

NOAA Technical Report NMFS Circular 428 Morphological Comparisons of North American Sea Bass Larvae (Pisces: Serranidae)

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# NOAA Technical Report NMFS Circular 428



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August 1979

# U.S. DEPARTMENT OF COMMERCE

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# Morphological Comparisons of North American Sea Bass Larvae (Pisces: Serranidae)

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## ABSTRACT

Larvae of 17 of the 23 nominal genera of American serranid fishes are described. Representatives of only two of these genera have been described previously from American waters. The genera fall into four groups which closely follow subfamilial groupings based on adult characters. Larvae of the Serraninae, representing seven genera, appear to be the most generalized and are most similar to Morone-like percichthyid larvae. They have some larval specializations but exhibit rather direct development of adult morphology. The serranine genera can be ranked in order of increasing larval specialization as follows: Serraniculus, Paralabrax, Centropristis, Diplectrum, and Serranus. Hypoplectrus and one type of Diplectrum, although considered serranines on the basis of adult characters, are quite different from the other serranine larvae observed. One line of divergence from the serranines is the Anthiinae, with larvae of four genera being represented in the present collections. These larvae have variously developed strong spines on the head and in the opercular region, also the pelvic fin spine and some dorsal fin spines are strong and develop precociously. These spines are serrated in more specialized genera. Among the anthiine genera described there is a progression of larval specialization as follows: Plectranthias, Pronotogrammus, Anthias, and Hemanthias. A third general type of serranid larvae is represented by members of the three American genera of the Epinephelinae and Gonioplectrus. These larvae all are similar in general appearance and specialized in having elongate, strong serrate spines-primarily the second spine of the dorsal fin and the pelvic spine. The fourth larval type is comprised of three genera whose affinities have been unclear. Liopropoma is generally considered by others to be a serranid of the subfamily Liopropominae, Pseudogramma has been placed by others in the family Pseudogrammidae, or considered to be a member of a subfamily of the Grammistidae, the family in which Rypticus, the third genus, is placed. Because of the similarity of their larvae and evidence from adult characters, I consider these genera to be members of the serranid subfamily Grammistinae. Larvae of these genera share some larval characters with the serranines. Their most outstanding larval feature is the development of one or two greatly elongated flexible dorsal fin spines.

## INTRODUCTION

Jordan and Eigenmann (1890) reviewed the American and European serranids known at that time. The limits of and relationships within the family have continued to be sources of study and, as presently understood, in American waters it consists of three of Jordan and Eigenmann's (1890) six subfamilies (Serraninae, Anthiinae, and Epinephelinae) plus the Liopropominae (Gosline 1966). Their Grammistinae has been elevated to familial status (Gosline 1966).

Serranid larvae are poorly known, although adults of most species are common and important commercially. Early descriptions of Mediterranean larvae indicated a diverse morphology (Fage 1918). The larvae have variously developed head and fin spination that seem related to the group within the family to which the species are assigned. Larvae of only 2 of the 100 or so species of American serranids have been described—*Epinephelus niveatus* by Presley (1970) and *Centropristis striata* by Kendall (1972). Descriptions of these and other serranid larvae indicate that the family may be subdivided based on specializations of the larvae. In this paper, subfamilial and generic characteristics of American serranid larvae are defined from material from western Atlantic and eastern Pacific waters and one representative of each of the four subfamilies is described in detail.

#### METHODS AND MATERIALS

Since only *Hypoplectrus*<sup>2</sup> and *Centropristis* (Hoff 1970) among American serranids have been reared beyond yolk exhaustion, the indirect method of assembling series of similar appearing larvae from plankton samples was used.

Representative larvae were drawn using a camera lucida attachment on a dissecting microscope. Pigment on the formaldehyde-preserved specimens was limited to melanophores which is variously referred to as it appeared on the larvae, e. g., as spots, patches, or blotches. Body proportion measurements were made with an ocular micrometer. The larval period was divided into three stages: preflexion (before notochord flexion), flex-

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<sup>&</sup>lt;sup>2</sup>W. J. Richards, National Marine Fisheries Service, Southeast Fisheries Center, Miami, pers. commun. January 1974.

ion (during notochord bending), and postflexion (after the notochord tip had completed flexion) following recommendations of Ahlstrom et al. (1976). Body length (BL), the reference for proportion measurements, was measured from the tip of the snout to the tip of the notochord (notochord length (NL) in preflexion and flexion larvae and in postflexion larvae it was measured from the tip of the snout to the margin of the hypural bones (standard length (SL) as in Ahlstrom et al. (1976). Some specimens were cleared and stained following Hollister (1934) and Clothier (1950). The ventral portion of the interopercular bone is not shown in the figures of the opercular area because its outline was hidden by overlying tissue in the cleared and stained specimens.

Specimens included materials from collections at the National Marine Fisheries Service (NMFS) Laboratories in La Jolla, Calif.; Miami, Fla.; Narragansett, R.I.; and Sandy Hook, N.J.

Most of the material was collected as part of one of three large-scale ichthyoplankton surveys—one in the Atlantic Ocean and two in the Pacific Ocean. The survey in the Atlantic was that of NMFS, Sandy Hook, aboard the RV *Dolphin* in 1965-68 when ichthyoplankton was sampled from Cape Cod, Mass., to Palm Beach, Fla. Most of the Pacific material resulted from the CalCOFI program, a long-continuing survey of waters off California and Baja California. The other major source of material from the Pacific Ocean was the EASTROPAC program, which consisted of three multivessel cruises in the eastern tropical Pacific Ocean. Appendix Table 1 lists collection data associated with specimens used for the illustrations.

#### RESULTS

## **Subfamily Serraninae**

The serranines have rather uniform characteristics which help distinguish them from other serranids (Table 1). They are represented by seven genera in North American waters with 52 species and are moderate to smallsized serranids apparently representing the base from which other subfamilies arose (Smith and Atz 1969; Kendall 1976). Most serranines are synchronous hermaphrodites; however, protogyny and secondary gonochorism are present in some species (Smith and Young 1966).<sup>3</sup> The lateral line is complete and not highly arched and the scales are moderate to large and strongly ctenoid (Jordan and Eigenmann 1890). The larvae of three European species of *Serranus* (Fage 1918; Bertolini 1933; Aboussouan 1972) as well as those of *Centropristis striata* (Kendall 1972) are the only serranines described.

Larvae of all but one (Schultzea) of the North American genera of serranines are herein described. Serranine larvae, except those of Hypoplectrus (see below), can be distinguished from larvae of other fishes on the basis of several characters. Development in serranines is direct and they do not possess many of the larval specializations of other serranids. They do not have elongate preopercular spines, rather a series of blunt points. The dorsal and pelvic fin spines are thin and only slightly elongate in some genera. Larval pigment generally consists of melanophores in characteristic positions mostly along the ventral midline. Generally, there are spots at the angle of the jaw, at the junction of the cleithra, between the bases of the pelvic fins, near the anus, at the bases of the anal rays and some on the caudal peduncle Some of these spots are intensified in some species. Pigment on other parts of the body is variable within the subfamily but some is consistent within genera. The body shape of the larva gradually changes to that of the adult, without abrupt changes in proportions.

Centropristis.—Centropristis occurs only in the northwest Atlantic where four species are recognized (Kendall<sup>4</sup>). These are moderately large protogynous hermaphrodites. Centropristis striata occurs farther north than any other serranid on the east coast. A closely related species, C. melana, is widespread in the Gulf of Mexico.<sup>5</sup> The two other species, C. philadelphica and C. ocyurus, cooccur with C. striata in the South Atlantic Bight. The species of Centropristis are distinguished by meristic and other characters (Table 1).

The eggs of C. striata were the object of one of the early detailed studies of fish embryology (Wilson 1891) and Hoff (1970) illustrated eggs and prolarvae of C. melana. Larvae of C. striata were not described until recently (Kendall 1972), although Sette (see Merriman and Sclar 1952) and Pearson (1941) had apparently recognized them in plankton samples.

I found only one type of larva assignable to *Centropristis* in the present material. The description of Kendall (1972) has been condensed and supplemented with recent observations in the following account.

Larval morphology of *Centropristis* (Fig. 1) is typical of other serranines. There is no armature development associated with the fin spines, the preopercular bone has only small, unserrate protruding spines (Fig. 2) and body shape, once the caudal fin has formed, approximates that of small adults. Fin spines are thin and not produced. Dorsal fin spines develop at about the same stage as the soft rays. Pelvic fins develop after the other fins have several rays ossified and grow isometrically throughout development.

In early larvae (<5 mm) there is some dorsal body pigment but afterwards nearly all larval pigment is asso-

<sup>&</sup>lt;sup>3</sup>Serranids studied to date are hermaphroditic (Smith 1965; Kendall 1977), i.e., male and female gametes are produced in each individual. Some genera are secondary gonochorists, i.e., the gonads show histological traces of both sexes but only male or female gametes are produced in each individual. Hermaphroditism takes on two forms in serranids: synchronous hermaphroditism, where both types of gametes are produced simultaneously in one individual, and protogyny, where individuals mature first as females and later in life the gonad transforms into testes and produces sperm.

<sup>&</sup>lt;sup>4</sup>A. W. Kendall. 1977. Biological and fisheries data on black set bass, *Centropristis striata* (Linnaeus). Sandy Hook Lab. Tech. Ser Rep. No. 7, 29 p.

<sup>&</sup>lt;sup>5</sup>Some (e.g., Miller 1959) consider C. melana a subspecies of C. striata.

													-				_	Laı	vae			-			4		
												Fin Spine Development				t			Pigment locations								
	Nun c spe	f		Adults								Precocious and/or elongate Serra		ate	Produced head spines –				Ven			ntral		Fin mem- branes			
Subfamily genus	Atlantic	Pacific		s of meris Fins Anal	tic charac	cters Vertebrae	Sexuality	RLA pattern	Predorsal pattern	Scale morphology	Body shape	Dorsal	Pelvic	Dorsal	Anal	Supra- occipital	Pre-	Inter- opercular	Jaw	Cleithrum	Pelvic insertion	Anus	Anal fin base	Caudal	Dorsal	Pelvic	-
Serraninae				III,	-											-	-									_	7
Serraniculus	1		IX-X,11	7	14-15	10 + 14	synchronism	9	0/0/0,2	III	Slender								X	X	X	X	Х	X			
Paralabrax		8	X-XI,12-15	6-8	15-19	10 + 14	sec. gonoch.	9	0/0/0.2	III	Slender										X	X	X	X	X	x	
Centropristis	4		X,11	7	15-20	10 + 14	protogyny		0/0/0,2	III	Slender									Х			X	X			
Diplectrum	3	9	IX-X,11-13	6-9	15-18	10+14	synchronism	9	0/0/0,2		Slender Slender <sup>1</sup>	Х	Х						Х			X X	Х	X X	Х	Х	
Serranus	13	5	IX-X.10-13	7-8	13-18	10 + 14	synchronism	9	0/0/0,2	III		3(some)	x							x		X	х		х	X	
Hypoplectrus -	7		X.14-16	7-8	13-10	10+14 10+14	synchronism		0/0/0,2	III	Slender	o(some)	Δ							л	х			X			
Schultzea	1	1	X,11-12	6-8	15-17	10+14 10+14	syncinomism	5	0/0/0,2	m	Siender				La	irvae	unkı	nown			А	Λ	Λ	л	Λ	Λ	
nthiinae			Х,																								
Plectranthias	1		16	7	13	10 + 16			0/00/2		Robust	3rd						x x				Х		Х			
Anthias	3	1	14-15	7-8	18-20	10+16	protogyny	9	0/00/2 or 0/0/2	III	Robust	1-3	Х			X (som		х х		Х			Х	Х	Х	Х	
Pronotogrammus	1	2	13-15	7-8	15-19	10 + 16		9		III	Robust	2-3	Х			X		x x	X				X	Х		Х	
Hemanthias	2	1	13-14	7-8	18	10-11+15-1	6		0/0/2		Robust	2-4		2-4 X	X			x x							X		
Holanthias	1	1	15-16	7-8	17-18	10 + 16										rvae											
Centristhmus		1	14	8	19	11 + 15										rvae											
Caprodon		1	19-20	8	17-18	10 + 16		9	0/00/2							irvae											
Epinephelinae																											
Gonioplectrus <sup>2</sup>	1		VIII, 13	7	16	10 + 14		None	0/0/1	II	Robust	2-3	Х	1-3 X	X			X									
Paranthias	1	1	IX,18-19	9-10	19-20	10 + 14	protogyny	None	0/0/1	II	"Kite" shaped	d 2-3	Х	1-4 X	Х			X		Х					Х	Х	
Epinephelus			X-XI, 14-20	8-10	16-20	10 + 14	protogyny	None	0/0/1	II	"Kite" shaped	d 2-3	Х	1-4 X	X			X							Х	Х	
Mycteroperca	8	5	XI,15-18	10-13	15-18	10+14	protogyny	None	0/0/1	Π	"Kite" shaped	d 2-3	Х	1-4 X	X			X		Х					Х	Х	
rammistinae																											
Liopropoma	5		VIII,12-13	III,8	12-15		sec.gonoch.			II	Slender with	2-3											Х		Х		
Pseudogramma	1		VII-VIII,15-24				synchronism	None	0,0/1	II	deep caudal	2-3						X							Х		
Rypticus	8	2	II-III,21-29	14-18	13-17		protogyny	None		II	peduncle	1													Х		
Pikea	3		VIII-IX,13-14	III,7-8	15	10 + 14		None	0,0/1	II						arvae u											
Jeboehlkia	1		VII,9	III,7	15	9 + 15									La	irvae	unkr	nown									

Table 1.—Some adult and larval characters of genera of North American serranids. Meristic characters and types of sexuality were compiled from several sources cited in the text. Ramus lateralis accessorius (RLA) patterns from Freihofer (1963). Predorsal patterns from Kendall (1976) and Kendall and Fahay (in press). Scale morphology from McCully (1961).

Diplectrum Type 2 larvae.

ω

<sup>2</sup>Provisionally placed in Epinephelinae.



Figure 1.-Larvae of Centropristis striata from the northwestern Atlantic Ocean: a) 4.7 mm; b) 8.3 mm.



Figure 2.—Spine-bearing bones of the opercular and posttemporal regions on a 10.6-mm *Centropristis striata* larva.

ciated with the ventral midline. Melanophores (spots) in characteristic positions are larger than others. Large spots are seen on the posterior margin of the angular, at the junction of the cleithra, between the bases of the pelvic fins, near the anus, and near the insertion of the anal fin. Several slightly smaller spots develop on the caudal peduncle, and still smaller spots are seen at the bases of the anal fin rays, between the larger caudal peduncle spots, and at the bases of some caudal fin rays. Several melanophores also occur on the posterior portion of the optic lobes and on the dorsoposterior lining of the coelomic cavity.

Paralabrax.—Paralabrax with eight species is the only North American serranine limited to the eastern Pacific (Table 1). It is ecologically similar to *Centropristis* in the Atlantic in that it is larger than most other serranines and occurs at higher latitudes than other serranines on the Pacific coast. Smith and Young (1966) indicated that *Centropristis* and *Paralabrax* are also closely related. The only species that has been studied is a secondary gonochorist, while most other serranines are synchronous hermaphrodites (Smith and Young 1966).

Paralabrax larval development is typical of serranines. Paralabrax larvae approach adult body proportions soon after tail flexion is complete (Fig. 3). The spinous and soft portions of the dorsal fin form at about the same rate, as they do in Centropristis. The fins of Paralabrax larvae are more heavily pigmented than those of Centropristis but the ventral melanophores are smaller and more uniform in size. Pelvic fins form with pigment on the membrane as the dorsal fin starts to form. Pigment develops ventrally at the base of the pelvic fin, near the anus, along the base and at the insertion of the anal fin, and on the caudal peduncle. Pigment also forms on the angular, on the dorsal surface of the brain, and at the base of the caudal fin. Some pigment develops dorsally at the base of the spinous dorsal fin and a large blotch of pigment develops on its membrane. The pectoral fin rays are pigmented on their distal third and the pelvic fin is heavily pigmented on and between the rays. Opercular spination is as in other serranines (Fig. 4): the preopercular has about three spines dorsal and



Figure 3.—Larvae of Paralabrax sp. from the northeastern Pacific Ocean: a) 6.0 mm, h) 5.0 mm.

two ventral to the one at the angle, on the preopercular ridge there are a few blunt spines, and the subopercular has a smooth posterior margin.

Diplectrum.—In contrast to reef-dwelling habits of many other serranids, Diplectrum occurs mainly over sand or mud bottoms on the continental shelves (Bortone 1977). These moderate-sized synchronous hermaphrodites have one or two clusters of strong and divergent spines on the preopercular which is produced into a bony flap. The Pacific species were reviewed by Rosenblatt and Johnson (1974) and the entire genus by Bortone (1977).

Diplectrum is the only serranine with larvae from both Atlantic and Pacific waters. Since species of Diplectrum have overlapping meristic features and geographic ranges, the larvae cannot be assigned to species. Two distinct larval types with the unique meristic characters of Diplectrum were found from both oceans. They will be referred to as Type 1 and Type 2 and discussed separately, since they share few larval characters in common.

Type 1—Larvae of Diplectrum called Type 1 from the Atlantic and Pacific Oceans are similar in development. They exhibit most of the features of other serranine larvae. The body shape approaches that of the adult and in later larval stages, after the fin rays form, they are among the most alender serranines (Figs. 5, 6). Fin development is modified from the serranine pattern (see page 2) in that the first dorsal fin spines and pelvic fin elements





form early. None of the early forming dorsail fin spines are very elongate, as they are in some Servation larvae. Figment on larvae from both oceans is present along the central midline in positions characteristic of servative larvae (Table 1). Individual melanophores are more uniform in size than those of Centropristic. A series of about



Figure 5.-Larvae of Diplectrum sp. Type 1 from the northwestern Atlantic Ocean: a) 5.8 mm; b) 10.0 mm.

five spots occur ventrally on the caudal peduncle of Atlantic larvae while there is only a spot at the insertion of the anal fin and one two-thirds of the way back on the caudal peduncle in Pacific larvae. At least one spot is present at the base of the caudal fin on larvae from both oceans. The membranes of the spinous dorsal and pelvic fins of Atlantic larvae are variably pigmented with scattered spots. Pacific larvae have intense pigment on the membrane of the spinous dorsal fin centered around the fourth spine. The pectoral and pelvic fins of Pacific larvae have pigment on and between the fin rays. The preopercular and subopercular have more armature than is seen in other serranine genera (Fig. 7).

Type 2—Larvae assigned here to *Diplectrum* Type 2 are distinct from *Diplectrum* Type 1. I have not found such intrageneric differences in larvae of any other serranid genus. This would indicate that either these larvae are not of *Diplectrum* but are of an undescribed genus, possibly even in a closely related family with representatives in both oceans, or that there are two quite distinct types of *Diplectrum*, possibly worthy of subgeneric rank.

While Type 1 larvae are similar to other serranine larvae, Type 2 larvae show specializations not seen in other genera. The general body shape is similar to that of Type 1 but the snout is more elongate and is concave in dorsal profile in smaller specimens (Fig. 8). The sequence and extent of fin ray formation is different from that in other serranines. The pectoral fin develops early, before most other fins, as a fan-shaped structure and extends to the anus. Only in grammistines is similar larval pectoral fin development seen. The pelvic fins form before the rest of the fins and are elongate, reaching beyond the anus. The distal third of the rays of the paired fins are covered with contracted melanophores. Elements of the dorsal, anal, and caudal fins all develop at about the same time. Pigment pattern differs from that seen in other serranines in that the body anterior to the anus is unpigmented before the fin rays are complete and later in development a large diffuse internal pigmented area forms between the lateral line and the anal fin, dorsal to the anterior half of that fin. The bones of the opercular region are similar to those of *Diplectrum* Type 1 except the subopercular margin is smooth and does not have the small spines seen in *Diplectrum* Type 1 (Fig. 9).

Serranus.—In the western Atlantic there are 13 species and in the eastern Pacific there are 5 nominal species assigned to Serranus (Table 1). These are rather small fishes (<200 mm) sharing 17 characters in common which, taken together, exclude all other genera (Robins and Stark 1961). Their median fin ray counts fall outside the ranges of other American serranids except Schultzea beta, which has only six branchiostegal rays (Robins and Stark 1961) and Diplectrum, which generally has more pectoral rays (Table 1).

Robins and Stark (1961) examined east coast *Serranus* species in some detail. Since *Serranus* in the eastern Pacific is poorly known with few specimens of some species taken, some species may prove invalid.

While no American Serranus larvae have been described, eggs and early larvae of Mediterranean species of Serranus were among the first serranids described



Figure 6.—Larvae of Diplectrum sp. Type 1 from the northeastern Pacific Ocean: a) 4.3 mm; b) 5.0 mm; c) 6.1 mm; d) 13.0 mm.



Figure 1.-Larvae of Centropristis striata from the northwestern Atlantic Ocean: a) 4.7 mm; b) 8.3 mm.



Figure 2.—Spine-bearing bones of the opercular and posttemporal regions on a 10.6-mm *Centropristis striata* larva.

ciated with the ventral midline. Melanophores (spots) in characteristic positions are larger than others. Large spots are seen on the posterior margin of the angular, at the junction of the cleithra, between the bases of the pelvic fins, near the anus, and near the insertion of the anal fin. Several slightly smaller spots develop on the caudal peduncle, and still smaller spots are seen at the bases of the anal fin rays, between the larger caudal peduncle spots, and at the bases of some caudal fin rays. Several melanophores also occur on the posterior portion of the optic lobes and on the dorsoposterior lining of the coelomic cavity.

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Paralabrax larval development is typical of serranines. Paralabrax larvae approach adult body proportions soon after tail flexion is complete (Fig. 3). The spinous and soft portions of the dorsal fin form at about the same rate, as they do in Centropristis. The fins of Paralabrax larvae are more heavily pigmented than those of *Centropristis* but the ventral melanophores are smaller and more uniform in size. Pelvic fins form with pigment on the membrane as the dorsal fin starts to form. Pigment develops ventrally at the base of the pelvic fin, near the anus, along the base and at the insertion of the anal fin, and on the caudal peduncle. Pigment also forms on the angular, on the dorsal surface of the brain, and at the base of the caudal fin. Some pigment develops dorsally at the base of the spinous dorsal fin and a large blotch of pigment develops on its membrane. The pectoral fin rays are pigmented on their distal third and the pelvic fin is heavily pigmented on and between the rays. Opercular spination is as in other serranines (Fig. 4): the preopercular has about three spines dorsal and



Figure 3.-Larvae of Paralabrax sp. from the northeastern Pacific Ocean: a) 6.0 mm; b) 9.0 mm.

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Type 1—Larvae of *Diplectrum* called Type 1 from the Atlantic and Pacific Oceans are similar in development. They exhibit most of the features of other serranine larvae. The body shape approaches that of the adult and in later larval stages, after the fin rays form, they are among the most slender serranines (Figs. 5, 6). Fin development is modified from the serranine pattern (see page 2) in that the first dorsal fin spines and pelvic fin elements





form early. None of the early forming dorsal fin spines are very elongate, as they are in some *Serranus* larvae. Pigment on larvae from both oceans is present along the ventral midline in positions characteristic of serranine larvae (Table 1). Individual melanophores are more uniform in size than those of *Centropristis*. A series of about



Figure 5.-Larvae of Diplectrum sp. Type 1 from the northwestern Atlantic Ocean: a) 5.8 mm; b) 10.0 mm.

five spots occur ventrally on the caudal peduncle of Atlantic larvae while there is only a spot at the insertion of the anal fin and one two-thirds of the way back on the caudal peduncle in Pacific larvae. At least one spot is present at the base of the caudal fin on larvae from both oceans. The membranes of the spinous dorsal and pelvic fins of Atlantic larvae are variably pigmented with scattered spots. Pacific larvae have intense pigment on the membrane of the spinous dorsal fin centered around the fourth spine. The pectoral and pelvic fins of Pacific larvae have pigment on and between the fin rays. The preopercular and subopercular have more armature than is seen in other serranine genera (Fig. 7).

Type 2—Larvae assigned here to *Diplectrum* Type 2 are distinct from *Diplectrum* Type 1. I have not found such intrageneric differences in larvae of any other serranid genus. This would indicate that either these larvae are not of *Diplectrum* but are of an undescribed genus, possibly even in a closely related family with representatives in both oceans, or that there are two quite distinct types of *Diplectrum*, possibly worthy of subgeneric rank.

While Type 1 larvae are similar to other serranine larvae, Type 2 larvae show specializations not seen in other genera. The general body shape is similar to that of Type 1 but the snout is more elongate and is concave in dorsal profile in smaller specimens (Fig. 8). The sequence and extent of fin ray formation is different from that in other serranines. The pectoral fin develops early, before most other fins, as a fan-shaped structure and extends to the anus. Only in grammistines is similar larval pectoral fin development seen. The pelvic fins form before the rest of the fins and are elongate, reaching beyond the anus. The distal third of the rays of the paired fins are covered with contracted melanophores. Elements of the dorsal, anal, and caudal fins all develop at about the same time. Pigment pattern differs from that seen in other serranines in that the body anterior to the anus is unpigmented before the fin rays are complete and later in development a large diffuse internal pigmented area forms between the lateral line and the anal fin, dorsal to the anterior half of that fin. The bones of the opercular region are similar to those of *Diplectrum* Type 1 except the subopercular margin is smooth and does not have the small spines seen in *Diplectrum* Type 1 (Fig. 9).

Serranus.—In the western Atlantic there are 13 species and in the eastern Pacific there are 5 nominal species assigned to Serranus (Table 1). These are rather small fishes (<200 mm) sharing 17 characters in common which, taken together, exclude all other genera (Robins and Stark 1961). Their median fin ray counts fall outside the ranges of other American serranids except Schultzea beta, which has only six branchiostegal rays (Robins and Stark 1961) and Diplectrum, which generally has more pectoral rays (Table 1).

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While no American *Serranus* larvae have been described, eggs and early larvae of Mediterranean species of *Serranus* were among the first serranids described



Figure 6.-Larvae of Diplectrum sp. Type 1 from the northeastern Pacific Ocean: a) 4.3 mm; b) 5.0 mm; c) 6.1 mm; d) 13.0 mm.



Figure 7.—Spine-bearing bones of the opercular and posttemporal regions on a 10.3-mm *Diplectrum* sp. Type 1 larva.

Figure 9.—Spine-bearing bones of the opercular and posttemporal regions on a 9.9-mm *Diplectrum* sp. Type 2 larva.



Figure 8.-Larvae of Diplectrum sp. Type 2 from the northeastern Pacific Ocean: a) 4.5 mm; b) 8.4 mm.

(Raffaele 1888). Larger larvae of Mediterranean species have since been illustrated and described (Bertolini 1933) and there are brief descriptions of *Serranus* larvae collected off Africa (Aboussouan 1972).

Serranus larvae were found in samples from the Atlantic; however, none were found in Pacific collections. Although there are differences among *Serranus* larvae in extent of fin ray elongation, pigment, and body shape, all found so far are separable from other larvae by the beginning of the flexion stage. More detailed study may allow descriptions of the several types and their assignment to species



Figure 10.-Larvae of Serranus sp. from the northwestern Atlantic Ocean: a) 3.7 mm; b) 5.0 mm; c) 5.5 mm; d) 9.4 mm.

Serranus development shows several modifications of the basic serranine plan (page 2). The body is considerably deeper from the head back to the anus from before notochord flexion until after all the fin rays have formed (Fig. 10). The pelvic fin forms before the other fins and the elements are elongate in some larvae. The first three to five spines of the dorsal fin form before the rest of the fin and in some the third spine is elongate. Among Serranus larvae described so far these fin spines are longest in S. cabrilla (Fage 1918).

In Serranus larvae some of the characteristic ventral pigment is intensified and some is eliminated. The more contracted melanophores of other serranines are absent in Serranus. Intensified melanophores are on the angular, at the junction of the cleithra, and near the anus. A spot at the insertion of the anal fin and one midway back on the caudal peduncle are the largest spots ventrally and are more pronounced in some larvae than in others. Dorsally, on at least some larvae, there is a spot near the base of the last dorsal spine. Another spot ventral to the posterior third of the second dorsal fin is variable in position from near the base of the fin to near the lateral line. This spot opposes the one at the insertion of the anal fin and in S. cabrilla these two spots are large and distinctive (Fage 1918). Pigment spots are scattered on the membranes of the spinous dorsal, anal, and pectoral fins in some larger larvae.

The opercular region is armed with blunt spines, which are generally more pronounced than those of other serranines (Fig. 11). There seems to be some variation in spine length among the species of *Serranus* since *S. cabrilla* has longer spines (Fage 1918) than the larvae I examined. The preopercular has two spines ventral to and three spines dorsal to the one at the angle. There are spines anterior to these on the ridge of the preopercular bone in some specimens. The subopercular has two spines dorsal to the one seen at its angle in other serran-



Figure 11.—Spine-bearing bones of the opercular and posttemporal regions on a 9.7-mm Serranus sp. larva.

ines. Among larval serranines, only *Diplectrum* has a more ornately armed opercular region.

Hypoplectrus.—This genus of brightly colored small reef fishes has long perplexed scientists. In the western Atlantic there are several nominal species with different color patterns but with identical meristic features and body proportions. At present, these are generally considered valid species; however, other species of serranids such as Mycteroperca rosacea and M. olfax have more than one color phase (Rosenblatt and Zahuranec 1967). Barlow (1975) observed spawning between two nominal species and so considered them synonymous. Thresher (1978) concluded that the color patterns observed in Hypoplectrus demonstrated mimicry of nonpredatory reef fishes. Apparently, coloration in Hypoplectrus is a plastic character; and with the possibility of clones in a synchronous hermaphrodite, different color patterns can become established locally in a relatively short time. The poorly known eastern Pacific Serranus lamprurus Jordan and Gilbert was placed in Hypoplectrus by Meek and Hildebrand (1925), but Robins and Stark (1961) stated it is indeed a Serranus and is close to S. flaviventrus of the Atlantic, although they gave no reason for their opinion. Hypoplectrus lamprurus is deeper bodied than Serranus and has a dorsal fin ray count of X, 14, whereas Serranus species generally have X, 12 (Table 1). Although a detailed study is needed, it seems that H. lamprurus should still be considered a Hypoplectrus.

No larvae assignable to Hypoplectrus were found in plankton collections. Their unique dorsal fin ray count (X, 14) among east coast serranines assured that if larvae had been present they would have been recognized. It is possible that Hypoplectrus larvae are planktonic for only a short time before they become demersal.

A series of *Hypoplectrus* sp. was reared from wild planktonic eggs at the NMFS Laboratory in Miami (Richards see footnote 2). I was able to examine the specimens briefly and copy drawings of them. Also, three cleared and stained specimens were examined in detail.

These specimens are different from other serranine larvae. It is unlikely that rearing produced these differences and it is difficult to consider them as modifications of serranine larval characters. These *Hypoplectrus* larvae are not similar to any known serranid larva and provide reason to doubt that *Hypoplectrus* belongs in the Serranidae.

The body shape indicates rather direct development from larval to adult proportions (Fig. 12). The first few spines of the dorsal fin develop early, during notochord flexure, but the associated membrane is more fleshy than in serranines. The pelvic fins form at about the same stage as the first dorsal spines but the rays are shorter than those of serranines with early developing pelvic fins. The membranes of these early forming fins are pigmented. The rest of the dorsal spines are progressively shorter than the third and the posterior few form late after the rayed portion of the fin is developed. Some of the rays of the second dorsal fin become longer



Figure 12.—Laboratory-reared larvae of Hypoplectrus sp. from eggs collected near Miami, Fla.: a) 3.4 mm; b) 4.7 mm; c) 5.7 mm; d) 8.5 mm.

than the longest spines. The rest of the fins form over a short length interval of 4.7-5.7 mm.

The head and particularly tissues around the mouth are fleshier than in serranines. The opercular region has spines developed on several bones; however, they do not appear on the larval drawings since they are covered by flesh. The preopercular is edged with about 12 subequal spines (Fig. 13). The subopercular has about three blunt spines on its margin. Besides the three definitive spines on the opercular, there are about four spines ventral to them, a condition not seen in serranines.

Pigmentation consists of irregular shaped and sized melanophores in characteristic positions. More pigment is present on *Hypoplectrus* than on most other serranines. A series of spots along the ventral midline consists of a spot near the base of the pelvic fins, one below the middle of the gut, one just anterior to the anus, one near the insertion of the anal fin, and another on the caudal peduncle. Spots ventral near the tip of the notochord come to lie at the base of the caudal fin rays as they form. A few spots near the base of the dorsal fin migrate to form the dorsal fin membrane pigment. A few spots are scattered on the dorsal surface of the brain posterior to the eyes. All the fin membranes have pigment in later larval stages. By 8.5 mm, small melanophores become scattered over the dorsal portion of the anterior two-thirds of the fish.



Figure 13.—Spine-bearing bones of the opercular and posttemporal regions on a 12.5-mm *Hypoplectrus* sp. larva.

Schultzea.—Schultzea is monotypic represented by S. beta of the western Atlantic (Table 1). It lives more pelagically than other serranines and is adapted to feed on small, free-swimming prey. The mouth is modified to be highly protrusible through extensive changes in the shape of the premaxillary (Robins and Stark 1961). The fin counts are similar to those of Serranus but there are only six branchiostegal rays instead of seven (Robins and Stark 1961). Two juvenile specimens (24.0 and 25.4 mm) collected by John McCosker (Steinhart Aquarium, San Francisco, CA 94118) provided for study did not retain any larval characters, so they cannot be compared with other serranines and their relationships within the group cannot be determined. However, from adult adaptations, it appears that *Schultzea* is the most highly modified American serranine.

Serraniculus.—Serraniculus contains one diminutive species (<80 mm), S. pumilio, in the northwest Atlantic (Table 1). Its life history has been studied and it is a synchronous hermaphrodite (Hastings 1973).

A serranine larval type from the Atlantic had meristic characteristics of *S. pumilio*, notably six branchiostegal rays as opposed to seven for all other serranines except *Dules auriga* and *Schultzea beta*, which occur south of the area where these larvae were collected.

Serraniculus pumilio (Fig. 14).-Meristic element development (Table 2)—A total of 41 specimens from 3.1 to 7.3 mm was studied to trace meristic character development. Since the smallest larvae have a straight notochord and vertebrae are the only ossified meristic elements, and the largest have adult complements of all meristic characters except gill rakers and scales, the pattern of meristic character development can be seen in this series. Vertebrae ossify from anterior to posterior except for the urostyle which ossifies before the two or three vertebrae anterior to it. The smallest larva examined (3.1 mm) had 1 ossified vertebra. Numbers of vertebrae gradually increase until by 4.6 mm some larvae have all 24 ossified. However, some larvae as large as 6.2 mm have only 23 vertebrae. Throughout the series, there is considerable variation in the number of ossified vertebrae at a given length. Branchiostegal rays are ossified in some larvae as small as 3.8 mm and the adult complement of six is seen in most specimens by 4.0 mm, when the notochord has completed flexion. Other meristic elements ossify when the notochord completes flexion at 4.0 mm and larvae as small as 4.6 mm have adult fin ray complements. Pelvic and spinous dorsal fin rays do not develop precociously as they do in other serranid subfamilies and even in Diplectrum and Serranus. The dorsal fin spines and rays each develop at about the same rate in S. pumilio.

Body proportions (Table 3)—Several body proportions of 21 larvae from 2.9 to 8.3 mm were measured and expressed as a percentage of body length (BL) to document changes in body shape during larval development. Total length increases rapidly from about 105% of BL at 2.9-3.9 mm, while the notochord is straight, to 115% of BL at 4.0 mm after notochord flexion is complete; thereafter, it increases gradually to about 125% of BL as the caudal fin forms. Preanal length increases from about 60% of BL in larvae <4.0 mm to about 65% of BL in 7.0to 8.0-mm larvae. Head length remains fairly constant at about 39% of BL throughout larval development. Eye length and snout length decrease slightly during development from about 12% to slightly less than 10% of



Figure 14.-Young stages of Serraniculus pumilio from the northwestern Atlantic Ocean: a) 3.8 mm; b) 5.8 mm; c) 55.3 mm.

BL. The greatest body depth decreases from 32% to about 28% of BL. Depth at anus increases during early development up to 4.0 mm and then holds constant at about 25% of BL. Caudal peduncle depth increases from <6% in BL in the 2.9-mm larvae to about 14% of BL in 4.4-mm larvae; thereafter, it changes little. A comparison of the proportions of the larvae after notochord flexion with those of the adult shows that the adult body shape of *S. pumilio* is established early in development, in larvae as small as 4.2 mm.

Pigmentation—Throughout larval development, S. pumilio is more heavily pigmented than any other

serranine. The characteristic serranine ventral spots are present, but they are supplemented by many other spots. Pigmentation is composed of small, individual melanophores making up a pattern, rather than the pattern being comprised of large melanophores in characteristic positions as seen in other serranids.

The beginning of the pattern is already established in 2.6-mm larvae with three rows of melanophores on the trunk: one along the dorsal midline, one along the lateral line, and the third along the ventral midline. Dorsally, there is a series of about four spots, which are larger than those in the other two rows. The anteriormost of these

Table 2.—Meristic character development of larvae of *Serraniculus pumilio*. Specimens between dashed lines are undergoing notochord flexion. For the caudal fin, "P" and "S" indicate primary and secondary fin rays.

Body length (mm)	Branchio- stegal		Pec-	Pel-	Caudal fin							
		Verte-	toral	vic	Dorsal		Ven	Ventral		Dorsa	l fin	Gill
	rays	brae	fin	fin	S	Р	Р	S	fin	Spines	Rays	rakers
3.1 NL		1										
3.4		3										
3.5		4										
3.5		8										
3.6		5										
3.6		11										
3.6		11										
3.7		10										
3.8	2	15										
3.8	2	10										
3.8		8										
		3										
3.8		3										
3.8												
3.8		16										
3.8	3	14										
4.0		12										
4.0		10										
4.0		16										
4.3		13										
4.4		14										
								N				
3.8		16		4								
4.1		17										
4.2		17										
4.3	2	17	1									
3.9	6	18	12	1,2	7	6			7	VI	4	
		*******		****		*****						
3.8 SL	6	19	13	I,3		8	8		II,7	VIII	9	1
4.4	6	22	15	I,3	1	9	8	1	III,7	IX	9	2
4.6	6	24	14	1,5	2	9	8	2	III,7	Х	11	4
4.7	6	22	9	Ι								2
5.0	6	24	14	1,5	3	9	8	3	III,7	X	10	3
5.2	6	24	15	I,5	3	9	8	2	Ш,7	Х	11	5
5.7	6	24	15	I,5	5	9	8	4	III,7	Х	11	5
5.8	6	21	6	I,4					II,1	IV		4
6.0	6	24	9	I,5			2		II,1	VIII		5
6.1	6	24	15	I,5	6	9	8	5	III,7	Х	10	5
6.2	6	23	8	I,4					II,1	VII		5
7.0	5	24	8	I,4					II,1	VII		4
7.0	6	24	13	1,5		3	6		П,1	IV		4
7.0	6	24	14	I,5		7	7		111,7	Х	11	5
7.2	6	24	15	I.5	7	9	8	6	Ш,7	X	11	6
7.3	6	24	14	1,5	7	9	8	6	III,7	X	11	6

spots is just anterior to the origin of the dorsal fin and remains pronounced throughout development. Additionally, a series of smaller spots forms along each side of the dorsal fin. When all of the dorsal rays are formed, one or two of the original large spots can be seen internal to the base of the fin and the smaller spots have developed into a series of nearly contiguous dashes on each side of the fin base.

The lateral line series begins on 2.6-mm larvae as a series of dashes from the head about two-thirds of the length of the trunk. These dashes seem to develop in association with the vertebrae and lie internally along the lateral septa. The spots above the gut become internal while those farther posterior remain on the surface. From the anus back, as the original dashes become internal, another series develops distal to them on the body surface. Superficial spots develop from the anus to the termination of the dorsal fin between the dorsal and lateral series of dashes. In larger larvae similar spots also extend ventrally to a lesser extent from the lateral dashes. These superficial spots are small but variable in size and position and appear as a single pigmented blotch. Superficial pigment also develops as a line on the head passing from the snout posteriorly at the level of the eye and another line on the opercular region in line with the lateral series of dashes on the trunk. A patch of small spots also develops laterally in the area of the pectoral fin. Ventrally, spots extend the length of the larva. A few spots are present on the tip of the lower jaw, along the isthmus, on the angular, and at the junction of the cleithra. A larger spot is present on the ventral midline between the junction of the cleithra and the base of the pelvic fins. Along the gut the ventral spots diverge slightly to form a series on each side of the midline. A few spots are also present on the midline ventral to the posterior third of the gut. The anteriormost of these is the largest

	Percent of standard length													
Body length (mm)	Total length	Body depth	Eye length	Head length	Snout length	Pre- anal length	Caudal peduncle depth	Depth at anus						
2.9 NL	103	32	13.0	39	10.0	58	5.7	19						
3.7	104	31	11.0	38	12.0	59	8.0	25						
3.9	107	33	12.0	38	10.0	63	10.0	27						
4.0	107	34	11.0	39	11.0	61	9.8	27						
4.0 SL	115	33	11.0	36	12.0	61	11.0	28						
4.2	118	34	12.0	39	10.0	63	13.0	28						
4.2	115	36	12.0	42	11.0	62	12.0	30						
4.4	119	33	11.0	39	10.0	63	14.0	29						
5.5	117	31	10.0	38	10.0	66	14.0	27						
5.7	122	31	11.0	38	11.0	59	13.0	25						
6.0	123	31	11.0	38	11.0	62	15.0	26						
6.1	123	29	10.0	36	9.3	65	14.0	29						
6.7	117	29	9.4	37	9.4	62	14.0	26						
6.8	120	31	11.0	38	9.0	67	14.0	27						
7.0	120	29	9.8	36	9.8	65	14.0	25						
7.7	125	23	9.8	32	7.4	61	13.0	28						
7.8	124	29	10.0	39	10.0	64	15.0	26						
7.9	117	29	11.0	38	9.5	64	14.0	25						
7.9	124	28	10.0	39	9.5	62	13.0	25						
8.3	125	27	9.9	39	9.9	66	14.0	26						
Adult		27-31	8.5-10	34.5-36	8.5-10.5		12-13.5							

Table 3.—Body proportions of larvae of *Serraniculus pumilio*. Specimens between dashed lines are undergoing notochord flexion.

Ginsburg (1952).

and is ventral to the deepest point of the gut. Posterior to the gut, a series of spots extends along the ventral midline to the caudal peduncle area in small larvae. As the anal fin develops, these spots are positioned on either side of its base. A series of spots also develops at the base of the anal fin rays and extends posteriorly onto the caudal peduncle. A spot develops ventrally near the tip of the notochord. When the caudal fin develops, this spot is situated ventrally at its base and several other spots develop along the base of the fin. The posterior third of the caudal peduncle is unpigmented throughout development. Other small spots present during development are on the membranes associated with the branchiostegal rays, pectoral and pelvic fins, and internally on the dorsolateral surface of the gut cavity.

Late in larval development the superficial spots intensify and coalesce giving the larva, particularly the trunk, a gray appearance and making *S. pumilio* the most heavily pigmented serranid larva found to date.

**Discussion**.—Of the seven genera of North American serranines, larvae of all but *Schultzea* have been examined. Larval material for five of these genera has been gleaned from plankton collections, and their development shows a similar pattern. Laboratory-reared material of the other genus, *Hypoplectrus*, showed a pattern of development dissimilar to that of other serranines. This suggests that its adult characters, upon which is presently understood affinities are based, need to be reexamined.

Two distinct types of larvae were found that had meristic characters of *Diplectrum*. Both types of larvae occurred in both oceans and more than two species of *Diplectrum* are known from each ocean. *Diplectrum* Type 2 larvae are not similar to those of other known serranines. They do not have the characteristic serranine ventral pigment, but have a large internal blotch dorsal to the anal fin. The fin rays of the pectoral, pelvic, and caudal fins are pigmented with small melanophores. The fin rays are thin, but longer than in other serranines. On the basis of larval characters, the affinities of *Diplectrum* Type 2 cannot be determined, but it does not appear closely related to any other serranine.

Among the other serranine genera, the extent of modifications of the basic pattern of development may indicate relationships. Among American serranids, the serranine genera Serraniculus, Centropristis, and Paralabrax show larval characters most similar to those of Morone-type percichthyids (Mansueti 1958, 1964). In these serranines the dorsal spines develop at the same stage of development as the dorsal soft rays and are not elongate. The pelvic fin rays are not precocious or elongate during larval development. Spines of the opercular region are less developed in these genera than in other serranine genera. Pigmentation of Serraniculus larvae is heavier than in other serranines and therefore, most closely resembles that of Morone-like percichthyids. Within the serranines it seems that there has been a trend from a uniformly heavily pigmented larva to one in which there are a few large spots in characteristic positions primarily along the ventral midline. Diplectrum Type 1 and Serranus show modifications of the basic serranine pattern in that the spinous dorsal fin develops before the rest of the fin, and in some species of Serranus

some of the dorsal spines are elongate and tipped with pigmented "flags." The pelvic fins are also early developing and become elongate, more so in Serranus than in Diplectrum Type 1. Serranus is deeper bodied than other serranines and Morone-type percichthyids. Also some large pigment spots develop dorsally in Serranus. Thus on the basis of larval characters, there seems to be a progression of specialization in the order: Serraniculus, Centropristis-Paralabrax, Diplectrum Type 1, Serranus.

## **Subfamily Anthiinae**

This subfamily is presently under study for revision by Anderson and Heemstra.<sup>6</sup> This is a cohesive group of small, brightly colored fishes that occur over hard bottoms near continental slopes. They are distinguished by several morphological modifications from serranine characteristics (Table 1). They have large scales (29-60 lateral line scales), an arched lateral line, deep bodies with rather large heads, and at least 14 gill rakers, but mostly more than 25 (Jordan and Eigenmann 1890, Heemstra see footnote 6). There are about 15 species of anthines in American waters grouped in seven genera. Four genera have representatives in both oceans but no species are common to both oceans.

Ten types of larvae assignable to four genera (Anthias, Pronotogrammus, Plectranthias, and Hemanthias) are present in the material I examined. No American anthiine larvae have been described previously although larvae of two species of Anthias from the Mediterranean Sea have been described (Bertolini 1933; Sparta 1932) and several anthiines from the southeast Pacific have been illustrated (Fourmanoir 1976).

Anthiine larvae have deep bodies and stout, produced preopercular spines. They also have strong spines in their dorsal, anal, and pelvic fins; but the spines are not as produced as they are in epinephelines. There seems to be a trend in anthiines toward development of armature in the form of serrations on the spinous fin rays and on spines of various head bones such as the opercular series, frontals, parietals, and supraoccipitals. In some species spiny scales develop at a small size, while the fish are still planktonic. Pigment consists of a few blotches in characteristic places on the trunk and head.

*Plectranthias.*—This genus is represented in the western Atlantic by one species (Robins and Stark 1961). The genus contains another species found in the Celebes and Arafura Seas. *Plectranthias garupellus*, the Atlantic species, is distinguished from other anthiines in the western Atlantic by the high number of dorsal soft rays (16) and the low number of pectoral rays (13) (Table 1). The spinous dorsal fin is quite angular with the third spine being the longest. There are two strong antrose spines on the lower limb of the preopercular. It is known from Florida and the Bahamas, but is apparently not readily available to normal collecting procedures.

Only a few P. garupellus larvae were found, so a detailed description is not possible. However, the larval characters indicate relationships of the species within the subfamily and will be discussed briefly. Plectranthias garupellus shows little development of characteristic anthiine larval features (Fig. 15). None of the fin spines are serrate. The third dorsal spine in small larvae is elongate but not stout. The head has spines in areas characteristic of other anthiine larvae but they are weakly developed and not serrate. A simple spine protrudes from the frontal ridge above the eye. Too few specimens were available for staining and illustrating the opercular series but the preopercular has two ridges of blunt spines with an elongate, thin spine at the angle of the posterior ridge. The interopercular has an elongate thin spine lying proximal to the long preopercular spine and the other opercular bones have some spines protruding. The posttemporal and supracleithral spines protrude bluntly. There is no protruding supraoccipital crest.

The pigment pattern of larval *P. garupellus* is distinctive. There are three characteristic blotches of pigment on the trunk. Two blotches are dorsal, one below the sixth and seventh dorsal fin spines, and the other below the four posteriormost dorsal soft rays. The third blotch is on the ventral midline just posterior to the insertion of the anal fin. Other spots occur on some specimens, such as one ventrally on the caudal peduncle.

Anthias.—Anthias is circumtropical with several species in the western Atlantic and one in the eastern Pacific Ocean (Table 3). They are rather small, brightly colored, deep-bodied fishes. Anthias anthias larvae have been described (Fage 1918; Roule and Angel 1930; Bertolini 1933) and they closely resemble Anthias larvae I have examined. I found four types of anthiine larvae in western Atlantic material and one type in Pacific material, which were quite similar and larger specimens had meristic features of Anthias species (Figs. 16-20). Only one western Atlantic type could be identified to species (Anthias tenuis) on the basis of meristic characters of the larvae. Anthias nicholsi seems to be the most common adult of this genus in the western Atlantic and Anthias Type 1 is the most common larval type collected; therefore, Anthias Type 1 may be Anthias nicholsi. Since there is only one Anthias species in the eastern Pacific (Anthias gordensis), the larvae are presumed to be that species (Fig. 20).

Anthias larvae are deep bodied and have large heads, as is characteristic of all anthiines. The second dorsal spine is elongate but thin in at least some species. The first three dorsal spines form while the rest of the dorsal fin is still an undifferentiated finfold. When all the dorsal rays have formed, the third spine is the longest and the spines approach the proportions of adults. The dorsal fin spines are rather stout during later larval development, but are never serrate. The elongate spine has pigment on its associated membrane, giving it a flaglike appearance. Pigment is retained on the membrane between the second and third dorsal spines into the late larval period. There is a deep notch in the dorsal fin, the last four

<sup>&</sup>lt;sup>6</sup>P. C. Heemstra, CSIRO, Cronulla, N.S.W., Australia, pers. commun. April 1973.



Figure 15.-Larvae of Plectranthias garupellus from the northwestern Atlantic Ocean: a) 5.5 mm; b) 8.0 mm.

spines being quite short. The pelvic fin forms early in *Anthias* larvae and the first soft ray is produced. The pelvic fin and first three spines of the dorsal fin develop before other fin rays. The membrane of the pelvic fin is pigmented, like the dorsal fin. The pelvic fin spine is stout but not elongate or serrate.

The dorsal and anal fins form concurrently except for the precocious anterior dorsal spines. The caudal fin completes formation after the dorsal and anal fins have formed. The pectoral fin is last to form rays, the dorsal rays of the pectoral fin forming first, as in all serranids studied to date.

Anthias larvae have characteristic head spines. In some species there is a simple supraoccipital spine. There is a serrate ridge above the eye. The degree of serration varies among the species, some having 3 to 6 serrae while others have up to 12. The most conspicuous spines are in the opercular region (Fig. 21). There are two spinescent ridges on the preopercular. The anterior ridge has 3 to 5 broad points. The posterior ridge has 4 to 8



Figure 16.-Larvae of Anthias sp. Type 1 from the northwestern Atlantic Ocean: a) 3.8 mm; b) 5.3 mm.

strong points, some of them serrate. This ridge is marked by a large serrate spine at the angle of the preopercular. Lying directly proximal to this preopercular spine is a similar spine on the interopercular, serrate and just as large. This spine is obscured by the one on the preopercular and is easily overlooked. The posttemporal region has a number of protruding spines, some of which are serrate.

Pigment on *Anthias* larvae varies among the species; however, there seems to be a generic pattern. Usually a small melanophore is at the posterior end of the anal fin, one is on the ventral edge of the caudal peduncle, one or a few spots are at the base of the central rays of the caudal fin, usually a few spots are on the skull above the optic lobes, and in some species there is a spot at the symphysis of the lower jaw. Dorsal trunk pigment varies among the species. In the Atlantic there are four types of *Anthias* larvae based on dorsal trunk pigment and other characters. *Anthias* Type 1 has a spot on the trunk musculature ventral to the middle of the dorsal fin (Fig. 16). In *Anthias* Type 2 there is a line of pigment ventral to the posterior part of the dorsal fin (Fig. 17). *Anthias tenuis* has some pigment between the dorsal body margin and the lateral line ventral to the last few rays of the dorsal fin (Fig. 18). *Anthias* Type 3 has no dorsal trunk pigment (Fig. 19).







Figure 18.-Larva of Anthias tenuis from the northwestern Atlantic Ocean, 6.7 mm.



Figure 19.-Larva of Anthias sp. Type 3 from the northwestern Atlantic Ocean, 5.1 mm.

These four types of *Anthias* larvae are distinguished by other characters also. Of the types, Type 2 and *Anthias tenuis* have a protruding supraoccipital crest. Also Type 2 is scaled while it is still pelagic and has larval preopercular spines, pigment, and body shape. Although there are not enough specimens for a thorough analysis, there appear to be differences in the number of spines above the eye with Type 1 and *Anthias tenuis* having the fewest (about 4), Type 3 having more, and Type 2 having the most.

Anthias gordensis has no dorsal trunk pigment, no protruding supraoccipital crest, and a moderate number of spines in the ridge above the eye. Thus, Anthias gordensis larvae correspond most closely to Anthias Type 3 larvae among the Atlantic types. As more becomes known about the relationships within this genus, clues about the identity of *Anthias* Type 3 may be sought in the Atlantic species most closely resembling the Pacific *Anthias gordensis*.

**Pronotogrammus.**—There are three American species of *Pronotogrammus: P. aureorubens* in the Atlantic and *P. eos* and *P. multifasciatus* in the Pacific. These fish are more slender and have smaller heads than other American anthiines.

In plankton samples, I found one larval type in each ocean which can be ascribed to *Pronotogrammus* on the basis of meristic features (Figs. 22, 23). The Atlantic type



Figure 20.-Larvae of Anthias gordensis from the eastern Pacific Ocean: a) 5.2 mm; b) 6.0 mm.

has meristic features of *P. aureorubens* and the Pacific type those of *P. eos.* The two larvae share common characters that differentiate them from larvae of other genera. None of the fin rays are serrate or much elongate but the second and third dorsal spines form before the other elements and the pelvic fin is formed early. The opercular region is heavily armed with several serrate spines (Fig. 24). The preopercular has a long serrate spine at its angle and the interopercular has a similar spine proximal to the one on the preopercular. The posttemporal and supracleithrum have protruding serrate spines. The supraoccipital crest protrudes as a simple ridge until it is "grown over" in late-stage larvae. There are several spines above the eye on a ridge of the frontal bone. Midlateral trunk pigment is characteristic of both types of *Pronotogrammus* larvae. In *P. aureorubens* this pigment consists of 5 to 12 dashes along the midlateral septum, roughly the length of the anal fin base. In *P. eos* 





the pigment consists of a group of melanophores that form a blotch of pigment laterally on the trunk over the last few rays of the anal fin. Other pigment consists of several melanophores on the surface of the optic lobes of the brain. A few spots of pigment are at the base of the caudal fin on both species, and on P. eos some pigment is on the pelvic fin membrane. Lower jaw pigment is present on P. eos and two ventral midline spots are on P. aureorubens—one at the insertion of the anal fin and one midway on the caudal peduncle.

*Hemanthias.*—*Hemanthias* is represented by three American species: *H. vivanus* and *H. leptus* in the Atlantic and *H. peruanus* in the Pacific.

I found one type of Hemanthias larvae in each ocean, the Atlantic species with 47 lateral line scales (Fig. 25) is presumably H. vivanus, the most northerly species. From larval catches, H. vivanus is the most abundant anthiine off the east coast of the United States. The larvae from both coasts share several characters which separate them from larvae of other genera. They are the most ornately spined anthiine larvae. They have welldeveloped spines in the opercular region, marked by an elongate, serrate spine at the angle of the preopercular and one underlying it on the interopercular. The interopercular also has a series of heavy spines ventral to the larger one. Both species have a protruding supraoccipital crest which is serrate, resembling a "cockscomb." There are numerous ridges of complex spines on the frontals and parietals. The frontals also have a ridge of spines on their ventral margins. The posttemporal and supracleithral bones have protruding, serrate spines. The second through fourth dorsal spines develop early and the third spine is quite elongate early in development. The first dorsal spine develops after these three. The pelvic fin also develops early. In both species the pelvic fin spine is serrate and stout. In H. vivanus the second and third dorsal spines as well as the first anal spine are also serrate. Pigment on *H. vivanus* consists of opposing spots on the trunk medial to the posterior extent of the second dorsal and anal fins. There is also a spot ventrally on the caudal peduncle and one at the caudal fin base. Spots also occur on the dorsal surface of the optic lobes. *Hemanthias peruanus* has pigment on the membranes of the spinous dorsal and pelvic fins (Fig. 26). Both species become scaled with ornate ctenoid scales while they still possess larval characters.

Hemanthias vivanus.-Meristic element development (Table 4)-In the smallest recognizable larvae on hand (3.1-4.0 mm), some meristic elements are already forming: the third dorsal fin spine and the pelvic spine are present. The third dorsal spine remains prominent throughout development with pronounced serrations. By 4.1-4.5 mm the dorsal fin has added one or two spines (the second and fourth) and some specimens are forming gill rakers. Between 4.6 and 5.0 mm the vertebral column has two to six vertebrae ossified, the first dorsal fin has three to five spines, the anal fin had one spine on about half of the specimens, and the branchiostegal rays range from two to six. By 5.1-5.5 mm, six branchiostegal rays, one spine, and one ray in the pelvic fin, and four to nine first dorsal spines are present. Between 5.6 and 6.0 mm the vertebral column is adding vertebrae and 14 to 20 are seen, the dorsal fin has 8 or 9 spines, there are 7 to 9 gill rakers, and branchiostegal ray complement is complete at 7. Between 6.1 and 6.5 mm there are 18 to 23 vertebrae, 9 or 10 dorsal spines, 1 to 4 pelvic rays, and 8 to 12 gill rakers. The second dorsal, anal, pectoral, and caudal fins are developing rapidly during this period showing wide ranges of numbers of elements formed. Between 6.6 and 7.5 mm, the same pattern of wide ranges of formed elements is seen, indicating rapid formation. Some specimens have adult complements of vertebrae, second dorsal, anal, caudal, and pelvic fin rays. By 7.6-8.0 mm, the adult complements of all characters examined except gill rakers are present. Notochord flexion takes place at 5.5 mm and specimens >6.0 mm are developing scales. That is, scales form when the only meristic character with its adult complement is the branchiostegal rays.

Serrae are well developed on the third dorsal spine and the pelvic spine. The second and fourth dorsal and the first and second anal spines also develop serrae.

Body proportions (Table 5)—Larvae from 3.1 to 9.2 mm were measured to trace the proportional development of several body dimensions. The only proportion that shows noticeable difference with size is total length, which increases from 110% of BL to 120% of BL as the larvae grow. This difference reflects the formation and growth of the caudal fin. Greatest body depth remains fairly constant ranging from 29 to 44% of BL; the depth at the anus is 30% of BL; and caudal peduncle depth is 12% of BL. Head length is about equal to greatest depth ranging from 34 to 46% of BL, snout length is 12% of BL as is eye diameter. The preanal length ranges from 53 to 65% of BL. Thus, *H. vivanus* larvae are large headed and deep bodied with a trunk that tapers quickly from the anus to the caudal peduncle.



Figure 22.—Larvae of *Pronotogrammus aureorubens* from the northwestern Atlantic Ocean: a) 4.6 mm; b) 6.0 mm; c) 9.0 mm.

Head spine development (Figs. 27, 28)—The serrate "cockscomb" spine protruding from the supraoccipital is pronounced in the smallest larvae (3.1 mm) observed. Serrate ridges above the eye and transverse ridges of spines on the surface of the cranium as well as beginnings of spines in the posttemporal and opercular region are also present. During larval growth, these spines increase in complexity and size, those in the opercular area showing the greatest change (Figs. 29, 30). The supraoccipital crest remains the largest cranial spine and is strongly serrate. The ridges on the cranium form a complex pattern covering the area between the eyes and the supraoccipital region (Fig. 28). The serrate supraorbital ridges develop about eight strong, blunt points. In the opercular region, the preopercular has a long serrate spine at its angle and several spines along the rest of the posterior margin of the bone (Fig. 30). The interopercular has a long serrate spine which lies directly proximal to the long spine on the preopercular and several smaller spines ventral to the long one. The subopercular has a few small spines on its posterior margin and some are serrate. The opercular bone develops the three spines characteristic of serranids on its posterior margin during the larval period. The posttemporal has several serrate spines and the supracleithrum has a posteriorly directed, elongate serrate spine. Apparently





Figure 23.—Larvae of *Pronotogrammus eos* from the eastern Pacific Ocean: a) 3.6 mm; b) 7.8 mm.

these spines are resorbed in the late larval or early juvenile period but specimens to describe these events are lacking.

Pigmentation-Pigmentation is present on the smallest larvae examined (3.1 mm) and remains essentially unchanged during larval development. Two spots are present on the ventral midline of the caudal peduncle, one just posterior to the insertion of the anal fin and the other, slightly smaller, at the anterior end of the caudal fin base. Another spot develops at the base of the ventral lobe of the caudal fin and extends along the bases of several rays. Dorsally a spot is present on some larvae at the insertion of the second dorsal fin. This spot seems to be quite superficial, seen on only one side of the larva in some cases, and apparently abraded off of other larvae. A few melanophores are present at the symphysis of the lower jaw, on the dorsal surface of the optic lobes of the brain, on the fin membrane between the third and fourth dorsal spines, and on the membranes between the rays of

Figure 24.—Spine-bearing bones of the opercular and posttemporal regions on a 9.5-mm *Prontogrammus aureorubens* larva.



Figure 25.—Larvae of Hemanthias vivanus from the northwestern Atlantic Ocean: a) 4.2 mm; b) 5.3 mm; c) 6.8 mm.



Figure 26.-Larva of Hemanthias peruanus from the eastern Pacific Ocean, 9.3 mm.



Figure 27.—Spine-bearing bones of the opercular and posttemporal regions of a 4.3-mm Hemanthias vivanus larva.

the pelvic fins. Internal pigment on the dorsolateral surface of the gut shows through the body wall.

Discussion.—Larvae of four genera of American anthiines have been found. These larvae are separated from other serranids by their deep bodies, large heads, produced preopercular and interopercular spines, a tendency for development of armature on the head, and serrations of fin spines. Within the anthiines, the genera can be ranked according to the development of these characters. *Plectranthias* has little development of these characters. The preopercular spine is elongate and serrate, but the interopercular spine is not serrate. There is no protruding supraoccipital crest, neither the frontal





ridge over the eye nor the fin spines is serrate. Anthias develops more extreme larval characters. The preopercular and interopercular spines are stronger and both are serrate. The ridge above the eye has several serrae. In some species there is a nonserrated protruding
	Branchio-		Pec-	Pel-		al fin				
length (mm)	stegal rays	Verte- brae	toral fin	vic fin	Dorsal S P	Ventral P S	Anal fin	Dorsa Spines	l fin Rays	Gill raker:
.2 NL								I		
.3								I		
.5								I		
.6								Î		
.6				Ι				I		
.7				I				Ĩ		
.7								·I		
.7								Ι		
7				Ι				Ι		
8				Ι				Ι		
8				Ι				Ι		
.8								Ι		
.8	2			Ι				III		
9								Ι		
.9				Ι				Ι		
.9				Ι				Ι		
.0				Ι				Ι		
0				I				I		
1	0			I I				II III		
1	2									
1				I I				II II		
.1 .2				I				П		
.2				I				П		
.2				I				II		
2				I				П		
.3	3			I				III		
.4	0			I				III		
.4				Ī				III		
.4	3	3		I				III		
.5	3	3		Ι				III		
.7	2	3		Ι				III		
.7	3	2		Ι				III		
.8	4	3		Ι				III		
.9	4	3		Ι				III		
.9	4	4		Ι				IV		
.9	5	4		Ι			Ι	IV		
.9	4	3		Ι			Ι	IV		
.9	5	5		I,1			Ι	IV		2
.9	6	3		Ι				III		
.0	6	6		I			I	V		2
.0	6	6		I			II I	V V		2
.2	6	5		I,1				VI		3
.3	6 C	5		I,1 I,1			II I	IV		0
.3	6 6	5 12		I,1 I,1			I	V		damag
.4										
.5	6	15		I,1			П	IX		5
.6 SL	7	20		I,1			II	IX		9
.6	7	14		I,2			II	VIII		7
.7	7	18		I,2			Π,1	IX		8
.8	7	16		I,2			II,1	IX		8
.8	7	16		I,2			II	VIII		8
.9	7	15		I,1			II	IX		7
.1	7	14		I,1			Ш	VIII		8
.3	7	18		I,2			II,1	X		9
.3	7	18		I,1	0	C	Ш	X		8
.3	7	23	11	I,4	8	6	II,9 II 1	X X		12 8
.4	7	18		I,2			II,1 II,1	IX X		9
5.5	7	20	0	• I,2	0	6	II,1 II,9	X	9	9 10
5.5	7 7	22	8	I,3 I,2	8	0	II,9 II,1	X		10
.8		23 20		I,2 I,2	2	3	П,1	X		11
5.8 5.8	7 7	20 26	14	1,2 I,5	2	8	П,1	X	14	13
	1	20	T.T	1,0	0	0	44,0			

Table 4.—Meristic character development of larvae of *Hemanthias vivanus*. Specimens between dashed lines are undergoing notochord flexion. For the caudal fin, "P" and "S" indicate primary and secondary fin rays.

Tabl	le .	1 -	Con	tin	ued.
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Body	Branchio-		Pec-	Pel-		Caud	lal fin					
length	stegal rays	Verte-	toral fin	vic	Do	rsal	Ver	ntral	Anal	Dorsal fin		Gill
(mm)		brae		fin	S	Р	Р	S	fin	Spines	Rays	raker
17.1	7	26	14	I,5		8	7		II,9	Х	14	13
17.3	7	26	16	I,5		9	8		II,9	Х	14	14
17.3	7	23	2	I,2		6	4		II,1	Х		12
17.7	7	26	17	I,5		9	8		II,9	Х	14	15
17.7	7	26	17	I,5		9	8		II,9	Х	14	15

Scales present.

 Table 5.—Body proportions of larvae of Hemanthias vivanus.
 Specimens

 between dashed lines are undergoing notochord flexion.

		Percent of standard length										
Body length (mm)	Total length	Body depth	Eye length	Head length	Snout length	Pre- anal length	Caudal peduncle depth	Depth at anus				
3.1 NL	106	36	14	34	12	60	8	28				
4.0	103	29	10	35	11	57	5	32				
4.4	114	39	11	37	14	53	11	31				
4.6	108	36	11	41	15	58	10	27				
4.6	112	38	12	42	15	55	10	30				
4.6	109	36	12	39	. 14	57	11	27				
4.6	109	38	12	42	14	59	11	27				
4.7 SL	116	41	15	43	16	61	12	35				
5.0	116	38	13	39	13	58	11	30				
5.0	113	41	15	48	15	60	14	38				
5.2	116	37	12	40	12	55	12	31				
5.2	118	39	13	41	16	60	13	31				
5.4	123	40	15	43	15	63	14	30				
5.5	117	44	16	43	15	62	14	36				
5.7	121	38	13	40	15	58	13	31				
6.0	118	43	16	46	13	65	16	35				
6.0	122	42	14	44	15	60	14	36				
6.3	122	39	13	44	13	60	14	31				
6.5	124	40	14	42	14	61	14	32				
6.8	117	33	13	38	14	61	13	29				
7.0	124	42	14	43	14	61	14	32				
7.8	124	37	14	42	14	59	13	29				
8.0	113	40	11	38	11	54	11	- 30				
8.1	122	40	15	41	14	60	11	32				
9.2	121	35	12	37	14	55	12	28				



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supraoccipital crest. The fin spines are strong and the third dorsal spine and the pelvic spine are elongate Some species develop ctenoid scales while retaining lavel val characters. *Pronotogrammus* develops more extrem larval characters including a strong protruding super occipital crest and heavy opercular armature. These lave, however, are not scaled. Among American anthime *Hemanthias* exhibits the most extreme development larval characters. The head is armored with a serra supraoccipital crest, numerous serrate ridges on the fro tals and parietals, and heavy serrate spines on bones the opercular series. Ctenoid scales develop during the larval period. In *Hemanthias vivanus* larval anthim characters reach their apex with the development of serations on several dorsal and anal fin spines.

Figure 29.—Development of the supraoccipital crest of *Hemanthias vivanus*: a) 4.3 mm; b) 5.8 mm; c) 6.6 mm.



Figure 30.-Details of the head spination on a Hemanthias vivanus larva, 7.2 mm.

#### Subfamily Epinephelinae

The Epinephelinae is represented by three genera in American waters from both oceans. These are *Paranthias* with 1 species, *Mycteroperca* with 13 species, and *Epinephelus* with 21 species grouped in 5 subgenera (Table 1). *Epinephelus* is worldwide in warm water while the other two genera are indigenous to the Americas. The monotypic genus *Gonioplectrus* has close affinities to the epinephelines based on larval and adult characters (Kendall and Fahay in press). Members of this subfamily are quite disparate in size as adults, some reaching only 30 cm, while others reach 180 cm and a weight of 320 kg. Until recently the subgroupings of *Epinephelus* were given generic status but Smith (1971) regarded them as subgenera.

Larvae of several species of Epinephelus have been illustrated and described. The species are outstanding in having the second spine of the dorsal fin and the pelvic spine strong, serrated, and produced to nearly the length of the larva. These larvae are frequently associated with the entire family and have been cited as representatives of the family (e.g., Rosenblatt and Zahuranec 1967; Smith 1971). Among the earliest published illustrations of Epinephelus larvae are those of Fage (1918) who called them Serranus scriba. Bertolini (1933) reviewed Fage's work and indicated that the fish was Epinephelus guaza. Sparta (1935) figured the eggs of Epinephelus guaza and the larvae of Epinephelus alexandrianus. Fage's (1918) figures and description were reviewed by Vodjanitzki and Kazanova (1954). Ukawa et al. (1966) and Mito et al. (1967) described larval development of reared Epinephelus akaara from Japan. Guitart Manday and Juarez Fernandez (1966) described eggs and early stage larvae of Epinephelus striatus obtained from aquarium held adults.

Aboussouan (1972) illustrated and described three types of larvae from the west coast of Africa that he ascribed to the genus Epinephelus. However, only one of these, E. aeneus, has the larval characteristics of an epinepheline. The other two do not have elongated fin spines; in fact, the spinous dorsal and pelvic fins develop after the soft dorsal and anal. The preopercular margin is comprised of several spines with the one at the angle only slightly longer than the rest and not serrate. Pigment is made up of small melanophores as opposed to the large caudal peduncle blotch of epinephelinesm. These larvae are almost certainly not epinephelines, rather one is possibly a sciaenid and the other a haemulid, judging from the number of fin elements and general larval morphology. Presley (1970) described Epinephelus niveatus larvae from the Florida Straits. Smith (1971) illustrated a larval Epinephelus from off the Carolinas. Fowler (1944) described a new genus and species (Serrihastaperca exul) from a larval fish from the eastern Pacific. As Heemstra (1974) has shown, this is probably a larval Epinephelus, possibly Epinephelus panamensis. Fourmanoir (1976) illustrated and briefly described three epinepheline larvae from the southeastern Pacific. Kendall and Fahay (in press) described a larval Gonio*plectrus hispanus* and concluded that although it had some characters of the anthiines, it was more closely related to the epinephelines.

Although the figures are not as detailed as might be desired, and the descriptions are generally brief, most Epinephelus larvae described thus far appear quite similar. They all possess stout, elongate, serrate pelvic fin spines and second dorsal spines. The preopercular is armed with an elongate spine at its angle and several smaller spines. The first spine of the dorsal fin is short and serrate, the second long and serrate, and the third somewhat elongate and serrate. The succeeding spines become progressively shorter and less robust until it is difficult to distinguish the last dorsal spine from the first dorsal soft ray. Pigmentation generally consists of a few spots on the surface of the skull, a spot at the junction of the cleithra, internal pigment lateral to the gut, and a large spot on the caudal peduncle. The elongate fin spines also have some pigmentation on their membranes.

The larval material I have examined contains many species of epinepheline larvae all agreeing closely with the above descriptions. There are no forms which possess only some of this suite of characters, rather they are all uniform and distinguishable from other types of serranid larvae. Besides specimens having meristic characters of *Epinephelus* sp., there are larvae representing the two other American genera, *Mycteroperca* and *Paranthias*. Larvae of these genera can be separated at present on the basis of meristic characters but not larval morphology.

**Paranthias**.—The genus Paranthias contains one species (P. furcifer) which is found on both sides of the Americas. It is separated from other epinephelines by morphology and habits. It converges with anthiines in several of its adaptations, although on skeletal and other characters its affinities clearly lie with the epinephelines (Table 1). As opposed to the demersal, piscivorous habits of other members of the subfamily, P. furcifer occurs in aggregations somewhat above the bottom where it feeds on plankton (Randall 1968). Morphological characteristics related to these habits include a deeply forked caudal fin, dorsal and ventral profiles nearly equally curved, a smaller head with a small upturned mouth, and more gill rakers (35-40) than other epinephelines (Smith 1971).

As larvae, the three genera of American epinephelines can only be separated using meristic characters. These are sufficiently formed only late in development. Separation of *Paranthias* from the other two genera depends on the number of dorsal fin rays. The posteriormost spines in the dorsal fin of epinephelines are short, late forming, and first form as rays. The total count of dorsal spines and soft rays in *Paranthias* (27-28) is commonly seen in members of the other two epinepheline genera also. At present, only large, well-developed larvae of *Paranthias furcifer* have been identified.

As mentioned, *Paranthias furcifer* larvae share larval characters with all other epinephelines found so far (Fig. 31). The pelvic spine and second spine of the dorsal fin are long and serrate. They bear pigmented "flags" near



Figure 31.-Larva of Paranthias furcifer from the eastern Pacific Ocean, 8.6 mm.

their tips, which are often abraded off in netted specimens. The first and third dorsal spines and second anal spine are also serrate. The third dorsal fin spine is moderately elongate. The spine at the angle of the preopercular is long and serrate and there are usually two spines on the preopercular bone dorsal and ventral to the spine at the angle. There is a serrate ridge of spines dorsal to the eye and the supracleithrum has a protruding blunt serrate spine. Pigment spots are present over the optic lobes of the brain and laterally over the gut. There is a large, intense blotch midlaterally on the caudal peduncle.

A 34-mm specimen collected at the surface as part of a large school showed loss of larval characters. The body was fully scaled and the supraocular ridge and the protruding supracleithral spines were unpronounced. The second dorsal spine was only slightly larger than the third and all were well formed and nearly equal in length. The second spine retained minute serrations. The pelvic spine also retained serrations and was about as long as the second dorsal spine, not reaching the posterior end of the pectoral fin. The first ray of the pelvic fin was longer than the spine. The spine at the angle of the preopercular was still slightly elongate and serrate; but rather than two spines on each side of the spine at the angle, there were several (6 ventral and 20 dorsal). The specimen I examined was cleared and stained so no assessment of pigment pattern could be made.

Epinephelus.—This is the only American epinepheline genus with representatives in other parts of the world. Epinephelus is the most species genus of serranids, containing 21 American species grouped in 5 subgenera. Fifteen species occur in the Atlantic and 11 in the Pacific, with 5 species common to both oceans. They are separated from other American epinephelines by a combination of characters (Table 1). Those species with IX dorsal spines have fewer than 18 rays, whereas Paranthias furcifer has a dorsal fin count of IX, 18-19. Epinephelus species differ from Mycteroperca by having 8 or 9 anal rays, rather than 10 to 12. Other diagnostic characters include characteristic skull crests and the presence of a postocular process (Smith 1971).

As discussed earlier, larvae of several species of *Epinephelus* from around the world have been described (e.g., Bertolini 1933; Mito et al. 1967; Fourmanoir 1976). Presley (1970) described larvae he assigned to *Epinephelus niveatus* from Florida. His description is rather brief, and considering the similar appearance of all epinepheline larvae that have been described and all those I have found, it is probably inadequate to separate that species from others in the area.

Larval epinephelines are not separable into genera until medial fin rays have formed. Only on the basis of these counts could *Epinephelus* larvae be distinguished from those of *Mycteroperca* (by a lower anal fin ray count) and from *Paranthias* (by a different dorsal fin count). Two larval specimens of *Epinephelus* are illustrated (Figs. 32, 33). They are both about the same length and appear similar. One specimen (Fig. 32) from the Atlantic has XI, 16 dorsal fin elements and III, 9 anal fin elements making it most likely a member of the *Epinephelus striatus* species group and probably either *E. morio* or *E. guttatus*. The other specimen (Fig. 33) is from the eastern Pacific with XI, 19 dorsal fin elements and III, 9 anal fin elements making it most likely either E. dermatolepis dermatolepis or E. alphestes multiguttatus. Although these specimens are in different subgenera, no characters other than meristics could be found to distinguish them from other genera within the subfamily.

The following account describes features of all larval Epinephelus specimens seen so far, since no characters have yet been found to identify the species. Most of the characters mentioned with the account of the subfamily apply to the specimens identified as Epinephelus sp. The second spine of the dorsal fin is elongate and serrate as is the pelvic spine. The first and third dorsal fin spines are also serrate and the fourth may be as well. The anal fin forms with only the first two spines as such until late in development. The third anal fin spine forms as a ray and later becomes a spine. The first two anal spines may be serrate. The preopercular margin is armed with an elongate, serrate spine at its margin and one or two blunt spines dorsal and ventral to the one at the angle. Later in development more spines form on this margin and it becomes serrate. There is a serrate ridge above the eye and the posttemporal and supracleithral bones have pro-



8.4 mm.

truding, serrate spines. The pigment pattern consists of a few melanophores on the surface of the optic lobes, some

on the lateral surface of the gut, and a large blotch on the caudal peduncle. The caudal peduncle blotch is var-

iously placed, from along the ventral midline to laterally on the lateral line. It tends to become internal on larger specimens. The elongate dorsal and pelvic spines are variously pigmented but the pigment is absent on many netted specimens. The pigment is seen on the membranes associated with the extended portion of the spines.

Besides the transformation of the third anal spine from a ray to a spine during development, as many as two posterior spines of the dorsal fin undergo similar transformation. The second dorsal fin spine is elongate and the third through seventh are progressively smaller. The 7th through the 11th dorsal spines are quite small during larval development. It seems that the first nine spines develop as such, but the last two develop as soft rays and later transform into spines. However, in specimens which have only 9 or 10 spines as adults, no such transformation may occur.

The bones in the opercular region of a 10-mm Epinephelus sp. (possibly E. niveatus) are characteristic of the genus (Fig. 34). The preopercular bone has the most produced spines of any of the bones in the region. As mentioned above, it has a long, serrate spine at its angle and two spines dorsal and ventral to the one at the angle. These spines may also be serrate. The opercular has a broad fan shape with three blunt spines. The area ventral to the lower spine is broad. The subopercular has a spine on its posteroventral margin. The interopercular has a spine on its posterodorsal edge. The posttemporal and supracleithrum each have a protruding serrate spine.





Mycteroperca.—This is the second most speciose epinepheline genus with eight species in the Atlantic and five in the Pacific Ocean (Table 1). They are distinguished from the other two epinepheline genera by having 10 to 13 anal rays and straight, parallel lateral skull crests that join the rim of the orbit anterior to the midorbital area (Smith 1971). Larvae with developed III, 10-13 anal fin elements and epinepheline larval characteristics were found in samples from both oceans. They had other diagnostic characters of Mycteroperca. These larvae had the full suite of characters of epinepheline larvae and, on the basis of larval characters, could not be separated from other epinepheline larvae. They had elongate, serrate second dorsal and pelvic spines and a long serrate spine at the angle of the preopercular. There was a serrate, bony ridge above the eye and protruding, serrate spines in the posttemporal region. They had a few pigment spots on the dorsal surface of the optic lobes of the brain, some on the lateral surface of the gut, and a large blotch on the caudal peduncle. Some pigment was present on the membranes of the elongate fin spines.

Mycteroperca microlepis (Figs. 35, 36).—The meristic characteristics of Mycteroperca microlepis fall within the ranges for several species of Mycteroperca in the western Atlantic (Table 1). However, among these species, M. microlepis is the most northerly occurring. Late larvae and early juveniles with characteristics of M. microlepis have been caught in the Middle Atlantic Bight.

In plankton samples from as far north as Cape Hatteras, N.C., large epinepheline larvae (>7 mm) with meristic characters of M. microlepis are frequently found. In these samples smaller larvae with similar larval characters but incomplete meristic characters are also found. The following description is based on these epinepheline larvae taken off North Carolina. Larger larvae and juveniles (12-35 mm) from nearshore and estuarine collections along the Atlantic coast from Florida to New Jersey were examined to note the development of juvenile pigment and the regression of the elongate spines of early larvae. No other species of Mycteroperca could be identified in the samples with certainty.

Meristic element development (Table 6)-Development of most meristic elements occurs over a length range of 4.0-9.8 mm. In the smallest larvae available (4 mm), the dorsal fin already has the first three spines ossified, the pelvic fin has one spine and one ray, and there are three branchiostegal rays and two gill rakers. Between 5 and 6 mm, the notochord is flexing and most meristic features are forming ossified elements. The ossified vertebrae increase from 4 to 18, forming from anterior to posterior except for the urostyle. Several vertebrae are partially developed in most specimens. The branchiostegal rays reach their adult complement of 7 and there are 6 to 10 gill rakers. The pelvic fin has three rays ossified and the pectoral fin starts to form rays. The dorsal fin increases from three to five spines and the anal starts to form. The caudal fin has its adult complement of nine dorsal and eight ventral primary rays as the notochord becomes fully flexed at 6 mm. When notochord flexion is complete, by 7 mm, most meristic features are well formed, approaching adult counts. Vertebrae increase to 22 with the urostyle forming prior to the 2 or 3 vertebrae anterior to it. The pectoral fin increases to 12 rays and the pelvic fin attains its adult complement of 1 spine and 5 rays. The anal fin increases rapidly having 2 spines and 11 rays. The first soft ray of the anal fin becomes the third spine later in development, as is characteristic of most adult serranids with three anal spines. The dorsal fin is difficult to count separately because the posterior spines are quite small at formation and, like the third anal spine, originate as soft rays. It appears that there are 10 spines and 15 rays in the dorsal fin. In addition to the 9 or 10 gill rakers on the lower limb, 1 forms on the upper end of the first gill arch. Procurrent caudal rays start to ossify. Between 7 and 10 mm, the meristic elements, except gill rakers and scales, reach their adult complements. Not until about 20 mm do the 3rd anal spine and 11th dorsal spine change from soft rays to spines.

Body proportions (Table 7)—Proportions of various measurements of larvae and juveniles of Mycteroperca microlepis to body length (BL) were examined. Most proportions show little ontogenetic change; however, total length increases sharply with the formation of the caudal fin and the depth at the anus and caudal peduncle depth also increase between 4 and 6 mm. The greatest body depth remains between 29 and 35% of BL throughout the size range examined. The head length stays about 31 to 43% of BL. The preanal length is 51 to 66% of BL. Eye and snout length are about 9 to 14% of BL. The elongated larval spines were measured to trace their relative growth. The second dorsal spine was broken on several smaller specimens but it appeared to increase from 40% of BL at 4.6 mm to 60% from 5 to 10 mm and then decrease to 11% by 35 mm. The pelvic spine showed a similar pattern of increase and decrease, reaching a maximum relative size of 68% of BL at 8.3 mm and decreasing to 12% of BL by 35 mm. The preopercular spine increases from about 0.5% of BL at 5 mm to 1.1% at 8 mm and decreases to 0.2% by 35 mm.

Pigmentation—The pigment pattern seen on the smallest larvae examined remains basically unchanged throughout larval development. On the heads of 4-mm larvae there is a spot on the dorsoposterior surface of each optic lobe, and there are several spots in the same area on 6-mm specimens. A spot develops internally on the nape near the dorsal fin origin which later occurs in the area of the neural spines of the first two vertebrae. The dorsolateral surface of the gut cavity is covered with rather dense pigment throughout larval development. Ventrally, on most specimens there is a spot at the cleithral junction. A large spot occurs on the ventral region of the caudal peduncle in small larvae. In 7.5-mm specimens this spot has moved dorsally to lie over the lateral line in the midlateral caudal peduncle area. This spot extends internally to the area of vertebrae 20 to 21. The size and vertical position of this spot varies somewhat among the specimens observed from along the ventral midline to the lateral line. A few small spots that develop on the ventral tip of the notochord lie near the bases of the caudal rays as the caudal fin is formed.

Opercular series spines (Fig. 36)—Spine-bearing bones of the opercular region of a 9.8-mm specimen of Mycteroperca microlepis appear similar to those of other epinephelines. The preopercular bone has an elongate, serrate spine at its angle which reaches a maximum of 1.3% of BL in 8-mm specimens. Smaller spines form along the vertical and ventral edges of the preopercular. During larval development, there are two spines in each area with all but the uppermost spine being serrated. Later in development, as the elongate spines regress, additional small spines appear along the edge of the preopercular to form the serrate margin of the adult. The interopercular bears two blunt spines along its posterior margin. The subopercular has one blunt spine at its ventralposterior angle. The opercular is fan-shaped with three blunt spines on its posterior margin. The supracleithrum has a posteriorly directed, serrate spine and the lateral posttemporal ridge is serrate.

Discussion.—The 35 presently recognized species of epinephelines in American waters constitute a cohesive group (Smith 1971). Recently, five genera have been given subgeneric rank, leaving the species grouped in only three genera. *Epinephelus*, the most speciose American genus with 21 species, is a speciose genus in other parts of the world also, e.g., there are 34 species in Japan (Katayama 1960). Among American genera, *Paranthias* has evolved obvious ecological and morphological distinctions from the general "grouper" characteristics. A clearer understanding of the relationships within this subfamily must await its comprehensive revision on a worldwide basis.

Epinepheline larvae representing all three American genera were found. Their identification was based solely on meristic characters. No larvae of epinephelines could be separated on the basis of any larval characters. They shared all recognized larval characters. Thus it appears that evolutionary differences within this group are not reflected in larval morphology.

Epinepheline larvae are quite distinct from larvae of other serranids. The other subfamily with serrated spines, Anthiinae, does not have the extremely elongate, serrate fin spines seen in epinephelines. In anthiines the interopercular has a produced spine which lies under the spine at the angle of the preopercular, both of which are usually serrate. Epinephelines have only a blunt spine on the interopercular. Anthiines also are heavier bodied than epinephelines. Gonioplectrus shares trenchant larval characters with epinephelines but has less variation in dorsal spine length and a stouter body, both reminiscent of anthiine larvae. These resemblances to anthiine larvae may represent convergence. However, Gonioplectrus may represent an evolutionary plateau between anthiines and epinephelines; this remains for further study to elucidate. Serranines have simple armature on the preopercular and no fin spine serrations. Grammistines have the second spine of the dorsal fin produced into a long, filamentlike structure, in contrast to its stout-serrated form in epinephelines. Apparently, in American waters at least, intermediates between epinephelines and other groups of serranids have been lost.





Figure 35.—Young stages of Mycteroperca microlepis from the northwestern Atlantic Ocean: a) 4.0 mm; b) 7.4 mm; c) 14.2 mm; d) 22.6 mm.

Table 6.—Meristic character development of larvae of  $Mycteroperca\ microlepis$ . Specimens between dashed lines are undergoing notochord flexion. For the caudal fin, "P" and "S" indicate primary and secondary fin rays.

Body	Branchio-		Pec-	Pel-		Cauc	lal fin					
length	stegal	Verte-	toral	vic	De	orsal	Ver	ntral	Anal	Dorsal fin		Gill
(mm)	rays	brae	fin	fin	S	Р	Р	S	fin	Spines	Rays	s rakers
4.0 NL	3			I,1						III		2
4.6	4			I,2						III		3
5.1	5	4		I,2		1	2			III		6
5.6	6	6		I,3		5	5			III		7
5.3	5	4		I,3		4	4			Ш		6
5.3	6	6	2	I,3		6	6			IV		8
5.3	6	8	2	I,3		7	7			IV		10
5.5	7	18	6	dama	ge	9	8		I,6	V		9
6.0 SL	7	20	9	I,4		9	8	1	П,9	X	11	1+9
6.1	7	19	6	I,4		9	8		I,6	VI		9
7.0	7	22	12	I,5	1	9	8	2	Π,11	Х	15	1+10
7.4	7	24	12 .	I,5	1	9	8	2	Π,11	X	15	2 + 9
7.9	7	24	14	I,5	3	9	8	3	П,13	Х	19	3+10
8.1	7	24	15	I,5	3	9	8	2	II,12	Х	18	3+10
9.2	7	24	17	I,5	4	9	8	5	Π,11	Х	18	3+12
9.8	7	24	16	I,5	5	9	8	5	II,12	Х	18	4+11

					Percent	of standar	d length				
Body length (mm)	Total length	Body depth	Eye length	Head length	Snout length	Preanal length	Caudal peduncle depth	Depth at anus	Second spine of dorsal fin	Pelvic fin spine	Preoper cular spine
4.6 NL	104	30.4	10.9	32.6	9.6	52.2	7.6	15.2	39.1		0.43
5.3	106	32.1	11.3	32.1	9.4	50.9	8.5	18.9	_	49.1	0.58
5.3	109	34.0	11.9	35.8	10.6	56.6	8.3	20.8	69.2	54.7	0.75
5.3	113	34.0	12.1	35.8	12.1	54.7	9.4	26.4	_	58.5	0.94
5.5	110	36.4	12.7	40.0	13.6	56.6	10.2	25.5	_	-	0.91
5.6	107	32.1	11.1	35.7	10.9	55.4	7.9	19.6	-	-/	0.55
5.9	112	32.2	10.8	42.4	-	64.4	10.5	22.0	11	-	1.02
6.0 SL	120	36.7	13.0	38.3	11.5	60.0	11.5	23.3	61.7	61.7	0.93
6.1	120	34.4	12.3	41.0	13.0	67.2	10.2	26.2	_	59.0	0.92
7.0	120	34.3	12.1	37.1	11.6	61.4	11.6	24.3	54.3	61.4	0.99
7.4	122	33.8	11.9	39.2	11.5	60.8	11.1	21.6	_	62.2	1.15
7.9	120	32.9	11.9	38.0	10.8	60.8	11.9	24.1	_	60.8	1.04
8.1	121	34.6	9.9	37.0	11.6	59.3	13.6	24.7	59.3	58.0	0.99
8.3	119	33.7	12.0	38.6	13.3	57.8	12.0	25.3	65.1	67.5	1.33
9.2	123	33.7	12.0	38.0	12.0	57.6	12.0	23.9	59.8	64.1	1.02
9.4	121	35.1	12.8	38.3	10.6	59.6	12.8	25.5	58.5	63.8	1.06
9.8	123	33.7	11.2	39.8	14.3	66.2	11.2	26.5	60.2	65.3	1.02
12.0	123	35.0	11.7	38.3	10.8	57.5	13.3	28.3	49.2	55.0	1.00
13.6	125	33.1	9.6	37.5	11.8	58.1	11.8	27.9	39.7	42.6	0.92
14.0	131	33.6	10.7	37.9	11.4	62.9	10.7	25.7	39.3	47.9	_
16.8	123	32.7	10.1	39.3	9.5	61.9	11.9	25.6	40.5	39.3	0.83
17.6	122	31.8	11.4	35.3	8.5	58.0	10.2	24.4	40.3	46.0	0,91
19.3	115	31.1	10.4	36.3	9.3	58.5	10.9	24.9	21.3	20.2	0.62
21.1	122	31.8	10.9	31.3	13.7	60.7	10.9	27.0	20.4	29.4	0.52
21.5	120	30.2	10.7	37.2	10.7	52.1	11.2	25.6	20.5	17.2	0.65
24.4 '	125	32.8	11.1	42.6	11.1	63.5	11.1	32.8	13.5	14.8	0.33
35.4	120	28.5	9.0	36.2	9.0.	61.6	10.7	27.1	11.0	12.1	0.14

Table 7.—Body proportions of larvae of *Myctoperca microlepis*. Specimens between dashed lines are undergoing notochord flexion.



Figure 36.—Spine-bearing bones of the opercular and posttemporal regions on a 9.8-mm Mycteroperca microlepis larva.

# **Subfamily Grammistinae**

Larvae of three genera, *Liopropoma* (larvae of *Pikea* may be included here), *Rypticus*, and *Pseudogramma*,

have been recognized and will here be considered members of a single group, the subfamily Grammistinae. These larvae are similar in appearance and readily separable from larvae of other fishes. Considerable work has been done on the taxonomic affinities of these fishes but their relationships remain perplexing. *Liopropoma* has been considered a member of the serranid subfamily Liopropominae (Katayama 1960). *Rypticus* has been considered a member of the family Grammistidae, a closely related offshoot of the serranids (Gosline 1966). *Pseudogramma* has been considered a pseudogrammid, a group which has been considered a subfamily of the grammistids or a separate family (see Randall et al. 1971). Reasons for considering these fishes members of a single group are detailed in Kendall (1976, 1977).

Liopropoma.—Pikea has been included with Liopropompa in the subfamily Liopropominae. They have identical predorsal bone patterns and similar meristic formulae (Table 1). Chorististium has been synonymized with Liopropoma. Two genera, Joboehlkia and Flagelloserranus, described from preadult material, apparently belong with this group. Pikea has three northwestern Atlantic species and Liopropoma includes five species in the northwest Atlantic, one in the eastern Pacific, and several from the central and western Pacific. Within this group, larvae of Liopropoma and/or Pikea have been found in material from the northwest Atlantic. These larvae appear similar to those described by Kotthaus (1970) as the genus Flagelloserranus. He described two species of Flagelloserranus, one from the Indo-Pacific Ocean and one from the western Atlantic Ocean. Fourmanoir (1971, 1976) indicated that similar specimens from near New Caledonia were young of Liopropoma. All the characters Kotthaus (1970) used to define this genus and separate it from Liopropoma appear to be transient larval or juvenile characters. The similarity of meristic and other characters, the unique predorsal bone pattern, and the lack of adults of Flagelloserranus indicate that these are larval Liopropoma or Pikea. Thus, Kotthaus (1970) provides descriptive material for larval development of Liopropoma-Pikea so it will be considered only briefly here.

I considered larval types resembling *Flagelloserannus*, one with pigment on the ventral caudal peduncle surface and one without, members of the genera *Liopropoma* and/or *Pikea*. However, since the meristic characters and areas of occurrence of the several species of these two genera overlap, I did not attempt to allocate the larvae to species.

Their general body shape is similar to that of the serranines, although the gut is shorter and there is a space between the anus and the origin of the anal fin (Fig. 37). The caudal peduncle is both longer and deeper than it is in serranines.

The most outstanding developmental feature is the presence, even in small larvae, of two elongate, thin dorsal spines. These develop before other fin rays, reach a length of up to three times the fish length and become the second and third dorsal spines. These spines are delicate and are broken in many specimens. Kotthaus (1970) described the presence of thick tissue surrounding these spines; the tissue around the second spine having two vanelike swellings on its distal third, the tissue around the third spine being tubular for its entire length. The distal portion of both spines is pigmented with several large melanophores. The remaining fin rays develop their adult proportions without any pronounced elongations. The ventral fins develop more slowly than those of most other serranids. The pectoral fins do not develop precociously, as they do in Rypticus and Pseudogramma.

Except for the pigment on the elongate dorsal fin spines, most larvae examined were unpigmented. Prior to notochord flexion some larvae bear a melanophore on the ventral midline anterior to the insertion of the anal fin. Whether this spot disappears in larger larvae or larger specimens with this pigment were not collected cannot be determined presently. Some spots develop on the hindbrain surface in larger larvae, probably representing the onset of juvenile pigment.

The bones of the preopercular region are armed with characteristic spines (Fig. 38). The preopercular has four blunt spines above and three below the one at the angle. *Flagelloserranus meteori* from the Indo-Pacific has a similar preopercular with two spines above and three below the one at the angle (Kotthaus 1970). *Flagelloserranus danae* from the western Atlantic has a similar preopercular except it has a hooked dorsalmost spine and the vertical limb is longer than in F. meteori (Kotthaus 1970). The opercular of the larvae examined in this study as well as those of Kotthaus (1970) is fan-shaped with three spines on its margin. Both the subopercular and interopercular have a blunt spine on the posterior edge in the larvae I examined; however, Kotthaus (1970) reported a smooth margin in both species he recognized. A low posttemporal ridge that penetrates the epidermis of the larvae I examined was not mentioned by Kotthaus (1970).

Rypticus.—Occurring in the Atlantic and eastern Pacific Oceans, this genus has meristic characters that are unusual among serranids (Table 1) and small, embedded cycloid scales. The unique gonadal morphology (Smith and Atz 1969) and predorsal bone patterns (Kendall 1976) also indicate that *Rypticus* is highly specialized and no other known fish can be derived from it. These are secretive, nocturnal reef fishes of small to moderate size (50-260 mm). Altogether, there are about 11 species, with 8 of them occurring in the western Atlantic (Randall et al. 1971). Atlantic members of the genus have been reviewed by Courtenay (1967).

Aboussouan (1972) illustrated and briefly described a single 9.0-mm larva as *Rypticus saponaceus* and a 4.5mm specimen as "*Rypticus* (?)." Courtenay (1967) illustrated a 15.5-mm juvenile of *Rypticus saponaceus*.

Only one larval specimen with meristic characters of Rypticus was found in collections from the Pacific, while the genus was represented by many specimens in collections from the Atlantic. Small larvae were so similar in body shape and lack of pigment to Liopropoma and Pseudogramma that it was difficult to separate them until some fin elements were well formed. The only pigment seen on the larvae was on the fleshy material enveloping the single elongated first dorsal spine (Fig. 39). This pigmented "flag" is more than half the body length; however, it is fragile and often broken in plankton-collected material. Aboussouan (1972) seems to show rather heavy pigment on the large fanlike pectoral fin of the 9.0-mm larva he illustrated; however, I saw none on the material I examined. Besides the elongate dorsal spine and the large pectoral fin, the rays of the second dorsal and anal fins are also uniformly long and the caudal fin appears rounded. The pelvic fins are quite short in contrast to their large size in most other serranids. In most fish larvae with an elongate dorsal spine, the pelvic spines are comparably elongate (Ahlstrom'); Rypticus, however, has an elongate dorsal spine but a relatively undeveloped pelvic fin. Aboussouan (1972) reported an element which resembled a spine in the anal fin; I found none in the specimens I examined. Most serranids have three anal spines, the third of which originates during larval development as a soft ray. Adult Rypticus have no anal

<sup>&#</sup>x27;E. H. Ahlstrom, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 22038, class notes, August 1971.



Figure 37.-Larvae of Liopropoma sp. from the northwestern Atlantic Ocean: a) 6.3 mm; b) 7.0 mm.

spines. If larvae of some *Rypticus* have an anal spine, it is apparently resorbed as the fish develops.

The body shape is similar to that of the serranines; but the nape is deeper and the bases of the second dorsal and anal fins are fleshier.

The bones of the preopercular region are similar in larval spination to those of *Liopropoma*, although specimens of the same size as those observed of *Liopropoma*  were not available for study, so comparisons may be invalid.

Pseudogramma.—Rhegma has been synonymized with Pseudogramma (Gosline 1960) and at times considered a serranid, a grammistid, or a pseudogrammid (Kendall 1977). Larval and other characters indicate that this genus is closely related to Rypticus and





Liopropoma and they all were derived from epinepheline serranids. *Pseudogramma* contains one species from each of the following areas: the central Pacific, the eastern Pacific, and the western Atlantic. They have incomplete lateral lines and moderate-sized scales (Schultz 1966).

Larvae assignable to this genus by their meristic features (Table 1) have been found in samples from the western Atlantic; and since this genus is represented in this area by a single species, it is assumed to be *Pseudo-gramma gregoryi*. Although there is only a small series in the present collections, it will be described in detail, since both of the other genera in this group contain several species, none of which could be identified using larval characters. Also *Liopropoma* has been dealt with previously (Kotthaus 1970).

**Pseudogramma gregoryi** (Fig. 40).—The proper generic name and number of species assigned to the Pseudogrammidae in the northwestern Atlantic have been sources of confusion. Gosline (1960) and Schultz (1966) listed three species, one in *Pseudogramma* and two in *Rhegma*. At present, *Pseudogramma gregoryi* is the only recognized pseudogrammid species in this area, all others being synonymized with it. However, the reported range of meristic characters among species synonymized with *P. gregoryi* indicates that there may be more than one valid species.

Meristic element development (Table 8)—A series of 18 larvae from 3.3 to 10.3 mm was cleared and stained. At 3.3 mm, the notochord is straight but 12 vertebrae (10 precaudal and 2 caudal), 4 branchiostegal rays, 15 pectoral rays, 1 dorsal spine, and 2 gill rakers are already ossified. The notochord undergoes flexion from 3.6 to 4.2 mm and during this time the vertebrae increase to 19, the branchiostegal rays to 6, the pectoral rays to 16, the dorsal spines to 2, and the gill rakers to 4. The caudal fin begins formation and has six dorsal lobe and six ventral lobe primary rays. The dorsal fin spines which become elongate during larval development are the second and third. Most of the meristic complements are complete in



Figure 39.-Larva of Rypticus sp. from the northwestern Atlantic Ocean, 6.6 mm.



Figure 40.—Larvae of *Pseudogramma gregoryi* from the northwestern Atlantic Ocean: a) 4.7 mm; b) 6.1 mm; c) 6.1 mm; d) 10.2 mm.

Table 8.—Meristic character development of larvae of *Pseudogramma gregoryi*. Specimens between dashed lines are undergoing notochord flexion. For the caudal fin, "P" and "S" indicate primary and secondary fin rays.

Body	Branchio-		Pec-	Pel-		Caud	al fin					
length	stegal	Verte-	toral	vic	Do	rsal		itral	Anal	Dorsa	l fin	Gill
(mm)	rays	brae	fin	fin	S	Р	Р	S	fin	Spines	Rays	rakers
3.3 NL	. 4	10 + 2	15							I		2
3.6	6	10+8	15							 II		
4.1	6	10+8	16			4	6			П		4
4.1	6	10+9	16			6	6			П		4
4.2	6	10+9	16			6	6			Ш		4
4.2 SL	7	10+14	16		1	9	8		I,13	IV	17	1+7
4.3	7	10+11	15			7	8		9	II		1+7
4.4	7	10 + 16	15		1	9	8	2	I,16	VIII	18	1+7
4.5	7	10 + 12	15			8	8		10	П		1+5
4.6	7	10 + 14	15			8	8	1	I,16	VIII	18	8
4.7	7	10 + 16	15	I,3	2	9	8	2	III,15	VIII	18	7
5.3	7	10 + 16	15	3	2	9	8	2	III,16	VIII	19	8
5.6	7	10 + 16	15	I,4	3	9	8	3	III.15	VIII	19	3+7
5.9	7	10 + 16	15	I,4	3	9	8	3	III,15	VIII	18	3+7
6.7	7	10 + 16	15	I,5	3	9	8	3	III.15	VIII	18	3+8
7.8	7	10 + 16	15	I,5	3	9	8	3	III.15	VIII	18	4+8
9.6	7	10 + 16	15	I,5	3	9	8	3	III,15	VIII	19	3+9
10.3	7	10 + 16	15	I,5	3	9	8	3	III,15	VIII	19	3+10

5-mm specimens (branchiostegal rays, vertebrae, pectoral rays, anal fin rays, dorsal fin spines and rays, and primary caudal fin rays). The pelvic fin is notably late in formation, relative to the other fins, and does not attain its adult complement of rays until 6.7 mm, after all other elements have reached their adult numbers. Thus, the sequence of meristic character development in *Pseudogramma gregoryi* is quite different from that of other serranids in that the pectoral fin forms before other fins and the pelvic fin forms last. The third anal spine develops as a spine rather than as a ray that transforms into a spine as it does in other serranids.

Body proportions (Table 9)—A series of larvae from 3.9 to 11.4 mm was measured to trace changes in body proportions during larval development. Due to the limited number of specimens available, some partly damaged larvae had to be used for these measurements; therefore, some measurements may not represent actual body shape. As the notochord flexes, total length increases from about 110% to about 125% of BL, caudal peduncle depth increases from 6-10% to about 14% of BL, and the preanal length increases from about 45% to about 55% of BL. The rest of the proportions remain rather constant over the size range at hand. The body depth is about 25% of BL (23.2-31.7%) and the depth at the anus is only slightly less (22.5-29.5%). The measurements associated with the head are: eye, 8.3 to 11.6% of BL; snout, 4.7 to 10.0% of BL; and head length, 26.6 to 37.8% of BL. Pseudogramma gregoryi then, is shallower bodied and has a shorter head and preanal length than other serranids.

Pigmentation—Larvae of *Pseudogramma gregoryi* are notable, as are those of *Liopropoma* and *Rypticus*, for their lack of pigment. The only body pigment of *P. gregoryi* during larval development occurs on the dorsolateral surface of the gut cavity. Some pigment develops on the membrane associated with the elongated second spine of the dorsal fin and also on the tips of the pectoral fin rays. Since many specimens were bleached, had broken dorsal spines or were in otherwise poor condition, it was not possible to determine exactly when this pigment first appeared. It was only present in larger larvae among those examined.

Spines in the opercular region (Fig. 41)-Several bones in the opercular region develop unserrated spines during the larval period. Their character was observed in a 10.3mm larva. The spines are more pointed in P. gregoryi than in Liopropoma. The preopercular has five subequal spines on its posterior margin. In contrast to other serranids where the spine at the preopercular angle is longest, the spine dorsal to the one at the angle is longest in P. gregoryi. The interopercular has a sharp spine on its posterior edge, as does the subopercular. The subopercular also has a strengthening ridge that lies under the opercular and extends posterodorsally near the opercular margin. The opercular has three posteriorly directed spines that are pointed and closer together than those of other genera examined. The posttemporal and supracleithrum lack noticeable spines protruding from the larval surface.

Discussion.—Larvae of the three genera described here (*Pseudogramma gregoryi*, *Liopropoma*, and *Rypticus*) share characters which unite them with each other and separate them from other groups of serranid larvae.

 They are practically devoid of pigment at all sizes. Some Liopropoma larvae have one to three melanophores on the caudal peduncle and the fleshy parts of the elongated dorsal spines are pigmented. Nevertheless, these genera have markedly less pigment than other serranid genera I examined.

They all possess one or two elongate, thin, dorsal spines with fleshy sheaths. These are broken in many

	Percent of standard length											
Body length (mm)	Total length	Body depth	Eye length	Head length	Snout length	Pre- anal length	Caudal peduncle depth	Depth at anus				
3.9NL	111	27.4	9.7	30.6	6.5	37.1	6.5	24.2				
4.1	106	29.2	9.2	29.2	7.7	46.2	9.2	26.2				
4.3	110	23.2	10.1	30.4	8.7	44.9	10.1	23.2				
4.3	110	25.0	10.2	30.9	8.8	44.1	8.8	25.0				
4.3	112	26.1	11.6	30.4	8.7	46.4	10.1	26.1				
4.6	112	25.7	9.5	31.1	-	50.0	9.5	23.0				
4.5 SL	120	26.8	11.3	32.4	7.0	52.2	14.1	26.8				
4.5	118	23.9	9.9	29.6	9.9	46.5	11.3	22.5				
4.8	113	27.6	10.5	27.5	6.6	42.1	13.2	26.3				
4.8	116	27.6	9.2	27.6	-	46.0	13.2	26.3				
4.8	118	26.3	9.2	30.3	9.2	50.0	14.5	23.7				
5.0	118	26.3	10.0	31.3	10.0	47.5	12.5	23.8				
5.2	117	31.7	9.8	37.8	9.8	59.8	11.0	24.4				
5.3	112	27.4	10.7	31.0	7.1	50.0	16.7	26.2				
5.7	122	26.4	9.9	29.7	7.7	50.5	15.4	25.3				
5.9	119	26.6	8.5	26.6	5.3	46.8	13.8	23.4				
6.0	121	26.0	10.4	34.4	8.3	45.8	14.6	25.0				
.6.1	120	26.8	9.3	29.9	8.2	48.5	15.5	25.8				
6.0	119	25.0	8.3	28.1	6.3	44.8	12.5	24.0				
7.2	121	26.7	9.5	29.5	6.7	50.5	16.2	27.6				
8.0	118	25.2	9.4	29.9	4.7	50.4	14.2	27.6				
9.7	125	26.0	. 8.4	31.8	9.1	53.2	13.0	27.3				
9.8	125	6.3	9.0	28.8	7.1	53.8	13.5	28.2				
10.4	122	28.3	9.0	30.7	6.6	56.0	14.5	29.2				
11.4	124	25.4	8.8	32.0	7.7	53.6	14.4	26.5				

Table 9.—Body proportions of larvae of *Pseudogramma gregoryi*. Specimens between dashed lines are undergoing notochord flexion.



Figure 41.—Spine-bearing bones of the opercular and posttemporal regions on a 10.3-mm *Pseudogramma gregoryi* larva.

field-collected specimens; but the bases of these elongate spines are larger than those of other spines and this is useful in recognizing these larvae.

3. The pectoral fins develop rays earlier and are larger than in other serranids. In other serranid genera the pectoral fins form last; however, in these genera (except *La propoma*) they form while only a few dorsal spines at caudal fin rays are developing.

4. The body shape is little elevated and the caudal p duncle is deep, producing a tubular-shaped body simil to that seen in some labrid and scarid larvae. Serran larvae in the subfamilies Anthiinae and Epinephelin are deeper bodied than grammistines. Only larvae serranines have the depressed condition of grammistine

These three genera have been considered members separate families or subfamilies; but on the basis of la val morphology and other characters (Kendall 1976 they appear more closely related to each other. Sever other genera have been aligned with those described he but their larvae are unknown, so an accurate assessme of the relationships within this group based on larval d velopment is not possible at present. However, Hub and Chu (1934) illustrated late larvae of Diploprion b fasciatum, a genus considered a grammistid by Randa et al. (1971). Their specimens had greatly elongated fle ible second and third dorsal spines. Jeboehlkia gladife described from a small specimen by Robins (1967), h an elongated but stiff first dorsal fin spine and is pro ably a small specimen of a species closely related to tho described here. Fourmanoir (1976) illustrated and brief described larvae of Grammistes sexilineatus ar Aporops bilinearis, both with an elongate dorsal spin and preopercular spines similar to the grammistines d scribed here. The unique first pterygiophore of gran mistine and related fishes (Kendall 1976) may help su port the elongate larval dorsal spines, as the enlarge predorsal bone supports the vexillum of larval carapids (Strasburg 1965). Possibly all fishes belonging in the Grammistinae have one or two elongated dorsal spines as larvae or have lost them secondarily. As larvae of more members of this group are described, relationships between them may become clarified.

# DISCUSSION

This study of larvae of most American serranid genera permits an examination of the phylogeny of the group on the basis of larval characters. Among the percichthyids, only the larvae of *Morone* have been adequately described (Mansueti 1958, 1964). Since they develop in estuarine areas whereas serranids develop at sea, their morphology may show adaptations not present in serranids. Nevertheless, the larvae of *Morone* appear generalized and it appears that unspecialized serranines could have been derived from them. Some of the larval characters of *Morone* considered trenchant in this respect are their late-developing spinous dorsal and pelvic fins, pigment consisting of evenly sized melanophores scattered over the body, and the lack of heavy armature in the opercular area.

Serraninae larvae demonstrate various degrees of specialization from the *Morone* pattern. There seems to be a trend among the genera toward a deeper body, earlier development of the spinous dorsal and pelvic fins, larger spines on bones in the opercular region, and pigment concentrated in blotches mainly along the ventral midline. *Hypoplectrus* and a type here designated *Diplectrum* Type 2 larvae do not show these features, so their taxonomic position based on other characters should be reevaluated.

Among the other serranids there seems two major lines of divergence from the serranines. These are the anthines and the epinepheline-grammistines (Kendall 1976).

Four genera of anthiine larvae (*Plectranthias, Anthias, Pronotogrammus,* and *Hemanthias*) were recognized and among them there appears to be a trend toward increased development of strong spines in the opercular region and on the head. Also fin spines in the dorsal and pelvic fins become strong. The strong ctenoid scales develop precociously. Serrations develop on the spines in the opercular region and on the thick fin spines. Among the anthiine genera and among the species within the genera these features are variously developed. These features probably afford protection against predation and thus make possible a longer planktonic larval period to increase the dispersion of these fish.

The American epinephelines contain three genera. One of these genera, *Epinephelus*, has several subgenera. Although there are considerable differences in size and body shape of adults of members of this subfamily, indicating different ecological requirements, the larvae are similar. Several species of epinepheline larvae have been described from other parts of the world and these are similar to American larvae. In fact, no characters were found to separate larval epinephelines to genera. Epi-

nepheline larvae possess a suite of specialized characters that apparently enable them to have a long pelagic existence. They have extremely elongate and serrate second dorsal and pelvic spines. The preopercular also has a long serrate spine at its angle and there is a serrate supraorbital crest. Pigment is generally confined to the ventral area of the caudal peduncle, the hindbrain, the lateral surface of the gut cavity, and the membranes of the elongate spines. Gonioplectrus larvae resemble epinepheline larvae in most respects, differences being in "degree" rather than "kind" (Kendall and Fahay in press). Whether Gonioplectrus should be considered an epinepheline awaits further analysis of adult morphology. Since there are no other larvae with only some of the epinepheline suite of characters or degrees of development of the characters, it is not possible to relate these fish to any others on the basis of their larvae. However, other evidence indicates that the epinephelines arose from serranine-type fishes (Smith 1971).

Larvae representing three genera in the grammistine line were found. No consensus on the relationship of these three genera is available; but their predorsal bone patterns (Kendall 1976) as well as larval similarity indicate that they are part of a single lineage. The most outstanding feature of these larvae is the development of one or two elongate, flexible, dorsal spines. Each spine has a variously pigmented membranous sheath around it. Otherwise, the larvae are practically devoid of pigment. In several features of development, these fish are similar to serranines. Their body shape is little elevated and there are no strong spines associated with the head or fins. The sequence of fin development is similar to that in serranines, except the pectoral fin develops early in Pseudogramma. In summary, it appears that these fishes could have developed from fishes with serranine-like larvae and that epinepheline larval specializations occurred in that lineage after the grammistine line diverged from it. Based on predorsal bone patterns, Pogonoperca is intermediate between serranines and epinephelinegrammistines (Kendall 1976) so its larvae may show partial development of epinepheline-grammistine characters.

#### SUMMARY

There are four distinct groups among the American serranids based on the morphology of their larvae. These groups represent the subfamilies Serraninae, Anthiinae, and Epinephelinae and the genera *Liopropoma*, *Rypticus*, and *Pseudogramma*, here grouped as the subfamily Grammistinae. Within the serranines and anthiines, larvae of several genera were found and a progression of morphological characters which seem to make the larvae better fit for a longer planktonic existence was seen.

The four groups of American serranid larvae can be partially characterized as follows (Figs. 42, 43):

Serraninae—Body proportions show rather direct development. There are no elongate spines in the opercular region, rather a series of blunt points. The fin spines are thin and only slightly elongated in some. Most larval



Figure 42.—Larvae representative of four groups of American Serranidae: a) Serraninae (*Paralabrax* sp., 6.0 mm); b) Anthiinae (*Anthias* tenuis, 6.7 mm); c) Epinephelinae (*Mycteroperca microlepis*, 7.4 mm); d) Grammistinae (*Rypticus* sp., 6.6 mm).



Figure 43.—Interoperculars of larvae of representatives of four groups of American Serranidae: a) Serraninae (*Centropristis striata*, 10.6 mm); b) Anthiinae (*Hemanthias vivanus*, 10.3 mm); c) Epinephelinae (*Epinephelus niveatus*, 10.2 mm); d) Grammistinae (*Pseudogramma gregoryi*, 10.3 mm).

pigment consists of melanophores in characteristic positions along the ventral midline.

Anthiinae—These are deep-bodied larvae with produced spines on several bones in the opercular region, some of which are serrated. The pelvic and some dorsal fin spines are strong, and serrate in some, but not very elongate. Pigment consists mainly of large blotches and dashes in characteristic positions on the trunk.

Epinephelinae—The body is roughly "kite" shaped, deepest at insertion of second spine of the dorsal fin and pelvic fin spine. Elongate serrate spines are present on the preopercular, but there are no serrations on other bones in the opercular series. The second dorsal fin spine and pelvic fin spine are greatly elongate and heavily serrate. Pigment mainly consists of a large blotch on the caudal peduncle, heavy pigment over the body cavity, and some pigment on the membranes associated with the produced fin spines.

Grammistinae—The body is roughly tubular with a deep caudal peduncle. Bones in the opercular series are armed with variously elongated, simple spines. One or two dorsal fin spines become quite elongate, but are thin and flexible with pigmented membranous sheaths around them. Bodies of the larvae are practically devoid of pigment throughout development.

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Appendix Table 1.—Data associated with larval fish used for illustrations. Institution abbreviations: NE: NMFS, Northeast Fisheries Center; SW: NMFS, Southwest Fisheries Center; SE: NMFS, Southeast Fisheries Center; UNC: University of North Carolina.

Figure	Species	Length (mm)	Insti- tution	ation         Cruise         State           NE         D-67-4         FF-           NE         D-71-5         N-2           NE         D-67-4         CC           SW         6509B         118           SW         S-5509         (Ca           SW         C-51         130           NE         D-67-4         GG           NE         D-67-16         HH           SW         5706S         107           SW         56	Station	Lat. (N)	Long. (W)		Date /Mo	
1a	Centropristis striata	4.7	NE	D-67-4	FF-5(1)	31°38′	79°56′	12	5	67
b	Centropristis striata	8.3	NE		N-2p	34°56′	75°55′	29	4	71
2	Centropristis striata	10.6	NE	D-67-4	CC-5(1)	32°20′	78°25′	14	5	67
3a	Paralabrax sp.	6.0	SW	6509B	118.39	28°19′	115°24′	17	10	65
b	Paralabrax sp.	9.0	SW				no precise			00
4	Paralabrax sp.	9.5	SW	C-51	130.30	26°21′	113°49′	10	8	53
En	Diplastrum on Tuno 1 (A+1)	5.8	NE	D 67 4	GG-4(1)	31°00′	80°51′	11	5	67
5a b	Diplectrum sp. Type 1 (Atl.) Diplectrum sp. Type 1 (Atl.)	10.0	NE		HH-5(2)	30°22′	80°48′	24		67
6a	Diplectrum sp. Type 1 (Pac.)	4.3	SW	5706S	107G02	29°42′	114°07′	20	6	57
b	Deplectrum sp. Type 1 (Pac.)	5.0	SW		107G02	29°42'	114°07′	20	6	57
с	Diplectrum sp. Type 1 (Pac.)	6.1	SW		107G02	29°42′	114°07′	20	6	57
d	Diplectrum sp. Type 1 (Pac.)	13.0	SW		143G100	29°19′	109°14′	11		57
7	Diplectrum sp. Type 1 (Atl.)	10.3	NE	D-67-4	CC-5(1)	33°20′	78°25′	14	5	67
8a	Diplectrum sp. Type 2	4.5	SW		157.10	22°35′	109°19′	4	7	54
b	Diplectrum sp. Type 2	8.4	SW	5612-H	160G30	22°39′	107°49′	3	7	56
9	Diplectrum sp. Type 2	9.9	SW	ETP	47.244	6°59′	84°54′	27	8	67
10a	Serranus sp.	3.7	NE	D-71-5	M-6	35°07′	74°55′	5	5	71
b	Serranus sp.	5.0	NE	1	4	35°03′	75°10′	11	4	72
с	Serranus sp.	5.5	NE	D-66-3	M-5(2)	35°11′	75°07′	20	4	66
d	Serranus sp.	9.4	NE	D-68-1	NN-2(2)	27°11′	80°03′	4	2	68
11	Serranus sp.	9.7	NE	D-66-12	L-4(1)	35°46′	75°05′	30	9	66
12a	Hypoplectrus sp.	3.4	SE	Reared at NI	MFS, Miami, F	la. from eg	gs collected	neart	ŊУ	
b	Hypoplectrus sp.	4.7	SE	Reared at N	MFS, Miami,	Fla. from	eggs collect	ed ne	arby	1
с	Hypoplectrus sp.	5.7	SE	Reared at NI	MFS, Miami, F	la. from eg	gs collected	neart	ŊУ	
d	Hypoplectrus sp.	8.5	SE	Reared at N	MFS, Miami,	Fla. from	eggs collect	ed ne	arby	7
13	Hypoplectrus sp.	12.5	SE	Reared at NI	MFS, Miami, F	la. from eg	gs collected	neart	уy	
14a	Serraniculus pumilio	3.8	NE	D-67-16	DD-4(1)	32°55′	78°51′	21	10	67
b	Serraniculus pumilio	5.8	NE	D-67-16	DD-5(2)	32°47′	78°44′	21	10	67
c	Serraniculus pumilio	55.3	NE		SA-2	29°51′	81°10′	3	9	71
15a	Plectranthias garupellus	5.5	NE	D-67-16	NN-4(1)	27°12′	79°51′	29	10	67
b	Plectranthias garupellus	7.0	NE		PP-2(1)	$26^{\circ}47'$	79°56′	4	2	68
16a	Anthias sp. Type 1	3.8	NE	D-66-5	N-4(2)	34°42′	75°48′	24	5	66
b	Anthias sp. Type 1	5.3	NE		BB-7	32°53′	77°26′	1	5	71
17a	Anthias sp. Type 2	4.7	NE	D-68-1	DD-6(1)	32°36′	78°34′	29	1	68
b	Anthias sp. Type 2 Anthias sp. Type 2	5.7			M-4	35°13′	75°12′	5	5	71
С	Anthias sp. Type 2 Anthias sp. Type 2	8.4	NE		EE-6	32°08′	79°10′	30	1	68
18	Anthias tenuis	6.7	SE	BLM	IV-2	26°10′	96°39′	30	5	76
19	Anthias sp. Type 3	5.1	NE	D-71-5	BB-8	32°39′	77°17′	1	5	71
20a	Anthias gordensis	5.2	SW	5706S	109G55	29°52'	113°04′ 112°44′	18 17	6	57 57
b	Anthias gordensis	6.0	SW	5706S	115G40	28°52′	112 44	17	0	51
21	Anthias sp. Type 1	10.2	NE	D-68-1	EE-6	32°08′	79°10′	30	1	68

Figure	Species	Length (mm)	Insti- tution	Cruise	Station	Lat. (N)	Long. (W)		Date //Mo	
22a	Pronotogrammus aureorubens	4.6	NE	D-68-1	PP-3(1)	26°47′	79°50′	4	2	6
b	Pronotogrammus aureorubens	6.0	NE	D-68-1	CC-7(2)	32°54'	78°07′	29	1	6
c	Pronotogrammus aureorubens	9.0	NE	D-68-1	AA-7	33°37'	76°47'	27	1	6
C	1 tonotogrammus aureorabens	5.0	INE	D-00-1	AA-1	00 01	10 41	21		U
23a	Pronotogrammus eos	3.6	SW	5706S	133G40	26°16′	110°50'	12	6	5
b	Pronotogrammus eos	7.8	SW	OP	052	00°04′	84°58'	19	11	6
24	Pronotogrammus aureorubens	9.5	NE	D-68-1	HH-7	30°19′	80°13′	1	2	68
25a	Hemanthias vivanus	4.2	NE	D-71-5	LK-5	35°59′	74°33'	5	5	7
b	Hemanthias vivanus	5.3	NE	D-71-5	BB-8	32°39′	77°17′	1	5	7
С	Hemanthias vivanus	6.8	NE	D-71-5	BB-8	32°39'	77°17′	1	5	7
26	Hemanthias peruanus	9.3	SW	6611J	147.30	23°36′	111°42′	13	11	6
27	Hemanthias vivanus	9.3	NE	D-71-5	N-7	34°13′	75°35′	29	4	7
28	Hemanthias vivanus	10.3	NE	D-68-1	HH-7	30°19′	80°13′	1	2	6
							00 10	1	2	0
29a	Hemanthias vivanus	4.3	NE	D-71-5	N-7	34°13'	75°35′	29	4	7
b	Hemanthias vivanus	5.8	NE	D-71-5	N-6	34°23′	75°39′	29	4	7
С	Hemanthias vivanus	6.6	NE	D-71-5	N-7	34°13′	75°35′	29	4	7
30	Hemanthias vivanus	7.2	SE	BLM-2	1-3 Day	27°34′	96°07′	10	4	7
31	Paranthias furcifer	8.6	SW	5612	157G10	22°30′	109°15'	3	12	56
32	Epinephelus striatus	7.6	NE	D-67-4	GG-7(2)	30°54′	80°00′	12	5	6
33	Epinephelus sp.	8.4	SW	OP	162	11°10′	92°00′	26	11	6'
34	Epinephelus niveatus	10.2	NE	D-67-16	GG-7	30°54′	80°00′	23	10	67
35a	Mycteroperca microlepis	4.0	NE	1	4	35°03′	75°10'	11	4	75
b	Mycteroperca microlepis	7.4	NE	3	2	35°03′	75°08'	27	4	7
С	Mycteroperca microlepis	14.2	UNC		- T-9	New River		26	4	7
d	Mycteroperca microlepis	22.6	UNC	(UNC 7934)	1-0	Bogue Sd		16	6	
0.0										
36	Mycteroperca microlepis	9.8	NE	D-71-5	AA-7	33°37′	76°47′	30	4	71
37a	Liopropoma sp.	6.3	NE	D-67-4	NN-4(2)	27°12′	79°51′	7	5	67
b	Liopropoma sp.	7.0	NE	3	2	35°03′	75°08′	27	4	72
38	Liopropoma sp.	12.0	SE	OR II 702	0-2-13	26°47′	84°34′	13	9	70
39	Rypticus sp.	6.6	NE	D-67-8	AA-4(1)	34°11′	77°11′	1	8	67
10-	D									
40a	Pseudogramma gregoryi	4.7	NE	D-67-4	MM-4(1)	27°46′	79°56'	8	5	67
b	Pseudogramma gregoryi	6.1	SE	OR II 7739	56	20°00′	80°13′	30	7	72
С	Pseudogramma gregoryi	6.1	NE	D-66-3	N-5(1)	34°33′	75°44′	20	4	66
d	Pseudogramma gregoryi	10.2	NE	D-67-4	JJ-6(1)	29°49′	80°14′	10	5	67
41	Pseudogramma gregoryi	10.3	SE	OR II 7239	56	20°00′	80°13′	30	7	72
42a	Paralabrax sp.	6.0	SW	6509B	118.39	28°19′	115°24′	17	9	65
b	Anthias tenuis	6.7	SE	BLM	IV-2	26°10'	96°39'	30	5	76
С	Mycteroperca microlepis	7.4	NE	3	2	35°03′	75°08'	27	4	72
d	Rypticus sp.	6.6	NE	D-67-8	AA-4(1)	34°11′	77°11′	1	8	67
43a	Centropristis striata	10.6	NE	.D-67-4	CC-5(1)	33°20′	78°25'	14	5	67
b	Hemanthias vivanus	10.3	NE	D-68-1	HH-7	30°19′	80°13'	1	2	68
С	Epinephelus niveatus	10.2	. NE	D-67-16	GG-7	30°54'	80°00′	23	10	67
d	Pseudogramma gregoryi	10.3	SE	OR II 7239	56	20°00'	80°13′	30	7	72

# Appendix Table 1.-Continued.