# Eggs, Larvae and Young of The Striped Bass, Roccus saxatilis

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# ABSTRACT

Detailed descriptions of the early development of the striped bass, *Roccus saxatilis* (Walbaum), with emphasis on variation in size and morphology, sequence of fin formation, changes in body form, and attainment of the full complement of meristic numbers. are presented and illustrated for the first time. The egg is spherical, transparent, non-adhesive and relatively large. It is pelagic and buoyant, although it sinks in quiet fresh water. When unfertilized, it averages 1.3 mm. in diameter, but is 3.4 mm. when fertilized and water-hardened. The granular yolk sac, green when alive and whitish-yellow when preserved, averages 1.2 mm., and the single amber-colored oil globule is about 0.6 mm. in diameter.

Newly hatched striped bass prolarvae, which range from 2.9-3.7 mm. in total length, are relatively undeveloped and nearly transparent, with no mouth opening, unpigmented eyes, and a greatly enlarged yolk sac with the large oil globule projecting beyond the head. When 5-6 mm. long the yolk sac and oil globule are assimilated and the postlarvae show advanced development of the internal anatomy. Although the fish is still transparent, scattered melanophores are found on the head and body and chromatophores in the eyes and the ventro-posterior edge of the body.

Postlarvae transform to young between 7 and 10 mm. in length when the finfolds are lost except in the dorsal, anal and caudal regions. The largest fish in this group possess a well-formed skeleton with a full complement of 25 vertebrae. Between 10 and 20 mm. in length all fish are fully transformed, muscular tissue renders most of the internal structure obscure, and the myotomes, which generally correspond in number with the vertebrae, are no longer visible. At fish lengths of 20-30 mm. scales are found on all specimens, and with the exception of the pectoral fin-rays, a full complement of meristic structures is present in all other fins. At this stage the body is pigmented uniformly with small spots. Linear regressions between several dependent variables and the independent variable of standard length indicate that the rate of development of head, eye, and snout to anus lengths is proportional to the length of the larvae and young. Body depth and standard length are non-linear among newly-hatched larvae.

Hatchery-reared striped bass demonstrated a slow rate of growth, and were regarded as "stunted," when compared to growth rates observed in another study and field collections. Observations were also made on abnormal eggs and teratological larvae and young. Blue-sac disease is tentatively identified and described for the first time in larvae and pugnosed larvae and young are also described for the first time in striped bass.

#### INTRODUCTION

The striped bass or "rock," Roccus saxatilis (Walbaum), is one of the most important migratory fish on both the Atlantic and Pacific coasts. It spawns in the headwaters of tidal fresh and slightly brackish waters in coastal estuaries, and has been investigated intensely in recent years, especially with regard to various aspects of its reproduction. Attempts have been made to: (a) delineate carefully the spawning areas (Hollis, 1955: 1-8; Tresselt, 1952: 98-110; Hatton, 1942: 65; Tiller, 1955: 1, 4; Tiller, 1956: 1, 2); (b) determine the egg density and survival of larvae and very young (Calhoun, 1953: 279-300; Calhoun and Woodhull, 1948: 171-188; Calhoun, Woodhull and Johnson, 1950: 135-145; and Erkkila, Moffett, Cope, Smith and Nielson, 1950: 2, 22-30); and (c) determine the distribution of postlarval and young stages (Mansueti, 1954: 4, 3-4; Rathjen and Miller, 1957: 43-60).

Such studies have been hampered by the lack of reliable and extensive diagnostic and detailed mensuration data on various stages in the early development. The headwaters of estuaries are spawning areas for serranid, percid, centrarchid, and other fishes with which it might be confused, especially in the mid and south-Atlantic coastal waters. This condition makes the problem of separating early stages of striped bass from these other species difficult and sometimes impossible.

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PLATE I. Eggs and prolarvae of the striped bass, Roccus saxatilis.

At the inception of this study, it was decided that a quantitative approach to this essentially qualitative problem could provide reliable discriminatory tools for identifying the different species that resemble one another.

Pearson (1938: 829-839) has made the most significant contribution to the problem of identification of eggs, larvae and young in striped bass. He described the egg immediately after fertilization, the different stages of larvae after hatching, and presented some brief data on the transformation of larvae to the young having adultlike features. He illustrated six egg stages, seven pro-larval stages, four post-larval stages and two young stages. Ryder (1887: 502-505) published good descriptions of larvae and criticized Agassiz (1881: 274-275) for his inaccurate diagnosis and description of certain larvae and young labeled as striped bass from salt water. Scofield and Coleman (1900: 109-117) also described some of the early developmental stages and published some very poor drawings of larvae. Merriman (1941: 19) provided photographs, not particularly useful for diagnostic purposes, of both egg and young. Mansueti and Mansueti (1955: 3) provided some provisional differences between the eggs and larvae of striped bass and white perch, Roccus americanus (Gmelin).

The author is greatly indebted to his wife, Alice Jane Mansueti, medical illustrator, for the drawings, for making many of the measurements, and for extensive help in rearing the larvae. All of her work was supported by a grant from the National Science Foundation. Mr. Arthur W. Dickson, fisheries investigator, North Carolina Wildlife Resources Commission, kindly provided facilities, help and striped bass eggs and larvae on two occasions at the Weldon hatchery in North Carolina. Dr. Richard Tiller and Mr. Earl Walker, formerly biologists at the Chesapeake Biological Laboratory, and Mr. Robert Behnke, summer biological aide in 1956 from the University of Connecticut, also aided in the study. Dr. L. Eugene Cronin followed the study with great interest and provided facilities and encouragement, and reviewed the paper in some detail. Appreciation is also extended to Messers G. Francis Beaven, David Cargo, John Longwell and Dr. Vagn

Flyger, staff members of the editorial board at the Chesapeake Biological Laboratory, for their work on the paper.

#### METHODS AND MATERIALS

Eggs were stripped from female striped bass into spawning pans, and fertilized by milt from male fish in the usual hatchery manner as described by Worth, (1910: 155-159); Pearson, (1938: 831); and Dickson (1957: 2-3). The female from which the eggs were procured weighed about five pounds, while the male fish that fertilized the eggs weighed about two pounds. The eggs were placed in large McDonald hatchery jars, where a constant stream of fresh water flowed among the eggs. After fertilization several series of about 30 eggs were preserved at the time intervals given in Table 1. The larvae hatched from 36 to 48 hours later. This stage of the study dealing with eggs was conducted at the Weldon, North Carolina, hatchery for striped bass, where ripe fish were procured from fishermen working in the Roanoke River nearby. A separate group of eggs were also stripped and fertilized from ripe striped bass taken from the upper tidal reaches of the Patuxent River, Maryland, and developed at a small, temporary hatchery at the Chesapeake Biological Laboratory, Solomons, Maryland (Table 6).

Larvae were preserved at hatching, and then at different intervals of time, usually every four hours immediately after hatching, while later stages were taken at time intervals as given in Table 7. After the larvae at Weldon were hatched, all from a single female, they were placed in a polyethylene plastic bag, filled almost to capacity with hatchery water, placed in an insulated cardboard box, and transported to the hatchery at Solomons, Maryland. There were virtually no mortalities during transit. Here they were placed in several 50-gallon aquaria and various other smaller containers to be reared. They were subjected to varying densities and concentrations of live food, the general results of which will be presented elsewhere. In all cases they were placed in water transported in glass carboys from tidal fresh water parts of the Patuxent River.

All descriptions of eggs, larvae and young are based on preserved material unless otherwise stated. Some measurements were made of live eggs and larvae before preser-



PLATE II. Postlarvae and young of the striped bass, Roccus saxutilis.

vation and these then were remeasured a week later to determine the effects of formalin. In all cases there was very small shrinkage in diameter of eggs and lengths of larvae, but the effects on the overall results were negligible. Measurements of eggs, larvae and young up to 29 mm. in total length were made with a stereoscopic microscope and an ocular micrometer. Some of the largest specimens were also measured with the aid of calipers. Measurements and counts of meristic numbers follow Hubbs and Lagler (1947: 8-15) and ment in short can be regarded as the successive deployment of a chain of reactions linked in sequence," a generalization that is very apt in this study. The early stages in the development of the striped bass are divided into four categories: (1) egg stage, which begins at fertilization and ends at hatching; (2) prolarva, which is the yolksac larva, with the obvious nourishing yolk to feed it during developmental changes this is the prolarva of Hubbs (1943: 260); (3) postlarva, which is the larva between yolk-sac absorption and completion of fin-



FIGURE 1. Fertilized egg (A) and an idealized larva (B) of the striped bass with the nomenclature employed for various parts of these structures.

Ahlstrom and Ball (1954: 244-245). Myotome counts are based on suggestions given by Blaxter (1957: 4).

Both standard length (in small specimens from the tip of the snout to the urostyle) and total lengths (in small specimens from tip of the snout to tip of the finfold or caudal fin) were determined. Conversion factors for various size groups can be easily calculated from the data for total and standard lengths in Table 7. For computing body proportions, only standard lengths were used, although total lengths are used in the text and discussion, and are designated as such. Original measurements were used to construct the curves showing growth rates of various body parts and changes in body proportion for reasons given by Marr, (1955: 28-31).

The general approach used by Ahlstrom and Ball (1954: 209-245) has also been followed in presenting larval development in the sequences of fin formation, body proportion and pigmentation. As Smith (1957: 336) has pointed out, "Developformation—this is the postlarva of Hubbs; and (4) young, which begins at completion of fin-formation, showing general ossification, and general outlines of all but mature fish—this is defined by Lagler (1952: 89). When the term "larvae" is used, it refers to both pro and postlarvae combined. The transition to the young stage occurs at about 20 mm. total length, although there is no sharp line of demarcation between the larval and young stages.

#### RESULTS AND DISCUSSION

#### **Development of the Striped Bass Egg**

**Description:** The egg of the striped bass is spherical in shape, non-adhesive, and relatively large when compared to many other fish eggs. It is pelagic and buoyant, and is characterized by a single, large oil globule, a lightly granulated yolk mass, a very wide perivitelline space and a clear, tough chorion or eggshell. Before swelling or water-hardening, the chorion is heavily corrugated (Figure 1B). The spermatozoa of striped bass have not been described,



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FIGURE 2. Unfertilized egg, 1.3 mm. in diameter. A. Non-water-hardened egg, showing lack of perivitelline space; B. Magnified view of chorion, showing shallow corrugations before it is stretched.

FIGURE 3. Fertilized egg, showing single blastomere, 1.6 mm. in diameter.
FIGURE 4. Fertilized egg, showing two-cell stage (lateral view), 2.0 mm. in diameter.
FIGURE 5. Fertilized egg, showing four-cell stage (dorsal view), 2.0 mm. in diameter.
FIGURE 6. Fertilized egg, showing four-cell stage (lateral view), 2.3 mm. in diameter.
FIGURE 7. Fertilized egg, showing four-cell stage (dorsal view), 2.3 mm in diameter.
FIGURE 8. Fertilized egg, showing five-cell stage, 3.3 mm. in diameter.
FIGURE 9. Fertilized egg, showing seven-cell stage, 3.4 mm. in diameter.
FIGURE 10. Fertilized egg, showing eight-cell stage, 3.4 mm. in diameter.

although Scofield and Coleman (1910: 113-114) described in some detail spermatozoa activity in relation to temperature.

The diameter of the fertile striped bass egg, based on measurements of almost 400 eggs in various stages of development and selected at random from live developing eggs under optimum hatchery conditions, averaged 3.4 mm. (range 2.4-3.9 mm.) after water-hardening (see Table 1). Table 2 summarizes chorion diameters for this study and from published accounts. Pearson (1938: 832) did not give a mean value, but stated that the egg diameter may range from 3.2-3.8 mm. after complete water absorption or water-hardening. Merriman

compares favorably with that given by Pearson (1938: 832) of 0.56 mm. The diameter of the yolk was 1.18 mm. (range 0.90-1.50 mm.) which is similar to Pearson's mean value of 1.10 mm. Thus, the yolk mass comprised about 35 per cent of the diameter, with about 65 per cent consisting of perivitelline space. Merriman (1941: 18) has made the point that this large space protects the embryo against injury from jarring, thus contributing to higher survival in waters that are rapid and rough. Ryder (1887: 502), on the other hand, stresses its function as a larger than usual "breathing chamber." Measurements of the yolk and oil globule during various

TABLE 1. Measurements of normal eggs of striped bass, *Roccus savatilis*, fertilized May 13, 1956, and maintained at a temperature of 62-63° F., at the Weldon Fish Hatchery, Roanoke River, North Carolina.

Age in hours	Number measured			Diameter ir	n Millimeters o	f	
	• • • • • • • • • • • • • • • • • •	Cho	rion	Ye	olk	Oil G	lobule
		Mean	Range	Mean	Range	Mean	Range
Unferti-		·· ·					
lized	30	1.32	1.25 - 1.35	1.08	0.90 - 1.25	0.52	0.40 - 0.65
0.1	30	1.58	1.25 - 1.80	1.12	0.90 - 1.25	0.53	0.45 - 0.65
0.3	30	1.77	1.30 - 2.30	1.11	0.90 - 1.30	0.54	0.45 - 0.70
0.7	30	2.23	1.90 - 2.50	1.10	1.00 - 1.25	0.63	0.45 - 0.75
1	30	3.35	2.40 - 3.65	1.15	1.00 - 1.40	0.59	0.45 - 0.70
2	60	3.51	2.95 - 3.80	1.23	1.00 - 1.50	0.64	0.45 - 0.75
4	30	3.39	3.00 - 3.55	1.17	1.00 - 1.30	0.55	0.50 - 0.70
8	30	3.36	2.85 - 3.60	1.21	1.00 - 1.40	0.59	0.55 - 0.80
12	30	3.48	2.90 - 3.70	1.19	0.95 - 1.45	0.61	0.45 - 0.75
16	45	3.34	2.50 - 3.75	1.26	1.00 - 1.35	0.62	0.50 - 0.75
20	30	3.37	3.00 - 3.60	1.24	1.05 - 1.45	0.67	0.50 - 0.70
24	65	3.22	2.95 - 3.75	1.26	1.10 - 1.35	0.72	0.55 - 0.85
36	30	3.42	2.90 - 3.85	Embry	yo present	Embry	70 present
48	30	3.57	3.05 - 3.90	Hatch	ing	Hatch	ing
Total & Mean	500	$3.40^{*}$	2.40-3.90	1.18	0.90-1.50	0.61	0.40-0.85

<sup>\*</sup> This mean is based on those eggs one or more hours old, since eggs carlier than this age are in the preliminary stages of water-hardening.

(1941: 19) measured 50 eggs from the North Carolina hatchery preserved one hour after fertilization and the mean was 3.63 mm., with a range 3.24-3.95. Table 1 shows that water-hardening of eggs used in this study was not completed until one or one and one-half hours later. Scofield and Bryant (1926: 60) gave the size of 1.27 mm. for the fully developed egg diameter, but apparently were referring to the egg size before fertilization.

The diameter of the oil globule averaged 0.61 mm. (range 0.40-0.85), and this figure

stages in the development of the striped bass egg are given in Table 1.

When alive, the yolk sphere was characteristically greenish or golden green, but amber-colored or whitish yellow, and dense and granular in appearance, in a preserved state. The vitelline membrane around the yolk mass must be quite thin for it was easily ruptured. Dead eggs were frequently observed and identified in the field with yolk material flooding the perivitelline fluid (Figure 40). In preserved material, many early-embryonic eggs (before closure of the blastopore) also showed a considerable amount of yolk diffusion into the perivitelline space (Figure 37 and 38). This lethal change was due to the mechanical rupture of the yolk membrane during collection and preservation of eggs, inasmuch as eggs in which the germ ring had encircled the yolk sphere did not show this damage (Figure 13). The size of the yolk mass remained the same in all egg stages during the early developmental stages.

The oil globule was amber-colored and approximately spherical in shape. In many of the preserved samples, however, the oil globule was irregularly distorted and fractured into several to many droplets. In some live, developing eggs, several much smaller oil globules were also observed, a feature that Pearson (1938: 832) noted also. The size of the oil globule also remained the same during the early developmental stages. melanophores appeared on the underside of the oil globule. During the later stage of embryonic development the oil globule became situated close to the head of the larva (Figure 15), a sequence that Pearson (1938: 832) also noted.

**Development:** The egg of the striped bass is slightly heavier than fresh water and sinks to the bottom in a container of undisturbed water. Slight agitation serves to float the eggs and keep them suspended near the surface in fresh water. The production of eggs in brackish waters, of greater density than the egg (see Tiller. 1955: 4, and Raney, 1952: 38-39, for further comments), would probably insure floatation, and hence survival, especially in quiet waters.

The embryonic development of striped bass eggs, as in many pelagic fish, is characterized by meroblastic cleavage. Of most concern are diagnostic characters that aid

TABLE 2. Comparison of egg measurements of the striped bass, *Roccus saxatilis*, based on various studies.

Chorion Diameter		Locality from which	Pofevonco
Average	Range	eggs originated	Reference
3.4	2.4-3.9	North Carolina	Present study
$2.7^{*}$	2.0 - 3.2	North Carolina	Present study
$2.2^{*}$	1.8 - 2.8	Maryland	Present study
3.6	3.2 - 4.0	North Carolina	Merriman (1941: 9
	3.2 - 3.8	North Carolina	Pearson (1938: 831
$1.3^{*}$		California	Scofield and Bryan (1926: 60)
3.6		Unknown	Brice (1898: 185)
3.6		North Carolina	Worth (1885: 226)

\* See text (page 7).

During the early stages of development, the oil globule was centered at the vegetative pole, usually opposite the developing blastoderm. As spherical, pelagic eggs characteristically float with the vegetative pole uppermost (Ahlstrom and Counts (1955: (297) the oil globule was at the top of the yolk mass. Great difficulty was encountered in studying and drawing devolopmental changes when the yolk and oil globule were so suspended in the perivitelline lluid since most examination was limited to vertical observation. In all cases, the chorion was burst in order to examine these features in detail. Immediately following the closure of the blastopore, a number of

in the identification of striped bass eggs developed at  $62^{\circ}$  to  $63^{\circ}$  F., and the descriptions given below are for eggs that developed at these temperatures. All times reter to intervals after fertilization. Table 3 summarizes the hatching time in relation to water temperatures of eggs of striped bass cited by various authorities. Table 4 summarizes the cleavage and development stages in relation to time and temperature. Brief descriptions of different stages in the development of striped bass eggs are as follows (refer to Tables 1 and 4):

(1) Unfertilized egg-average size was 1.32 mm. with little, or no, perivitelline space. Yolk was green when alive and



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- FIGURE 11. Fertilized egg, showing 32-cell stage, 3.6 mm. in diameter.
- FIGURE 12. Fertilized egg, many-celled stage or early blastoderm, 3.5 mm. in diameter.
- FIGURE 13. Fertilized egg, germ ring and embryonic shield stage, 3.5 mm. in diameter.
- FIGURE 14. Fertilized egg, early embryonic stage (lateral view), 3.5 mm. in diameter.
- FIGURE 15. Fertilized egg, early embryonic stage (dorsal view), 3.5 mm. in diameter.
- FIGURE 16. Fertilized egg, fully developed embryo, chorion--3.5 mm., embryo--2.5 mm.

amber or opaque yellow when preserved. Oil globule was amber-colored, located at top of yolk mass, and about one-half the diameter of eggshell. Chorion was clear, transparent in life but translucent after preservation, and was covered with shallow corrugations. When touched by hand they felt like friction ridges. See Figures 2A and 2B.

TABLE 3. Hatching time of eggs of striped bass, *Roccus saxatilis*, in relation to water temperature, based on present and published studies.

Incuba- tion period in hours	Average H <sub>2</sub> O temp. in degrees F.	Locality from which adult fish originated	Reference
36-48	62-63	North Carolina	Present study
30	72	North Carolina	Merciman (1941: 9)
72	59	North Carolina	Merriman (1941: 9)
48	64	North Carolina	Pearson (1938: 831)
72		California	Scofield & Bryant (1926: 62)
74	58	Unknown	Bigelow & Welch (1925: 256)
48	67	Unknow n	Bigelow & Welch (1925: 256)
80	54 ?	California	Scofield & Coleman (1910; 115)
74	58	Unknown	Brice (1898: 185)
48	66-67	North Carolina	Ryder (1887: 502)
36	71	North Carolina	Worth (1885: 226)
64	65	North Carolina	Ferguson & Hughlett (1880: xxiii-xxvi)

(2) Immediately after fertilization to about five minutes after fertilization, the eggs began to develop a perivitelline space. Well-defined blastomeres, two-, four-, and cight-cell stages, as well as transition stages, were recognized about 20 to 40 minutes later. The blastodisc was differentiated at one pole of the yolk sphere. The cleavages observed in this study were somewhat earlier than the two-hour delay before cleavage that was recorded by Scofield and Coleman (1910: 113), although generally lower water temperatures prevailed in their work, which may have caused a slower rate of cell division. See Figures 3-10.

(3) At one hour, the 4- and 8-cell stages predominated, and the perivitelline space was even greater, hence the chorion was larger in diameter, but had not reached full capacity. The stretched chorion was now less corrugated.

(4) At one to two hours, blastomeres were evident, the perivitelline space had reached its greatest capacity, and the eggshell was thin, transparent and fragile. Thus, the increase in average diameter of the egg is a result of the absorption of water with an accompanying expansion of the eggshell and development of the perivitelline space. From this stage of development until hatching, the eggs and oil globules maintained about the same average diameter and range of sizes. The yolk mass varied in shape, of course, as the embryo develops and as some of the yolk material was metabolized.

(5) At two hours, some eggs had reached the 32-blastomere stage, although the 16cell stage predominated. See Figure 11.

(6) At four hours, the blastoderm was well-formed and berry-like in its late cleavage stages. See Figure 12.

(7) At eight hours, the blastoderm was granular in appearance. See Figure 13.

(8) At 12 hours, the blastoderm had grown halfway down over the yolk. Pearson (1938: 832), who did not record changes between 15 minutes after fertilization and 12 hours later, stated that the blastoderm was in late cleavage and the periblast was clearly differentiated about the yolk mass and becomes a paler green with age at this stage. This condition also was true in this study.

(9) At 16 hours, the blastocoel or cavity in the yolk below the blastoderm was forming. The germ-ring thickened around the periphery of the blastoderm. See Figure 13.

(10) At 20 hours, the embryo was developed and neural ridges and eyes were visible. Pigmentation was present around the embryo and the oil droplet. See Figures 14 and 15.

(11) At 24 hours, the embryo was well differentiated and extended about half way around the circumference of the yolk, as indicated first by Pearson (1938: 832). The embryo became even more intensely pigmented on the dorsolateral parts of the body and the adjacent blastoderm.

(12) At 36 hours, the larvae within the egg were approximately 1.6-2.0 mm. in total length (Pearson 1938: 832 gives the size at 1.5 mm.) and were well developed. Some were almost ready to hatch. Eyes were well-differentiated but lack pigment. The posterior part of the embryo body was free from the yolk-sac. See Figure 16.

(13) At 48 hours, the prolarvae were hatching and were 2.9-3.7 mm. long at this

time. Pearson states that the prolarvae is about 2.5 mm. upon leaving the egg, but measurements in the present study indicate that this figure is low. The newly hatched fish tended to settle to the bottom of an aquarium filled with unagitated water despite swimming efforts to remain at the surface.

TABLE 4. Cleavage and developmental stages of the eggs of striped bass, *Roccus saxatilis*, in relation to time and temperature at 62-63° F.

	B1	astor	nere	Num	bers	and	Deve	lopm	ental	Sta	ges
Age in hours	<b>H</b>	8	4	w	16	32	64	Blasto- derm	Gas- trula	Embryo	Ilatch- ing
0.1	x							-			
0.3	x	х	х								•
0.7		х	х	х							
1			N	х	N			× -			
2	•	*****	х	x	х	х					
4			х	х	х	х	х				
8		~~	-		x	х	х	х			·
12						х	х	х	х		
16						· -	N	х	N	~	~ .
20			-						х	х	
24		· - ·						· - ·	~	х	
36		·						·		x	N
$48^{\circ}$			• ~							х	X

\* All eggs hatched at about this age in hours.

Variation in eggshell diameters: Some variation has been observed in diameters of striped bass eggs in this study. Tables 5 and 6 show that a group of small eggs from another female striped bass at the Weldon, North Carolina, hatchery and from another group taken and fertilized from striped bass in the Patuxent River, Maryland, were abnormally small when compared with published accounts. Other field workers in Maryland have found striped bass eggs with advanced stages of cleavage and embryos that were also characterized by abnormally low diameters of the chorion, but with normal-sized yolk masses and oil globules. Tables 5 and 6 show that average sizes of the yolk masses and oil globules from eggs with small chorion diameters do not differ greatly from the average diameters of volk masses and oil globules given for normal-sized eggshell diameters in Table 1. As yet there is no evidence to shed light on why abnormally small eggshell diameters occurred in the eggs measured in Tables 5 and 6, or taken by other field workers in Maryland waters. Three possibilities should be investigated: (a) striped bass eggs deposited in fresh water but carried too rapidly into very brackish or salt water, in the case of the Patuxent River eggs, may have the expansion of the chorion diameter arrested by osmotic pressure of the external environ-

TABLE 5. Measurements of abnormally small eggs from striped bass, *Roccus saxatilis*, fertilized May 5, 1955, and maintained at a temperature of  $62-63^{\circ}$  F. at the Weldon Hatchery, Roanoke River, North Carolina.

ge in ours	umber asured		Diame	eter in	Millime	ters o	ť
A R	ñŽ	C}	norion		Yolk	Oil	Globule
		Mean	Range	Mean	Range	Mean	Range
0	39	1.28	1.20-1.35	1.03	0.90-1.15	0.54	9,45-0.60
1	36	2.54	2.25-2.70	1.15	0.95 - 1.25	0.61	0.40-0.75
4	39	2.43	2,00-2.65	1.07	0.95-1.25	0.57	0.50-0.65
12	30	2.87	2.70-3.05	1.12	0.90 - 1.25	0.56	0.50-0.70
24	30	2.83	$2.55 \cdot 3.15$	1.06	0.90-1.20	0.63	0.55 - 0.75
Total &							
Mean	150	2.67*	2.00 - 3.15	1.69	0.90 - 1.25	0.58	0.49-0.75

\* This mean is based on those eggs one or more hours old, since eggs earlier than this age are in the preliminary stages of water-hardening.

ment; (b) fertilized eggs produced from very small sexually mature female and male striped bass may be considerably smaller than those produced by larger fish (Brown,

TABLE 6. Measurements of abnormally small eggs from striped bass, *Roccus saxatilis*, fertilized April 21, 1955 from the Patuxent River, and maintained at a temperature range of 69-79° F. at a small hatchery in the Chesapeake Biological Laboratory, Maryland.

ge in Iours	asured		Diame	ter in	Millime	ters o	f
4 Y	Σ́θ	Ch Mean	vorion Ranze	Mean	Yolk Range	Oil Mean	Globule Range
					1 40 1 0		A 47 6 40
8	30	2.18	2.00-2.30	1.11	1.00-1.3;	0.08	0.45-0.60
12	30	2.19	1.95 - 2.40	0.97	0.90 - 1.30	0.63	0.45 - 0.65
16	39	2.28	2.05-2.45	1.08	0.95-1.30	0.58	0.40 - 0.70
$28^{*}$	22	2.23	1,85-2,75	1.02	0.85-1.3	5 0.68	0.55-0.75
Total &							
Mean	112	2.22	1.85-2.73	5 1.94	0.85-1.8	5 0,62	0.40-0.75

\* All evgs perished after the 28-hour period.

1957: 376, on the basis of growth studies in trout, states that the final size of the eggs depends both on the size of the female parent and on her level of nutrition during the period preceding spawning: larger fish and fish with a more abundant food supply generally produce larger eggs): (c) there may be considerable differences in average egg diameters between striped bass from North Carolina, California and Maryland waters, from which measurement data is available. The data summarized in Table 2 and measurements of eggs from plankton collections from the Patuxent River. Moryland, however, do not support this latter thesis.

#### Larvae and Young

State of development at hatching: The striped bass hatches and begins its postembryonic existence before the mouth forms and before the eyes become pigmented. The young of many other migratory and estuarine fish with pelagic eggs, including the American shad, hickory shad, alewife herring and glut herring are in a similarly undeveloped state at hatching.

The details presented herein are based on a study of 145 larvae and young ranging from 2.9 to 29.0 mm. in total length, reared under hatchery and laboratory conditions. The larvae were chosen periodically at random from the laboratory-reared fish in aquaria. After preservation, measurements were taken and details of pigmentation and changes in body form were recorded. All these sequences can be observed on the drawings accompanying the text (Figures 17-28).

The period of larval development is considered to extend from hatching to the completion of fin formation, but the end of the larval and beginning of the young stage are not sharply defined in the striped bass. All fins are apparently fully formed after about 22 mm, total length, but there appears to be considerable variation in the development and terminal formation of any one fin in relation to other features.

#### Stages of development at various sizes:

(1) At batching—the prolarvae were about 36-18 hours old after fertilization, and ranged from 2.0-3.7 mm, total length. They possessed a very large yolk sac with a large oil globule, which projected beyond the head. The eyes were not pigmented. See Figure 17.

(2) At about 5 mm, they were about 2-5 days old, were more slender, with part of their volk sac absorbed. They also pos-

sessed a smaller oil globule. Ryder (1887: 503) illustrates a Jarva this size that is 16 days old after hatching. He described the tail of this specimen, as are specimens in the present study, as distinctly spatulate and rounded; and he also noticed the presence of an air bladder and pronounced hooked teeth in both jaws, which were not observed in fish of this size in the present study (see Table 9). In this study, melanophores were observed along the ventral surface, and the eyes were pigmented with yellow, orange and black. The jaws were differentiated and the digestive tract, with some pigmentation along the edges, had begun to form. Myotomes were easily counted. The pectoral buds had formed a fan-like fin. See Figure 18 and 19.

(3) At about 7.5 mm, they were 10to 15 days old, quite slender, with the volk sac fully absorbed and with no oil globule visible. No fins were visible except the pectorals. The fin-folds became lost except in the dorsal, anal and caudal regions, with the first dorsal and pelvics not indicated. Pigmentation extended along the ventral part of the body, over the upper surface of the well-formed air bladder, and the visceral mass. Branching melanophores were also evident on the side of the head, the lower jaw and along the lateral portions of the tail regions behind the position of the anus. Teeth were visible. Some fish were in various stages of transformations. See Figures 22 and 23.

(4) At about 10 mm, they were 20 to 30 days old. The dorsal and anal fin-rays were somewhat differentiated, although the first dorsal elements and pelvic fins were absent. These fin-rays were made up of well-defined longitudinal fibers. The notochord curved dorsally in the area of the urostyle, although the caudal portion was not vet homocercal as shown in Pearson (1938: 836). The caudal fin-rays, however, were well-developed. Pigmentation was heavier in the same regions as in the smaller larvae, although it was not as profuse on the top of the head as in Pearson's figure for a 9 mm. fish. Although the skeletal structure (see Figure 29), teeth and other features of the head were advanced, they were not as well-developed as Pearson suggests. Myotomes were correlated with the number of



# STRIPED BASS PROLARVAE

FIGURE 17.	Prolarva, soon after hatching, 3.3 mm. long.
FIGURE 18.	Prolarva, 5.3 mm. long. A. Lateral view. B. Dorsal view.
FIGURE 19.	Prolarva, 5.5 mm, long.
FIGURE 20.	Prolarva, 6.0 mm. long. A Dorsal view. B. Ventral view.
FIGURE 21.	Prolarva, 6.3 mm. T. L., almost indistinguishable from early postlarva.

vertebrac. Some fish were well along toward transforming from postlarvae to young. See Figures 21 and 25.

(5) At about 15 mm, they were 30 to 40 days old. Although the specimens reared in this study were apparently stunted in growth, at this stage they were almost fully transformed, with soft dorsal, anal and caudal fins well-differentiated, the last fin being homocercal in shape. The spinous and pelvic fins however, were not welldeveloped at this size. The fin-rays were segmented, and some fish had two while others had three anal spines. The skull structure was highly developed, with most of the bones characteristic of the fingerling fish, and was largely ossified. All the vertebrae were visible only in translucent specimens (Figure 29). None of the specimens exhibited the fin-fold connection between the spinous and solt dorsal fins described and illustrated by Pearson (1958: 836), as can be seen in examples illustrated in Figures 25-28. The specimens in this study were much more slender than the description and illustration of a relatively robust fish in this general size range given by Pearson (1938: 837). In many fish, muscular bands of tissues obscured the skeletal and abdominal elements, and they were generally opaque, compared to 10 mm. fish which were translucent or transparent. Myotomes could no longer be counted. Pigmentation was still not fully developed, although melanophores were concentrated on the head, sides of the abdomen and along both sides of the body posterior to the anus. Pearson's fish seems to be more heavily pigmented at this stage. Worth (1904: 226) stated that "The four-weeks old specimens, about one-half inch long. were reared in a crudely constructed pool near the hatchery door. Their fins are easily discernible, and when they were being introduced into the vial, the stripes down their sides could be seen." Stripes were not evident in any fish in the present study, nor did Pearson (1938: 837) observe stripes in any fish less than 11/2 inches long that were reared during his study.

(6) At about 20 mm, they were 50 to 70 days old. These fish were markedly stunted in growth, when compared to fish of the same general age taken from the Patuxent River (see Figures 27 and 28). The spinous dorsal, although not complete,

was evident, while the other fins, except the larval pelvic fin were in various stages of maturity as far as attaining the full complement of meristic structures. Although most fish had three anal spines, a lew still possessed two, and in these the hist solt dorsal ray was in various stages of ossification and desegmentation. Scales were observed for the first time in the largest fish in this general size group. Pigmentation was heavier laterally from the head to tail regions than in smaller specimens. The fins were also pigmented. See Figure 27.

(7) At about 25 mm, they were 60 to 80 days old. All these fish were covered with scales over the entire body (Figure 30), three anal spines, and generally possessed the full complement of meristic characters (see Table 7 for exceptions). Although well-pigmented, there still was no indication of the longitudial striping found on older fingerlings. The body was covered with small melanophores that provided a diffuse spotting effect.

(8) At about 30 mm, they were 70 to 100 days old. These fish were also considerably stunted from sizes attained by wild lish at the same general age (see Figure 36). Pugheaded features in abnormal specimens were quite striking at this size (Figure 50). The meristic numbers were almost complete except for pectoral fin-rays Pigmentation was present over most of the body and fins, and less so on the abdomen, in the form of minute black dots scattered over the entire body such as described and illustrated for a 36 mm. fish about 20 to 30 days old taken in the field by Pearson (1938: 837). The series of about nine oblique V-shaped lines observed by Pearson along the lateral line of the fish were not observed in the fish of this general size range in this study. See Figure 28.

**General comments:** The results of the present study were similar to the other studies cited above of the striped bass eggs. larvae and young based on material from known parents. The only exception is the study of larvae taken from plankton collections and not based on known parents and hatchery-rearing. The postlarvae and young described here were compared with those described and illustrated by Agassiz (1881: 371-275), and it is certain that he ap-



#### STRIPED BASS POSTLARVAE

FIGURE 22. Postlarva, 6.7 mm. long (early stage).

FIGURE 23. Postlarva, 8.1 mm. long (early metamorphosis). Brine shrimp eggs can be observed in the intestine.

FIGURE 24. Postlarva, 9.3 mm. long (metamorphosing).

FIGURE 25. Young, 12 mm. long (largely metamorphosed).

parently did not have striped bass. His specimens, beginning at about 3.5 mm. in length, were collected with tow nets in salt water, and are not based on rearing studies. He has given eight illustrations purporting to be postlarval and young striped bass, all of which have many striking differences from those reared in this study, and from descriptions of specimens from known parents given by Ryder (1887: 502-505) and Pearson (1938: 829-839). In fact, Ryder (1885: 503), corroborated by Ehrenbaum (1905: 17), both after careful consideration of available material, firmly rejected the identification of Agassiz's flsh as striped bass (see also Tracy, 1910: 44-45, 121-122).

Larval activity: Immediately after hatching, the movements and position of prolarvae were directed largely by the large oil globule in the anterior part of the yolk sac. Typically, it caused the individual to assume a perpendicular position, with head toward the surface of the water. The newly hatched prolarva also tended to settle to the bottom of a still aquarium despite swimming efforts to remain near the surface. As Pearson (1938: 832) and Dickson (1957: 3) pointed out, a strong current of water enables the fishes to remain suspended and in more or less continuous motion. After one or two days their activity and movements were random near the surface, without any apparent orientation except when a light was placed at one end of the aquarium. They were positively phototropic, moving toward lights placed in front of the aquaria. This response was useful in concentrating phototropic plankters and fish in a single area. There was a tendency in the aquaria for the prolarva to attach to floating detritus or dead larvae. Feeding activities of larval and young fish will be described in another paper dealing with rearing problems. About two weeks after hatching, the postlarvae began dying out catastrophically, and for a period of 3 to 5 days, dead and dying fish continued to be found. Dying fish floated perpendicularly in a vulnerable manner, and some were caught and devoured by hydra and other predators that could not be completely controlled in the aquaria. Surviving postlarvae and transformed young foraged about on the bottom for food, coming to the surface only when food was

introduced. When not feeding, young striped bass remained near the bottom of their containers.

**Changes in pigmentation:** Although pigmentation is meager, there is considerable variation in the amount and quality of pigment that is found on striped bass larvae of comparable size. The newly hatched larva (Figure 17) has a pigment pattern similar to that of an embryo in a late stage egg. Melanophores were generally concentrated on the following locations: (a) on dorsolateral aspects of the head; (b) over the anterior and lateral aspects of the oil droplet; (c) along the dorsal surface of the yolk sac; and (d) irregularly along the lateral portion of the trunk and tail.

Before yolk-sac absorption was completed (Figures 17-20), however, the melanophores had migrated or coalesced to form the three conspicuous pigment areas characteristic of striped bass larvae: (a) conspicuous ventrolateral pigmentation by stellate melanophores along the posterior two-thirds of the trunk and tail; (b) a heavy concentration of pigment along the dorsal peritoneal wall, on the dorsolateral and ventrolateral wall of the yolk and along the gut: and (c) heavy concentration around the oil droplet. The eyes were heavily pigmented with melanophores and yellow or orange chromatophores shortly after hatching, and frequently there were scattered block spots on the lower jaw and belly. The pigmentation cited above was characteristic of larvae 4 to 10 mm. total length.

Pigment was added gradually and individuals between 7 to 10 mm. showed a more prominent display of melanophores. Figures 22:24 show typical individuals with a heavy coalesced spot under the otocyst, and on the developing air bladder. Occasional melanophores appeared on the sides of the head and along the lateral portions of the trunk of the tail, even on the caudal fin. Some orange chromatophores were observed along the trunk of the tail. There was no conspicuous pigmentation of the head except those mentioned above.

Among larvae between 10 and 22 mm. long, pigment was distributed as follows: (a) on head, snout and above and behind



STRIPED BASS YOUNG

- FIGURE 26. Young, 14 mm. long.
- FIGURE 27. Young, 16 mm. long.
- FIGURE 28. Young, 29 mm. long.

eyes and on the upper parts of the opercular flaps; (b) on dorsolateral portion of body; (c) along posterior midline of body dividing the upper and lower halves of myotomes; (d) along posterioventral keel at hatching, with the greatest body depth at or behind the pectoral fin. The body narrows generally behind the anus. The digestive tract underlies only the anterior one-half of the body, the distance from



FIGURE 29. Drawing of an almost metamorphosed striped bass larva, 10 mm. long, showing details of the skeletal structure. Dotted parts within the outline are unossified structures.

of trunk, at base of anal fin, and on the abdomen; and (e) scattered pigment on the caudal fin. The fins never became heavily pigmented in striped bass less than 29 mm. long. (See Figure 28).

Chromatophores on larvae in general were sparse. None were observed on prolarvae, but yellow and orange chromatosnout to anus being approximately 62 per cent of the standard length. The intestine is continuous and unlooped, readily seen in small larvae before it is obscured by overlying musculature. The changes in body form from prolarva to young are best seen in the various attached drawings (Figures 17-28).



FIGURE 30. Drawing of scales from young striped bass, recently metamorphosed. A. Fish, 20 mm. long; scale,  $0.24 \times 0.31$  mm.; B. Fish, 20 mm. long; scale,  $0.26 \times 0.31$ ; and C. Fish, 24 mm. long; scale  $0.33 \times 0.39$  mm.

phores were observed in the eyes, on the head and slightly posterior to the base of the anal fin in developing live specimens ranging from 6 to 10 mm. These colors became more intense in postlarvae and voung.

**Changes in body form:** The striped bass larva is moderately elongate, except

Measurements are summarized in Table 7, and are based on average values. Those in Table 8 represent proportions of various body features to standard length. Very small larvae were well represented in the tables but as they increased in size mortalities increased and the sample size for each size interval decreased greatly. The standard length of striped bass larvae and young

i				:						<u> </u>	e columns	respective	nelvic in	d larval	boral an	arval pect	$[LP \simeq ]$		
X		17	11.0	III	I-11	XI	1-5.0	14.0	~1	}		15.70	5.70	2.90	7.75	25.00	29.00	1	29.0-30.0
, 1			ļ	Ì		ł		ł	ļ	1	-	}		ļ	ſ			ł	28.0-29.0
×		17.0 -	11.5	111	I-11.0	XI	- I-5,0	18.5	7.0	ļ	ļ	15.28	5. <del>.</del> .	2.52	7.30	24.00	27.50	61	27.0 - 28.0
1	}		ł	1	1		1		i	ļ	-	ł		-	1		-	٩	26.0-27.0
X		16.3 -	11.3	ш	I-10.7	VII-IX	J-5.0	13.0	7.0	ļ	1	14.30	5.52	2.38	7.07	22.50	25.38	ట	25.0-26.0
1			 1	1	1		, 1 ,		ļ	{	i	i		ļ	]	ŀ	:	ł	24.0-25.0
X		16 -	12.0	III	1-10	XI	I-4	12	~1	ļ	-	13.65	5.65	2.50	6.20	21.30	23.95	1	23.0-24.0
х		16 .	12.0	III	I-11	VII	ΓÞ	12	-1		-	12.86	5.27	2.33	5.92	20.12	22.82	<b></b>	22.0-23.0
x		16 -	10.0	III	I-11	VIII	LP	12	~1	ļ	ì	12.10	4.90	2.10	5.60	19.00	21.66	1	21.0-22.0
X		16 .	12.0	II	I-10	VIII	LP	12	~1		i	11.30	4.35	1.89	5.00	17.70	20.17	-	20.0-21.0
[		-		}		1	i 1		:		ļ	5	l	1	ļ	;		ļ	19.0-20.0
I		16 .	12.0	Ш	I- 9	VII	LP	12	-1		-	10.51	3.99	1.73	4.63	16.38	18.69	1	18.0 - 19.0
ļ		16 .	11.0	111	I- 9	V	$\mathbf{LP}$	12	-1		-	10.03	3.76	1.60	4.30	15.57	17.71	1	17.0-18.0
1		15.5	11.0	П	I-10.5	VI-V	$\mathbf{I}'\mathbf{P}$	12.0	7.0	ł	-	9.20	3.50	1.40	4.30	14.20	16.50	2	16.0-17.0
		15.7 .	12.7	11-111	I-10.7	Ν	ЧЛ	11.7	7.0	1	ļ	7.93	3.35	1.21	3.68	12.80	15.12	60	15.0-16.0
ļ	}	16.0 -	13.0	11	I-11.3	III-IV	l,P	11.7	7.0	[	1	7.94	3.26	1.14	4.03	12.45	14.50	ట	14.0 - 15.0
{		15.5 -	13.0	Ш	I-10.5		ľ	12.0	7.0			7.05	2.65	0.98	3.42	11.85	13.25	19	13.0 - 14.0
ļ	12 25	15.3	12.7	п	I-10.7	III-IV		11.0	7.0		ł	6.92	2.52	1.00	3.48	11.13	12.62	ಒ	12.0 - 13.0
1	12.5 25.3	15.7	13.0	п	I- 9.7		1	10.7	7.0		ļ	6.27	2.45	0.88	3.00	10.50	11.63	ಜ	11.0-12.0
{	13 27	16	:	I	I-11	п	1 :	11	-7	ĺ	, 1 1	6.05	2.17	0.85	3.00	9.70	10.38	1	10.0-11.0
1	12 26	16	11	II	I-10	1	i	11	~1			5.24	2.07	0.73	2.41	8.72	08.6	-	9.5 - 10.6
ł	12 25	16	10	I	I- 9	п	-	10				5.03	1.96	(0, 69)	2.19	8.42	9.33		9.0-9,5
ł	13 26	10	x	Ţ	I- 8	4 { 1		30	~1	ļ	-	4.80	1.84	0.67	1.90	8.10	8.70	1	S.5-9.0
ł	12 25		1	i	I- 6	, i		LP	6	0.19	0.48	4.51	1.72	0.62	1.78	7.73	8.23	-	8.0- 8.5
	12.5 25.5	14	-7		I- 4.0	П	1	I,P	4.0	l i	0.52	4.26	1.53	(.59)	1.60	7.36	7.76	14	7.5- 8.0
1	12 25					ļ		LP	r V	ł	0.50	4,05	1.48	(1.52)	1.65	7.09	7.33	1	7.0-7.5
ł	12.7 24.9			+	}	-		LP	ļ	0.43	0.45	3.63	1.19	0.46	1.27	6.35	6.60	:	6.5-7.0
	12.0 23.5				1	-	1	гЪ	+	 i	0.54	3.31	0.86	0.40	1.06	5.85	6.10	2	6.0- 6.5
1	12.4 24.1		-			н Ц.		LP		-0.51	1.44	2.99	0.94	0.34	1.02	5.47	5.68	51	5.5-6.0
i	12.0 22.8					i	+	LP	į	0.53	1.82	2.90	1.09	0.28	0.76	5.05	5.24	24	5.0- 5.5
i	12.5 23.5	ļ							ł	0.68	1.74	2.72	0.94	0.26	0.70	4.56	4.78	2	4.5- 5.0
ì	11.4 23.4	İ		ļ	ļ		ļ	ł	•	0.57	2.04	2.40	1.38	0.30	0.63	4.07	4.22	4	4.0-4.5
1	10.6 22.1	İ					-		]	0.63	1.83	2.17	1.10	0.24	0.57	3.50	3.57	30 27	3.5 - 4.0
I	10.8 22.4		}	ļ	[			Į	í	0.61	1.85	2.17	1.12	0.24	0.54	8.36	3.41	27	3.9- 3.5
1	9.7 18.3						1		; {	0.66	1.82	2.06	1.23	0.20	0.40	2.78	2.38	7	2.5- 3.0
$\Pr$	s/a tot.	Ca F	A Se R	A Sp	S (sei Do	Spi (fi Do	Pe I	Pec H	Bra ste R	Glo Dia	Y S Lei	Sno Ani	Gre De	I Le	H Le	Sta: Le (S	T Le (T	fish	mm.
esence o Scales	Myotomes	udal 'in	nal oft- ays	nal ines	oft cond) orsal	nous rst) rsal	lvic Tin	etoral Fin	nchio- egai ays	Dil Dule meter	olk Sac ngth	out to 1s s/n	entest epth	lye ngth	ead ngth	ndard ngth .L.)	otal ngth '.L.)	ber of	inter- vals (T.L.)
of				unts	eristic Co	M					,el's	1 Millimet	ements ir	Measur	Average		1		Size

TABLE 7. Measurements and meristic counts of larval and young striped bass, Roccus saxatilis, reared under laboratory hatchery conditions.

ECC' TVEAVE VAD AODAG OF THE STRIPED BASS, ROCOG SAXATLES

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was the independent variable in all comparisons of various morphometric features that were employed as dependent variables. In all cases the relationships were found to be essentially linear, except for body depth. Lund (1957: 3) in his similar study of much larger striped bass ranging from 31 to 420 mm. also described linear relationships for similar and other variables.

Head: The head grows at a constant rate in relation to the standard length during the early development, increasing 0.34 mm. in length for every millimeter increase in standard length (see Figure 31). This was shown for larvae and young between 2 and 25 millimeters standard length, where actual measurements were plotted. When head length, expressed as a percentage of standard length, was plotted against the standard length (Figure 32), a different type of plot resulted. The advantage of the former over the latter method of plotting data has been pointed out by Marr (1955: 28-29).



FIGURE 31. Regression of head length on standard length of the striped bass. Each dot is the average of a group of measurements. The regression line is fitted by the method of least squares. The outline drawings of the larval and juvenile stages are not drawn to scale.

The head length was approximately 15 per cent of the standard length in newly hatched larvae, increasing to about 30 per cent at 10 mm. and remaining at this approximate value to the largest young in this sample. Thus, at hatching, the head was a smaller part of the standard length, but as the larva increased in size a uniform rate of increase of the ratio of head length to standard length took place. Lund (1957: 6) found that the relation of head length to standard length is linear in larger striped bass ranging from 31 to 420 mm. long.



FIGURE 32. Regression on head length, expressed as a percentage of standard length, on standard length of striped bass. The curve is fitted by eye from statistics given in Table 8.

Snout to anus length: The anus is located roughly two-thirds of the distance back along the body, and it retains this relative position throughout larval and young stages (see Table 8). The distance from snout to anus increased 0.65 mm.



FIGURE 33. Regression of the snout to anus length on standard length of striped bass. Each dot is the average of a group of measurements. The regression line is fitted by the method of least squares. The outline drawing of the larval and juvenile stages are not drawn to scale.

for each millimeter increase in the standard length. Since the relation is constant, this is an important taxonomic character. Figure 33 illustrates this relationship.

Body depth: The greatest body depth, usually at or behind the pectoral fin, increases more rapidly during the early part of its development than during the later part (see Table 8). Figure 34 shows that as the fish grows from 2.8 and 5.8 mm. in length there was an absolute decrease, in body depth, but between 6.4 and 25.0 mm. there was a proportional increase. Thus, the very early larval stages decreased 0.26 mm. in body depth for each millimeter increase in standard length, but the later larval and young stages, increased 0.26 mm. for each millimeter increase in standard length. It is evident also that the striped bass larvae and young become progressively more slender with increase in size. Lund (1957: 3) found that the relation of body depth length to standard length is linear in larger striped bass ranging from 31 to 420 mm. long.



FIGURE 34. Regression of greatest body depth on standard length of striped bass. Each dot is the average of measurements. The regression lines are fitted by the method of least squares. The outline drawings of the larval and juvenile stages are not drawn to scale.

**Eye:** The eye of the striped bass larva is round, with a ventral cleft developed to a varying degree. It grows at a relatively uniform rate throughout the larval and the young stages (Figure 35). The distance from the snout to the anterior margin of the eye was about 1/3 to 2/3 the diameter of the eye, the proportional distance being greater among the later stages. The eye diameter measured horizontally increased 0.12 mm. for each millimeter increase in standard length.

Myotomes: In general, myotome development was from anterior to posterior. These segments were assumed to correspond generally to the number of vertebrae (Norman, 1948: 167; and Blaxter, 1957: 3, 12). The various drawings indicate that each myotome was shaped like an "S". On either side each of these segments was further divided into an upper and lower half by a groove running along the length of the fish. Although myotomes were evident on larvae within the eggs they could not be reliably counted.



FIGURE 35. Regression of eye diameter on standard length of the striped bass. Each dot is the average of a group of measurements. The regression line is fitted by the method of least squares. The outline drawings on the larval and juvenile stages are not drawn to scale.

The formation of visible myotomes proceeded slowly among very small larvae. The full complement of 25 myotomes was not evident until the larvae were over 7 mm. standard length (see Table 7). Between 6 and 12 mm. the total number of myotomes varied around the mean of 25, with a range of 23-27, although Blaxter (1957: 12-13) found that the number of myotomes on the average was about 5 per cent more than the number of vertebrae in counts made on the same herring larvae. The average number of myotomes counted between the snout and anus generally increased in numbers as the larvae increased in size at the very early stages in development, but the number soon stabilized at about 12 after a length of 5 mm. was reached. There was also an apparent increase in myotome counts between hatching and absorption of yolk sac. This increase is undoubtedly due to the myocommata developing in the tail after hatching; the myotome tissue is present but is not

differentiated. These conditions have been observed also in the sea herring, *Clupea harengus*, by Blaxter (1957: 6). At present it is difficult to say at what stage in the development the number of myotomes is determined in the striped bass, but the observation above suggests that it is soon after hatching. After about 13 mm., the myotomes could no longer be counted (see Table 7).

TABLE 8. Body proportions of striped bass larvae and young.

		Body P Percent	roportion age of S	is Expres tandard	sed as Length
Size Intervals in Total Length	Standard Length	Hend Length	Eye Diameter	Greatest Depth	Distance from Snoat to Anus
2 50- 3 00	2.78	14.3		14.2	7.4.1
3 00- 3 50	3.36	16.0	7.1	33.3	64.6
3 50- 4 00	3.50	16.3	6.8	29.8	62.0
4 00= 4 50	4.07	15.5	7.4	33.0	58.9
4 50= 5 00	1.58	35.4	5.7	20.6	59.6
5.00- 5.50	5.05	15.0	5 5	21.6	57.4
5 50- 6 00	5.47	15.6	6.2	17.9	51.7
6.00- 6.50	5.85	18.1	6.8	14.7	56.6
6.50+ 7.00	6.35	29.0	7.2	18.7	57.2
7.00- 7.50	7.09	23.2	7.3	20.9	57.1
7 50- 8.00	7.36	21.7	8.0	20.7	57.9
8 00- 8,50	7 73	23.0	8.0	22.2	58.3
8.50- 9.00	× 10	23.4	8.8	22.7	59.2
9,00- 9,50	8.42	26.0	8.4	23.3	59.7
9.50-10.00	8.72	27.6	8.8	23.7	60.1
10.00-11.00	9.70	30.9	8.8	22.4	62.4
11.00-12.00	10.05	29.8	8.8	24.4	62.4
12.00-13.00	11,13	31.3	8.9	22.6	62.2
13.00-14.00	11.85	28.9	8.3	22.4	59.5
14.00-15.00	12.45	32.4	9.2	26.2	63.8
15.00-16.06	12,80	28.1	9.4	26.2	61.9
16.00-17.00	14.20	30.3	9.8	24.6	64.8
17.00-18.00	15.57	27.6	10.3	24.1	64.4
18,00-19,00	16.38	28.3	10.6	24.4	64.2
19.00-20.00					
20,00-21,00	17.70	28.2	10.7	24.6	63.8
21.00-22.00	19.00	29.5	11.0	25.8	63.7
22.00-23.00	20.12	29.4	11.6	26.2	63.9
23.00-24.00	21.30	29.1	11.7	26.5	64.1
24.00-25.00					•
25.00-26.00	22.50	31.4	10,6	24.5	63.6
26.00-27.00					·- ·
27.00-28.00	24.00	30.4	10.5	24.0	63.7
28.00-29.00	·····				
29.00-30.00	25,00	31.0	11.6	22.8	62.8

The paucity of larger specimens reared in the laboratory did not allow a detailed study of vertebral development and the sequence of ossification. Some observations are available on the vertebrae. Figure 29 shows a specimen 10 mm. long that pos-

sessed a full complement of 25 vertebrae. With the aid of transmitted light under stereoscopic observation, vertebrae were visible in specimens beginning at about 7 mm. in length. In general, vertebral development seemed to be from anterior to posterior. Figure 29 also shows that some of the head bones were well-developed and ossified at a size over 10 mm. in total length. The caudal and abdominal vertebrae were distinct from one another. The caudal vertebrae, including the hypural plate, consisted of 13 vertebrae, while the abdominal vertebrae numbered 12, as reported by Jordan (1905, 1. 48) and Merriman (1940: 59). The vertebrae were found in some fish to correspond in number with the myotomes, thus serving to emphasize the general usefulness of the latter in meristic counts. In a few specimens. differences of  $\pm 2$  myotomes to the vertebrae were observed, indicating that caution is necessary in making these counts.

**Branchiostegal rays:** Table 7 indicates that these rays were visible when the fish were over 7 mm. The full complement of 7 rays was formed at the very small size of 8 mm. The sequence of ossification seemed to be from upper to lower rays.

Teeth: Teeth were evident on the mandible at about 6 mm. in a late prolarva which displayed a single fang-like tooth on the mandible. On postlarvae metamorphosing to the young stage at 8 mm the premaxillary teeth were evident. Table 9 shows that the mandibular teeth appeared first and maintained slightly greater number throughout the larval growth and transformation. Teeth on both jaws were unevenly spaced and tended to vary in size. All were slender, conical and recurved, the anterior showing the most curvature. Just before a length of 12 mm. is attained the teeth on both jaws became biserial, and in fish of about 20 mm. this feature was most pronounced, although counting is complicated by the irregular grouping of these teeth. The teeth of the inner row on either jaw were slightly longer and pushed backward. Ryder (1887: 503) found teeth on both jaws in larvae only 5 mm. long.

Gill rakers: Although gill rakers could be observed clearly in a few specimens, in

most cases counts were so unreliable as to render the effort wasted. Dissection was considered a drastic measure since the number of specimens was low. Lewis (1957: 5) stated in his exhaustive study of this character in O and I age groups (one and two summers old, respectively) of striped bass from throughout its range that: "Gill raker counts were not made on fish below 26 mm, due to the difficulty of removing the entire arch." He found that there was no change in the number of gill rakers in the first two years of growth in these advanced fingerlings. The mean value for the total number of gill rakers in young fish for Chesapeake Bay was 24.48; for Albemarle Sound, North Carolina, was 24.51. These means were not significantly different when analyzed by standard statistical procedures.

TABLE 9. Teeth in larval and young striped bass, according to size.

Size	Count of a side	all teeth on one of jaw
	Mandible	Premaxilliary
6.2	3	0
6.5	1	0
6.7	5	0
8.2	6	5
9.3	6	6
12.0	36	35
15.0	40	42
18.5	56	48
22.0	72 +	66 +

**Opercular and preopercular spines:** Opercular spines were poorly indicated on recently transformed juveniles at about 12 mm. Figure 29 shows the development in a fish 8.2 mm. long. Three well-developed spines were observed on the preopercle on a 12 mm. juvenile where the headbones were well-developed (Figure 24). In the larger individuals the preopercle possessed more, but smaller, spines (Figures 26-28). The small opercular spines were either single or double in the large juveniles.

In addition to the opercular spines, certain other features of the head may be useful in identification of young striped bass. Woolcott (1957: 6) has discovered the fact that in the striped bass the diameter of the sensory canal in the strong compact bones forming the lower jaw is smaller than in the white perch, *Roccus americanus*, with which it is most often confused during the postlarval and early young stages. In the latter species, the lower jaw appears frail because of the large sensory canal and pores. For this reason, Woolcott thinks that this character may serve in separating young white perch from striped bass.

**Scales:** Scales were first observed on striped bass juveniles when they attained a size of 21 mm. (Table 7). Imbrications were observed at a slightly smaller size. The scales on the smaller fish were deciduous and on the larger fish they were more firmly attached. Figure 30 indicates the appearance of these scales from various sizes of juveniles. No observations were available to show the sequence of scale formation. The larger fish in Table 7 were heavily scaled and, except for the lack of markings, have the important features of larger striped bass.

**Pectoral fins:** The larval pectoral fins, which consist of a fleshy base and non-rayed fan-shaped membrane, was first observed on prolarvae about 5 mm. long. Superficial rays made their appearance at about 6 mm. in length, and these were not counted with certainty until about 8 mm. (see Table 7). After this size, the rays could be counted, and the number gradually increased to, but never attained, the full complement of 16 rays. It appeared that the full complement was achieved at a size beyond 30 mm.

Caudal fin: The caudal fin of the striped bass young was typically homocercal, but in larvae the tail was spatulate and rounded. The first evidence of caudal fin formation occurred when a ventral thickening was observed near the posterior end of the notochord where the urostyle becomes ossified at a size as small as 5 mm, in length (see Figure 17). Rays were also distinguished in some fish slightly larger than this. At 6 mm. most prolarva possessed these superficial rays. The rays formed at an oblique angle, and were equally distributed on either side of what will be the center of the caudal fin when formed. Figure 24 shows that all principal rays are ventral in origin, and as they were being laid down the urostyle goes through the flexion that brings the principal rays into

the terminal position they occupy in the fully formed caudal. They seem to be laid down at about 8 mm. The hypurals appeared to be developed at about 10 mm.

The caudal fin was articulated with the last three vertebrae (Figure 29). Table 7 indicates that the increase in number of rays from fish over 8 mm. is slow. The largest fish represented in the table had attained the full complement of 17 caudal rays, of which 15 were branched. Figures 24-25 show the critical size when the fins attain their homocercal characteristic.

Pelvic fins: The pelvic fins were the last important meristic element to form in young striped bass. An abnormal juvenile, one of the largest specimens reared, did not develop any pelvic fins (see Figure 50). Pelvic buds could be seen at about 10 mm. but the larval pelvic fins were evident first in fish about 14 mm. in length and were retained by transformed young juveniles until about 23 mm. The full complement of one spine and 5 rays was attained shortly after the rays were first discerned.

Spinous dorsal fin: The first dorsal fin did not appear or become fully developed until a considerable period after the appearance of the soft or second dorsal fin. The anterior rays of this fin appeared to develop first. Table 7 shows that the spines were discernible first at about 8 mm. in length, and that additional spines were added slowly. In smaller sizes, individual spines were difficult to find. The full complement of nine spines was attained at about the same time the full complement of pelvic rays was formed, i.e., at about 24 mm. in length. Figures 25-28 show the relative sizes of the various spines during this development: these were very much like those present in large fingerling and adult fish.

Soft dorsal fin: The second dorsal fin showed greater development and sharper differentiation than the first dorsal fin (Figures 23-28). At about 7 mm. in length in some specimens (see Table 7) the number of rays was about one third the full complement. The spine was also present at this early stage. The increase in the number of soft-rays was rapid until the fish was about 15 to 20 mm. in length when the full complement of 1-11 rays

were evident. Figures 25-28 show the relative sizes of the various spines during the development. As pointed out earlier, a fold connecting the first and second dorsal fins was not observed.

Anal fin: The differentiation of this fin occurred when the larva was about 7 mm. in length, but clearcut evidence of a spine and a countable number of soft-rays was not evident until 9 mm. in length. Between this length and 15 mm. most of the fish possessed two anal spines, although a few still possessed a single spine. After 15 mm, three anal spines were clearly evident, the third being formed from the ossification of the first soft-ray immediately behind the second spine as shown by Mansueti (1958: MS). The present study corroborated this anal spine study in all details, except that three spines were found in a few fish smaller than 20 mm. in this study. The number of soft-rays varied as shown by Table 7, but the full complement of about 11 soft-rays was evident when the three anal spines were present beginning at about 20 mm.

Rate of growth: Data on the growth rate of striped bass from larvae through transformation are presented in Table 10 and Figure 36. The estimates of growth from hatchery-reared striped bass were compared with sizes attained by fish reared in a pond beginning May 7, 1931, by Pearson (1938: 832-837) and with the average sizes of naturally-spawned fish taken by seine during the month of June, July and August, 1956, from the Patuxent River. The peak of spawning was observed to be between May 1-19, 1956, in this area so that the hatching dates were roughly comparable with that of Pearson's and the hatchery-reared material. Striking differences in growth rates were observed between them and the hatchery-reared striped bass in the present study, and it was obvious that the latter fish were greatly "stunted." The average sizes attained by naturally-produced fish in the Patuxent River during summer months in 1956 have also been observed during other years in the Patuxent River and clsewhere, and along with similar data obtained by Vladykov and Wallace (1952: 150), the growth rate of young during this period can be regarded as normal. Interestingly

enough, the small amount of data from Pearson when fitted by eye with a curve can be provisionally combined with the absolute growth curve of Patuxent River young, forming the classical sigmoid growth curve. In spite of the differences in years, spawning periods, and growing seasons, it appears likely that growth of striped bass larvae and young, under natural conditions during spring and summer, will be similar to Pearson's data and the Patuxent River fish curves combined.

TABLE 10. Growth data, based on average sizes for various ages, of larval and young striped bass, *Roccus savatilis*.

Hatche I (Prese	ry-re Pish nt sti	nred idy)	Patu (Seine	xent Fish colle	River ections)	Pearse (1958:	on's 1 832-	Fish 837)
Оbserved иде	Number of fish	Av. total length mm.	Estimated age in weeks	Number of fish	Av. total length mm.	Observed age	Number of fish	Av. total length mn.
0	10		• • •	- •		0	• • •	
hatching	12	2.9				hatching	1	5.2
i day	18	3.6	-					
152 days						1½ days	1	4.4
2 days	30	5.1	··· ·			2 days		
3 days	15	5,6				3 days	1	5.2
4 days	-			-		4 days	1	5.8
6 days			~ -			6 days	1	6.0
8 days			· · -			8 days	1	9.0
2 weeks	10	8.1			<del>-</del>	16 days	1	13.0
3-4 weeks		****				3-4 weeks	1	36.0
4	F	11 5	4	10	10.0			
Currents	ມ 	10.0	weeks	10	44.0	. –		
n weeks	i)	10.0						
8 Weeks	5	20.1	- 8 Wooke	21	69.6			
10 poole	5	09.9	weeks	- 51	00.0			
12 weeks		20.0						
1 weeks	-	÷0.11	7.4					
weeks	1	29.0	weeks	91	75.0			Para-

The depressed growth curve of the hatchery-reared fish was probably a product of many complex factors. Overcrowding (Brown, 1957: 372-375, 377, 385, 395-396, Davis, 1953: 48-50), lack of sufficient and proper food during different phases of growth (Brown, 1957: 380-391), variable effects of metabolites in the aquaria (Brown, 1957: 396), endocrine disturbances brought on by artificial environment, (Brown, 1957: (393), and many other factors that were present, where few of these variables were fully understood or could be rigidly controlled, have been known to affect fish growth. Among hatchery-reared fish, Smith (1957: 341) has developed the thesis that high growth rates and high respiration rates occur together. It is conceivable that low growth rates can be produced in fish whose oxygen consumption was dictated by the low levels and high water temperatures present in rearing aquaria. Without trying to account precisely for the stunted nature of the fish, it was possible that the ontogenetic features of these fish were unaltered by this phenomenon. except to delay the sequence of morphological events in time. In other words, size, not age, determines the appearance and development of body parts and numbers. This is consistent with the findings of Martin (1949: 27-28, 64-65), who showed that the body form is influenced by five relative-growth stanzas, punctuated by four inflections found at approximately the eyed-egg stage, hatching, ossification, and sexual maturity. Body size at these points is an influencing factor on the determination of the relative size of the body parts. Perhaps the appearance and development of meristic features is also more affected by body size than age. Martin also indicated that the immediate environment can alter body size and hence proportions dur-



FIGURE 36. Comparison of growth rates of hatchery-reared striped bass with average sizes of this species recorded during various dates by Pearson (1938: 832-837) after hatching May 7, 1931, and from seine collections made during summer months 1956 in the Patuxent River, Maryland.

ing a considerable period of time. This generalization can probably be carried to conditions present in a laboratory hatchery. Nevertheless, the unusually small sizes and the teratological individuals described below require that all features in the early development of the eggs, larvae and juveniles be further studied under more controlled conditions. Since the appearance Abnormal eggs: Anyone culturing the eggs of striped bass is confronted with the frequent occurrence of dead and abnormal eggs that display a wide variation in the



ABNORMAL EGGS OF STRIPED BASS

FIGURE 37. Abnormal fertilized egg, 2.2 mm. in diameter, showing broken oil droplets.

FIGURE 38. Abnormal fertilized egg, 2.2 mm. in diameter, showing complete disintegration of oil droplets and yolk.

FIGURE 39. Abnormal fertilized egg, 2.3 mm. in diameter, showing yolk sac and oil globule broken down. A. Lateral view; B. Dorsal view.

FIGURE 40. Abnormal fertilized egg, 3.7 mm. in diameter, containing white coagulated material within the chorion.

of many or most morphological features and meristic numbers are a function of size rather than age certain other diagnostic features, such as stripes and the full number of pectoral rays, that are at present unrecognized, may be observed among the larger-sized, recently-transformed young especially between 30 and 40 mm. in length. internal breakdown of yolk-sac and oil globule. Worth (1910: 156-158) and Scofield and Coleman (1910: 110-111, 113) have provided detailed descriptions of dying, dead and abnormal eggs, and some of the conditions accompanying them. Since dead and abnormal eggs are frequently taken with live eggs in plankton samples, some of the most common features will be described briefly for diagnostic purposes. Unfortunately, conditions in the hatchery were not under sufficient control to provide data that might elucidate causative factors.

Figure 37 shows a live egg that had not fully water-hardened with oil droplets that were beginning to break apart from the oil globule to float to the top of the vitelline fluid. It was 2.2 mm. in diameter and was about 3½ hours old. This condition was occasionally observed in normal eggs where it was apparently arrested and the eggs developed as if unaffected. In abnormal conditions, the endpoint of oil droplet disintergration is illustrated in Figure 38. This egg was also 2.2 mm. in diameter and was 10 hours old. The yolk material was almost completely separated from oil droplets that were in various stages of suspension in the perivitelline fluid. Such eggs were frequently characterized by a heavy opaque and coagulated yolk around the circumference of the egg. Other areas of such eggs were clear and transparent.

Another type of egg that died before the complete swelling of the chorion takes place is illustrated by Figure 39A. It was 2.3 mm. in diameter and 8 hours old. The oil globule was disengaged from the yolk, and the latter had disintegrated and had concentrated on the bottom as a coagulated mass. A large cavity was occasionally seen in the oil globule, and the contents from this space are illustrated as a dark mass at the bottom of the egg in this view of the egg. Figure 39B is a dorsal view of the same egg.

Among fully water-hardened dead eggs as illustrated by Figure 40, the most frequently encountered anomaly were those that are fully or partially clouded with coagulated fluid. The oil globule may be free or still attached to a partially disintegrated or irregular yolk. These eggs died tollowing the rupture of the vitelline membrane surrounding the yolk. Striped bass eggs were apparently quite susceptible to rapid changes in oxygen supply, temperature, water movement, and other unknown factors up to the time of closure of the blastopore, one-third of the way between fertilization and hatching. After this period, when the yolk sac becomes covered with several layers of cells, the eggs are apparently less susceptible and can stand rough handling, as has been reported by many workers for eggs of other species of fish.

Abnormal larvae: Abnormalities among fish larvae were commonly observed in the laboratory. Among striped bass, the most prominent deviation from the normal appearance were the pugheaded individuals, which are described in a separate section below. The possibility of the occurrence in plankton samples of such abnormalities cannot be completely ruled out. Those described here may have been largely induced by artificial conditions, but similar abnormalities may occur in nature. A number of variations other than those that are illustrated have also been observed so that this discussion is merely an introduction to the subject. In the case of larvae, as well as with eggs, environmental conditions in the laboratory could not be sufficiently controlled to provide information about how such deviations are brought about.



FIGURE 41. Dorsal views of abnormal prolarvae, recently hatched, showing blisters on body.

Abnormal behavior of larval striped bass could occasionally be traced to debilitation from gas bubble disease. Among afflicted fish very small bubbles either became attached to the larvae or were swallowed so that bubbles were clearly seen in the intes-

tines. The fish developed white spots on the yolk sac and died. The disease was apparently associated with waters supersaturated with atmospheric gases. Gas embolism also may be due to an excess of nitrogen, which is frequently found in well water (see Marsh, 1910: 898-901; Marsh and Gorham, 1905: 343-376; and Dannevig and Dannevig, 1950: 211-215). Early experiments with well water during this study resulted in many mortalities apparently from this nitrogen excess and/or oxygen deficiency, which is another characteristic of well water. Figure 41 shows newly hatched prolarvae with bulges and blister-like features along the body, the causes of which are unknown.

One of the most common abnormal conditions observed in newly-hatched striped bass larvae from 48 to 72 hours old and about 4.5 mm. long is illustrated in Figure 42. The head was bent back and the eye was perpendicular to the body. Very little pigmentation was evident on the body except for melanophores on the oil globule. There was also a lack of pigment in the eyes, a characteristic of newly hatched One of the most pronounced larvae. pathological features of this type of larva was the settling of the yolk material in an odd-shaped mass in the posterioventral part of the yolk sac. Among newly hatched larvae under turbulent water conditions or those roughly handled, catastrophic mortalities occurred that were marked by the spectacular rupturing of the oil globule into the water (see Worth, 1904: 215-226).

Several other atypical larvae that were poorly defined are illustrated by humpbacked individuals in Figures 43 and 44 that were observed before preservation. The first was characterized by a specimen with much of the yolk material and a large oil globule retained. The other showed a larva in the same group with most of the yolk material absorbed and a large oil globule retained, suggesting some kind of metabolic disturbance. Usually yolk sac and oil globule were more or less absorbed simultaneously.

One of the most serious pathological features of striped bass in the hatchery, encountered in both pro- and postlarvae, were the symptoms tentatively identified as bluesac disease. The following characteristics of this essentially circulatory disease have

been observed in striped bass larvae: (1) hemorrhages in the head and thoracic region (Figure 45 and 46); (2) blisters on the sides of the body above the pectoral fin and above the yolk sac (Figure 46); (3) fluid-filled coelom which is a light blue, hence the name of the disease; (4) kyphosis, in which only a slight curvature of the spine was noted; (5) general circulatory system damage in which blood vessels ceased to pass blood, deteriorated. and in which clots of blood cells were (6) "lock-jaw" or the openformed: mouthed condition indicating that respiratory movements were being curtailed; (7) lighter anemic coloration than usual, resulting from decreased blood flow and increase in clots; and (8) white spot formation in the yolk sac. In all cases where blue-sac disease developed, death followed presumably due to immobility and suffocation.

Blood in healthy striped bass larvae was characterized by arterial flow on top and venous flow beneath the notochord, easily observed within the posterior part of the body. The heart in the cephalothoracic region beat with a steady and vigorous rhythm in healthy fish. Among diseased fish, the early stages were characterized by clots of blood cells chiefly in the forward portion of the head, and the irregular heart beat and an abnormally elongated heart. The fish became increasingly debilitated, lying on their sides. Healthy fish continued to swim about normally. When afflicted fish began their gaping movements the internal structure was already deteriorated. This was accompanied by the coagulations in the yolk sac, developing into prominent white spots. They eventually died from asphixiation as indicated above.

All the symptoms described above agree with classical descriptions given by Wolf (1954: 51-59) who reported the occurrence of the disease in three families of fishes (Salmonidae, Coregonidae and Catostomide). The disease has an unknown etiology, in spite of a large amount of work in this field. Whether the disease is infectious or not has not been demonstrated. Healthy striped bass, mixed among larvae with the disease, were reared through transformation to the juvenile stage. Once again, environmental factors such as oxygen ten-



FIGURE 42. Abnormal prolarva, 4.5 mm. long, showing constricted head. FIGURE 43. Abnormal prolarva, 4.5 mm. long, showing constricted head. FIGURE 43. Abnormal postlarva, 5.7 mm. long, showing humpback and enlarged oil globule. FIGURE 46. Abnormal postlarva, 6.2 mm. long, with blue-sac disease. FIGURE 46. Abnormal prolarva, 6.2 mm. long, with blue-sac disease. Or sand enlarged hody eropares.

clots and enlarged body grooves. Figure 47. Abnormal postlarva, 5.6 mm. long, showing an almost total lack of pigment. sion, temperature and other factors, either singly or collectively, cannot be ruled out from the many causative agents that have already been suggested for the disease.

Figure 46 shows a completely transparent and pigmentless larvae 5.6 mm. long, a condition induced artificially by confinement in total darkness for a two week period after hatching. A group of larvae were confined thus for survival purposes, and the results described here are a secondary effect. Orange pigmentation along the ventrolateral aspect of the body and the gold-flecked eyes present on normal larvae of the same general age and size were absent in these individuals. Small melanophores, however, were present.

Development of abnormal pugheaded larvae and young: Shortly after the transformation of many of the postlarval striped bass, it was noted that some of the individuals exhibited the typical pugheaded anomaly occasionally observed among adult striped bass in commercial catches and described and illustrated as "Mopskopf" fish by Schaeperclaus (1954: 618-620). These fish were characterized by (a) lack of a snout and most of the upper jaw, (b) marked bulging of the eyes, steep forehead, and top of head flat, (c) well-defined projection of lower jaw beyond the straight bar-like structure of the upper jaw, and (d) partial exposure of the tongue and minute pigmentation in cavity of lower jaw. About one-third of the hatcheryreared young that survived during the summer of 1956 were pugheaded fish, and these included some of the largest individuals. Figures 48-50 show some of the essential characteristics. Thus, some pugheaded features, notably the unequal placement of the upper and lower jaws are evident in the postlarvae (Figure 48). Figure 48 and 50 show the unequal closure of upper and lower jaws that was observed on most of the normal larvae. Figure 49 more nearly approximates the abnormal "Rundkopf" type described and illustrated by Schaeperclaus (1954: 620).

The present experiments have produced the first well-defined examples of pugheaded characteristics in larval and young striped bass, although Gudger (1930: 1-19) had thoroughly summarized all the observations of this pathological condition in adult

striped bass up to the date of his publication. Since that time additional specimens have been found by fishermen in Chesapeake Bay and deposited in the Chesapeake Biological Laboratory, and accounts have appeared in newspapers (Covell, 1957: C-4), indicating that this is not a unique condition in striped bass or other species. Ryder (1887: 503, 548), in addition to publishing the first illustration of a postlarval striped bass, described and illustrated what he considered "... a hybrid between the shad and rock-fish, the former being the female and the latter the male parent." This illustration was discussed with Dr. E. C. Raney, who agreed with the author that the drawing probably represented a pugheaded striped bass, and that, on the basis of present state of knowledge that negates interfamilial breeding of fishes, it certainly was not a hybrid between the two species. There are a number of similar references dealing with hybridization of striped bass with shad, white perch, and yellow perch that have been overlooked by workers in recent years (Roosevelt, 1885: 510-515: Ryder, 1882: 187; and Ryder 1887: 504-505). Ryder, who remarked, "That the eggs of the shad . . . might be fertilized with the milt from the male striped bass seems almost incredible," was confident nevertheless, that the hybrids were good, although the evidence he presented was very poor. Carl Hubbs (1955: 1-20) listed no cases of successful hybridization above intergeneric level, and Clark Hubbs and Strawn (1957: 55-56) carried out some interfamilial matings that were essentially unsuccessful. Thus, considering the primitive conditions under which these so-called hybrids were produced and reared, it is possible that any such larvae were actually one species or another. It is conceivable that Ryder's specimen could have been introduced from the river into boxes or jars containing his so-called shad-striped bass hybrids and that confinement may have produced the pugheaded example that he illustrated.

Gudger (1930: 18-19) indicated that there was no information available to show how pugheaded striped bass feed. Incidental observations in this study showed that they exhibited no difficulty in feeding, in fact, as indicated earlier, some of the largest specimens that survived were pugheaded. In all cases they were observed to open their mouths widely when pursuing brine shrimp or daphnia, engulfing the prey and then expelling water through

substantiate the claim that it is due to a mechanical injury (Covell, 1957: C-4). Gudger (1930: 18) and Schaeperclaus (1954: 620) established the fact that with



#### PUGNOSED STRIPED BASS

FIGURE 48. Abnormal postlarva, 6.7 mm. long, showing pugheaded condition. Eggs and larvae of brine shrimp are shown in the stomach.

FIGURE 49. Abnormal young, 15 nm. long, showing pugheaded condition. FIGURE 50. Abnormal young, 29 mm. long, showing pugheaded condition.

the gill openings. Pugheaded fish did not appear at a disadvantage in their ability to feed when compared to normal-headed individuals.

The cause of pugheadedness in fish is still conjectural. There is no evidence to

other species of fish it arises as a germinal defect in the embryo and that its course may be directed by endocrine disturbances affected by an adverse environment. The effects of environment, unfortunately, are usually not clearly separated from genetic in many of the references cited. Schaeperclaus (1954: 618-620) and Tschoertner (1956: 124), for example, have reviewed the extensive European literature and have discussed the influence of environmental factors, especially oxygen deficiency, in producing pugheadedness in cod, trout, pike, carp and yellow perch. The origin of some normal and some pugheaded individuals from phenotypically normal striped bass parents in the present study leaves the roles of both environment and genetic factors undetermined.

# SUMMARY AND CONCLUSIONS

1. Detailed descriptions of the early development of the striped bass, *Roccus* saxatilis (Walbaum), with emphasis on variation in size and morphology, sequence of fin formations, changes in body form, and attainment of the full complement of meristic structures, are presented and illustrated for the first time.

2. The eggs, which are pelagic, buoyant, but slightly heavier than freshwater, are spherical, transparent, nonadhesive and relatively large when compared to the eggs of other estuarine and anadromous fish. When unfertilized, they are about 1.3 mm. in diameter, and about 3.4 mm. when fertilized and fully water-hardened. The granular yolk sac is green in live eggs and whitish yellow when preserved, and is about 1.2 mm. in diameter. The single, amber-colored oil globule is about 0.6 mm. in diameter.

3. Striped bass prolarvae hatch in 36 to 48 hours at an average water temperature of about 63°F., and range from 2.9-3.7 mm. in total length. They are relatively undeveloped, with no mouth opening, unpigmented eyes, and a greatly enlarged yolk sac and oil globule projecting beyond the head. When about 5-6 mm. long the yolk sac and oil globule are partly or wholly assimilated and they become postlarvae. The jaws and teeth, digestive tract, air bladder, gills, circulatory system and other internal structures are clearly distinguish-They are transparent, except for able. some scattered melanophores and a few orange chromatophores on the body and eves.

4. Postlarvae transform to juveniles between 7-10 mm, when the fin-folds are lost except in the dorsal, anal and caudal

regions. Fin rays begin to differentiate in the larger fish in these regions. The tip of the urostyle flexes dorsally and the rounded, spatulate tail of the larvae becomes homocercal when the principal rays take a terminal position. The largest fish in this group possess a well-formed, but partly ossified skeleton with the full complement of 25 vertebrae, which are generally correlated in number with the myotomes. Melanophores are more concentrated on the head, sides of the abdomen, and along both sides of the body posterior to the anus at these sizes, although the distribution of chromatophores is about the same as in prolarvae.

5. Between 10-20 mm. all postlarvae complete metamorphosis, with segmented fin-rays in the various fins. Muscular bands of tissues have obscured the skeletal structure and internal viscera, and myotomes can no longer be counted. Some have the full complement of three anal spines characteristic of the family Serranidae, and other meristic characters are well-developed.

6. Between 20-30 mm., scales are found on all young, and with the exception of pectoral fin-rays, a full complement of meristic structures is attained. The body is uniformly yellow-brown colored, and is spotted with many small melanophores, but the striping found in older and larger fish is not evident.

7. Linear relationships is found between the dependent variables of head length, eye length, and snout to anus length, and the independent variable of standard length of larvae and young; the relationship between standard length and body depth in the smallest larvae was nonlinear. These data indicate that, with the latter exception, in all of these body parts the rate of development is proportional to the length of the fish, a condition that has been observed in larger striped bass in another study.

8. The sequence of fin formation is as follows: larval pectorals (without rays), caudal fin, second dorsal, first dorsal, anal fins (more or less simultaneously), pectoral fin (with rays) and pelvic fin. The third anal spine develops from the first terminally segmented soft-ray between 15-20 mm. total length, so that all young striped bass below 15 mm. possess two anal spines, and all above 21 mm. possess three. 9. Myotomes are evident on larvae within the eggs, but are countable only in the larvae. Between 6-12 mm. total length, the total number varies around the average of 25, with a range of 23-27, indicating that the myotomes apparently do not exactly equal the 25 vertebrae, a phenomenon observed in the sea herring in another study.

10. Striking differences exist between the growth rate of hatchery-reared striped bass, those based on another study, and those obtained from field collections. The young in the present study were stunted, a condi-

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tion which may have been induced by overcrowding and inadequate feeding.

11. Observations made on dead and abnormal eggs and teratological larvae and young are presented. Blue-sac disease is tentatively identified for the first time in larval striped bass. Pugheadedness is also described for the first time in hatcheryreared striped bass, and possible causative factors are discussed.

12. A detailed discussion and review of the literature dealing with the early development of the striped bass is included in the text of this paper.

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PLATE I. Eggs and prolarvae of the striped bass, Roccus saxatilis.