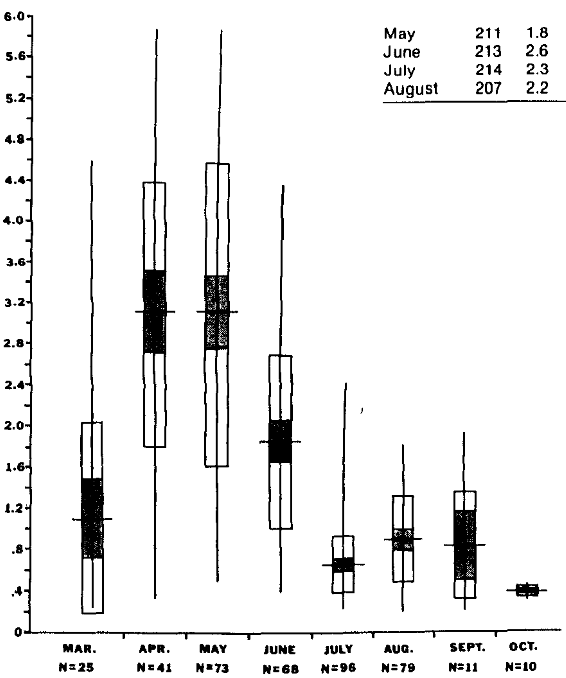


FIGURE 1.—Seasonal variation in gonosomatic index of 403 female giant western Atlantic bluefin tuna collected from 1965 through 1968 and 1974 through 1978. The number, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

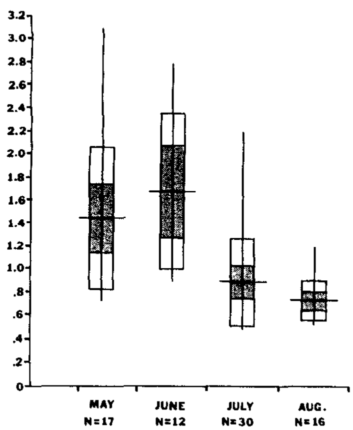


FIGURE 2.—Seasonal variation in gonosomatic index of 75 female giant eastern Atlantic bluefin tuna collected during 1963 by Rodríguez-Roda (1967). The number, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each of the mean (shaded box) are shown.

and reached a peak during April and May as indicated by the highest GSI. Sampling was inadequate for November through February. Well-developed ovaries were present mainly during May and June in eastern Atlantic giant bluefin tuna from the traps at Barbate (Rodríguez-Roda 1967). In May, the mean GSI for the western Atlantic was greater than that for the eastern Atlantic. No great difference was found between the mean GSI for the western and eastern Atlantic giant bluefin tuna for June, July, and August for which data were available for comparison. The plots of the GSI indicate that giant bluefin tuna spawning occurs earlier in the western Atlantic (the drop in GSI occurring in June) than in the eastern Atlantic (the drop in GSI occurring in July).

Heterogeneity of Egg Diameters

A significant difference in egg diameters was found for the center, midregion, and periphery of the anterior section of an ovary from a mature fish ($F=6.1$; df $=2, 631$; $P<0.005$). No significant difference in egg diameters was found for the center, midregion, and periphery of the middle or posterior sections of the ovary. A significant difference in egg diameters was also found among the anterior, middle, and posterior sections ($F=11.6$; df $=2, 1{,}843$; $P<0.001$). Because some heterogeneity occurred, estimates of fecundity were based on eggs from each section of both ovaries. Heterogeneity of egg size within an ovary has also been shown for albacore, *Thunnus alalunga*, (Otsu and Uchida 1959); swordfish, *Xiphias gladius*, (Uchiyama and Shomura 1974); and white marlin, *Tetrapturus albidus*, (Baglin 1979).

Histology of the Ovaries

Microscopic examinations were made of ovarian tissues from 119 small and medium bluefin tuna and 173 giant bluefin tuna. Diameters measured from these prepared slides were considerably smaller than those measured from whole eggs fixed in 10% Formalin (see footnote 5).

The oocytes were grouped into the following stages of oogenesis using the system of Kraft and Peters (1963), Smith (1965), and Moe (1969).

Stage 1—Thin layer of cytoplasm surrounding a relatively large nucleus with a single nucleolus; oocytes are <0.03 mm in diameter.

Stage 2—Dark cytoplasm and many peripheral nucleoli are in the nucleus oocytes are 0.03 mm through 0.13 mm in diameter (resting stage).

Stage 3—Yolk vesicles appear in cytoplasm; the membrane called the zona radiata, also referred to as zona pellucida (Hoar 1969) and vitelline membrane (Bodola 1966), appears at the end of this stage; oocytes are 0.17 mm through 0.30 mm in diameter (early vitellogenic stage).

Stage 4—Thick zona radiata, yolk vesicles, and yolk globules are present; oocytes are 0.33 mm through 0.63 mm in diameter (late vitellogenic stage).

Stage 5—This final stage was seldom observed during histological analysis. It evidently takes place during a short period of time immediately before ovulation. Eggs in this stage have a lightly staining granular yolk mass with few yolk vesicles and yolk globules, a thin zona radiata, and an irregular shape caused by sectioning.

Histological examination of female bluefin ovary sections from the Middle Atlantic Bight revealed the following:

Age 1—Very little sexual differentiation was present in age 1 bluefin tuna ($N=17$) collected during May, June, July, and August. Some oogonia were observed within the lamellae.

Age 2—The first appearance of oocyte development occurred in age 2 bluefin tuna collected during July ($N=4$). Both stage 1 and stage 2 oocytes were present, although stage 2 oocytes were most numerous.

Age 3—Many stage 2 oocytes and a few stage 1 oocytes were found in age 3 bluefin tuna collected during January and June ($N=13$). Only stage 2 oocytes were found in age 3 bluefin tuna collected during July and August ($N=10$).

Age 4—Stage 2 oocytes were present in all age 4 females collected during June ($N=36$) (Fig. 3). Also in 11% of these fish, some vitellogenic stage 3 oocytes undergoing absorption were present. Only stage 2 oocytes were present in age 4 bluefin tuna collected during July and August ($N=10$).

Age 5—Mostly stage 2 oocytes were present in age 5 fish collected during June ($N=16$),

FIGURE 3.—Ovarian tissue from an age 4 bluefin tuna (119 cm, 33.6 kg) collected off the Middle Atlantic Bight during June 1977. Stage 2 oocytes are present, as indicated by arrow.

although a few stage 1 oocytes were also observed. Also, in 44% of these fish some stage 3 oocytes were present, many undergoing absorption. One individual also had some stage 4 oocytes present. These oocytes were in the process of degeneration. Mostly stage 2 oocytes were present in age 5 fish collected during July ($N = 2$). Both of these fish also had some stage 3 oocytes present, which were undergoing absorption. Stage 2 oocytes were present in all fish collected during August ($N = 4$). Only one of these fish had stage 3 oocytes present. These stage 3 oocytes were also undergoing absorption.

Age 6—The majority of oocytes observed in age 6 bluefin tuna collected during June ($N = 12$) were in stage 2 of development and only a few stage 1 oocytes were observed. Many of these fish (83%) had some stage 3 oocytes present, most undergoing the process of degeneration (Fig. 4). One individual had some stage 4 oocytes present, which were also degenerating. Only stage 2 oocytes were found in an age 6 bluefin tuna collected during August.

Age 7—Mostly stage 2 oocytes were found in age 7 fish collected during June ($N = 15$). Also, some stage 1 oocytes were present in most of these fish and 47% had stage 3 oocytes present, many of which were undergoing absorption. Only stage 2 oocytes were found in an age 7 fish collected during July and another age 7 fish taken during October.

Some gonadal development, therefore, occurs in these medium female bluefin tuna. However, the simulation of gonadal maturation by young fish that probably do not spawn has been reported for king mackerel, *Scomberomorus cavalle*, (Beaumariage 1973) and Atlantic sailfish, *Istiophorus platypterus*, (Jolley 1977). These authors based their determination on the size of the stage 4 oocytes, on their compactness within the lamellae, and on the appearance of many degenerating oocytes. My observations of medium bluefin tuna seem to correspond with the findings of the above authors, although the most

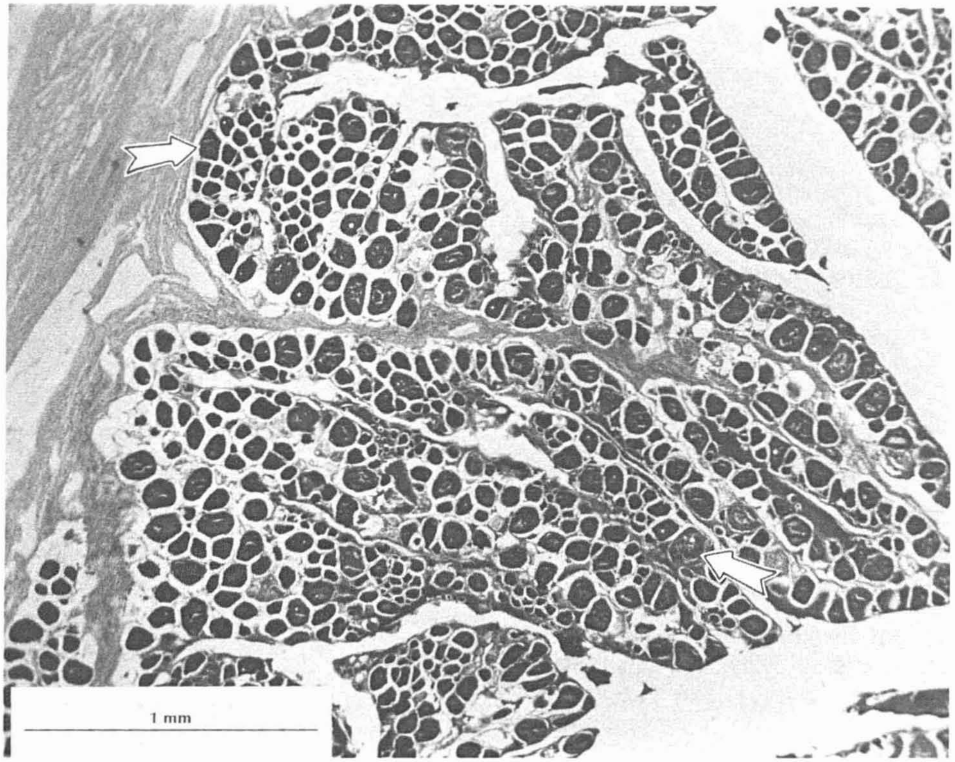


FIGURE 4.—Ovarian tissue from an age 6 bluefin tuna (153 cm, 59.5 kg) collected off the Middle Atlantic Bight during June 1976. Resting stage 2 oocytes are present (upper arrow), as are stage 3 oocytes undergoing the process of degeneration (lower arrow).

developed oocytes in the majority of fish that I examined were in stage 3 of development, and the average were in stage 2 based on the mean size of the oocytes measured (Fig. 5).

I believe, therefore, that the Middle Atlantic Bight is not a significant spawning area during the summer and probably not at any other time of the year, but samples are not available for other seasons. Also, recently there has been speculation by Rivas (1978) that some of these medium bluefin tuna may migrate during May and June across the Atlantic to the Mediterranean Sea to spawn. According to Sella (1929) eastern Atlantic bluefin tuna begin to reproduce in their third year, when they attain a weight of about 15 kg. Rodríguez-Roda (1967) found that 50% of eastern Atlantic bluefin tuna females are mature at 97.5 cm or 3 yr of age. However, the smallest bluefin tuna that he estimated fecundity for was 130.5 cm and 54 kg, which corresponds to an age 5 fish according to Coan (1976). Frade and Manaças (1933) found very little development in age 3 females from the eastern Atlantic. Cort et al. (1976) found developing oocytes in eastern Atlantic bluefin tuna measuring 148 and 152 cm from the Gulf of Gascony. These fish would be age 6 according to Coan (1976).

The only published record I have found of age of maturity of western Atlantic bluefin tuna is that of Westman and Neville (1942). Observing the gross morphology of ovaries, they indicated that western Atlantic bluefin tuna 5 yr of age appeared to be mature, although the gonads gave no indication of the presence of eggs. I have also examined the unpublished cruise report of the MV *Delaware*, June 1957. Using the conversion table of Coan (1976), all age 3 female bluefin tuna were judged immature, and most age 4 (2 out of 3) were judged immature. No description of the ovaries on an age 5 fish was given, and 67% of age 6 females ($N = 6$) had well-developed eggs.

My analysis of western Atlantic bluefin tuna ovaries indicates that age 6 would probably be

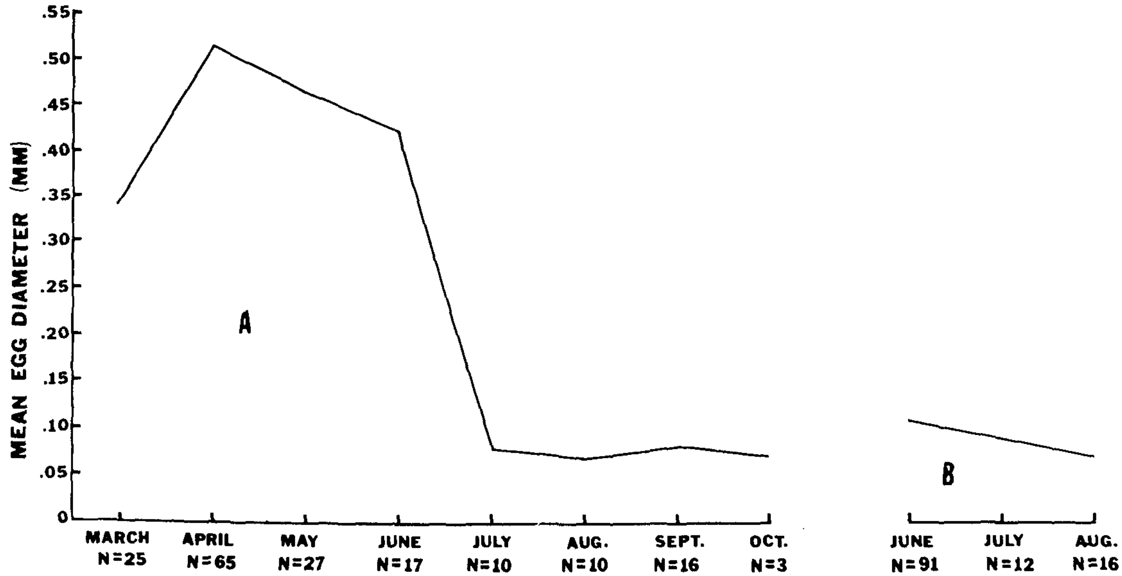


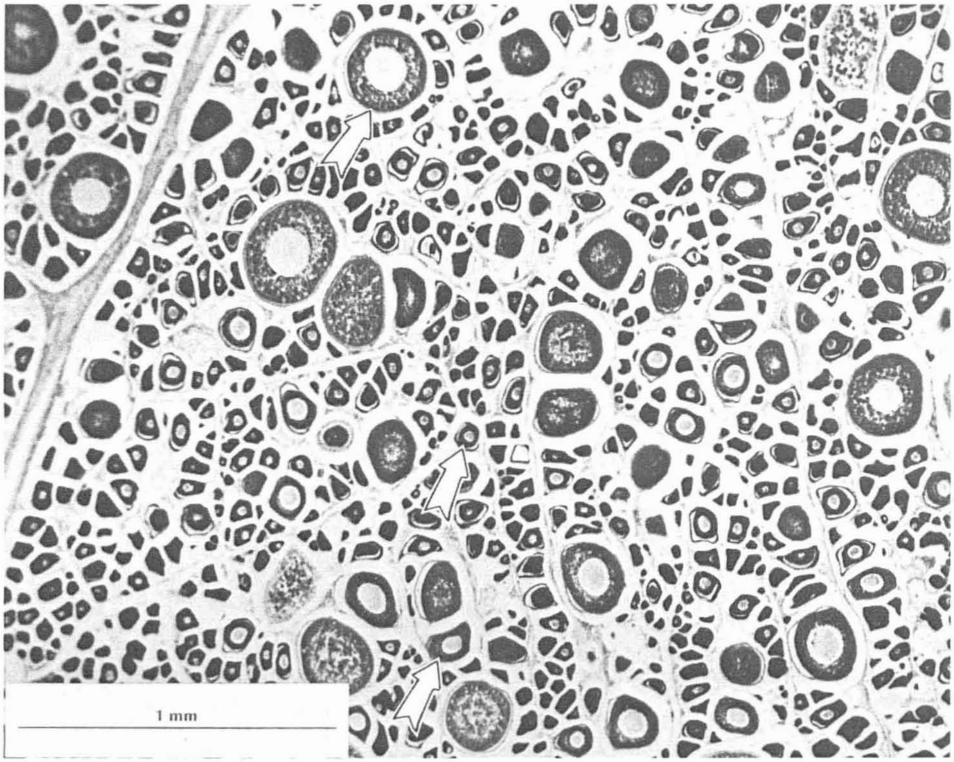
FIGURE 5.—Mean egg diameter of largest ovarian egg as determined from histological sections from monthly samples (N) of A) female giant bluefin tuna from the Gulf of Mexico and the Florida Straits (March through June 1955, 65-67, 76-78) and from off New England (July through October 1974-75, 77), and B) female bluefin tuna ages 3-7 from off the Middle Atlantic Bight (June through August 1974-77).

the earliest age at which a majority of females could possibly reach maturity. However, a majority of vitellogenic oocytes in these age 6 fish were being absorbed and most likely would not have been spawned during the years when these fish were taken. As previously noted, I observed no vitellogenic oocytes in age 3 fish, but if Sella (1929) and Rodríguez-Roda (1967) are correct, eastern Atlantic bluefin tuna may reach maturity at an earlier age than their western Atlantic counterparts.

Vitellogenic oocytes were not found in the two giant bluefin tuna (205 and 207 cm) taken during the March 1966 MV *Delaware* Cruise 66-2 (lat. 37°24′N, long. 67°32′W). Vitellogenic oocytes were found in one of three giant fish (190-213 cm) taken during April 1965 on the MV *Delaware* Cruise 65-3 (lat. 35°54′N, long. 72°51′W). Evidently this area of the western North Atlantic was not an important spawning area for bluefin tuna during March-April.

Vitellogenic oocytes (stages 3 or 4) were present in all giant bluefin tuna taken from the Gulf of Mexico and Florida Straits during 1955, 1967, 1976, 1977, and 1978 during March (N = 24), April (N = 61), and May (N = 54) (Figs. 6, 7). In one of two fish taken in June 1967 and 1977, stage 3 and stage 4 oocytes were present; in the other fish all the vitellogenic oocytes had been spawned or absorbed. On the average, the largest oocytes in all of the fish for July (N = 10), August (N = 10), September (N = 16), and October (N = 12) from off New England during 1974, 1975, and 1977 were in stage 2 (Fig. 8). Vitellogenic oocytes were generally absent from these fish.

I found degeneration and absorption of advanced unovulated eggs more common as the season progressed. This agrees with the findings of Frade and Manaças (1933) for eastern Atlantic bluefin tuna. Distinctive atretic bodies, formed from the remnants of oocytes that were not shed, were present in the female giant bluefin tuna collected during March through October. Topp and Hoff (1971) also reported atretic body formation in the ovaries of a single giant female collected from the west Florida coast during May. As previously described by Smith (1965), these atretic bodies form a characteristic brownish mass, the corpus atreticum, and are made up of amorphous brownish granules, phagocytes, and clear yellow pigment globules (Fig. 9). I found that empty follicles left behind after the ripe oocytes are released degenerate rapidly. This was also observed for eastern Atlantic bluefin tuna by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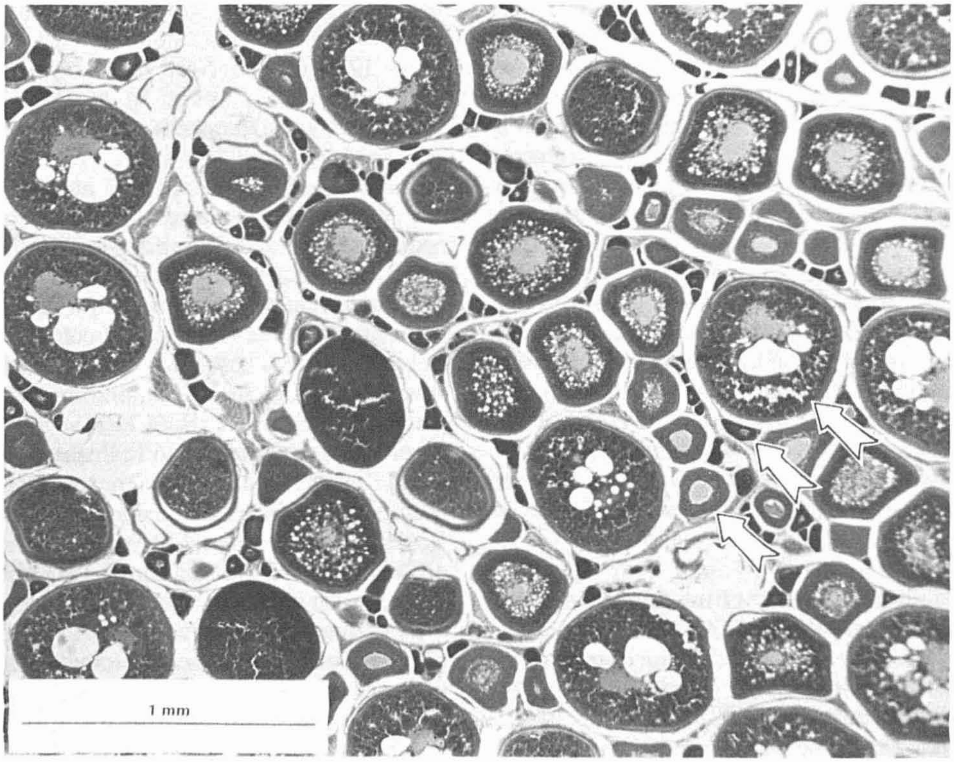
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FIGURE 6.—Ovarian tissue from a giant bluefin tuna (250 cm) collected off the Gulf of Mexico during March 1978. Early stage 4 oocytes (upper arrow), stage 2 oocytes (middle arrow), and stage 3 oocytes (lower arrow) are present.

FIGURE 7.—Ovarian tissue from a giant bluefin tuna (205 cm) collected off the Gulf of Mexico during May 1978. Late stage 4 oocytes (upper arrow), stage 2 oocytes (middle arrow), and stage 3 oocytes (lower arrow) are present.

Frade and Manaças (1933), who speculated that the rapid degeneration of the follicles could be caused by pressure exerted by neighboring oocytes. My findings also confirm that western Atlantic bluefin tuna released eggs intermittently during April, May, and June, the majority during May.

Fecundity Estimates

Fecundity estimates were obtained for 28 western Atlantic bluefin tuna, which were collected from the Gulf of Mexico and Florida Straits during April, May, and June of 1967, 1968, 1974, 1975, 1976, and 1978 (Table 4). The reliability of the dry gravimetric method was tested by estimating the fecundity of an individual fish by counting and weighing eggs from four subsamples. Based on these four estimates, the average number of eggs >0.46 mm in diameter was 41.6 million with a range from 40.0 to 43.0 million and a standard error of the mean (SE) of 0.76. The average number of eggs >0.32 mm in diameter was 76.0 million with a range from 72.5 to 82.5 million and SE = 2.2.

I am presenting two estimates of potential fecundity, and the estimate based on eggs >0.32 mm in diameter essentially coincides with the size of 0.33 mm used by Rodríguez-Roda (1967) for eastern Atlantic bluefin tuna. This would be the potential number of eggs that could be spawned, assuming there was no degeneration or absorption of advanced unovulated eggs. My histological examinations of bluefin ovaries,

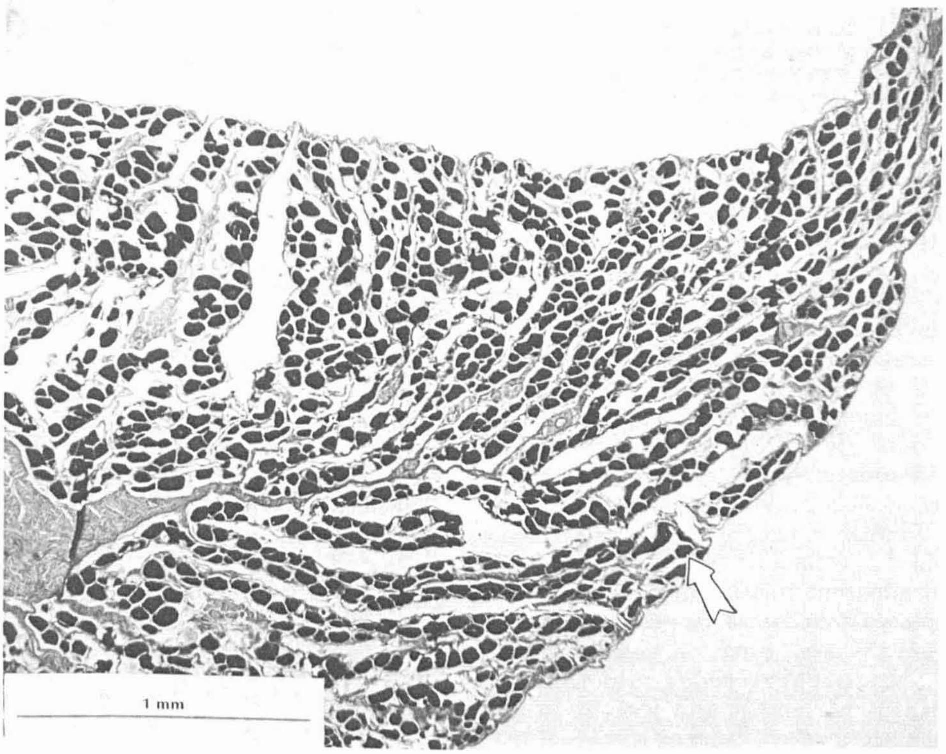

FIGURE 8.—Ovarian tissue from a giant bluefin tuna (256 cm, 268 kg) collected off the northeast coast of the United States during August 1975. Stage 2 oocytes are present, as indicated by arrow.

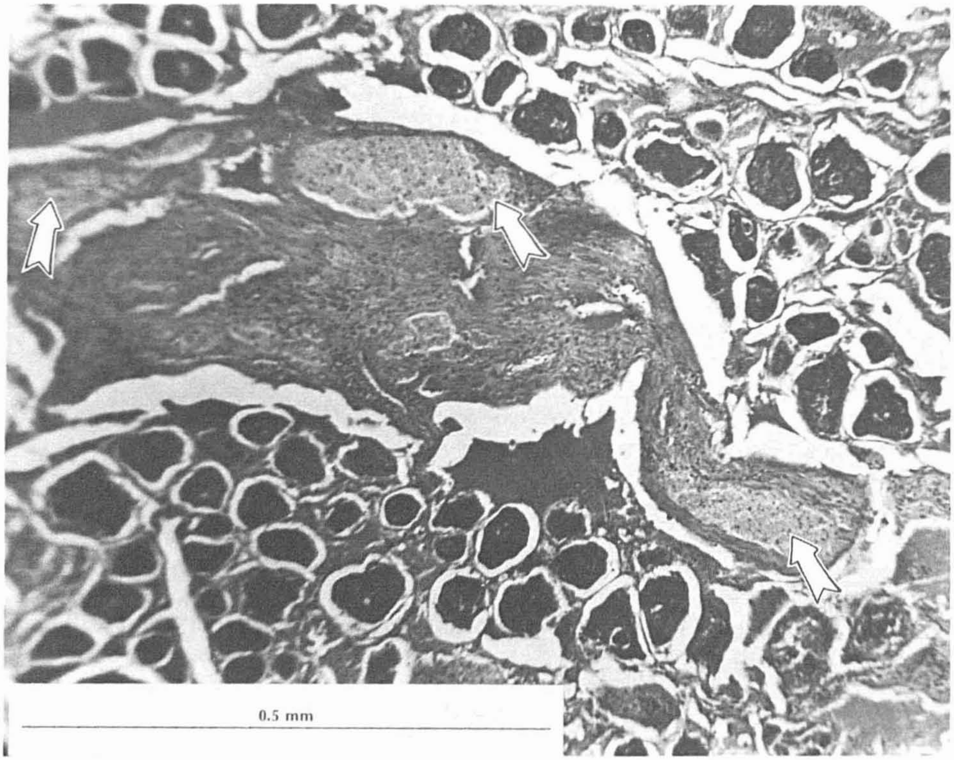

FIGURE 9.—Ovarian tissue from a giant bluefin tuna (264 cm, 297 kg) collected off the northeast coast of the United States during July 1975. Brown bodies are present, as indicated by arrows.

however, revealed the presence of atretic bodies. It was impossible to quantify the number of eggs constituting these atretic bodies, although I assume that absorption would occur principally with the smaller vitellogenic ova. Therefore, I have also estimated the number of eggs >0.46 mm in the most advanced size mode that could potentially be spawned during one spawning season. For bluefin tuna 205-269 cm FL and 156-324 kg round weight, the average number of eggs 0.33 mm in diameter and larger was estimated as 60.3 million (SE = 4.04) and the average number of eggs 0.47 mm in diameter and larger was estimated as 34.2 million (SE = 2.15). No apparent relationship was found for fecundity as a function of length or estimated weight for the size range of bluefin tuna I studied. MacGregor (1968) said that the relationships of length and weight to egg production are masked in many species of fish, because egg production occurs over a relatively short range in size, and because variation in number of eggs produced at each length is great. Bailey (1964) found no obvious relationship between fecundity and fish size for American smelt, *Osmerus mordax*. Schenck and Whiteside (1977) and Loesch and Lund (1977) found a great amount of variability in fecundity for a given fish size for the fountain darter, *Etheostoma fonticola*, and blueback herring, *Alosa aestivalis*. Since histological examinations of ovaries and estimated GSI showed that the bluefin tuna are multiple spawners, it is possible that some of the fish selected for fecundity estimates had previously shed eggs. Also the rate of absorption of vitellogenic ova could have varied for the fish selected for fecundity estimates. I found, however, that the dry weight of eggs could be used for estimating fecundity. The following relationships were found:

$$F = 5.2895 + 0.0167\ W\ (R^2 = 0.64),$$

where F is the number of ova >0.46 mm in diameter and W is the dry weight of all eggs separated from the ovarian connective tissue.

TABLE 4.—Length, weight, and gonadal data for 28 female western Atlantic bluefin tuna from the Gulf of Mexico and the Florida Straits collected during April, May, and June 1967, 1968, 1974, 1975, 1976, and 1978. The mean and standard error of the mean are given at the bottom of the columns.

Body length (cm)	Estimated body weight (kg)	Dry weight of eggs (g)	Gonosomatic index (%)	Estimated no. of eggs >0.46 mm diameter (millions)	Estimated no. of eggs >0.32 mm diameter (millions)
205	156	1,260	5.3	13.6	32.7
222	[1]188	696	2.1	16.7	22.7
229	217	1,202	3.1	24.2	46.4
229	217	2,177	5.0	55.5	96.0
229	217	1,481	2.8	33.9	64.4
231	224	1,330	4.4	26.8	41.1
236	[1]197	1,329	3.2	28.4	40.3
236	[1]189	1,404	3.2	29.6	44.7
238	246	1,788	4.1	39.0	63.9
238	246	1,703	4.2	40.1	64.5
238	246	1,796	3.8	34.4	61.7
241	254	1,483	3.4	29.8	62.4
241	254	2,436	4.8	48.0	84.9
241	[1]247	1,560	3.9	33.0	44.0
244	263	1,750	3.6	25.2	56.7
244	263	1,452	3.4	23.2	42.1
244	263	2,121	5.0	49.3	93.3
252	289	2,770	4.7	39.6	94.6
254	298	1,942	2.9	41.6	76.0
—	307	1,681	2.5	32.0	59.2
256	307	1,950	2.6	42.2	79.5
257	[1]232	1,200	2.9	24.3	33.8
257	309	750	1.9	16.2	26.2
259	316	2,750	4.2	32.6	76.9
259	316	2,500	4.4	48.8	80.6
261	[1]272	1,488	2.6	31.4	42.3
262	[1]324	2,593	4.5	57.6	81.6
269	[1]284	1,950	4.6	40.6	74.8
$\bar{x}$ 243	255	1,734	3.7	34.2	60.3
SE 2.78	8.37	102.79	0.18	2.15	4.04

[1]Actual weight determined.

$$F = -0.9057 + 0.0353\, W (R^2 = 0.81),$$

where F is the number of ova >0.32 mm in diameter and W is the dry weight of all eggs separated from the ovarian connective tissue.

A reduction in fecundity in older fish has been reported by Bodola (1966) for gizzard shad, *Dorosoma cepedianum*, and by Loesch and Lund (1977) for blueback herring. No such decline in number of eggs was found for western Atlantic bluefin tuna.

My fecundity estimates for western Atlantic bluefin tuna are considerably greater than the estimate given by Williamson (1962). He, however, did not describe how he arrived at his estimate for a western Atlantic bluefin tuna. My estimates more closely agree with estimates presented by Frade (1950) and Rodríguez-Roda (1967) for eastern Atlantic bluefin tuna. Although my estimates were based generally on larger fish, it appears that western Atlantic bluefin tuna are considerably more fecund than eastern Atlantic bluefin tuna.

ACKNOWLEDGMENTS

I thank L. R. Rivas and W. J. Richards of the Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA and C. L. Smith of the American Museum of Natural History for their many helpful comments on the manuscript. I also thank the two anonymous reviewers who read the manuscript and offered helpful suggestions.

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