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The Nature of Post-larval Transformation in *Tylosurus acus* (Lacépède)

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(Plate I; Text-figures 1-9)

INTRODUCTION

THE transformation of the post-larvae of *Tylosurus raphidoma* (Ranzani) has been shown by Breder & Rasquin (1952) to include a process of sloughing off melanic areas of the dorsal fin. Since that report was published, data on comparable stages of development for the related and in many ways similar *Tylosurus acus* (Lacépède) have been obtained. There are, however, rather remarkable and striking differences, the demonstration of which forms the bulk of this communication.

Since the two species are sympatric, it has seemed strange that with their close superficial similarities they would apparently occupy the same environmental locus. The detailed data of this paper should improve understanding of the reasons for this situation. The comparisons it has been necessary to make in order to clarify differences and similarities should be useful in the taxonomic separation of these two forms at any stage of development.

The studies and new material reported herein were made possible by the Lerner Marine Laboratory on Bimini, Bahamas.

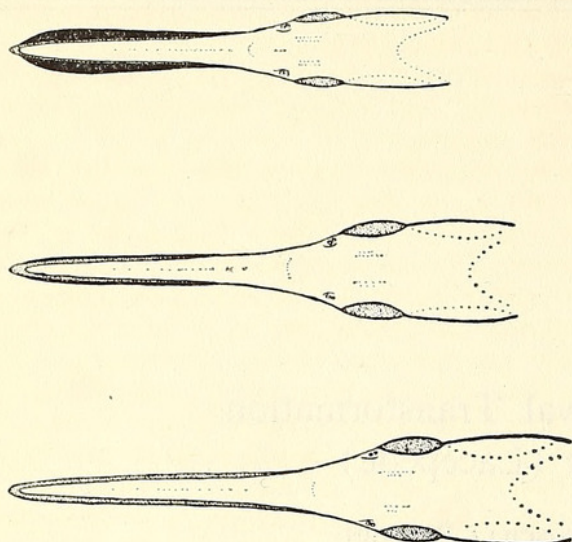
DESCRIPTION OF TRANSFORMATION

The gross changes in any fish at the time of transformation from a post-larval individual to the adult form are obviously a function of growth in the sense of increase in size and the differential rates of various aspects of this growth, or heterogony. This is based in final analysis on the behavior of the cellular components of the tissues involved and properly belongs in the province of histology. For this reason this descriptive section is divided into

two parts, the first dealing with the gross changes in the fish and the second with the accompanying histological changes.

Growth and Heterogony. — In the earliest stages known, the lower jaw of *Tylosurus acus* protrudes considerably beyond that of the upper in a manner not unlike that of many species of the related genus *Strongylura*. This is the so-called "halfbeak" condition of the young of these fishes in which they resemble the adult in the related Hemirhamphidae. The beak reduces rapidly as the growth rate of the upper jaw exceeds that of the lower so that at a length of about 250 mm standard length the two jaws are very nearly the same length. This condition they retain throughout life. At about the same time, i.e., when the adult form of the beak is attained, there is a transient development of mandibular lappets which quickly reduce themselves to a mere dark line on the jaw. The sizes at which this change takes place are shown in three stages in Text-fig. 1, from the maximum development to the loss of the appendages.

Concurrently appearing with the loss of this "halfbeak" condition is the development of an elevation of the posterior part of the dorsal fin, which becomes intensely black. This too reduces but does not disappear until some time later. The reduction of this area of the fin is shown in Text-fig. 2. Before the dark elevation of the posterior of the dorsal fin has reached its fullest development, the anterior rays begin to increase in length. On attaining a certain size the anterior rays retain that increased proportion for the remainder of the fish's life so that the fully adult fish has a dorsal fin high anteriorly and low posteriorly.

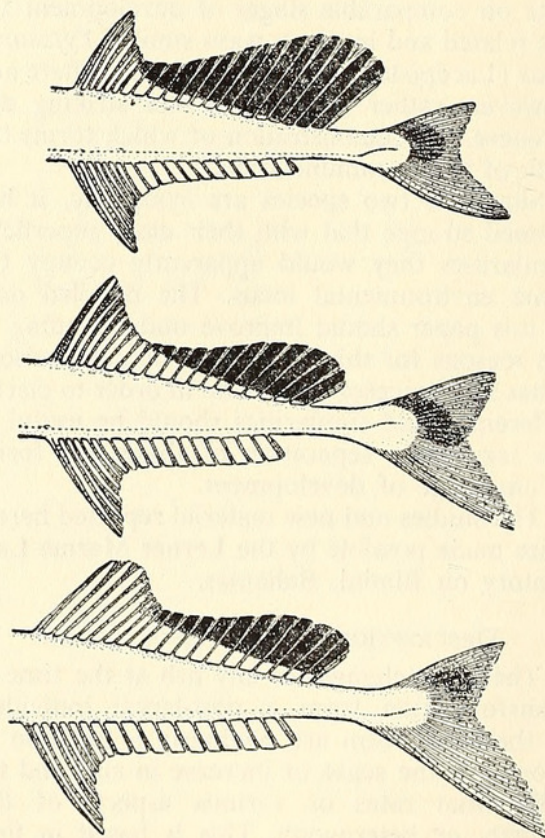


TEXT-FIG. 1. Heads of *Tylosurus acus*, showing the maximum development of the mandibular lappets and their subsequent reduction. Upper, 205 mm, s.l., middle, 205 mm s.l., lower, 242 mm s.l.

Numerical data supporting the above will be found in Tables I, II and III. The changes in the anterior and posterior heights of the dorsal fin are shown graphically in Text-fig. 3 with these values shown as percentages of the standard length of the fishes. Text-fig. 5 shows the same data expressed in millimeters. The interesting differences in these two sets of curves based on the same data are a measure of the heterogony responsible for these transformations. Text-fig. 7 shows graphically the changes in the head, beak and mandibular lappets. The comparison with *Tylosurus raphidoma* which these several graphs present is given consideration in the discussion.

Histology of Fin Transformation.—A post-larval fin was removed from a specimen fixed in Bouin's solution and an intermediate stage fin was removed from a formalin-fixed specimen. Both were sectioned at right angles to the long axis of the fin rays at seven microns and alternate slides were stained with Harris's hematoxylin and eosin and Masson's trichrome connective tissue stain. These are comparable to two fins of *T. raphidoma* studied by Breder & Rasquin (1952) and two photographs from that report are republished here for the purpose of comparison. Plate I, Figure 1, is a detail of the intact fin of *T. raphidoma* before the onset of disintegration and may be compared with Figure 2 which is a photomicrograph of a fin of *T. acus* before the onset of resorption. Figure 3 shows the inter-radial membrane of the disintegrating part of the dorsal fin of *T. raphidoma* and may be compared with Figure 4, which is a detail of the inter-radial membrane of the dorsal fin of *T. acus* during the period of resorption.

Fundamentally the structure of the dorsal fin of *T. acus* is the same as that of *T. raphidoma*, described by Breder & Rasquin (1952). Actinotrichia are present on the tips of the rays extending distally from between the most distal segments of the lepidotrichia. Nerves, blood vessels and connective tissues are arranged in the fin elements in the same way in both species. The area about the first ray of the fin is broader than around the rest of the rays and contains more connective tissue. Here the blood vessels are larger than capillaries, although still extremely thin-walled, and contain coarse granular eosinophiles. In fact these cells are more frequently seen than erythrocytes. At the level where the last division of the lepidotrichia of the first ray is seen, the coarse granular cells are found in the connective tissue spaces as well. In this area also the blood vessels appear filled with an acellular material that is coarser and more granular than serum usually appears in section. It seems possible that the acellular fluid found in these blood vessels is less dilute than that found in other parts of the body, owing to the accumulation of products of beginning dissolution of the fin tissues. Coarse granulocytes are common in the blood vessels at the



TEXT-FIG. 2. Tails of *Tylosurus acus*, showing the maximum development of the black posterior dorsal fin and its subsequent reduction. These fish are the same as those of Text-fig. 1.

TABLE I. MEASUREMENTS (IN MILLIMETERS) OF THE DEVELOPMENT OF THE DORSAL FIN OF *Tylosurus acus*

Standard length	Posterior dorsal height	Anterior dorsal height	P.D.H./S.L.	A.D.H./S.L.
23	1.27	0.18	0.06—	0.01—
35	1.56	0.70	0.04+	0.02
79	2.10	2.97	0.03—	0.04—
205	17.00	15.00	0.08+	0.07+
215	11.50	16.50	0.05+	0.08—
242	11.50	17.00	0.05—	0.07+
620	12.00	36.00	0.02—	0.06+

Note. Fish in the 200 mm class from Bimini, others from the Dry Tortugas.

base of the fin where it meets the dorsal musculature. In both fins of *T. acus* these coarse granular eosinophiles are never at any place as numerous as they appeared in *T. raphidoma*, although they are more numerous in the resorbing fin than in the intact one.

Breder & Rasquin (1952) have suggested that the appearance of quantities of coarse granular eosinophiles is associated with a function of preserving fat from the degenerating tissue for the further physiological economy of the fish. These cells are also often found in abundance in parasitized teleosts. They were extremely abundant in the fins of *T. raphidoma* that also showed many encysted worms. The sections of *T. acus* studied for the present report showed no parasites, and while the coarse granulocytes were not so abundant as they were in the parasitized fish, they were still found in great numbers. Jordan & Speidel (1931) have suggested that they are responsible for the transportation of fat in the African lungfish. Their presence in degenerating fins of *Tylosurus acus* also seems to indicate that they have some function in the resorption of tissue unrelated to the presence of parasites.

The striking differences in histological structure between the dorsal fins of the two species lie in the structure of the epithelium and in the number of melanophores. In *T. acus*, the covering epithelium of the young intact fin may be from six to ten cell layers deep while in *T. raphidoma* it is extremely thin, being only one or two layers thick. Within the covering epithelium in the fin of *T. acus* the connective tissue shows two lines of melanophores and between them can be seen an occasional capillary and connective tissue fibers and cells. In *T. raphidoma* these details are obscured by the density of the melanic tissue (Plate I, Figures 1 and 2).

The resorbing fin of *T. acus* contrasts sharply with the disintegrating fin of *T. raphidoma*. Where the latter shows naked rays devoid of epithelium, and ragged, disintegrating inter-radial membranes, the resorbing fin of *T. acus* shows the epithelium to be intact over the entire surface of the fin. There appears to be some breakdown of the cellular boundaries of the melanophores. In many places, melanin granules are seen in the epithelium being passed through to the surface. These discrete granules are obviously not contained within melanophores. At the base of the resorbing fin the connective tissue is filled with coarse granular eosinophiles and macrophages. The phagocytic cells are filled with cellular debris and melanin granules. Many of the coarse granulocytes appear to have disintegrated, liberating their granules into the meshes of the loose connective tissue.

These three items—the loss of melanin through the epithelium of the fin and phagocytosis of melanin at the base of the fin, the abundance of coarse granulocytes, and the phagocytosis of cellular elements—are the only histological signs of resorption of tissue. The resorbing fin is somewhat more delicate in structure than that of the post-larval form in that the epithelium contains fewer layers of cells and the connective tissue of the inter-radial membrane is less dense and shows fewer nuclei. Unlike the disintegrating

TABLE II. DEVELOPMENT OF THE BEAKS OF *Tylosurus*. (BASED ONLY ON SPECIMENS WITH UNBROKEN BEAKS).

Standard length	Upper jaw ¹	Lower jaw ¹	Difference	Per cent difference
<i>Tylosurus acus</i>				
23	1.2	3.0	1.8	60
28	3.0	6.5	3.5	54—
30	2.0	4.0	2.0	50
35	5.0	8.5	4.1	41
42	6.5	11.5	5.0	43
97	21.0	30.0	11.0	37—
205	38.5	41.0	2.5	6+
215	45.0	48.0	3.0	6+
242	52.0	53.5	1.5	3—
590	134.0	138.0	4.0	3—
660	130.0	134.0	4.0	3—
<i>Tylosurus raphidoma</i>				
11	0.5	0.8	0.3	37+
19	1.9	2.1	0.2	10—
44	21.2	22.0	0.8	4—
149	28.2	29.8	1.6	5—
231	48.6	50.1	1.5	3—
500	106.0	109.5	3.5	3—

¹ Measured from eye. All in millimeters. From Breder (1932) with additions.

TABLE III. PROPORTIONS OF MANDIBULAR APPENDAGES COVERING ONLY THE PERIOD OF THEIR PRESENCE. (ALL MEASUREMENTS IN MILLIMETERS. BASED ONLY ON SPECIMENS WITH UNBROKEN BEAKS).

Standard length	Length of lower jaw	Mandibular appendages ¹		Percent of lower jaw	
		Greatest width	Distance of G. W. from jaw tip	Greatest width	Distance from tip
<i>Tylosurus acus</i>					
97	30.0	—	—	—	—
205	41.0	6.0	24.0	15—	59—
215	48.0	4.0	24.0	8+	50
242	53.5	—	—	—	—
<i>Tylosurus raphidoma</i>					
11	0.8	—	—	—	—
19	2.1	0.6—	0.4—	29—	19—
44	22.0	10.0	4.0	45+	18+
149	29.8	10.9+	7.0—	37—	23+
231	50.1	—	—	—	—

¹ The specimen nearest in size above and below those with mandibular appendages is given in each species.

dorsal fin of *T. raphidoma*, that of *T. acus* shows no breakdown of connective tissue elements, no sloughing off of epithelium, and no sign of weakening of the structure of the rays. The loss of tissue from this fin is not accomplished by a violent disruption of tissue structures.

DISCUSSION

Comparison with Tylosurus raphidoma.—Aside from the aberrant and much flattened *Ablennes hians* (Cuvier & Valenciennes), *Tylosurus acus* and *T. raphidoma* are the only members of the family Belonidae in the West Indies and adjacent waters which reach a length of several feet or more. The smaller species, usually going under the generic name *Strongylura*, differ from these two species in many respects, a number of which are not easily handled by conventional taxonomic methods. The characters usually used to separate these two quite different types of fishes are at best trivial. This has led to the suppression of *Tylosurus* by various recent authors. We have followed a more conservative usage in the retention of the name *Tylosurus* for these larger and more widely ranging forms with higher dorsal and anal fin formulae, pending more satisfactory analysis of the status and limits of genera in this family.

In ontogeny various characters in the West Indian species of the two groups show the following readily recognized differences.

- a. Beak usually not more than 2 times rest of head in adults; dorsal and anal fins with 20 or more rays; juveniles pass through a stage with a high dark-colored prolongation of the posterior part of the dorsal and possess dark mandibular lappets; dark vertical

bars are present under certain conditions of environment.

Tylosurus

- b. Beak usually more than 2 times rest of head in adults; dorsal and anal fins with less than 20 rays; juveniles pass through no such stage as described above, but the "half-beak" stage is much more marked, this being somewhat suppressed in *Tylosurus*; a narrow, longitudinal, dark or iridescent stripe on the sides usually present, but no vertical bars.

Strongylura

The larger and more widely ranging West Indian species of *Tylosurus* are more given to open and deep water while the smaller *Strongylura* favor water shallower and more confined, such as about docks and in mangrove passages.

Although there is no real taxonomic difficulty in separating large specimens of the two species of *Tylosurus* under consideration, some of the developmental stages may present difficulty. The following data should be helpful in questionable cases and, together with certain of the included diagrams, should make clear separation possible in all instances.

ADULTS

- a. Beak about 2 times rest of head (about 66% of head). Scales about 380-400. Body depth 18.5 to 22 in standard length (about 4-5%) 6-7 in head, (about 12-16%). Dorsal surface usually notably bluish. Tends to stay outside of harbors. Pupil about 2¾ in longest diameter of eye (about 36%). Umbelacrum larger and accompanied with a patch of corneal pigment.

Angle of visual deflection about 13-140° below the horizontal¹. *Tylosurus acus*

- b. Beak about 1½-1⅝ times rest of head (about 57-60% of head).

Scales about 350.

Body depth 13.3-18 in standard length (about 5-7%), 4.35-5.8 in head, (about 17-23%).

Dorsal surface usually notably greenish.

Tends to stay inside harbors.

Pupil about 2⅓ in longest diameter of eye (about 42%).

Umbelacrum smaller and with corneal pigment reduced to a few flecks.

Angle of visual deflection about 9-10° below the horizontal¹.

Tylosurus raphidoma

JUVENILES

- a. A definite "halfbeak" condition is passed through; see Text-fig. 7.

Labial folds slightly developed and not angulated; see Text-fig. 7.

Pectorals usually uniform hyaline or dusky.

Tylosurus acus

- b. No pronounced "halfbeak" condition at any time, jaws nearly co-terminous at all sizes; see Text-fig. 7.

Labial folds well developed and angulate; see Text-fig. 7.

Pectoral tips usually blackish.

Tylosurus raphidoma

¹ The angle of visual deflection is most easily measured by taking from the fish the distance between the orbital rims at top (interorbital distance) and at bottom and the vertical diameter of the eye. Then with this data the angle which the optical axis (at rest) makes with the horizontal may be calculated according to the following formula. Let

a = distance between opposite orbital rims at top

b = distance between opposite orbital rims at bottom

c = vertical diameter of eye (measured along its face, not as a projection on a vertical plane)

These values define a symmetrical trapezoid with the lower base, b, smaller than the upper base, a, and the two non-parallel sides each equal to c. The altitude on this figure, which may be called d, forms a leg of a right triangle with hypotenuse c and the other leg $\frac{a-b}{2}$.

A perpendicular from c to the opposite angle, the right angle of this triangle, forms a smaller and similar triangle with its hypotenuse $\frac{a-b}{2}$. Since $\frac{a-b}{2}$ is horizontal and the perpendicular to c is parallel to a perpendicular at its midpoint (the optical axis), the angle between $\frac{a-b}{2}$ and the perpendicular to c is the angle sought.

Since this triangle is similar to the larger triangle on which it is based, this angle is equal to the angle between c and d which is opposite $\frac{a-b}{2}$ in the larger triangle. Calling this angle A, then

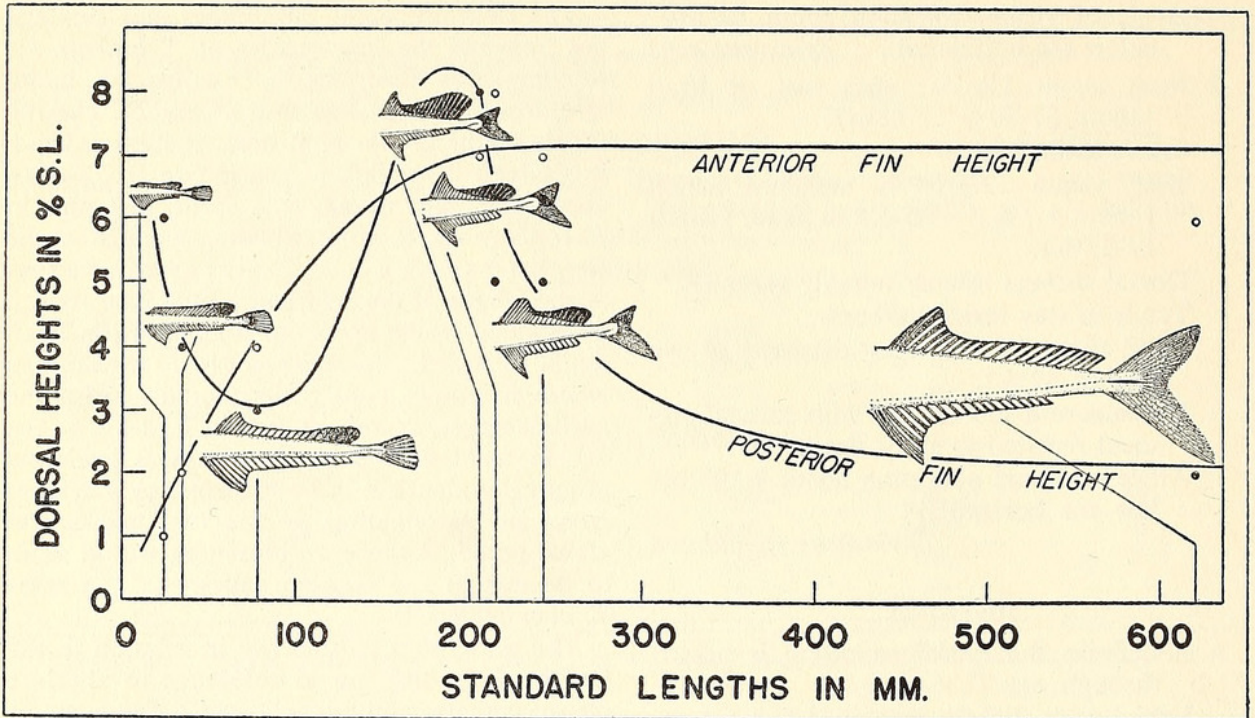
$$\sin A = \frac{a-b}{2c}.$$

The developmental differences and similarities between the two species of *Tylosurus* are so completely illustrated in Text-figs. 3-9, inclusive, that little explanation is necessary. The full development of the high dark posterior dorsal is attained at a slightly larger size in *T. acus*, about 200 mm as against about 150 mm in *T. raphidoma*. It is noteworthy, too, that at the very early stages it is relatively higher in respect to the length of the fish than a little later, which gives a depression in the curve as shown in Text-fig. 3. This deflection is absent in *T. raphidoma*, where it simply rises proportionally from the earliest stages, as may be seen in Text-fig. 4. The development of the anterior rays is evidently practically identical in both forms, as is evident from an examination of the two text-figures above noted. Apparent differences would seem to be due to the relative paucity of the rarer *T. acus* material.

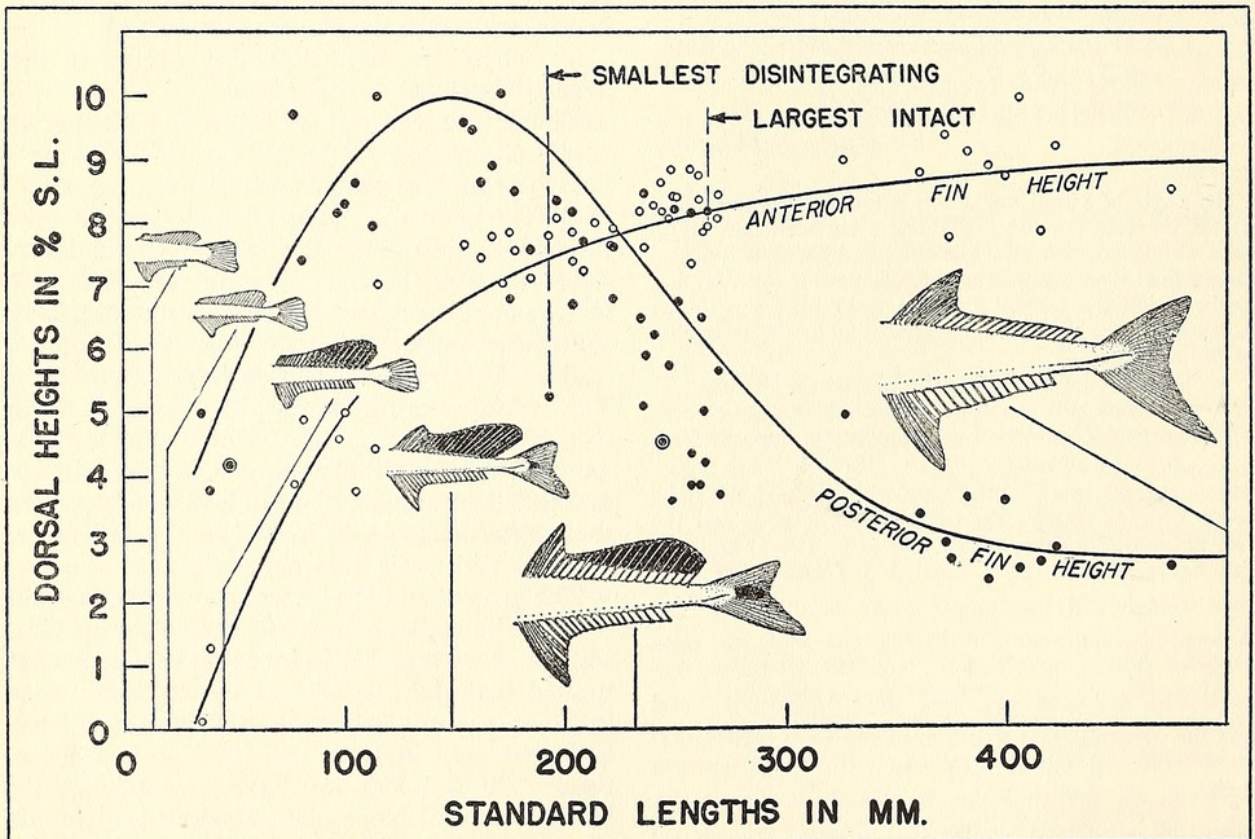
The same data plotted not in relation to the length of the fish but in reference to absolute measurements, emphasize these differences, as indicated in Text-figs. 5 and 6. The similarity of the growth of the anterior part of the dorsal fin in both species and the sloughing of the posterior lobe in *T. raphidoma* and its disappearance by resorption in *T. acus* is clearly indicated. Here it is seen that *T. acus* reaches the peak of its posterior lobe development at just about the place where the first sloughing occurs in the most precocious *T. raphidoma*.

The development of the beaks of both species is plotted comparatively in Text-fig. 7. By plotting the standard length against the percentage of difference of the excess of the lower jaw over the upper, from Table II, the ontogenetic differences between the two forms in respect to this feature are clearly developed. This diagram indicates how much farther the suppression of the "halfbeak" juvenile condition has progressed in *T. raphidoma* as compared with *T. acus*. It again shows the relative sizes at which the development of the mandibular lappets is at maximum and the illustrations point out how much greater these structures are developed in *T. raphidoma*, together with their different outlines.

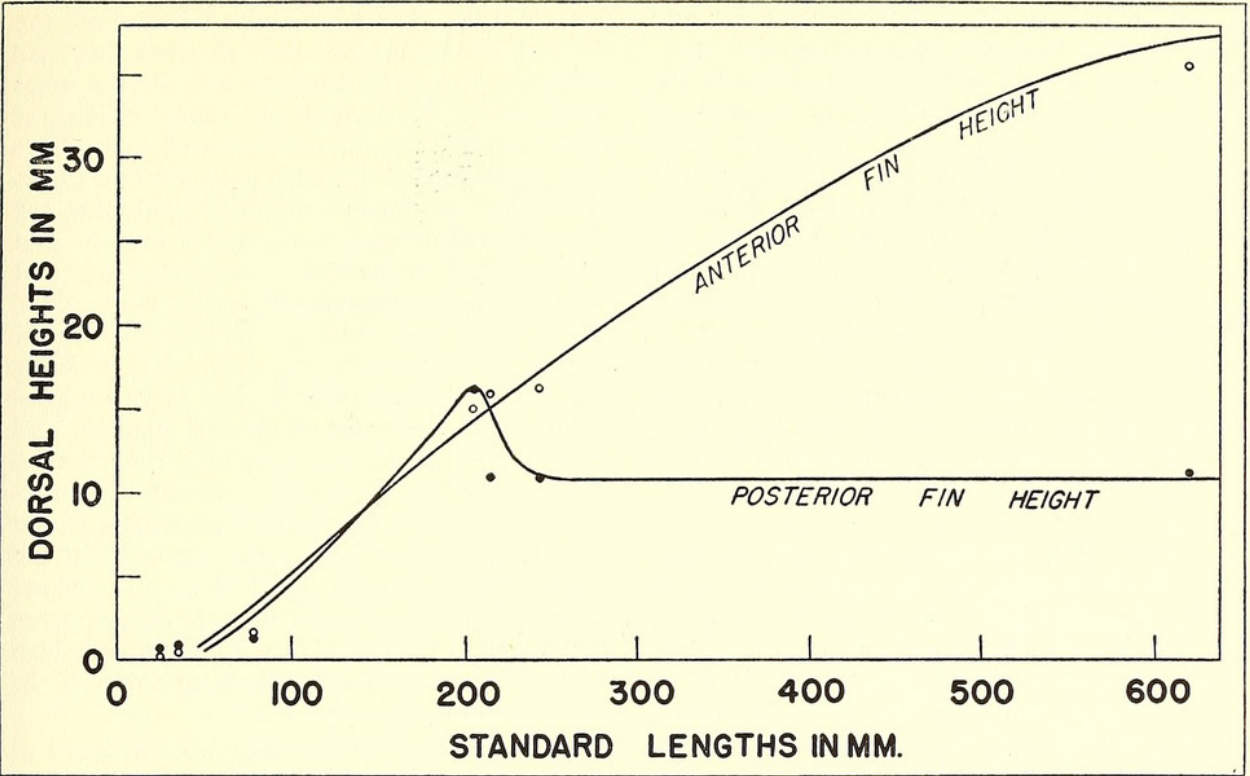
The growth and attainment of maturity would seem to be rather similar in these two species, insofar as we are able to interpret the somewhat limited material. Text-fig. 8 shows clearly that in *T. acus* young fish under 100 mm have been collected only in June and July while fish between 200 and 250 mm have been taken only in October and November. Various individuals that were seen about the laboratory dock in January and February, 1952, under conditions that made catching out of the question, were carefully estimated to be about 300 mm in standard length. The Florida fish of 150 mm



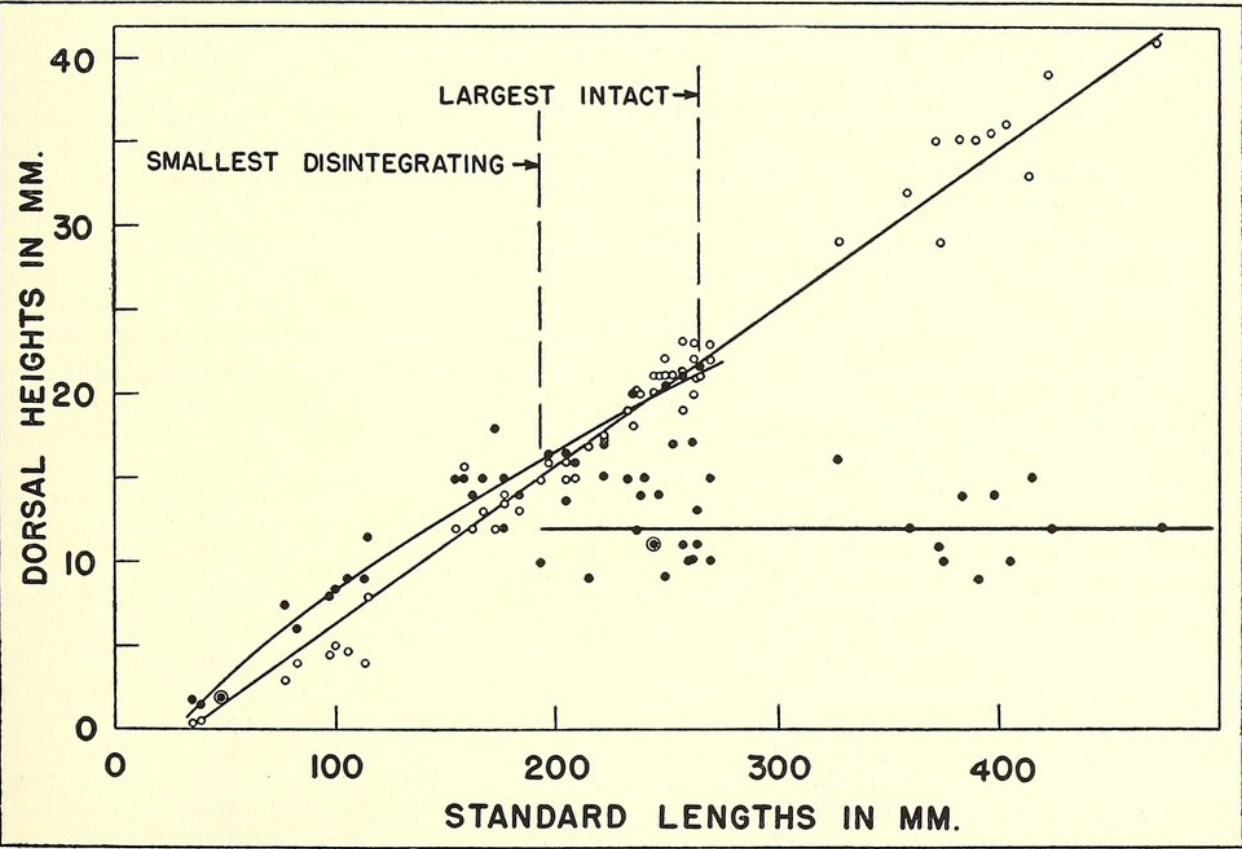
TEXT-FIG. 3. Changes in anterior and posterior heights of the dorsal fin of *Tylosurus acus* with increase in length of fish. Dorsal heights expressed as per cent of standard lengths. White circles represent anterior fin height. Black circles represent posterior fin height. Curves are freehand approximations of the mean. The illustration of the three smallest and the largest stages have been taken from Breder (1932). These with the new material show the appearance of the fish at the indicated lengths. Data from Table I.



TEXT-FIG. 4. Changes in anterior and posterior heights of the dorsal fin of *Tylosurus raphidoma* with increase of length of fish. Dorsal heights expressed as per cent of standard lengths. White circles represent anterior fin height. Black circles represent posterior fin height. Curves are freehand approximations of the mean. No account is taken here of the mechanics of the changes in the posterior height. The illustrations of various indicated stages at their respective lengths have been taken from Breder (1932). Text-figure from Breder & Rasquin (1952) for direct comparison of these two sympatric species.



TEXT-FIG. 5. Changes in the anterior and posterior heights of the dorsal fin of *Tylosurus acus* with increase in length of fish. Unlike Text-fig. 3, to which this should be considered complementary, the dorsal heights are expressed not in relation to the length but in absolute units. White circles represent anterior fin height. Black circles represent posterior fin height. Curves are freehand approximations of the mean. Data from Table I.



TEXT-FIG. 6. Changes in anterior and posterior heights of the dorsal fin of *Tylosurus raphidoma* with increase of length of fish. Unlike Text-fig. 4, to which this should be considered complementary, the dorsal heights are expressed not in relation to the length but in absolute units. White circles represent anterior fin height. Black circles represent posterior fin height. Curves are freehand approximations of the mean. Account is taken of mechanics of the posterior height indicating its disruptive nature. From Breder & Rasquin (1952) for direct comparison of these two sympatric species.

in April may have been a late-spawned fish and somewhat retarded, as is suggested on the graph, or may be a very precocious individual of the first year. Partly spent females were seen at the Dry Tortugas in July, 1929. This agrees well with the sizes of the small fish and suggests that sexual maturity is attained at about the same size and age as in *T. raphidoma*. The large fish listed in Table IV, over 1,000 mm long, is not included in Text-fig. 8, as it could not be placed with any degree of reasonable judgment. It would seem most likely to be in its 4th or 5th year, but could be considerably older if the life span of these fishes permits such ages. More material than is at present available would be necessary to warrant further analysis along this line.

Although these are considered sympatric species and in fact both species have been caught in a single setting of a gill net, the fact remains that they show differential response to the finer details of their environment. *T. acus* is much less likely to be found in the harbor at Bimini than is *T. raphidoma*, which is regularly present, including large sized individuals that may frequently be seen chasing *Hemirhamphus* and other small prey. No *T. acus* were taken or seen in the harbor until a considerable amount of dredging had materially changed the depths about the dock. Almost immediately the dock-side fauna altered in the direction of more oceanic species. These included young *T. acus* as well as small *Cypselurus*, *Coryphaena*, *Histrio*, etc.

The large *T. acus* caught outside the harbor by angling are normally a brilliant ocean blue on the back, a color common to many truly

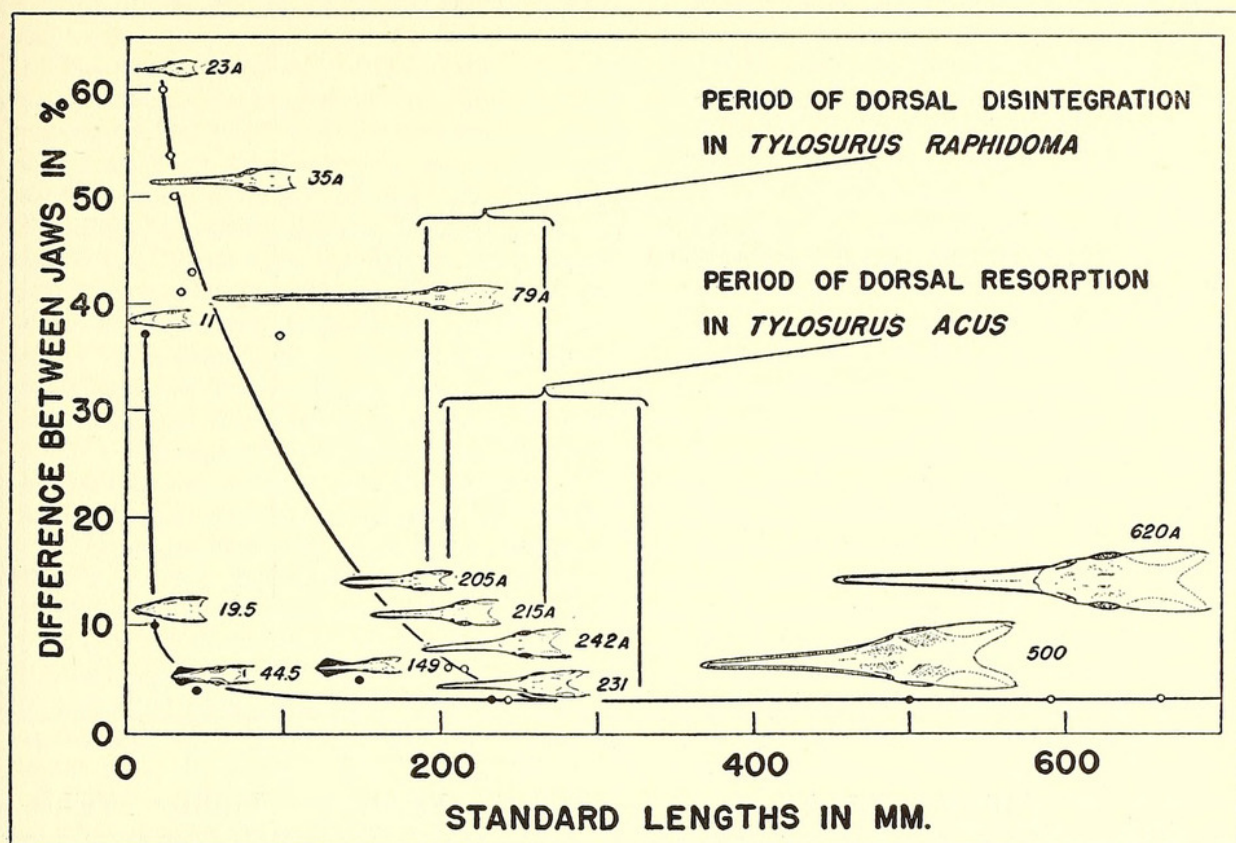
oceanic fishes. The young ones taken about the dock showed the blue color also but they had evidently just entered the harbor. On the other hand, large *T. raphidoma*, taken inside the harbor, near its mouth or over shoal water, have been noted in each instance to be a bright green. Both these colors are evidently matching the two different environments, and it may be that this is strictly a pigmentary response and that both species are capable of showing both colors. If this is so, then this noted difference surely reflects environmental choice, which is evidently different in the two forms. The large umbelacrum, greater amount of corneal pigment and smaller pupil in *T. acus* may be a reflection of this also, as this fish is fully exposed at the surface of the sea in open water to a greater extent than *T. raphidoma*. The depression of the visual angle, which is more marked in the former species, may be associated with danger from more nearly directly below than that from which *T. raphidoma* would be likely to suffer in its more shallow environs.

Both species are voracious and will strike at nearly any fish or other organism small enough to be managed. Two *T. acus* of about 200 mm were maintained in a 12-foot circular pool for eight days with a large school of *Jenkinsia*. The latter performed with regard to temperature as described in detail by Breder (1951); that is, they would come to a thermal barrier of a fraction of a degree and refuse to go into the differently temperatured water, regardless of the presence or driving influence of man or the small *Tylosurus*. These latter had no such regard for the finer differences of temperature and ranged at will about the pool, picking off *Jen-*

TABLE IV. DATES OF COLLECTION AND STANDARD LENGTHS (IN MILLIMETERS) OF *Tylosurus acus*.

Locality	Date	No. of fishes	Min.	Modes ¹ or Means	Max.
Nassau, Bahamas ²	2/11/30	1	—	620	—
Dry Tortugas ²	6/4/29	1	—	97	—
	6/13/29	14	16	22	42
	7/1/29	1	—	38	—
	7/6/29	1	—	660	—
	7/19/28	1	—	805	—
Sandy Hook, N. J. ²	6/—/18	10	30	35	46
Key West, Fla. ²	4/20/17	1	—	circa 152	—
Biscayne Bay, Fla. ³	7/27/86	1	—	circa 1,219	—
Woods Hole, Mass. ³	10/25/51	3	205	221	242
	11/2/51	1	—	203	—
	11/10/51	3	194	209	232
	11/2/49	1	—	190	—
	1-2/—/52	10+	—	est. 300+	—

¹ Where possible, modes are used in preference to means; the former are in italics.
² From Breder (1932).
³ From Nichols & Breder (1926).



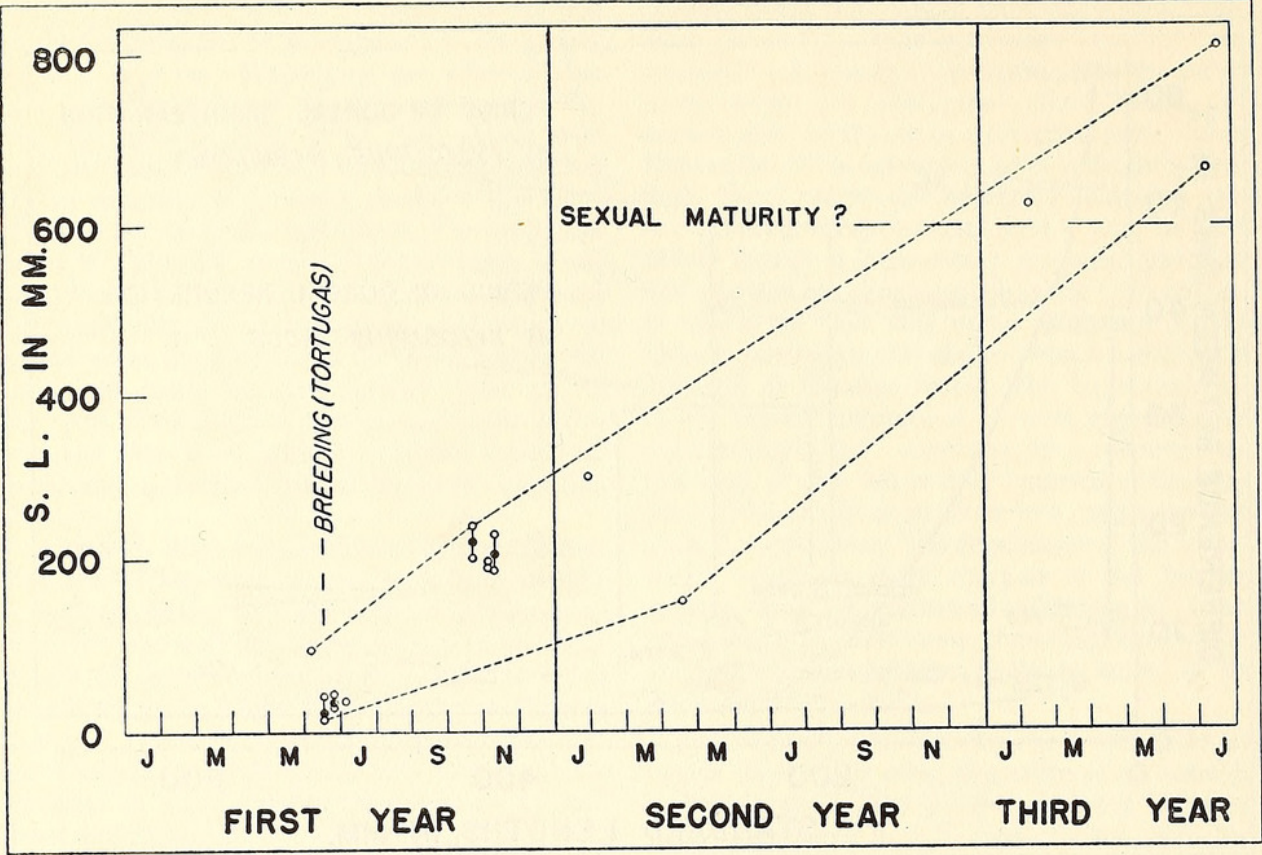
TEXT-FIG. 7. Changes in the relative lengths of the upper and lower jaw in *Tylosurus acus* and *T. raphidoma*. The illustration of the various indicated stages of the beak and its mandibular appendages are taken from Breder (1932) in the case of the latter species, as well as the former except for additional material presented herewith. The numbers near the fish heads indicate standard length of fish in mm. An "A" after such numbers indicates *T. acus*, while lack of a letter following the number indicates *T. raphidoma*.

kinsia at short intervals. This caused no great commotion in the school of these fish, only a slight "shock wave" passing through it, as when a pebble is dropped. The presence of the predatory *Tylosurus* as such seemed to have no special significance for the herrings; they were evidently regarded merely as any other solid object to be avoided, provided such behavior did not violate the fine regard these fishes have for both temperature and light variations.

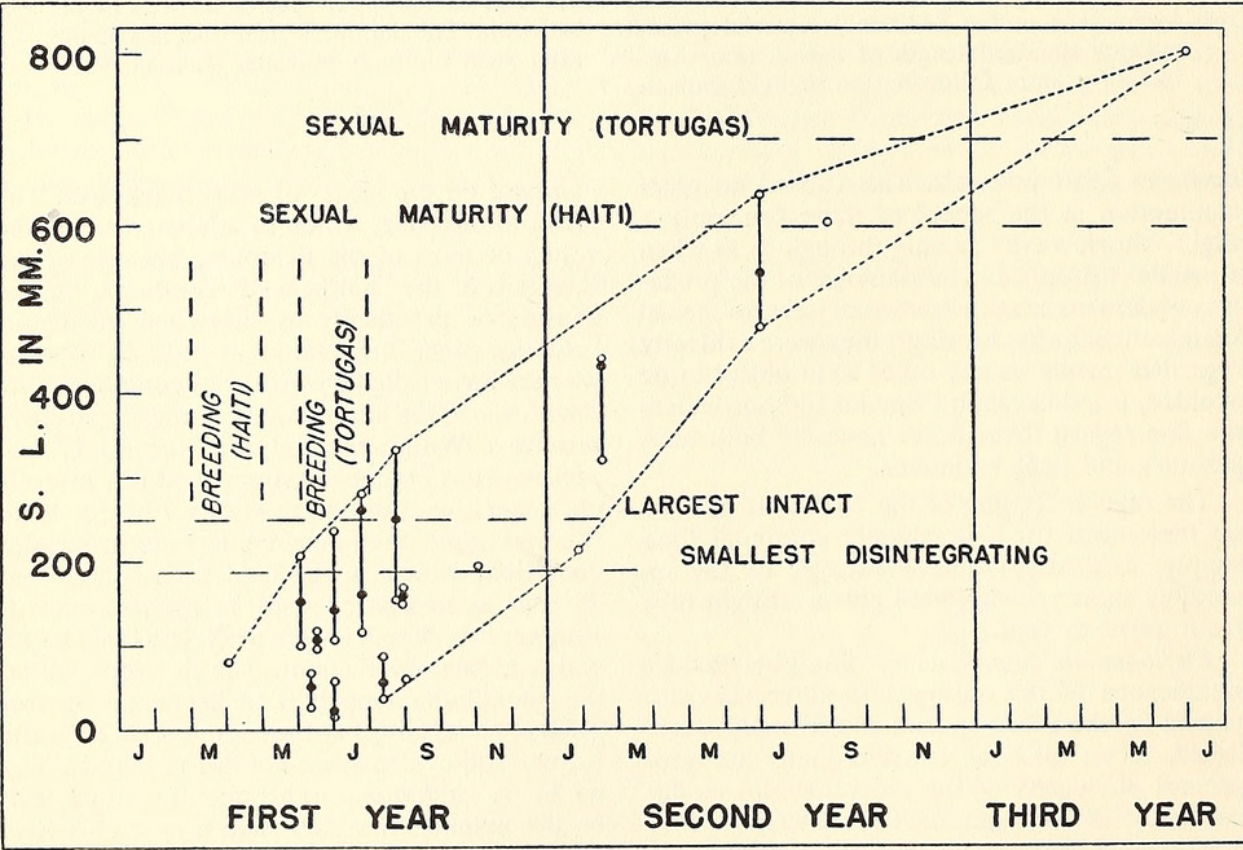
The regular feeding of the *Tylosurus* pointed up their need for a practically continual food supply, evidently required because of the incredibly short syntentognath gut—a straight tube from gullet to vent.

Phylogenetic Significance.—The phylogenetic significance of the ontogenetic differences displayed by these two species is not easily established. If we take the conventionally accepted general phylogeny of the syntentognaths as discussed by Schlesinger (1909), Regan (1911) Sewertzoff (1927) and Nichols & Breder (1928) and reinforced by de Beer (1951), *T. acus* could be placed as more primitive than *T. ra-*

phidoma on the basis of several features. The Hemirhamphidae, which as adults resemble the young of most of the Belonidae because of the retention of the "halfbeaked" condition, can be considered practically as shortened neotenus belonids. Since this feature is reduced in what we here have called *Tylosurus* as compared with *Strongylura*, the latter could be considered more primitive. Within the *Tylosurus* group *T. raphidoma* has practically suppressed this juvenile character, far more so than has *T. acus*. With this has gone a change from a more slender condition, which is reflected in the fact that *T. acus* as compared with *T. raphidoma* is a slimmer fish, with a longer beak, less body depth and a higher scale count. The development of the mandibular lappets is in keeping with this general change in that they are narrower in the former and evidently do not last as long as they do in *T. raphidoma*. This feature might well be the manner in which such a new character puts in its appearance. The fact that there are "erratic" presences and absences of barbels throughout the order may only be a case of the



TEXT-FIG. 8. Standard lengths of *Tylosurus acus* and their respective dates of occurrence.



TEXT-FIG. 9. Standard lengths of 279 *Tylosurus raphidoma* and their respective dates of occurrence. From Breder & Rasquin (1952) for direct comparison of these two sympatric species.

suppression or expression of the genetic potentialities of the group.

The whole problem in this group, as in so many others, is clouded by the fact that the phylogenetic "tree" may be inverted. A good many years ago Dr. George S. Myers discussed verbally the possibility of the non-exocoetid synentognaths being derived from or near the exocoetids rather than the reverse, as has generally been accepted. Breder (1938) discussed some of these inferences insofar as they concern the Exocoetidae. A very good case can be made out for the inversion. The most cogent reason against it, however, is given by de Beer (1951) who agreed with the earlier taxonomic workers in considering that the halfbeak features are the results of neoteny. Sewertzoff (1927) considered the very early stages of *Belone*, before either of the jaws began to lengthen, as passing through a stage equivalent to that of the short and equal-jawed flying fishes. It is believed, however, that this is a spurious resemblance since practically any fish embryo at the stages studied by Sewertzoff have short equal jaws; the point is that all fish jaws start off from such an early condition irrespective of what strange development subsequently may take place.

If the other synentognaths can be derived from the exocoetids, then the lengthening jaws, first the lower one in the hemirhamphids and finally both in the belonids, would have to be considered, in the usage of de Beer, as a hypermorphosis. If this were the case the series would be moving from short-bodied large-scaled forms to long-bodied fine-scaled forms. Whichever direction evolution moved, it is obvious that the transformations through which these fishes have gone is well in accord with the principles of distorted grids as discussed by Thompson (1942).

It should be evident that the determination of the direction of evolution in this group is of great importance in the interpretation of problems arising from the differences in the ways these two closely related fishes eliminate the juvenile high dark posterior lobe of the dorsal fin. So far as known the function of this appendage in *T. acus* would be similar to that supposed for *T. raphidoma* and discussed at length by Breder & Rasquin (1952). Since there are no data on the young of the former other than that contained in this paper, it would be pointless to speculate on whether the young of *T. acus* behaves in a manner similar to that of the young of *T. raphidoma* or whether this feature is employed in some other fashion.

However, it may be of some profit to speculate on which method of elimination of the dark dorsal lobe is antecedent. If we consider the

condition found in *T. raphidoma* as the earlier, based perhaps on an organism's successful attempt to arrest an invasive melanosis, as has been suggested by Breder (in press), this would be then the first step in the reintegration of the organism's regain of control. The next step would be finally to substitute the ordinary process of resorption as seen in *T. acus* for the more violent and unusual one of sloughing off an intensely melanic area. That in both species the mandibular lappets are simply resorbed would suggest that only the large area involved in the dorsal fin made necessary an initial elimination by sloughing. Such would seem to be the case if the phylogenetic tree were inverted as above suggested. If, however, the more conventional position be accepted, the reverse would follow. Under such a supposition, the then more primitive *T. acus* with its moderately developed dorsal lobe transformed by the standard method of resorbing juvenile features. On the other hand, in *T. raphidoma*, in which this feature is actually more marked, as may be seen by reference to the several text-figures, it became no longer possible to resorb this material and recourse was made to the process of sloughing it off. If this is in truth the case, then the latter form may be "the end of the line." That is, if the sloughing process is no longer sufficient to preserve the integrity of the organism the next stage could conceivably be invasion and death. Actually, only one questionable case of fish melanoma has been reported to show metastases, Schlumberger & Lucké (1948) discussing Takahashi (1929). In the melanomas of the xiphophorin fishes extensively studied by Gordon (e.g., 1948 and 1951) death follows from invasive process only. Presumably in *Tylosurus*, if the area of melanosis were not sloughed off but went on to develop as a melanoma, the speed would be sufficient to preclude reproduction.

Such thought cannot help but make one wonder how many lines may have been eliminated in an evolutionary sense by some similar process. It would be perhaps inevitable in the in-and-out-breeding of organisms that this would follow. It would seem likely that more than occasionally an old line would reach some point where the gene combinations were such that it was impossible for the individuals to maintain organic integrity long enough to perpetuate their kind in adequate abundance.

It should be noted in conclusion that the raw data are adequate only to form a bare sketch of the ontogeny of *Tylosurus acus*. In the area available for collecting and study, *Tylosurus raphidoma* is much more abundant, as is evident from a comparison of the tabular data herein and that of Breder & Rasquin (1952) and Breder

(1932). It is also clear from the tables on both species that data during the height of the hurricane season, September and October, are virtually non-existent. Also much to be desired is further material of the larger sizes in sufficient quantity to make frequency studies. Only the availability of much more material suitably spread over the year can reduce the life history aspect of these species to a more refined and definitive form.

SUMMARY

1. The loss of the high, dark posterior lobe of the dorsal fin is accomplished by a process of resorption in *Tylosurus acus* in contradistinction to *T. raphidoma* in which the loss of a homologous structure is accomplished by sloughing off the area.
2. Histologically, the post-larval dorsal fin of *T. acus* differs from that of *T. raphidoma* in that the epithelium covering the surface is six to ten cell layers thick, contrasted with the extremely thin epithelium of *T. raphidoma* of only one or two cell layers.
3. Melanophores are so few in the dark fin area of *T. acus* that connective tissue elements of the inter-radial membrane are readily visible, whereas in the same locus of *T. raphidoma* such details are completely obscured by melanin.
4. These two sympatric species occupy contiguous and overlapping ranges but are adjusted to different ecological factors, *T. acus* favoring a more offshore and *T. raphidoma* a more inshore environment.
5. The above-noted differences are reflected in a variety of structural, developmental and behavioristic details.
6. Because of the scant data on which the phylogeny of the group rests it is impossible at this time to evaluate clearly the difference between the methods of eliminating the post-larval dark posterior dorsal fin lobe.
7. It is tempting, however, to think of the dark area as an invasive area of melanosis which has been arrested in *T. raphidoma*, resulting in a sloughing off, and finally in *T. acus* as an integrated part of the life history in which the material is taken care of by the less violent process of resorption.

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EXPLANATION OF THE PLATE

PLATE I

- FIG. 1. Detail of the intact dorsal fin of *T. raphidoma* before the onset of disintegration, showing thin epithelium and intense concentration of melanin. Magnification 450 \times . After Breder & Rasquin (1952).
- FIG. 2. Detail of the intact dorsal fin of *T. acus* before the onset of resorption, showing thick epithelium and connective tissue elements and melanophores. Magnification 450 \times .
- FIG. 3. Detail of the inter-radial membrane of the disintegrating dorsal fin of *T. raphidoma*, showing the loss of the epithelial layer and disintegration of connective tissue and melanophores. Magnification 450 \times . After Breder & Rasquin (1952).
- FIG. 4. Detail of the inter-radial membrane of the resorbing dorsal fin of *T. acus*, showing no disintegration. Magnification 450 \times .

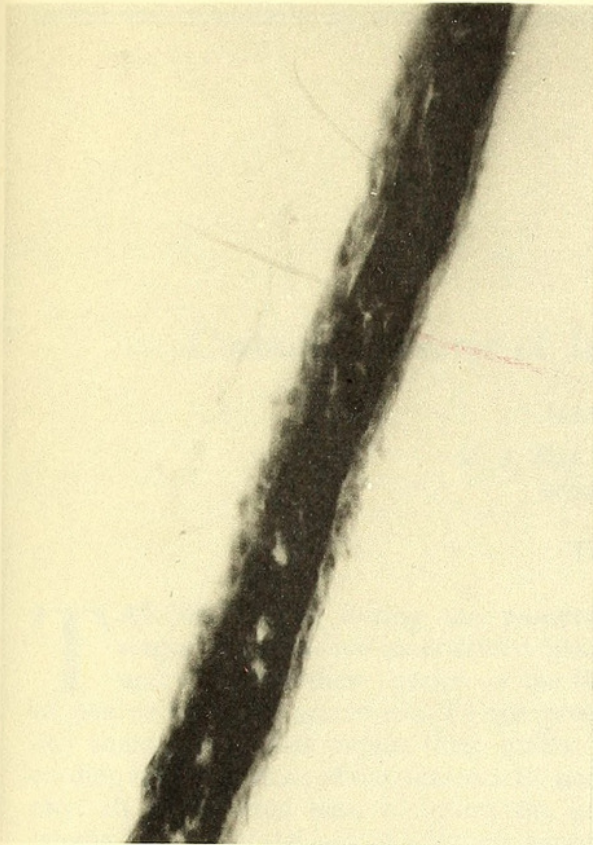


FIG. 1

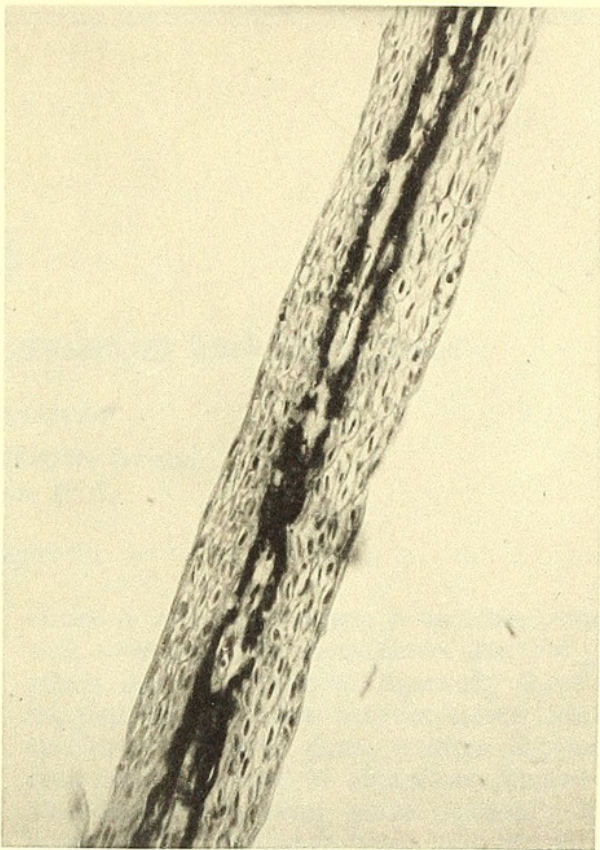


FIG. 2



FIG. 3

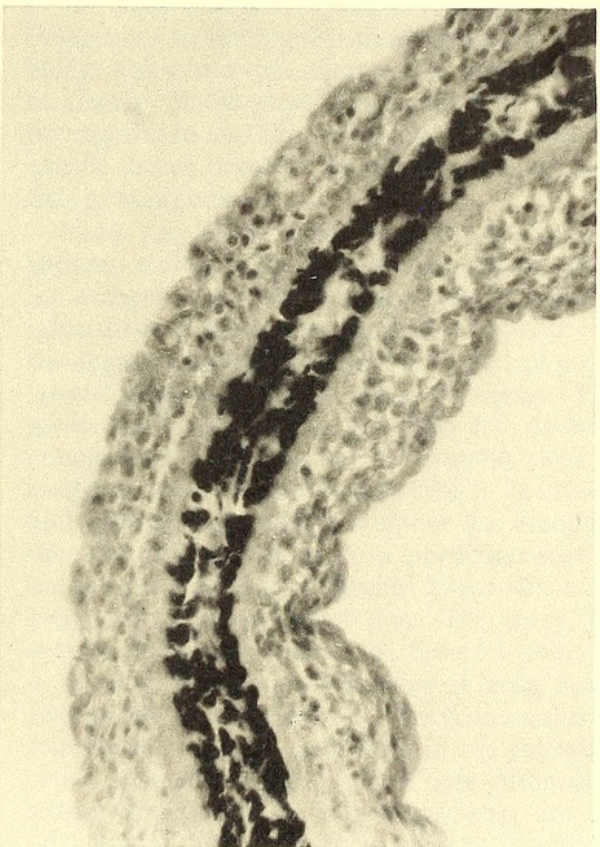


FIG. 4

THE NATURE OF POST-LARVAL TRANSFORMATION
IN TYLOSURUS ACUS (LACÉPÈDE)



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