

OSTEOLOGICAL DEVELOPMENT AND VARIATION IN YOUNG TUNAS, GENUS *THUNNUS* (PISCES, SCOMBRIDAE), FROM THE ATLANTIC OCEAN¹

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ABSTRACT

The development and variability of osteological and meristic features obtained from 427 juvenile *Thunnus* from 8 to 117 mm SL are described. The juveniles of *T. atlanticus*, *T. thynnus*, and *T. alalunga* can be identified. *Thunnus obesus* cannot be separated from *T. albacares*, but both are separable as the "*Thunnus* spp. complex" from the other three species. Identification methods are discussed with emphasis on the features of the axial skeleton, number of gillrakers over the ceratobranchial bone, pterygiophore pattern under the second dorsal fin, and the shape of the lateral line.

This paper describes the development of osteological features and their variability for the identification of juvenile *Thunnus* from 8 to 100 mm standard length (SL). To date, this has not been attempted in an orderly and systematic fashion for the species in the Atlantic Ocean, mainly because all juveniles have the same general external appearance as *T. atlanticus* shown in Figure 1. Nevertheless, some species have been previously identified by using mostly external characters: Sella (1924), Schaefer and Marr (1948), Wade (1950, 1951), Mead (1951), Padoa (1956), Jones (1960), Matsumoto (1961), Marchal (1963a, b), and Yabe, Ueyanagi, and Watanabe (1966). The identifications were probably correct, although other species of juvenile *Thunnus* could fit these same descriptions. Scaccini (1961) published on a series of juvenile *Thunnus* from the Mediterranean and stated that they were *T. thynnus*, but he did not reveal how he arrived at his identifications. Ueyanagi (1967) mentioned the occurrence of small *T. alalunga* in the North and South Atlantic Oceans, but he gave no identification methods. Klawe and Shimada (1959) and Klawe (1961) examined juvenile *Thunnus* material, using external and osteological characters, but they had doubts as to the correctness of their identifications. Watson and Mather (1961) used the soft X-ray method to distinguish between the species. One of their major characters was the

vertebral position of the first ventrally directed parapophysis. I found this character to be of limited value, because the vertebral position of the first parapophyses changes with growth. Potthoff and Richards (1970) used osteological characters to identify two species of juvenile *Thunnus* from bird stomachs, and Juárez (1972) described larvae of *T. atlanticus*, also on the basis of osteological methods. Other researchers have used adult osteological characters on specimens larger than 100 mm (Yabe et al., 1958; Nakamura and Kikawa, 1966).

I was not entirely successful in separating all species. Using osteological characters, *T. albacares* and *T. obesus* were not separable from each other as juveniles (from 8 mm to about 100 mm SL), but together they can be separated from the other three *Thunnus* species in the Atlantic Ocean. Thus, I have lumped them together as the "*Thunnus* spp. complex."

Adult characters from the works of Kishinouye (1923), Frade (1932), Godsil and Byers (1944), de Sylva (1955), Watson (1964), Nakamura (1965), and Gibbs and Collette (1967) formed the basis for my study. At first I identified the largest fish in my collection and then worked down to the smaller sizes, noting changes that occurred.

METHODS

The specimens used in this study were first measured with dial calipers or calibrated ocular micrometers and the standard length (SL) from

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FIGURE 1.—*Thunnus atlanticus*, 85 mm SL. Specimen was cleared and stained later for species determination.

the anterior tip of the upper jaw to the posterior edge of the hypural plate was taken. After determining length measurement the right opercular plates were removed and the specimens were then cleared and stained (Taylor, 1967). All counts were made on cleared and stained material that was preserved in 100% glycerin, using a binocular microscope with 100 \times magnification. On a few of the larger specimens 25 \times magnification was used. Counts on the gill arches, fins, and vertebral column were made on the right side of the specimen, except for the pectoral finrays and lateral line scales, which were counted on both sides. The side with the higher count was used for tabulation. Small gillrakers and finrays that were just beginning to appear in their first stage of development were always included in the counts. Structures such as the pterygiophores, neural and haemal spines, zygapophyses, etc., were always counted, although in smaller specimens some of these structures were very small and showed very weak ossification. The hypural complex (parhypural, hypural plates, and ural centrum) was considered as the last vertebra. I was unable to make every count on all of the specimens because of damage or their developmental stage. For these reasons, the number of specimens used for the various counts may vary.

The osteological terms used in this paper are mainly from Eaton (1945) and Gibbs and Collette (1967). The terms transforming and juvenile are defined for scombrid fishes as follows: specimens of the transforming stage can be identified with the aid of larval pigment characters but have attained most adult gross anatomical features,

such as number of vertebrae and median fins; juveniles attain the juvenile pigmentation which obliterates the larval pigmentation. The transition from larval to transforming to juvenile stages is gradual in scombrids and allows for individual subjective judgment. In my opinion, the larval stage for *Thunnus* lasts to about 9 mm SL, the transforming stage to about 13 mm SL, and the juvenile stage to sexual maturity.

MATERIAL

Most of the *Thunnus* used in this study were collected with a dip net, using a strong light at night. A few were collected by plankton nets and some were taken from fish or bird stomachs. The numbers and standard lengths of all specimens examined for this study are shown in Figure 2. Their numbers and size ranges for general capture areas are shown in Table 1.

VERTEBRAL COLUMN

Number of Vertebrae (Figures 3 to 6; Tables 2, 13)

The species of *Thunnus* usually have 39 vertebrae, including the hypural plate: 18 precaudal and 21 caudal vertebrae for all species except the western Atlantic *T. atlanticus*, which usually has 19 and 20, respectively. In juveniles the centra in the anterior two-thirds of the vertebral column are already ossified at 8 mm SL, but are still developing in the posterior third. About 9 mm SL, ossification of all centra is completed. Pleural ribs

start on the 3rd precaudal vertebrae attached to the parapophyses and to the tips of the haemal arches. Caudal vertebrae lack pleural ribs and their haemal arches continue as one haemal spine. In transforming specimens, it is sometimes difficult to distinguish pleural ribs from haemal spines, but one can use the first large anal pterygiophore as a demarkation point because it is

always found in the interhaemal space anterior to the first haemal spine.

Knowledge of the variability of precaudal and caudal arrangement and number of vertebrae is important in the identification of specimens, particularly in the 8- to 14-mm-SL size range where fewer characters are available. However, great differences in vertebral variability exist from

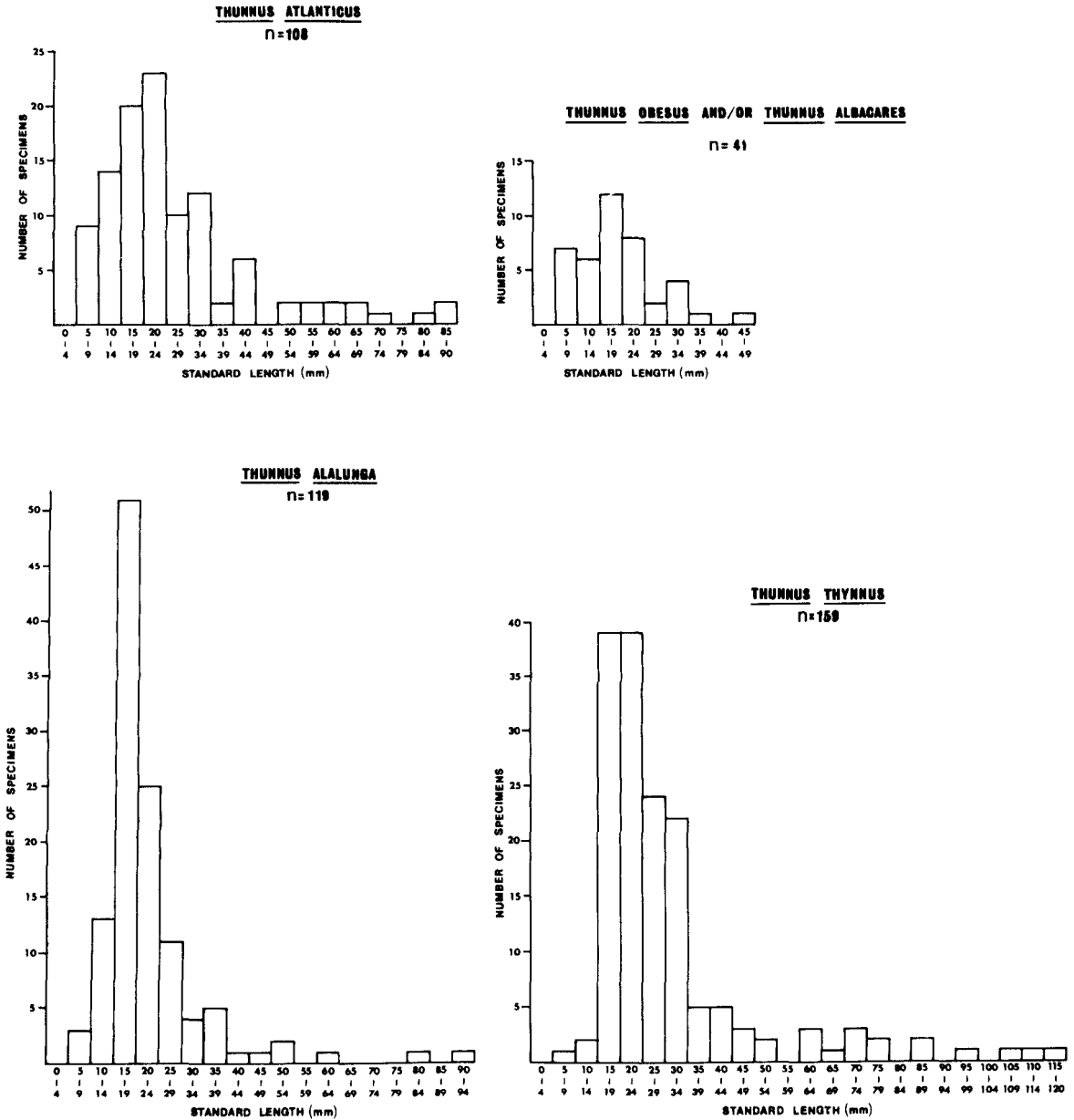


FIGURE 2.—Length distribution by species of all specimens examined for this study.

TABLE 1.—Capture areas, species, number, size range, and mean standard length for specimens studied.

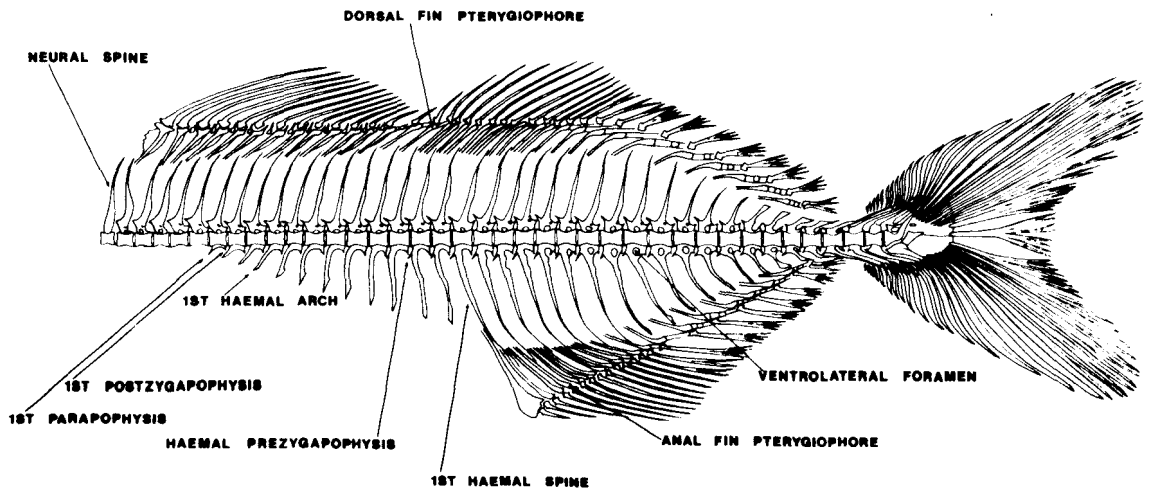
Area	Species	No.	Size range SL (mm)	Mean SL (mm)
Northeast Pacific Ocean	<i>Thunnus</i> spp.	23	14-31	19
Northwest Atlantic Ocean	<i>T. thynnus</i>	14	8-71	32
Northwest Atlantic Ocean	<i>T. alalunga</i>	1	9	
Northwest Atlantic Ocean	<i>T. atlanticus</i>	35	9-71	34
Northwest Atlantic Ocean	<i>Thunnus</i> spp.	4	18-33	27
Gulf of Mexico	<i>T. thynnus</i>	15	17-115	45
Gulf of Mexico	<i>T. atlanticus</i>	65	8-87	23
Gulf of Mexico	<i>Thunnus</i> spp.	1	32	
Caribbean Sea	<i>T. alalunga</i>	9	15-22	19
Caribbean Sea	<i>T. atlanticus</i>	7	8-85	35
Mid-North Atlantic Ocean	<i>T. alalunga</i>	1	18	
Equatorial East Atlantic Ocean	<i>Thunnus</i> spp.	11	8-47	17
Mediterranean Sea	<i>T. thynnus</i>	78	14-117	33
Mediterranean Sea	<i>T. alalunga</i>	102	9-91	23
Unknown	<i>T. thynnus</i>	52	13-44	23
Unknown	<i>T. alalunga</i>	6	16-41	24
Unknown	<i>T. atlanticus</i>	1	11	
Unknown	<i>Thunnus</i> spp.	2	16. 20	

various reports, probably because of insufficient sample size and population differences. I have found variability in precaudal and caudal arrangement, as well as in total vertebrae. Vertebral numbers ranged from 38 to 40, and total variability from the normal counts of $18 + 21 = 39$ and $19 + 20 = 39$ ranged from 1.9% for *T. atlanticus* to 14.6% for *Thunnus* spp. Frade (1932) found 13.6% variability for *T. thynnus* compared to my 5.1%, and he reported eight specimens with 38, six with 40, and one with 41 vertebrae. Gibbs and Collette (1967) doubted Frade's (1932) high counts of 40 and 41 vertebrae, but they confirmed Godsil and Byers' (1944) specimen of *T. thynnus* with 38 vertebrae. Otherwise, they report no

variability in vertebral numbers from more than 200 skeletons, except for three abnormalities where two adjacent centra were fused. I found one such "fusion abnormality" in a *T. thynnus* with $16 + 22 = 38$ from more than 400 *Thunnus* specimens examined.

First Ventrally Directed Parapophysis (Figure 3)

Ventrally directed parapophyses are already present on the anterior centra in the smallest (8 mm SL) specimens. There are two parapophyses per centrum. Posteriorly, these two structures become larger and finally join to form the haemal

FIGURE 3.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus thynnus*, 24 mm SL.

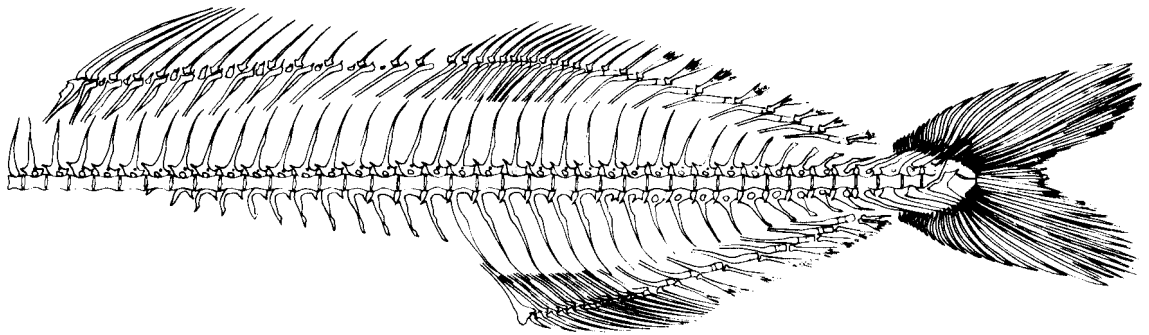


FIGURE 4.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus alalunga*, 22 mm SL.

arches. The first (anteriormost) ventrally directed parapophysis occurred on the 8th or 9th vertebra on specimens 10 mm SL and smaller. In fish larger than 10 mm SL the first ventrally directed parapophysis occurred on the 6th, 7th, or 8th vertebra. I could not determine specific differences in the position of the first ventrally directed parapophysis. Differences reported by Watson and Mather (1961), Watson (1964), and Gibbs and Collette (1967) occur only in specimens larger than 80 mm SL. In juveniles less than 80 mm SL, the first ventrally directed parapophysis is one to three vertebrae anterior to the adult position. As the fish grow, some of the anterior-most parapophyses move to a lateral position on the centra.

First Closed Haemal Arch
(Tables 3, 13)

The closed haemal arches are formed quite early. Even the smallest (8 mm SL) specimens of

Thunnus that I examined had their first anterior-most closed haemal arch on the diagnostic vertebra. The arch is formed by the fusion of the distal ends of the elongated two parapophyses on each centrum. At times it is difficult to determine whether the parapophyses have actually fused or are only lying close together. Care should be taken to determine this fact. The position of the first closed haemal arch is a character of some value, since it forms at very small sizes. Posteriorly, the arches become more elongated in a dorso-ventral direction, forming spines at their distal points (Figures 3 to 6). The vertebral position of the first closed haemal arch separates the species of the genus *Thunnus* into two groups. In *T. thynnus* and *T. alalunga* the first arch occurs on the 10th vertebra; in *T. atlanticus* and *Thunnus* spp. it occurs on the 11th. The variability of this character ranges from 1% to 12% for the various species. *Thunnus alalunga* is the most conservative for this character, and *T. thynnus* is the most variable.

TABLE 2.—Precaudal and caudal arrangement of the vertebrae and total vertebral number in juveniles of *Thunnus*.

Item	<i>T. thynnus</i>	<i>T. alalunga</i>	<i>T. atlanticus</i>	<i>Thunnus</i> spp.
Total variability from mode (%)	5.1	3.4	1.9	14.6
Precaudal, caudal, and total number of vertebrae				
16 + 22 = 38	1			
18 + 20 = 38		2		
19 + 19 = 38			1	
17 + 22 = 39	1			5
18 + 21 = 39	149	114	1	35
19 + 20 = 39	2	4	105	
18 + 22 = 40	1			
19 + 21 = 40	1			1

First Ventrally Directed Haemal Postzygapophysis
(Figures 3 to 7; Tables 3, 13)

The haemal postzygapophyses begin to develop a little later than the parapophyses. In 12- to 15-mm-SL fish, they first appear as tiny bony projections on the ventral posterior edge of the centrum. They develop anteriorly and posteriorly from the center of the vertebral column. At about 13 to 16 mm SL, the position of the first haemal postzygapophysis becomes a diagnostic character. A 100× magnification should be used in the

smaller specimens. The species of *Thunnus* can be separated into two groups by the vertebral position of the first haemal postzygapophyses. *Thunnus thynnus* and *Thunnus* spp. have the first haemal postzygapophyses most often on the 7th vertebra; *T. alalunga* and *T. atlanticus* on the 8th. *Thunnus thynnus*, *T. atlanticus*, and *Thunnus* spp. develop the haemal postzygapophyses on their respective diagnostic vertebrae at about 13 to 14 mm SL; *T. alalunga* develops them at about 15 to 16 mm SL.

I examined seven prepared skeletons from young adults for all species from 400 to 700 mm SL and found that the position of the first ventrally directed haemal postzygapophyses was one vertebra posterior to those of juveniles. I attribute this difference between juveniles and adults to the lateral movement of the structures during growth and also to differential growth between the centrum and the haemal postzygapophyses. The elongate haemal postzygapophyses that characterize the adult *T. atlanticus*, i.e., the longest haemal postzygapophysis is equal to or longer than the centrum (Gibbs and Collette, 1967), develop only gradually in juveniles of that species, and no specimens below 80 mm SL can be separated on the basis of this character. The same is true for adult *T. albacares*, which approach the condition of *T. atlanticus*. I was unable to follow this through on juveniles in the *Thunnus* spp. complex because I lacked specimens in the larger sizes. All my *Thunnus* spp. specimens had haemal postzygapophyses no larger than those of all the other species in their comparable size groups.

Haemal Prezygapophyses (Figures 3 to 7; Table 3)

The haemal prezygapophyses develop almost at the same time as the haemal postzygapophyses, but later than the parapophyses. They first show up as minute bony projections on the two anterior parts of the haemal arches near the centra in about 10- to 13-mm-SL fish. Development, in order of appearance, proceeds from the anterior to the posterior vertebrae and varies slightly with species and size. Young *T. atlanticus* develop them at 10 mm SL, the remaining species between 12 and 13 mm SL. High magnification (100×) should be used on specimens that just develop this structure. Most specimens of *T. thynnus* and *T. alalunga* have their first haemal prezygapophyses under the 15th or 16th vertebra, *T. atlanticus* under the 16th and 17th, and *Thunnus* spp. under the 14th. There is however considerable overlap with apparent bimodal tendencies for the various species.

In small juvenile *Thunnus*, all haemal prezygapophyses arise from the haemal arches. Only in specimens larger than 80 mm SL are the haemal prezygapophyses on the centra and then only posterior from about the 30th vertebra. In adult *Thunnus* the haemal prezygapophyses arise from the centra posterior from about the 25th vertebra (Gibbs and Collette, 1967).

The position of the anterior haemal prezygapophyses on the haemal arches or centra varies for the species of the adults of *Thunnus*. Adult *T. alalunga* have their more anterior haemal

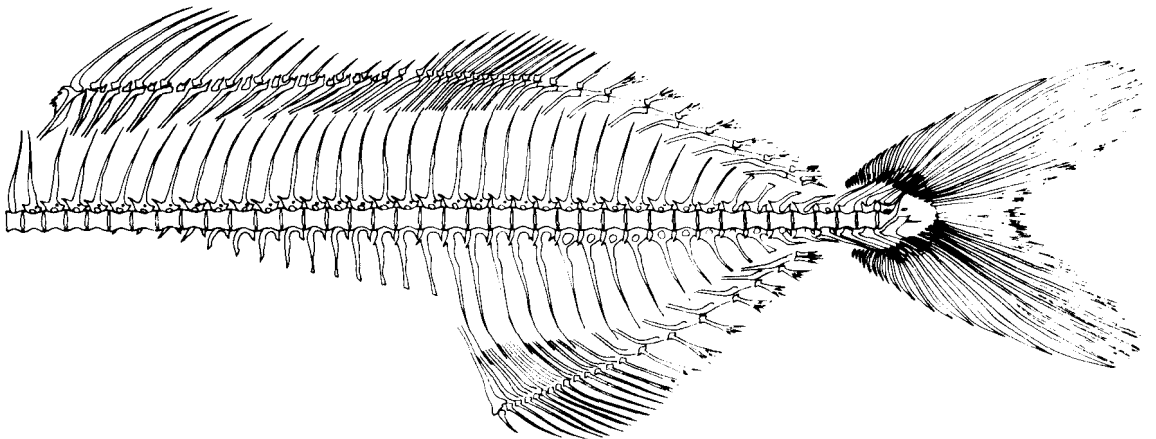


FIGURE 5.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus atlanticus*, 23 mm SL.

TABLE 3.—Vertebral position of the first closed haemal arch, first ventrally directed postzygapophysis, first haemal prezygapophysis, and first ventrolateral foramen for juveniles of *Thunnus*.

Species	Vertebra																	Modal variation %	Size range mm SL						
	6	7	8	9	10	11	12	13	14	15	16	17	18	20	21	22	23			24	25	26	27		
	Position of first closed haemal arch																								
<i>T. thynnus</i>				1	137	18																12	8-117	156	
<i>T. alalunga</i>				1	115																	1	9-91	116	
<i>T. atlanticus</i>					2	101	4															6	8-87	107	
<i>Thunnus</i> spp.					2	38	1															7	8-47	41	
	Position of first ventrally directed haemal postzygapophysis																								
<i>T. thynnus</i>	2	153	2																			3	13-117	157	
<i>T. alalunga</i>		3	97	4																		7	15-91	104	
<i>T. atlanticus</i>			86																			0	13-87	86	
<i>Thunnus</i> spp.	3	28																				10	14-47	31	
	Position of first haemal prezygapophysis																								
<i>T. thynnus</i>							2	2	16	81	49	6												13-117	156
<i>T. alalunga</i>								1	15	55	32	9	1											12-91	113
<i>T. atlanticus</i>								1	4	7	46	32	5											10-87	95
<i>Thunnus</i> spp.								8	14	7	2													13-47	31
	Position of first ventrolateral foramen																								
<i>T. thynnus</i>															1	12	16	20	18	6	2			25-117	75
<i>T. alalunga</i>																	3	13	5	3	1			25-91	25
<i>T. atlanticus</i>																		14	9	—	1			25-87	42
<i>Thunnus</i> spp.															1	3	4							27-47	8

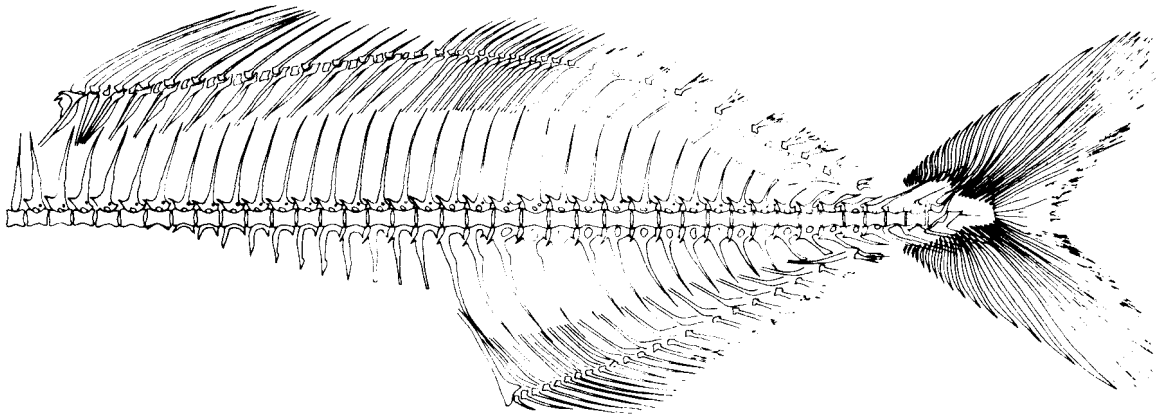


FIGURE 6.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus* spp., 31 mm SL.

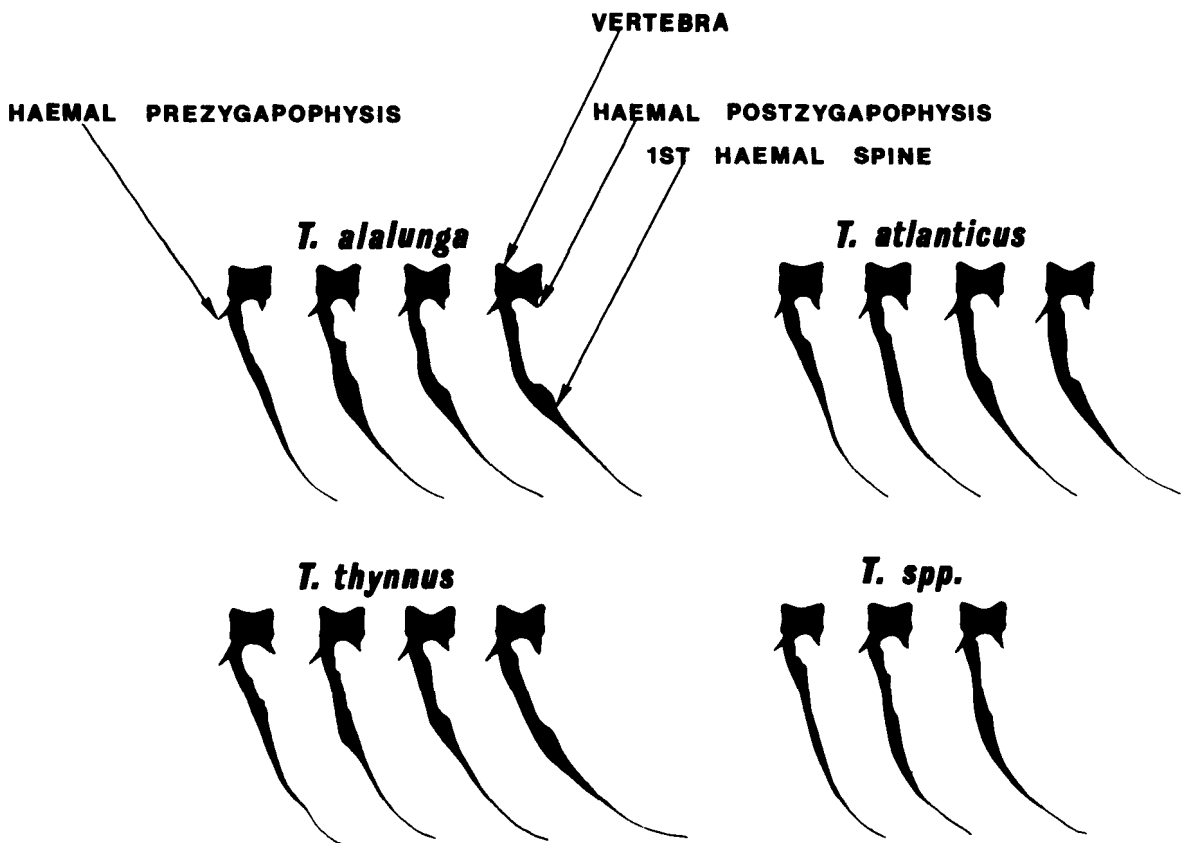


FIGURE 7.—Shape of the first haemal spine for juveniles of the *Thunnus* species. From left to right: *T. alalunga* 17, 34, 61, 91 mm SL; *T. atlanticus* 18, 34, 64, 85 mm SL; *T. thynnus* 17, 33, 65, 100 mm SL; *Thunnus* spp. 16, 33, 47 mm SL.

prezygapophyses on the centra, *T. thynnus* and *T. obesus* have them near the centra but on the haemal arches, and *T. albacares* and *T. atlanticus* have them well ventrad of the centra on the haemal arches (Gibbs and Collette, 1967). In juveniles below 50 mm SL, this specific difference for the adults is not apparent because the more anterior haemal prezygapophyses arise at about the same position on the anterior parts of the haemal arches for all species. In specimens larger than 50 mm SL, the differences between the species can be gradually perceived with increased size.

In my collection not even the largest juvenile *T. alalunga* (91 mm SL) had its anterior haemal prezygapophyses on the centra; instead, they were close to the centra on the haemal arches as in *T. thynnus*. The largest juvenile *T. atlanticus* (87 mm SL) had the anterior haemal prezygapophyses well ventrad on the haemal arches. Consequently, large juveniles of *T. alalunga* and *T. thynnus* cannot be separated by the position of their anterior haemal prezygapophyses, but large juvenile *T. atlanticus* can be separated from *T. alalunga* and *T. thynnus* because the shift of the more anterior haemal prezygapophyses to ventrad is accomplished at a smaller size in *T. atlanticus* than the shift dorsad to the edge of the centra in *T. alalunga*. Lack of larger *Thunnus* spp. specimens prevents their separation by this character. I am certain that large juveniles (>100 mm SL) of the *Thunnus* spp. complex could be separated to the species on the basis of the position of the anterior haemal prezygapophyses since differences have been observed on adult *T. albacares* and *T. obesus* as mentioned above.

Ventrolateral Foramina (Figures 3 to 6; Table 3)

The ventrolateral foramina are the last gross anatomical feature to develop on the vertebral column. They begin to form as projecting bony bridges from the anterior edges of the haemal postzygapophyses to the posterior edges of the haemal arches in specimens from 19 to 22 mm SL. On rare occasions 17-mm-SL fish may show beginning development of the structure. The very first developing ventrolateral foramen can be located beneath any vertebra from the 27th to 30th, but it is most often found beneath the 28th. During growth, new structures are added beneath

the centra, anterior and posterior to the first foramen. All of the ventrolateral foramina are developed at about 25 mm SL, generally from the 22nd to the 36th vertebra. There is considerable overlap for all the species with some modal separation for specimens greater than 25 mm SL in the vertebral position of the first ventrolateral foramen. The ventrolateral foramina can be found posteriorly to the 36th vertebra on all 25- to 35-mm-SL specimens of all species. After 35 mm SL, some posterior openings are gradually filled in by ossification. Juvenile *T. thynnus* from 71 to 117 mm SL had the last ventrolateral foramen on the 32nd and 33rd vertebra, *T. alalunga* from 54 to 91 mm SL on the 31st, and *T. atlanticus* from 52 to 87 mm SL on the 29th or 30th. My largest *Thunnus* spp. specimen (47 mm SL) had the last ventrolateral foramen on the 34th vertebra. In adult *Thunnus* the last foramen is found on the 29th to 30th vertebra according to my own examination of seven skeletons of adults (400 to 700 mm SL). Gibbs and Collette (1967) found it on the 29th to 33rd vertebra.

All species of *Thunnus* have initially circular or nearly circular shaped openings, which gradually decrease in diameter posteriorly. Juveniles larger than 60 mm SL lose the circular shape on the anteriormost foramina, acquiring a more triangular or oval shape. Specific differences in the size and shape of the anterior openings are not distinct for juveniles as they are for adults (Gibbs and Collette, 1967).

First Haemal Spine (Figure 7)

The first haemal spine is located on the haemal arch of the first caudal vertebra. It is a considerably elongated process. Anterior to this process, in close proximity, are the first two anal pterygiophores (Figures 3 to 6). The preceding haemal processes on the haemal arches of the precaudal vertebrae are shorter than the first haemal spine and also have at their tips flattened parapophyses for rib articulation. Yabe et al. (1958), Matsumoto (1963), and Yoshida (1965) reported on the flattening of the first haemal spine in *T. alalunga* and stated that this character may be unique to the species. I believe that this is true for the adults but not for the juveniles because in all *Thunnus* species the first haemal spine goes through a variety of flattened shapes during

its ontogeny. In addition, there is great individual variability in the shape of the first haemal spine within each species. Nevertheless, *T. alalunga* exhibits the greatest flattening of the first haemal spine during its ontogeny and *Thunnus* spp. the least. *Thunnus thynnus* and *T. atlanticus* generally show less flattening than *T. alalunga* but more than *Thunnus* spp.

In *T. alalunga* the first haemal spine begins to flatten a little at 21 mm SL. Flattening continues to increase to about 35 mm SL. From this size on changes in shape occur, but the degree of flattening remains essentially the same. *Thunnus atlanticus* does not show any flattening before 60 mm SL and *T. thynnus* not before 30 mm SL. *Thunnus* spp. showed slight flattening at 47 mm SL.

As the shape of the first haemal spine is a character of degree and cannot be accurately assessed, I suggest that only persons familiar with the Atlantic species of *Thunnus* juveniles in all sizes use this character.

FINS AND FIN SUPPORTS

First Dorsal Fin (Table 4)

All species develop the full complement of spines in the first dorsal fin before 8 mm SL. Fourteen spines were regularly counted in the first dorsal, even in the smallest specimens (8 mm SL). The count of 14 spines is remarkably constant for juveniles with a variability of 0% to 3% for the various species. This remarkably constant count of 14 can serve as a generic character to separate juveniles of the genus *Thunnus* from other scombrid genera in the Atlantic Ocean such as *Euthynnus* (15-16), *Katsuwonus* (15-16), and *Auxis* (10-12) (Potthoff and Richards, 1970); *Scomberomorus* (15-19) (W. J. Richards, pers. comm.)³; *Scomber* (9-13) (Matsui, 1967); *Acanthocybium* (24-26) (Rivas, 1951); *Sarda* (20-22); and *Orcynopsis* (13) (Collette and Chao, 1973).⁴ There is conflict between the consistency of first dorsal fin counts in juveniles and greater variation of counts in adults (Frade, 1931; Rivas, 1951;

³Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

⁴Collette, B. B., and L. N. Chao. 1973. Systematics and anatomy of the bonitos (*Sarda* and their relatives). Unpublished manuscript.

TABLE 4.—Variability of spine and ray counts of the dorsal and anal fins in the various species for juveniles of *Thunnus*.

Species	Spines, first dorsal fin				Number of specimens	Variability from mode %
	13	14	15	16		
<i>T. thynnus</i>	1	144	1	1	147	2
<i>T. alalunga</i>	—	112	1	—	113	1
<i>T. atlanticus</i>	2	97	1	—	100	3
<i>Thunnus</i> spp.	—	37	—	—	37	0

Species	Rays, second dorsal fin and finlets			Number of specimens	Variability from mode %
	22	23	24		
<i>T. thynnus</i>	4	134	4	142	6
<i>T. alalunga</i>	—	104	4	108	4
<i>T. atlanticus</i>	4	89	1	94	5
<i>Thunnus</i> spp.	—	30	—	30	0

Species	Rays, anal fin and finlets					Number of specimens	Variability from mode %
	20	21	22	23	24		
<i>T. thynnus</i>	—	5	127	6	2	140	9
<i>T. alalunga</i>	—	2	101	5	—	108	6
<i>T. atlanticus</i>	1	85	6	—	—	92	8
<i>Thunnus</i> spp.	—	1	28	1	—	30	7

Bullis and Mather, 1956; Gibbs and Collette, 1967). In some adults the posteriormost spines become embedded in the dorsal groove and surrounding tissue and are consequently overlooked.

The first dorsal fin can be easily separated from the second dorsal fin because the last spine of the first dorsal is always shorter than the first element in the second dorsal (Figures 3 to 6), and the spacing between spines of the first dorsal fin is greater than that between rays of the second dorsal. The space between the last spine of the first dorsal and the first element of the second dorsal is wider than the following spaces between the rays of the second dorsal. This difference in spacing is due to the shape, structure, and spacing of pterygiophores, which support the visible elements of the fins.

Second Dorsal Fin and Finlets (Table 4)

Eight-mm SL larvae of all species have already acquired the full complement of rays in the second dorsal fin, but lack two or three of the posteriormost finlets. By 11 to 13 mm SL all finlets are developed. *Thunnus atlanticus* develops its second dorsal rays and finlets to a full complement at a slightly smaller size, usually by 10

to 12 mm SL. A total count of 23 rays was obtained most of the time for the second dorsal fin and finlets of all the species (Frade, 1931; Bullis and Mather, 1956; Gibbs and Collette, 1967). Although the variability was greater than that for the first spinous dorsal fin, it did not exceed 6% in the second dorsal fin. I included the dorsal finlet counts with ray counts of the second dorsal fin because in larvae and juveniles of *Thunnus*, and perhaps with all other scombrid genera, it is impossible to determine precisely the break between the last posterior second dorsal fin soft-ray and the first anterior dorsal finlet even in cleared and stained specimens. Figures 3 to 6 show this gradual intergradation from soft-rays to finlets. The last ray of the second dorsal fin can be separated from the first finlet by their pterygiophore structure in specimens larger than 50 mm SL. Finlet pterygiophores have two clearly visible bony parts from a lateral view and second dorsal fin pterygiophores have only one clearly visible part. Figures 3 to 6 show specimens that have not yet developed the two clearly visible parts in their finlet pterygiophores.

Anal Fin and Finlets (Tables 4, 13)

The anal fin develops similarly to the second dorsal fin. At 8 mm SL, all rays in the anal fin are present with three or four of the posteriormost finlets lacking. By 11 to 12 mm SL all finlets are developed. *Thunnus atlanticus* typically has 21 anal elements (rays plus finlets), and the remainder of the species have 22 (Frade, 1931; Bullis and Mather, 1956; Gibbs and Collette, 1967). Variability for this character ranges from 6% to 9%. The counts of the anal finlets were included in the anal ray counts for the same reasons given previously for the second soft dorsal fin.

Pectoral Fins (Table 5)

Development of rays in the pectoral finfold had already started in my smallest (8 mm SL) specimens. The increase in number of pectoral rays and their sequence of development was similar for all the species. Wide ranges in number of pectoral fin rays were common for equal size groups. These

wide ranges narrow in the 25 to 29 mm SL size groups where adult counts of more than 30 rays are attained (Frade, 1931; Bullis and Mather, 1956; Gibbs and Collette, 1967). The rays in the pectoral fins were counted on both sides for each specimen. The side that yielded the highest value was taken for tabulation. In 34% of all specimens counted there was no difference in counts between the two pectoral fins; in 47% of the specimens, a difference of one ray was noted; 11% of the specimens had a difference of two rays; 6% had a three ray difference; and 2% differed by four rays. Only one specimen differed by five rays. At 8 mm SL, 8 to 12 rays were developed on the dorsal side of the finfold. Development of rays proceeded progressively ventrad until the finfold was completely occupied with rays. At 20 mm SL, very few juveniles have the adult count of more than 30 rays. At 23 mm SL, about one-half of the specimens have adult counts, and at 27 mm SL all have adult counts. Adults and all juveniles >27 mm SL have more than 30 pectoral fin rays, usually 31 to 34, sometimes 35, rarely 36 or 37. My data are corroborated by Schaefer and Marr (1948) and Mead (1951).

Pelvic Fins

All the fin elements of the pelvic fins were visible in my smallest (8 mm SL) specimens of *Thunnus*. A count of six fin elements was obtained for each fin throughout the size range sampled. I could not be certain if the first element was a spine but all have 1,5 as adults.

TABLE 5.—Range of variation in pectoral fin ray counts for selected sizes in juveniles of *Thunnus* of all the species combined.

Size mm SL	Range of variation, Number of pectoral fin rays	Most frequent number of pectoral fin rays
8	8-12	—
9	10-19	10,14
10	9-24	—
11	13-23	18
12	16-20	17
13	15-24	18,19,21
14	18-25	23
19	26-31	27,28
20	26-32	27,29
21	28-31	29,30
22	28-31	29,30
23	28-33	29,31,32
24	29-35	31
25	29-34	31,32
26	29-33	32
27	31-34	31,32
28	32-33	32

Caudal Fin (Table 6)

At 8 mm SL, a total of 27 to 31 rays is developed on the caudal fin. If the total was an even number then an equal number of rays was found dorsad and ventrad to the midline. If it was an uneven number then the dorsal side of the caudal fin always carried one more ray. As the larvae grow, additional procurrent rays are added equally on the caudal fin to the dorsal and ventral side. The last rays to develop are the anteriormost. There is a difference in caudal ray development between *T. thynnus* and the other species. *Thunnus thynnus* usually has fewer caudal rays than the other species at all sizes, particularly from 14 to 22 mm SL. At 17 mm SL, few *T. thynnus* have the maximum caudal counts of more than 48 rays. At 23 mm SL, about one-half of the *T. thynnus* specimens had maximum counts and only after about 35 mm SL did all but two specimens have maximum caudal counts. Collectively, the remaining species differ from *T. thynnus* in that, at 15 mm SL, a few specimens had already acquired the maximum complement of caudal rays. At 18 mm SL, one-half of the specimens had maximum counts, and all but one specimen had the maximum counts at 24 mm SL. I noted three exceptions to the above statements: one 34-mm-SL *T. atlanticus* had 48

rays and two *T. thynnus* had 47 and 44 rays at 40 and 50 mm SL, respectively. From my data I believe that all *Thunnus* juveniles >24 mm SL have a maximum of more than 48 caudal rays, usually 49 to 51, rarely 52. I also believe the maximum juvenile counts represent the adult complement of caudal rays, although I did not examine any adult fish. Frade (1931) found 46 caudal rays as the most frequent number for adult *T. thynnus*. The difference is likely due to difficulty in counting the anteriormost rays on adults. For this study, I did not attempt a detailed examination of the principal caudal rays or of the hypural complex. A study of the ontogeny of the caudal skeleton in *T. atlanticus* will be published in the future.

Dorsal and Anal Fin Supports (Figures 8 to 10; Tables 7, 13)

The spines, rays, and finlets of the dorsal and anal fins are supported within the body by pterygiophores. The pterygiophores are made up of two or three bony parts referred to as radials. Spines and rays have a proximal and a distal radial; finlets have an additional middle radial. The distal radials of the posterior rays of the second dorsal fin and finlets and of the anal fin and finlets cannot be seen from a lateral view because they are hidden by the bifurcate bases of

TABLE 6.—Range of variation in total caudal fin ray counts for selected sizes and species groups of juveniles of *Thunnus*.

Size mm SL	Range of variation, number of total caudal fin rays		Most frequent number of total caudal fin rays	
	<i>T. alalunga</i> , <i>T. atlanticus</i> , <i>Thunnus</i> spp.	<i>T. thynnus</i>	<i>T. alalunga</i> , <i>T. atlanticus</i> , <i>Thunnus</i> spp.	<i>T. thynnus</i>
8	27-31	—	—	—
9	32-40	—	33,37	—
10	34-43	—	—	—
11	39-46	—	—	—
12	41-43	—	—	—
13	42-45	—	45	—
14	45-47	41	45	—
15	44-49	43	47	—
16	45-49	46-47	46,47,48	47
17	46-49	45-49	47,48,49	47
18	47-50	47	48,49	47
19	48-51	46-49	49	47
20	47-51	47-48	49	47
21	47-51	47-49	49,50	47,48
22	49-51	47-49	49	47
23	47-51	48-50	50	49
24	48-51	47-49	50,51	49
25	49-51	47-50	51	49
26	50-52	49-51	50	50
27	48-50	48-49	50	49

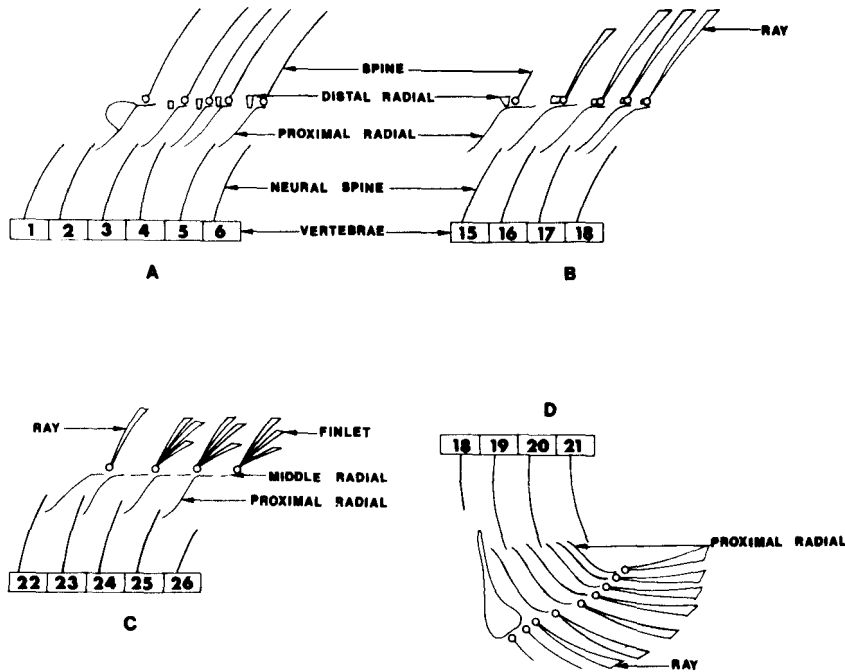


FIGURE 8.—Schematic representation of the relationship between vertebrae, pterygiophores, and fin elements in juveniles of *Thunnus* (lateral view). A. Anterior portion of first dorsal fin, pterygiophores, and vertebrae; B. Last spine of first dorsal fin, anterior portion of second dorsal fin, pterygiophores, and vertebrae; C. Last ray of second dorsal fin, anterior finlets, pterygiophores, and vertebrae; D. Anterior portion of anal fin, pterygiophores, and vertebrae.

the fin elements. Generally, all species of *Thunnus* have 37 dorsal fin elements (XIV-15-8) but only 36 pterygiophores; the first pterygiophore supports the first two spines. In actuality, the first pterygiophore is serially associated with the second spine but has captured and fused to it the distal radial of the first spine (Figure 8A). The proximal radial of the first spine has been lost. The first spine is therefore only secondarily associated with the first pterygiophore. Posteriorly, each fin element is serially associated with a pterygiophore, but each fin element also rests atop the adjacent posterior pterygiophore in a secondary association (Figure 8). Thus, two pterygiophore fin element associations exist. The serial association is most often overlooked. The last fin element (finlet) in the dorsal fin assembly is serially associated with its pterygiophore. It also rests in a secondary association on a very small bone, which I assume to be a reduced proximal radial of a lost finlet without its serial middle and distal radials. The distal radials of the spinous dorsal that, to me, resemble the horns

of a moose (Kramer (1960) uses the term "alate"), form in part and rigidly support the dorsal groove and become smaller in size in a posterior direction. The distal radials are still present in the second dorsal fin, although their semblance to moose horns has disappeared ("non-alate"). They decrease in size posteriorly (Figure 8B) until they disappear from the lateral view at about the 9th ray. Dissection of posterior fin rays and finlets revealed the presence of the distal elements between the bifurcate bases of the rays or finlets (Figure 9B, C). Spines, on the other hand, do not have bifurcate bases (Figure 9A). Instead, the distal radials are located anterior to the base of the spine.

The anal fin and finlet pterygiophores are structurally similar to the pterygiophores of the second dorsal fin and finlets with one exception: The first anal pterygiophore in *Thunnus* is derived from two cartilaginous parts which fuse at about 8 mm SL. It has two anal fin elements in serial association and one in secondary (Figure 8D). Thus, all Atlantic species of *Thunnus*,

except *T. atlanticus*, have 22 anal fin elements (15-7) but only 20 pterygiophores. *Thunnus atlanticus* has 21 fin elements (14-7) but only 19 pterygiophores. As in the second dorsal fin, all the anal fin rays and finlets have a bifurcate base that contains a small distal radial (Figure 9B, C). The last anal finlet, as well as the last dorsal finlet, is serially associated with a pterygiophore but has a secondary association with a small bone that I assume to be a greatly reduced proximal radial of a lost finlet.

Pterygiophore development is more or less synchronous with fin spine and ray development. My smallest 8-mm-SL *Thunnus* specimens lacked about two to four posteriormost pterygiophores dorsally and ventrally (see earlier fin sections). At 13 mm SL, all specimens had acquired a full count of pterygiophores. *Thunnus atlanticus* has a full count at the slightly smaller size of 11 to 12 mm SL. In the very small sizes of 8 to 11 mm SL, the pterygiophores cannot be differentiated into proximal, middle, and distal radials. At about 11 mm SL, differentiation first begins under the anteriormost section of the first dorsal fin. A few of the distal radials begin to separate from the main mass of the pterygiophores in tiny nonalate blocks. The separation and development sequence is in a posterior direction. At 20 to 35 mm SL, all the distal radials are separated under the first dorsal fin, are well ossified, and gradually assume an alate shape.

The middle radials under the finlets (usually eight dorsal and seven ventral) begin to separate and ossify over a great size range. Some specimens showed no separation at 30 mm SL, whereas others showed some separation and ossification as small as 22 mm SL. The middle radials of the finlet pterygiophores separate and develop in an anterior direction. First to develop are the posterior middle radials of the last finlets. Most specimens had all their ventral middle radials developed by 40 mm SL, but a few still lacked the first (e.g., anteriormost) dorsal middle radial. By 60 mm SL, all specimens had their eight dorsal middle radials developed.

In juvenile *Thunnus* it is difficult to determine, externally, the exact number of finlets because of the gradual intergradation from fin ray to finlet. A finlet can now be precisely defined as having a middle radial serially associated with it. I think that at 50 mm SL one can, with some certainty, count middle radials to determine finlet number. Caution is warranted, however, because a few

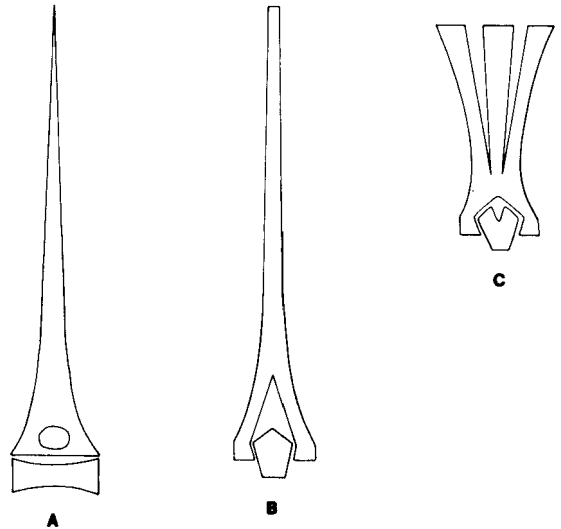


FIGURE 9.—Schematic representation of the relationship between fin elements and distal radials (anterior view) in juveniles of *Thunnus*. A. First dorsal fin spine and distal radial near base; B. Second dorsal fin ray and distal radial within bifurcate base; C. Finlet and distal radial within bifurcate base.

specimens may still lack the first (e.g., anteriormost) dorsal middle radial. Table 7 has been compiled from my specimens above 40 mm SL. There was not enough material available in the larger sizes to assess variability and specific differences in the number of middle finlet radials. The most common combination of middle dorsal and ventral radials is 8/7. Variability from this combination seems to be low in *T. atlanticus* and *T. alalunga* and high in *T. thynnus*.

Most of the interneural and interhaemal spaces bounded by the neural and haemal spines are occupied by one or more pterygiophores in *Thunnus* (Figures 3 to 6). The association of pterygiophores with the interneural and interhaemal spaces is limited to smaller juveniles. By 100 mm SL, the anteriormost pterygiophores under the first dorsal fin are already situated above the neural spines and do not insert into any interneural spaces. As the juveniles grow, more pterygiophores lose their association with their respective interneural spaces. I did not examine specimens larger than 117 mm SL and cannot say if all pterygiophores, dorsally and ventrally, pull away by the time the fish become adults. For the identification of juveniles, however, the serially associated pterygiophores of the second dorsal fin can be used successfully in

TABLE 7.—Number of dorsal and ventral middle radials of the finlets in three species of juveniles of *Thunnus* (41-117 mm SL).

Species	Middle radials					n	
	Dorsal Ventral	7 7	8 7	9 7	8 8		9 8
<i>T. atlanticus</i>		1	14	—	1	—	16
<i>T. alalunga</i>		2	5	—	—	—	7
<i>T. thynnus</i>		—	9	2	6	2	19

separating *T. thynnus* from *T. alalunga* and *T. alalunga* from the *Thunnus* spp. complex. All of my *T. alalunga* specimens (n = 116) had their first three second dorsal interneural spaces occupied with only one pterygiophore (Figure 10, Table 13). The following five spaces were filled with two and one with three pterygiophores, and the last posteriormost second dorsal interneural space again had only one pterygiophore. This pattern of pterygiophore insertions under the second dorsal fin is most characteristic of *T. alalunga*, but may occur in the other species to a lesser degree. Figure 10 and Table 13 also show the percentages of occurrence for the second dorsal pterygiophore insertion sequences which are most characteristic for that species. Ninety-five percent of my 148 *T. thynnus* specimens had their first two second dorsal interneural spaces occupied with only one pterygiophore. The following five spaces were filled with two and one with three pterygiophores, and the last two posteriormost second dorsal interneural spaces had only one pterygiophore. The remaining 5% of my *T. thynnus* specimens had the identical *T. alalunga*

second dorsal pterygiophore insertion sequence. Ninety-eight percent of my 41 *Thunnus* spp. specimens resembled *T. thynnus* and 2% *T. alalunga*. *Thunnus atlanticus* was the most variable in the second dorsal pterygiophore insertion sequence; 46% of my 92 specimens resembled *T. alalunga*, 19% resembled *T. thynnus*, and 35% had six interneural spaces occupied with two pterygiophores but did not have a space with three pterygiophores (Table 13).

Counting from anterior, the first 12 occupied interneural spaces associate in *Thunnus* with the first dorsal fin. The diagnostic second dorsal interneural spaces are the 13th through the 21st. Following, in the 22nd to 30th spaces are the finlet pterygiophores (Figure 10). The interneural spaces occupied by three or zero pterygiophores for the second dorsal fin and finlets are depicted in Figure 10 on the basis of where they most often occurred, but they could vary as much as two spaces in an anterior or posterior direction. The percentages in Figure 10 refer only to the arrangement under the second dorsal fin.

The distribution of pterygiophores under the anal fin (Figure 10, Table 13) present too much variability to be useful for species separation, except perhaps in *Thunnus* spp. and *T. atlanticus*. The first five anteriormost interhaemal spaces are occupied by two or three pterygiophores in *T. thynnus* and *T. alalunga*. The 6th and 7th spaces, which complete the anal fin association, always have only one pterygiophore. The anal finlet pterygiophores insert into the 8th to 14th spaces, one to a space. The last or 14th interhaemal space that is occupied by the last or

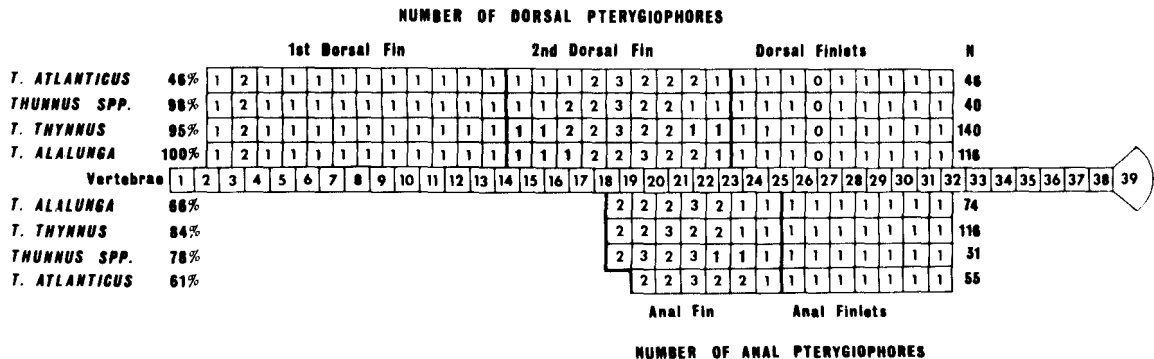


FIGURE 10.—Representative arrangement of pterygiophores in relation to the fins and vertebrae for the juvenile *Thunnus* species. Percentages and number of specimens (N) are for the occurrence of the commonest arrangement under the second dorsal fin only; other arrangements given in Table 12. Modified after Matsui (1967).

posteriormost pterygiophore is directly opposite the last or 30th interneural space that is occupied by the pterygiophore of the last dorsal finlet. *Thunnus* spp. and *T. atlanticus* deviate from this pattern. In 78% of my 40 *Thunnus* spp. specimens, only the first four interhaemal spaces were occupied by more than one pterygiophore, the 5th through 7th spaces had only one. *Thunnus atlanticus* differed by having only six interhaemal spaces available for the anal fin. Thus, 61% of a total of 89 fish had their first five spaces occupied with more than one pterygiophore and the 6th space with one.

BONES AND RAKERS OF THE FIRST GILL ARCH (Figures 11, 12)

In *Thunnus* the gillrakers develop within the epithelium that overlies the three bones of the first gill arch and their connective cartilage. In its first stage of development, the raker can be observed on cleared and stained preparations, under 100× power, as a tiny speck of weakly stained material within the translucent epithelium. As the speck grows it gradually assumes the triangular shape of a raker. The tip of the raker will finally break through the epithelium, and its broad base remain anchored in the tissue close to the bone. Ankylosed rakers were not observed on the bones of the first gill arch, even in the larger specimens. As the epithelium is opaque in preserved specimens, gillraker counts

for smaller juveniles should be made only on cleared and stained material for accuracy. Mead (1951) noted that no gillrakers could be seen in fish smaller than 15 mm. I believe that he referred to untreated specimens, because in my collection all species of *Thunnus* had six or seven rakers at their smallest size (8 mm SL).

The ceratobranchial bone of all species has six to seven rakers at 8 mm SL. Development and acquisition of rakers over the ceratobranchial proceeds distally from the angle towards the hypobranchial bone. The raker in the angle is always included in the ceratobranchial count. It develops at about 8 mm SL.

At 14 mm SL some specimens of all the species develop a raker on the epibranchial bone next to the angle. One exception was noted: an 11-mm-SL *T. atlanticus* with one raker on the epibranchial. Additional rakers over the epibranchial bone develop distally from the angle.

The last bone of the gill arch to acquire rakers is the hypobranchial. The size of the juveniles when this occurs depends on the size at which the ceratobranchial becomes entirely occupied with rakers. In the hypobranchial count I have included the rakers (usually one, sometimes two) found over the cerato-hypobranchial cartilage.

The first rakers to appear are usually located over the cartilage but are considered hypobranchial rakers. Occasionally rakers appear over the hypobranchial bone leaving the cartilage empty. *Thunnus atlanticus* has the lowest adult gillraker counts and completes its entire cerato-branchial complement at the smallest size (9-15

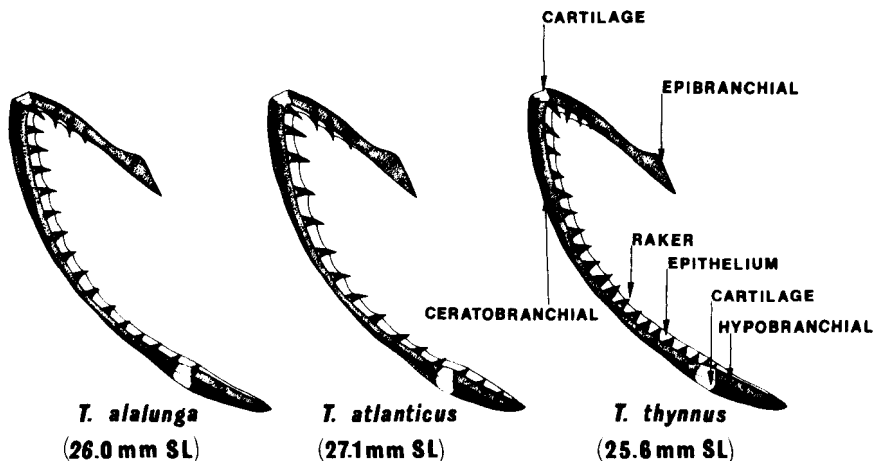


FIGURE 11.—First right gill arches of juveniles of three *Thunnus* species.

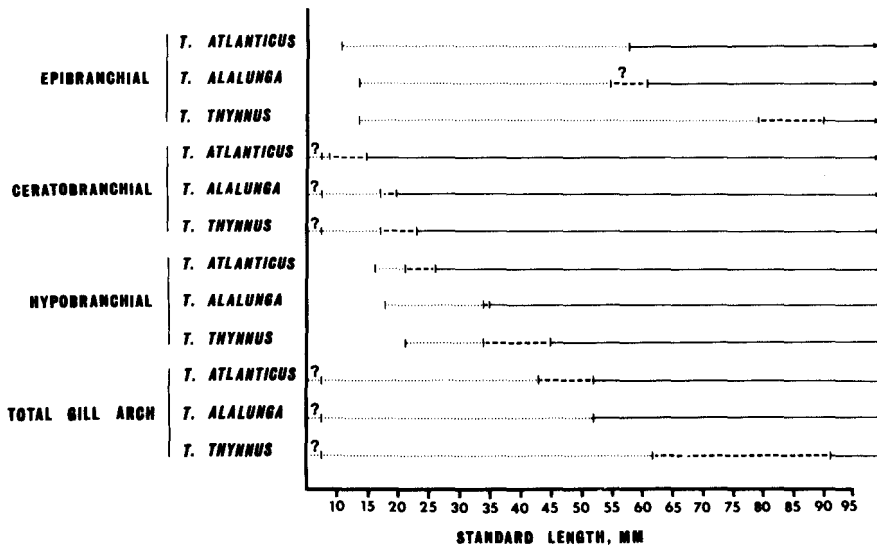


FIGURE 12.—Representative scheme of gillraker development with increase in size over the three bones of the first gill arch for juveniles of three *Thunnus* species. Dotted line: developmental stage, one or more rakers present; dashed line: adult gillraker complement present in some specimens; solid line: adult gillraker complement present in all specimens; question mark: assumed, no data available.

mm SL) of the Atlantic species. Therefore, some juvenile *T. atlanticus* have their first raker over the hypobranchial at 16 mm SL, and all have at least one raker over the hypobranchial at 20 mm SL. Some *T. alalunga* and *Thunnus* spp. juveniles have their first raker over the hypobranchial at 18 mm SL, and all have at least one raker over the hypobranchial at 22 mm SL. *Thunnus thynnus* has the highest adult gillraker counts and adds its first rakers to the hypobranchial at the largest size of all the species; they begin to appear on some of the 21-mm-SL specimens from the western Atlantic and on some of the 23-mm-SL specimens from the Mediterranean. Not until 28 mm SL do all *T. thynnus* have at least one raker over the hypobranchial.

Summarizing the data from Tables 8 to 11, one can conclude that:

1. The species differ in size at which they attain the maximum gill raker counts on each bone of the first gill arch.
2. Each species differs from the others in maximum number of rakers that it can have on some or all of the three bones of the first gill arch.
3. All species of *Thunnus* first attain the maximum complement of rakers over the ceratobranchial bone.
4. The range of the maximum number of rakers

over the ceratobranchial bone shows the greatest interspecific difference.

Thunnus atlanticus (Table 8; Figures 11, 12). The maximum gillraker count over the epibranchial bone of 7 to 9 rakers was first present in specimens of 58 mm SL. The diagnostic maximum count of 11 to 13 rakers over the ceratobranchial bone was first present in a 9-mm-SL specimen, but it was not until 15 mm SL that all specimens had the diagnostic count. Maximum counts over the hypobranchial bone (including the cerato-hypobranchial cartilage) of 4 to 6 rakers were first observed on 21-mm-SL specimens, but not before 26 mm SL did all juveniles attain the maximum count. The maximum total count for the first gill arch of 23 to 27 rakers was first observed in a 43-mm-SL specimen and all specimens larger than 52 mm SL had maximum total counts. The maximum total count is attained in some specimens at a smaller size than the maximum epibranchial count. This discrepancy is explained by the range in number of rakers over the ceratobranchial and hypobranchial bone. Gibbs and Collette (1967) give 19 to 25 rakers as the total number over the first arch for *T. atlanticus*. Because all specimens larger than 34 mm SL had more than 20 gillrakers, I believe that

TABLE 8.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus atlanticus* juveniles. *n* = 104.

(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

N	SL (mm)	Epibranchial									Ceratobranchial							Hypobranchial							
		0	1	2	3	4	5	6	7	8	9	6	7	8	9	10	11	12	13	0	1	2	3	4	5
7	5-9	7										1	—	4	1	—	—	1		7					
14	10-14	12	2											3	1	2	5	3		14					
19	15-19		8	8	3												4	15		4	6	7	2		
23	20-24			6	16	1											2	20	1			6	9	8	
10	25-29			1	7	2											2	8				1	8	1	
12	30-34				3	8	1										1	10	1				8	4	
1	35-39						1											1					1		
6	40-44				2	2	1	1									6					1	—	5	
2	50-54							2									2							2	
2	55-59									2						1	—	1						1	1
2	60-64									2							1	1						1	1
2	65-69										1	—	1				2						1	—	1
1	70-74										1							1						1	
1	80-84											1							1					1	
2	85-89										2						1	1						1	1

		Total gillraker count																														
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27									
7	5-9	1	—	4	1	—	—	1																								
14	10-14				3	1	2	5	1	2																						
19	15-19									3	7	1	6	—	2																	
23	20-24											3	5	9	5	1																
10	25-29													4	4	1	1															
12	30-34														4	3	4	1														
1	35-39															1																
6	40-44																2	3	—	1												
2	50-54																	2														
2	55-59																								1	1						
2	60-64																								1	—	1					
2	65-69																			1	—	—	—	1								
1	70-74																			1												
1	80-84																							1								
2	85-89																								2							
*120	>300																									1	7	29	59	21	2	1

T. atlanticus may actually not fully develop or may lose some rakers during its later life. Potthoff and Richards (1970) already mentioned this possibility.

Thunnus alalunga (Table 9; Figures 11, 12). The maximum gillraker count over the epibranchial bone of 7 to 8 rakers was first obtained in a 61-mm-SL specimen. Most likely, however, maximum counts over the epibranchial would first show in the 55- to 59-mm-SL size range, but the lack of specimens for those sizes precludes a definite statement. Bullis and Mather (1956) counted 7 to 9 rakers on four adult specimens. The diagnostic maximum count of 14 to 16 rakers over the ceratobranchial bone was first present in a few 17-mm-SL specimens. At 20 mm SL, all specimens had the diagnostic maximum count. This count overlaps with the *Thunnus* spp. complex. Maximum counts over

the hypobranchial bone (including the ceratohypobranchial cartilage) of 5 to 6 rakers were first observed on a 34-mm-SL specimen; all specimens larger than 35 mm SL had the maximum count. The maximum total count for the first gill arch of 27 to 29 rakers is attained at 53 mm SL. Gibbs and Collette (1967) give 25 to 31 rakers as the total number over the first gill arch for adult *T. alalunga* from the western Atlantic. Our difference is due to my smaller sample size and population variance.

Thunnus thynnus (Table 10; Figures 11, 12). The maximum total gillraker count over the epibranchial bone of 12 to 13 rakers was first present in one 79-mm-SL specimen. Because I lack data in the larger size ranges, I can only estimate that all *T. thynnus* have a full epibranchial after they have reached 90 mm SL. The diagnostic maximum counts of 17 to 20

rakers over the ceratobranchial bone were first observed in 17-mm-SL specimens from the western Atlantic. It was not until 23 mm SL that all specimens, including the Mediterranean samples, had the diagnostic maximum count. Maximum counts over the hypobranchial bone (including the hypo-ceratobranchial cartilage) of 7 to 9 rakers were first observed on a 34-mm-SL specimen from the western Atlantic, but not before 45 mm SL did all juveniles, including the Mediterranean samples, attain the maximum count. One exception was noted at 71 mm SL with 6 hypobranchial rakers. The maximum total count for the first gill arch of 36 to 41 rakers was first observed in a 62-mm-SL specimen; all juveniles in the 90- to 94-mm-SL size range will probably have the maximum total count. As in *T. atlanticus*, the maximum total gill arch count is reached in some *T. thynnus* specimens at a smaller size than the maximum epibranchial count. This discrepancy

is again explained by the range in number of rakers over the ceratobranchial and hypobranchial bone. Gibbs and Collette (1967) give 34 to 43 rakers as the total number over the first arch for the western Atlantic *T. thynnus thynnus*. Our difference is due to my smaller sample size and population variance.

Thunnus spp. (Table 11). Juvenile *T. albacares* and *T. obesus* could not be separated and were grouped together under *Thunnus* spp. Lack of enough specimens in a proper size range prevented me from making observations on gill-raker ontogeny. There is considerable overlap between the *Thunnus* spp. complex and *T. alalunga* in number of rakers and their development over the three bones of the first arch. The maximum counts of 14 to 16 rakers over the ceratobranchial bone are identical for *Thunnus* spp. and *T. alalunga*. At 15 mm SL, one *Thunnus* spp. specimen had the maximum ceratobranchial count and at 20 mm SL all

TABLE 9.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus alalunga* juveniles. *n* = 118.

(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

N	SL (mm)	Epibranchial								Ceratobranchial										Hypobranchial							
		0	1	2	3	4	5	6	7	8	6	7	8	9	10	11	12	13	14	15	16	0	1	2	3	4	5
3	5-9	3								1	—	—	1	—	1												3
13	10-14	10	3							2	—	—	—	5	2	3	1										13
50	15-19	5	28	11	6											13	8	11	17	1							38
25	20-24		1	6	18													8	16	1							2
11	25-29			1	6	4												2	8	1							2
4	30-34				2	2												2	2								2
5	35-39					1	4											1	3	1							5
1	40-44						1													1							1
1	45-49							1																			1
2	50-54								2										2							2	
1	60-64									1									1							1	
1	80-84										1								1							1	
1	90-94											1							1							1	

Total gillraker count																															
6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31						
				1	—	—	1	—	1																						
					2	5	2			2	2																				
						2	12	7	4		11	4	8	1	1																
											1	2	5	5	8	3	1														
													1	2	4	1	2	1													
															1	—	2	—	1												
																			2	2	1										
																					1										
																						2									
																						1									
																							1								
																								1							
																									1						
55	>700																								1	1	10	20	15	6	2

specimens had it. Therefore, the juveniles of the *Thunnus* spp. complex can only be separated from *T. alalunga* by the vertebral position of the first haemal arch, by the shape of the first haemal spine, by the vertebral position of the first ventral postzygapophysis, and by the pterygiophore pattern of the second dorsal and, perhaps, anal fins. However, caution should be used in applying any separating character because of variability. Percentages for variabilities can be found in the respective tables.

LATERAL LINE SCALES

(Figure 13, Table 12)

All species develop the first lateral line scale at 16 to 18 mm SL. The scale originates near the dorso-posterior edge of the pectoral girdle. It is rectangular in shape, with strong ossifications on the dorsal and ventral sides. These strong ossifications develop into two plates that project vertically to the base of the scale. As growth proceeds, more scales are added posteriorly, forming a distinct broken line, which at first slopes ventrad then dorsad and levels off in a posterior direction. At about 60 mm SL, lateral line scales cannot be counted because the scales fuse to form a continuous line. Fusion of the scales occurs first

on the anterior portion of the lateral line and proceeds posteriorly.

Sella (1924) and Watson and Mather (1961) noted specific differences in the shape of the lateral line. I have examined this character in detail and found that *T. thynnus* can be separated from all the other *Thunnus* species. Eighty-one *T. thynnus* from a total of 159 were undamaged and large enough to show the lateral line contour. In all 81 specimens the first three scales formed a posteriorly descending straight line, whereas the following scales formed a posteriorly ascending line at an angle approximately 90° to the first line. At the 8th or 9th scale the line curved in a posterior direction, parallel to the body axis. At 19 mm SL, some *T. thynnus* can be separated on the basis of the lateral line contour because at this size some have acquired four scales. The 4th scale in *T. thynnus* is always aligned at a 90° angle to the preceding three. At 22 mm SL, all *T. thynnus* have acquired four or more scales and are therefore totally separable from the other species.

In the remaining species a descent and ascent in the lateral line is also present, but it forms a smooth curve instead of a right angle. In all specimens (29 *T. alalunga*, 46 *T. atlanticus*, and 14 *Thunnus* spp.) the last scale to descend

TABLE 11.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus* spp. juveniles. n = 40.
(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

N	SL (mm)	Epibranchial							Ceratobranchial										Hypobranchial															
		0	1	2	3	4	5	6	7	6	7	8	9	10	11	12	13	14	15	16	0	1	2	3	4	5	6	7						
6	5-9	6							1	—	4	—	1															6						
6	10-14	3	3										1	2	—	2	1										6							
12	15-19		9	3												2	5	5									8	3	1					
8	20-24			3	4	1											3	5									1	3	1	3				
2	25-29					2												2											1	—	1			
4	30-34					1	2	1										4										1	2	1				
1	35-39							1										1												1				
1	45-49						1												1												1			
		Total gillraker count																																
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33					
6	5-9	1	—	4	—	1																												
6	10-14					1	2	—	—	2	1																							
12	15-19									2	3	4	1	1	1																			
8	20-24											1	—	1	3	1	1	1																
2	25-29																	1	—	1														
4	30-34																		1	—	2	—	1											
1	35-39																														1			
1	45-49																														1			
*127	>600 <i>T. albacares</i>																								6	11	33	37	30	9	1			
*55	>600 <i>T. obesus</i>																								5	13	15	17	4					

TABLE 12.—Number of lateral line scales for selected sizes of juveniles of *Thunnus*.

SL (mm)	<i>Thunnus alalunga</i>													<i>Thunnus thynnus</i>														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6	7	8	9	10	11	12	13
16			2																									
17		4													2	2	3											
18		2	1	1	1											1	1	1										
19			2												2	—	—	5	3	1								
20				1	4	—	—	—	2									2	5	1	1							
21					2													1	1	4	1							
22								2	1	2	—	1									1	—	3	—	1			
23											1	1									4	—	—	1	—	1	—	1

SL (mm)	<i>Thunnus atlanticus</i>													<i>Thunnus spp.</i>														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6	7	8	9	10	11	12	13
16																												
17															1	1												
18			1	1											1	—	2											
19			1	1	1										1	1	1											
20				1	1	—	1													2								
21					1	—	—	—	—	1	1	1								1	1	1					1	
22									1	—	1	—	—	1														
23												1	1	4														

posteriorly is the 4th or 5th, never the 3rd as in *T. thynnus*. If the lines of the curve that show descent and ascent were to subtend an angle, it would be larger than 90°. Some specimens of these species have also acquired four or more scales by 19 mm SL. They can be distinguished from *T. thynnus* by their 4th scale that stays in line on a descent with the 3rd. At 21 mm SL, all specimens have four or more scales. Slight differences in the curvature of the lateral line were noted between *T. alalunga*, *T. atlanticus*, and *Thunnus spp.*, but these differences were not distinct enough for separating the species.

IDENTIFICATION
(Table 13)

The generic external characters of transforming and juvenile *Thunnus* have been adequately documented by a number of workers as pointed out in the introduction. Richards and Potthoff (in press) concluded that if accurate identifications to species are necessary, the only choice is to use osteological characters, even though this involves the time-consuming task of clearing and staining.

Only three characters are available to separate the species from 8 to 14 mm SL: the number of precaudal and caudal vertebrae, vertebral position of the first closed haemal arch, and the pterygiophore pattern under the second dorsal fin. Assuming a specimen is not a variant in

any of the three characters, it can be identified as follows:

Character	Species separated
Number precaudal + caudal vertebrae	<i>T. atlanticus</i> from <i>T. thynnus</i> , <i>T. alalunga</i> , <i>Thunnus spp.</i>
First closed haemal arch	<i>T. atlanticus</i> + <i>Thunnus spp.</i> from <i>T. thynnus</i> + <i>T. alalunga</i>
Pterygiophore pattern	<i>T. alalunga</i> from <i>T. thynnus</i> + <i>Thunnus spp.</i>

Although the vertebrae are not yet developed posteriorly at 8 mm SL, they nevertheless can be counted by noting chondrified neural and haemal spines which are present above and below the notochord. Care should be taken not to count the parhypural bone as a haemal spine. The parhypural belongs to the hypural plate but resembles a haemal spine during early development. The position of the first closed haemal arch is difficult to determine in small specimens but it can be done with diligence and patience. The pterygiophores may not be entirely ossified at 8 mm SL, but they are present as chondrified struts. Varying the substage light, by moving the mirror below the microscope, will bring them into view.

The vertebral position of the first haemal postzygapophysis becomes available as a character on specimens from 15 to 20 mm SL. In this size range, only *T. atlanticus* acquires the diagnostic

TABLE 13.—Comparison of diagnostic characters for juveniles of *Thunnus*. Parentheses indicate rare occurrence.

Character	<i>T. thynnus</i>	No.	%	<i>T. alalunga</i>	No.	%	<i>T. atlanticus</i>	No.	%	<i>Thunnus</i> spp.	No.	%
Number of vertebrae, precaudal and caudal	18 + 21 = 39 [16-19]+[20-22] = 38-40	149	95	18 + 21 = 39 19 + 20 = 39	114	97	19 + 20 = 39 [18,19]+[19,21] = 38,39	105	98	18 + 21 = 39 [17,19]+[21,22] = 39,40	35	85
First haemal arch on vertebra number	10 11, (9)	137	88	10 (9)	115	99	11 12, (10)	101	94	11 10,12	38	93
First haemal post-zygapophysis on vertebra number	7 (6),(8)	153	97	8 7,9	97	93	8	86	100	7 6	28	90
Number of anal fin elements, including finlets	22 21,23,(24)	127	91	22 (21),23	101	94	21 (20),22	85	92	22 21,23	28	93
Pattern of single second dorsal fin pterygiophores for interneural spaces	1,1-----1,1 1,1-----1	140	95	1,1,1,-----1	116	100	1,1,1,-----1 1,1-----1 1,1-----1,1	42	46	1,1-----1,1 1,1,1-----1	40	98
Pattern of single anal fin pterygiophores for interhaemal spaces	-----1,1 --1--1,1 -----1,1,1 }	116	84	-----1,1 --1--1,1	74	66	-----1 -----1,1	55	61	-----1,1,1 -----1,1	31	78
Gillraker number over ceratobranchial bone	17,18,(19,20)	102		14,15,(16)	81		11,12,(13)	92		14,15,16	27	
Shape lateral line	right angle			smooth curve			smooth curve			smooth curve		

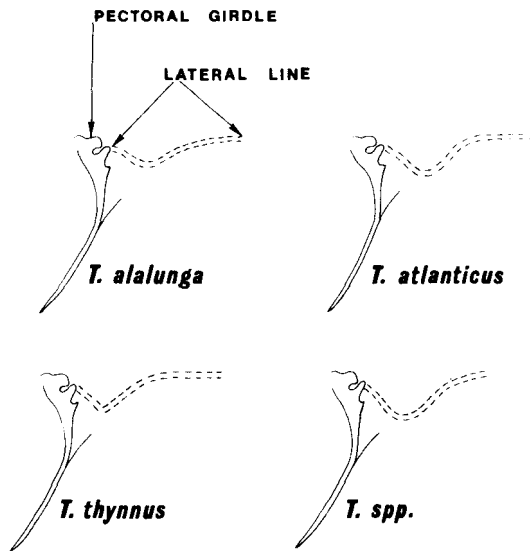


FIGURE 13.—Outline of the lateral line for juveniles of the *Thunnus* species. Each pair of dashes in the lateral line represents one scale.

count of gillrakers over the ceratobranchial. The juveniles can be identified as follows:

Character	Species separated
Number precaudal + caudal vertebrae	} <i>T. atlanticus</i> from <i>T. thynnus</i> , <i>T. alalunga</i> , <i>Thunnus</i> spp.
Ceratobranchial filled with 11-12 rakers	
First closed haemal arch	<i>T. atlanticus</i> + <i>Thunnus</i> spp. from <i>T. thynnus</i> + <i>T. alalunga</i>
Pterygiophore pattern	<i>T. alalunga</i> from <i>T. thynnus</i> + <i>Thunnus</i> spp.
First haemal postzygapophysis	<i>T. alalunga</i> + <i>T. atlanticus</i> from <i>T. thynnus</i> + <i>Thunnus</i> spp.

Juveniles in this size range are easier to identify for two reasons. First, they are further advanced in development, they stain better, and the characters are more readily discernible. Second, the availability of two additional characters permit cross-checking so that it is possible to identify "one character" variants. For example, a specimen with 18 + 21 vertebrae and the ceratobranchial filled with 12 gillrakers is a vertebral variant of *T. atlanticus*. Although gill rakers over the ceratobranchial bone can vary over a range,

specific ranges do not overlap except for *T. alalunga* with the *Thunnus* spp. complex. Thus, the ceratobranchial count, if available, should take precedence over the vertebral count. The first haemal postzygapophysis may be very small and high magnification should be used when viewing this character.

All characters listed in Table 13 are available for identification on specimens past 21 to 23 mm SL. The following features can be used to identify a specimen:

Character	Species separated
Number precaudal + caudal vertebrae	<i>T. atlanticus</i> from <i>T. thynnus</i> , <i>T. alalunga</i> , <i>Thunnus</i> spp.
Gillraker number over ceratobranchial	All species separable except <i>T. alalunga</i> from <i>Thunnus</i> spp.
First closed haemal arch	<i>T. atlanticus</i> + <i>Thunnus</i> spp. from <i>T. thynnus</i> + <i>T. alalunga</i>
Pterygiophore pattern	<i>T. alalunga</i> from <i>T. thynnus</i> + <i>Thunnus</i> spp.
First haemal postzygapophysis	<i>T. alalunga</i> + <i>T. atlanticus</i> from <i>T. thynnus</i> + <i>Thunnus</i> spp.
Shape lateral line	<i>T. thynnus</i> from <i>T. alalunga</i> , <i>T. atlanticus</i> , <i>Thunnus</i> spp.

It is not difficult to identify specimens larger than 21 mm SL. Sufficient characters are available and bones are well ossified and stained. However, variability should be taken into account and characters with the least variability should be relied upon the most. The number of gillrakers over the ceratobranchial bone and the shape of the lateral line should take precedence over the other characters. I have never observed the range for the number of ceratobranchial rakers in one species overlap with that of another, except *T. alalunga* with *Thunnus* spp., and I have never seen a *T. thynnus* with a smoothly curved lateral line.

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