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The Patterns of Sexuality and the Classification of Serranid Fishes

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Classification of the family Serranidae is notoriously unsatisfactory, largely because the serranids and their allies are generalized perciform fishes and the assignment of genera to this complex is often based on the absence of recognized specializations rather than on the presence of basic similarities. Consequently there is little agreement as to the limits of the family, and arrangements within the family are also unsatisfactory.

Many serranids, however, are specialized in their reproductive mechanisms and have structural and functional patterns of sexuality that can be utilized in phylogenetic studies. Some species have separate sexes, others are synchronous hermaphrodites that can produce eggs and sperm at the same time, and still others are protogynous hermaphrodites in which the male tissue develops after the female tissue has ceased to function. Moreover, the testes of gonochoristic species differ in structure from those of hermaphroditic forms, and there are several distinct arrangements of ovarian and testicular elements in hermaphroditic gonads.

The present paper describes the general structure of the serranid gonads that exhibit three types of hermaphroditism. As more species are studied, it is expected that additional patterns will be found.

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MATERIALS AND METHODS

The following species were collected in the vicinity of the Lerner Marine Laboratory, Bimini, Bahamas, in 1963–1964:

Cephalopholis fulva (Linnaeus)
Petrometopon cruentatum (Lacépède)
Serranus tigrinus (Bloch)
Epinephelus striatus (Bloch)
E. adscensionis (Osbeck)
E. guttatus (Linnaeus)
Rypticus arenatus Cuvier

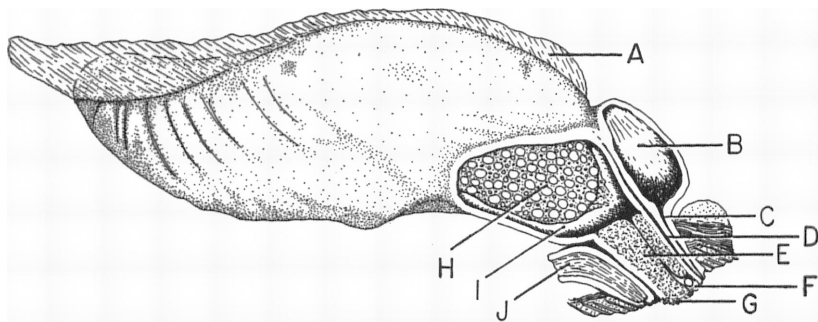


FIG. 1. Longitudinal section through the reproductive tract of a spawning female *Cephalopholis fulva*. The right ovary appears in medial view. A. Supporting mesentery. B. Urinary bladder. C. Urinary duct. D. Sperm duct. E. Oviductal plug. F. Egg canal, with an egg ready to be released. G. Genital mound. H. Ovarian lamellae. I. Lumen of the right ovary. J. Rectum.

A series of *Roccus chrysops* (Rafinesque) was collected in the vicinity of the Franz Theodore Stone Laboratory, Put-in-Bay, Ohio, from June to August, 1963.

Rypticus saponaceus (Bloch and Schneider) was collected at the Bermuda Biological Station in 1956 and 1957.

The gonads were removed and fixed separately in Bouin's fluid immediately after the animal was killed. Later they were transferred to technicon S 29 dehydrant, then embedded in paraffin and sectioned at 7 to 10 microns. For preliminary and survey examination, six slides were prepared from near the center of the gonad. Two were stained with Harris' hematoxylin and eosin, two were stained with Masson's trichrome, and two were kept for future use or special stain. Serial longitudinal and cross sections were then prepared as needed for checking on special features or anatomical details.

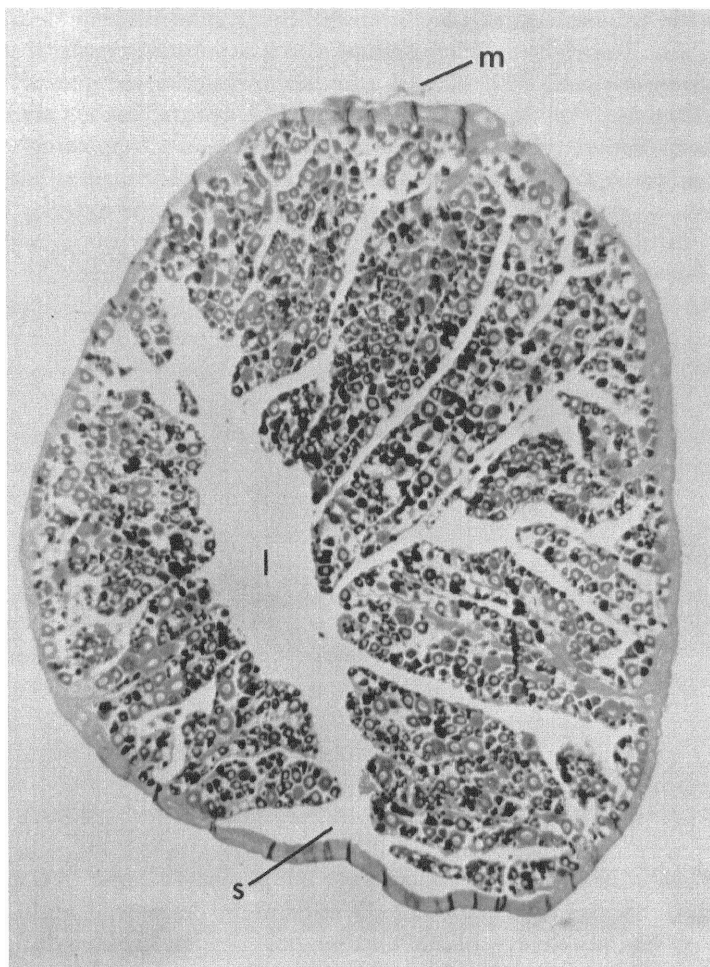


FIG. 2. Cross section through the gonad of *Cephalopholis fulva*, showing ovarian lamellae projecting into the lumen and the ventral sector without lamellae.

Abbreviations: l, lumen; m, dorsal mesentery; s, ventral sector.

GONAD STRUCTURE

In gross appearance the gonads of all the hermaphroditic serranids are similar (fig. 1). Each organ consists of a hollow sac, lying below and behind the posterior part of the air bladder and connected to it by mesenteries. The gonads are relatively small; for example, they accounted

for less than 5 per cent of the total weight in a spawning female *Cephalopholis fulva*. The right and left organs, which are usually unequal in size, join posteriorly and descend as a common oviduct to the genital region immediately behind the anus. The urinary bladder and its duct are closely bound to the posterior face of the common oviduct. Supporting mesenteries continue forward from the anterior end of each gonad as ligaments that join a complex of ligaments and mesenteries at the anterior end of the swim bladder. The genital arteries and veins enter the gonad from these ligaments and continue in the dorsal walls of the gonads. The veins lie approximately below the lines of attachment of the mesenteries and the arteries slightly medial to them. Segmental branches of the arteries and veins supply all parts of the organs.

The wall of the gonad is covered externally with a peritoneal layer. The wall itself is composed of smooth muscle and connective tissue, large organs having relatively more connective tissue than small organs. In gonochoristic species [(e.g., *Lutjanus synagris* (Linnaeus))], there is usually an outer layer of longitudinal muscle fibers and an inner layer of circular muscle fibers, but in hermaphroditic serranids, longitudinal, oblique, and circular fibers are intermixed. The lumen is lined with germinal epithelium which forms the surface layer of a series of longitudinal, slightly oblique folds or lamellae (fig. 2). The central part of each lamella is composed of loose connective tissue and blood vessels. As the oocytes enlarge, they fill and distend the lamellae (fig. 3). There are no lamellae in the common oviduct or in the ventrolateral sector of the gonad proper. This alammellar sector possibly allows distension of the gonad with ripe eggs without injury to the germinal epithelium.

The oocytes can be grouped into stages following the system used by Kraft and Peters (1963) in members of the perciform genus *Tilapia*:

Stage-1 oocytes are small (12-30 microns in diameter), with a thin layer of basophilic cytoplasm surrounding the rather large nucleus. There is a single nucleolus.

Stage-2 oocytes are larger (20-125 microns) and have very dark cytoplasm and many peripheral nucleoli in the nucleus.

Stage-3 oocytes (90-250 microns) have less strongly basophilic cytoplasm in which yolk vesicles gradually develop. At the end of stage 3 the zona radiata begins to appear.

State-4 oocytes (375-500 microns) have a thick zona radiata and both yolk vesicles and yolk globules (platelets). There are prominent lampbrush chromosomes in the centrally located germinal vesicles.¹

¹ No oocytes of 250-375 microns were seen.

Stage 1 is premeiotic, stage 2 is previtellogenic, and stages 3 and 4 are in vitellogenesis. Later stages have been observed only as ovulated eggs, never as oocytes still within the lamellae. In these late stages the nucleus is eccentric, the zona radiata has disappeared, leaving a thinner oölemma, and the yolk globules are no longer separate bodies. Apparently the final maturation process takes place immediately before ovulation,

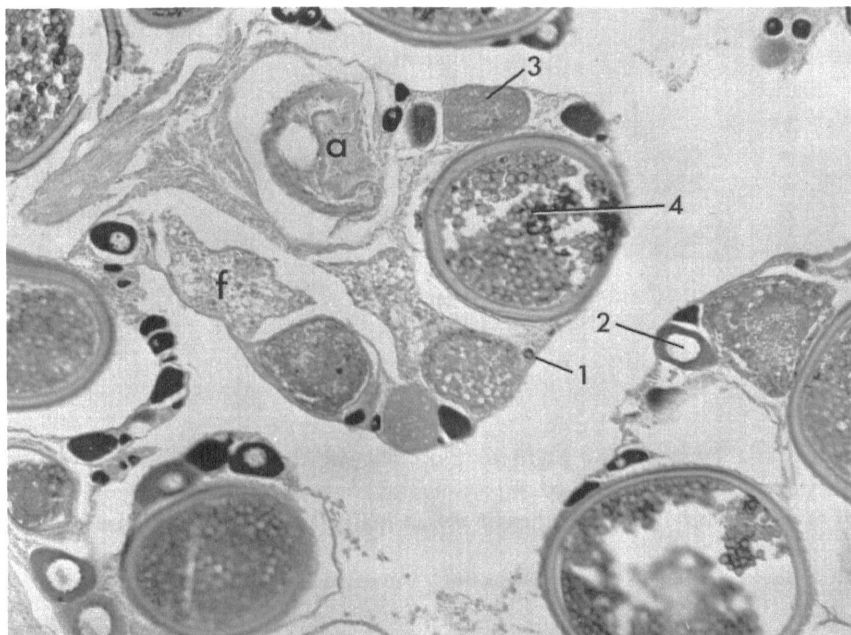


FIG. 3. Partial cross section of the gonad of a spawning female *Cephalopholis fulva*. 1, 2, 3, 4. Oocyte stages.

Abbreviations: a, atretic body forming from unovulated egg; f, empty follicle filled with granulosa cells.

perhaps in a matter of minutes or, at the most, a few hours. Sprecher (1938) noted a similar rapid ripening of eggs in certain centrarchids.

Egg follicles develop with the ova. Stage-2 oocytes are surrounded by a single layer of squamous cells. During stage 3 an inner granulosa layer develops next to the egg. After ovulation the collapsed follicle shrinks, and the granulosa cells proliferate and fill the lumen (fig. 4). The follicles then gradually disappear.

A certain proportion of the oocytes are never shed, and these undergo

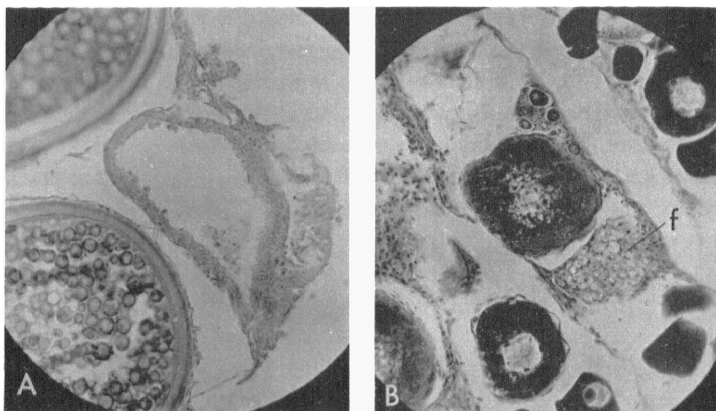


FIG. 4. Post-ovulatory follicles in *Cephalopholis fulva*. A. Empty follicle soon after ovulation. B. Later stage, with vacuolated cells filling the follicle.

a characteristic type of degeneration (fig. 5). The contents of the follicle become disorganized, the membranes, if they have already formed, collapse, and gradually the cell debris is withdrawn by adjacent cells, forming a characteristic brownish mass, the corpus atreticum. These distinctive atretic bodies contain amorphous brownish granules, phagocytes, and clear yellow pigment globules. In the protogynous groupers they remain near the blood vessels in the central part of the lamella, and it is likely that many represent the remains of more than one oocyte.

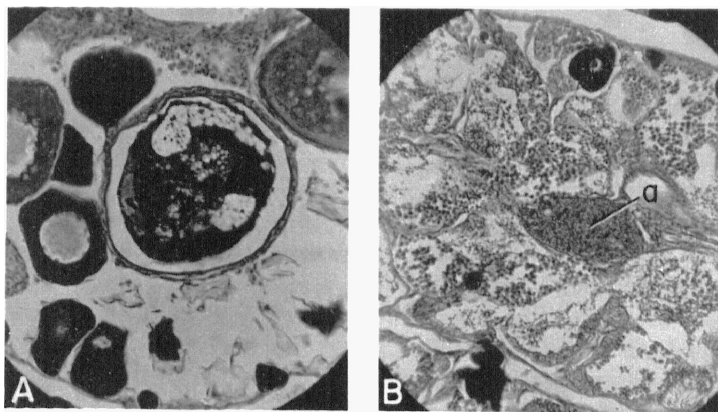


FIG. 5. Stages in the formation of atretic bodies. A. Loss of organization in an unovulated egg. B. Final appearance of atretic body (a) in the male phase.

Since similar bodies are sometimes seen in liver, gut, and elsewhere, I interpret them as unspecific end products of degenerative processes representing, in this case, the last vestiges of oocytes.

The external genitalia lie in a shallow depression immediately behind the anus and consist of a low mound covered by a convoluted epidermis with abundant superficial mucous cells and a deeper layer of melanophores. The urinary and sperm ducts open at the posterior end of this genital mound.

Ovulated eggs are released into the lumen and travel down the common oviduct. Except during the spawning season, the oviduct is occluded by

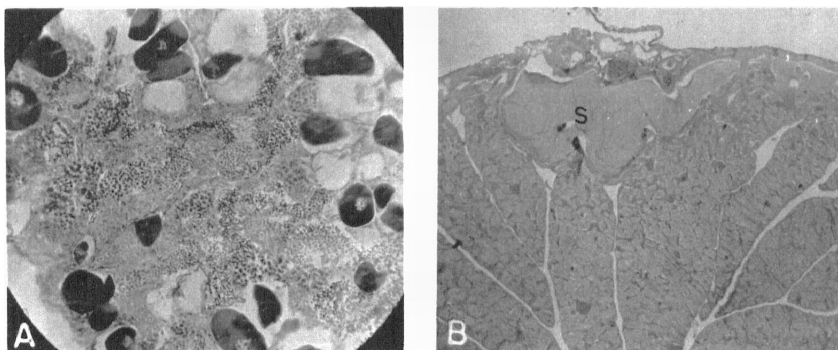


FIG. 6. Testes of *Cephalopholis fulva*. A. Recently transformed, with remnants of stage-2 oocytes. B. Older male, with sperm sinus (s) filled with sperm.

a mass of vascular connective tissue that is continuous with the genital mound. This tissue ruptures at the time of ovulation to allow the eggs to pass out of the ovary. Sperm, however, never enter the lumen. A separate sperm duct in the posterior wall of the oviduct terminates with the urinary duct at the posterior end of the genital mound. The main sperm duct is fed by spaces (sperm sinuses) which develop within the wall of the gonad near the genital veins (fig. 6).

There are no accessory glands ("seminal vesicles") like those reported in toadfish (Hoffman, 1963), gobies and blennies (Eggert, 1931; Tavolga, 1955), and some catfishes (Sneed and Clemens, 1963).

The male tissue of the hermaphroditic serranids is of the acinus type (Felix, 1906) in which sperm are formed in small, more or less spherical crypts (acini), and all the cells within a given crypt are at the same stage of meiosis (fig. 6). These crypts are surrounded by connective tissue membranes that break down when the sperm reach maturity. Thus the groups

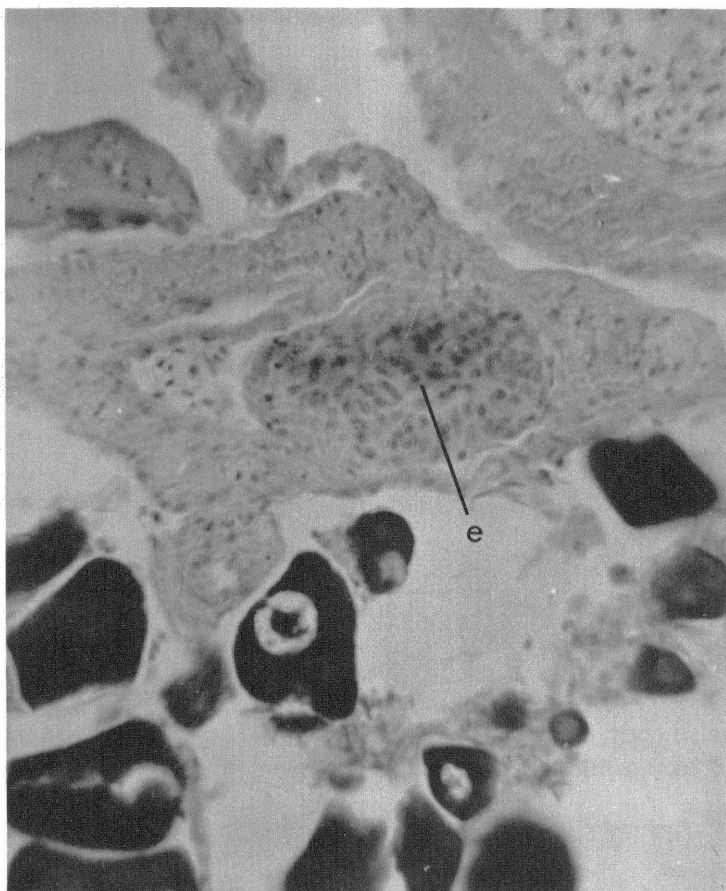


FIG. 7. Suspected endocrine tissue (e) in *Cephalopholis cruentata*.

of sperm cells are isolated during spermatogenesis and merge when the sperm are fully developed. Prespawning individuals have some crypts containing tailed sperm, many crypts with spermatogonia, many with primary spermatocytes, and many with secondary spermatocytes. At the height of sexual activity most crypts are filled with mature sperm, and only a few contain spermatogonia. After spawning, most crypts are empty, but it is nearly always possible to find a few sperm in crypts or ducts.

Several workers (Hjort, 1910; Schaeffer and Orange, 1956; Bowers and Holliday, 1961) have designated maturity stages of teleost gonads in

order to facilitate the recording of observations related to breeding cycles. These systems are designed primarily for use in the field and are based on the gross appearance of the gonads of bisexual species. They are not strictly applicable to hermaphroditic forms, in which it is exceedingly difficult even to distinguish the sexes by gross examination. The following system is proposed for designating stages in the sexual tissues:

IMMATURE OVARY: Stage-1 and stage-2 oocytes present; no atretic bodies

INACTIVE MATURE OVARY: Stage-1, stage-2, and stage-3 oocytes, or stages 1 and 2 and atretic bodies (indicating past spawning), present

ACTIVE MATURE OVARY: Stages 1, 2, 3, and 4 present. Presence of empty follicles indicates that spawning has actually occurred

POST-SPAWNING OVARY: Has empty follicles (with or without hypertrophied granulosa layers) and degenerating stage-4 oocytes

IMMATURE TESTIS: Tissue consists of groups of cells not organized into distinct crypts

MATURE INACTIVE TESTIS: Crypts well organized, some containing mature sperm, others with primary and secondary spermatocytes

RIPENING MATURE TESTIS: Many meiotic figures; many primary and secondary spermatocytes; relatively few mature sperm

RIPE TESTIS: Most crypts filled with sperm; very few earlier spermatocyte stages

POST-SPAWNING TESTIS: Very few sperm; very few primary or secondary spermatocytes; testis dominated by spermatogonia and connective tissue

TRANSITIONAL OVOTESTIS: Remains of stage-2, stage-3, and stage-4 oocytes; atretic bodies present; seminiferous crypts proliferating in the germinal epithelium. (A gonad with fully formed crypts is regarded as a testis even though it may contain abundant remains of oocytes.)

In the vicinity of the main vein and artery lie groups of cells of unknown function (fig. 7). This tissue occurs in disjunct masses, not in continuous cords. It is somewhat encapsulated and well supplied with blood vessels. The nuclei tend to be ovoid, with a well-developed reticular chromatin network. The cytoplasm is somewhat granular and stains a light pink (eosin) or red (ponceau). The cells are elongate, and sometimes they appear to be oriented around a lumen, with the nuclei situated basally (away from the lumen). Lavenda (1949) has suggested that this material is medullary adrenal tissue, but this hypothesis has not been confirmed. In protogynous hermaphrodites the tissue appears to be the same in the juvenile, female, and male phases.

PATTERNS OF HERMAPHRODITISM

The basic plan of the gonad and the cellular structure of testicular and ovarian tissue seem to be similar in all the hermaphroditic Serranidae so far studied. The relationships of the ovarian and testicular portions differ, however, and it is now possible to recognize three distinct types of

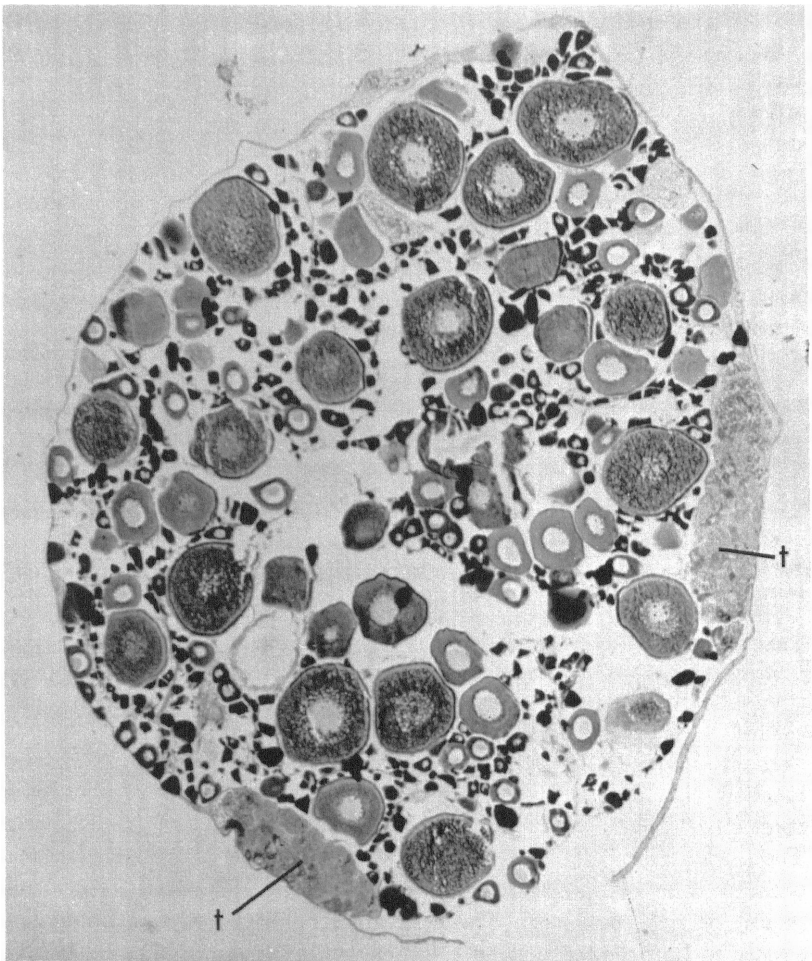


FIG. 8. Cross section of the ovotestis of *Serranus tigrinus*, showing two bands of testicular tissue (t).

serranid hermaphrodites: the *Serranus* type, the *Rypticus-Anthias* type, and the *Epinephelus* type.

The *Serranus* gonad (fig. 8) is predominantly ovarian, with the male tissue confined to the posteroventral region. Reinboth (1962) gave an excellent account of the gonad of *Serranus cabrilla* (Linnaeus), and I have found essentially the same pattern in the West Indian species *S. tigrinus* (Bloch). I have also observed the same pattern in gross dissections of

Serranus baldwini (Evermann and Marsh), *Serranus phoebe* Poey, *Serranus tabacarius* (Cuvier), and *Hypoplectrus unicolor* (Walbaum). Ginsburg (1952), Clark (1959), and Robins and Starck (1961) report similar patterns in several other species of this genus.

The testicular tissue is arranged in two narrow cords running along the ventral part of each gonad (fig. 9). These fuse anteriorly, forming a loop. Posterior to the confluence of the gonads, the mesial bands fuse and the lateral bands continue backward in the wall of the common oviduct to the sperm duct.

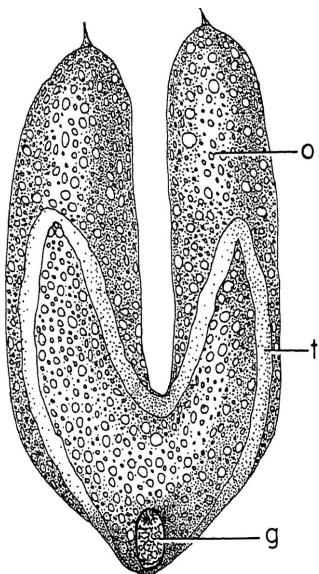


FIG. 9. Sketch of the gonads of *Serranus tigrinus* in ventral view.

Abbreviations: g, genital mound; o, ovarian tissue; t, testicular tissue.

The testicular part of the gonad is well separated from the ovarian part, and, although these are functional at the same time, they have entirely separate ducts; hence there is little possibility of internal self-fertilization. Dufossé (1856) and Clark (1959), however, have reported that some species can fertilize their own eggs. D'Ancona (1952) has called this separation of testicular and ovarian tissue "territorial hermaphroditism."

The *Epinephelus* type of hermaphroditism stands in contrast to the *Serranus* type in that the entire gonad is an admixture of ovarian and testicular tissue. The ovarian tissue functions first, then the gonad appears to transform into a testis. Since the sexes are separated temporally, there is no possibility of self-fertilization. Evidence for this mode of reproduc-

tion has now been accumulated for six species of *Epinephelus*, five species of *Mycteroperca*, *Cephalopholis fulva* (Linnaeus), *Petrometopon cruentatum* (Lacépède), *Alphestes afer* (Bloch), and *Centropristes striatus* (Linnaeus) (Van Oordt, 1933; Lavenda, 1949; Smith, 1959). The current investigation has been primarily directed at *Cephalopholis fulva* and *Petrometopon cruentatum* because these small species are convenient to work with and abundant in the vicinity of the Lerner Marine Laboratory. In these smaller gonads, structural features can be seen more easily than in large gonads, in which there is more abundant connective tissue.

During the juvenile and female phases, the testicular tissue is present

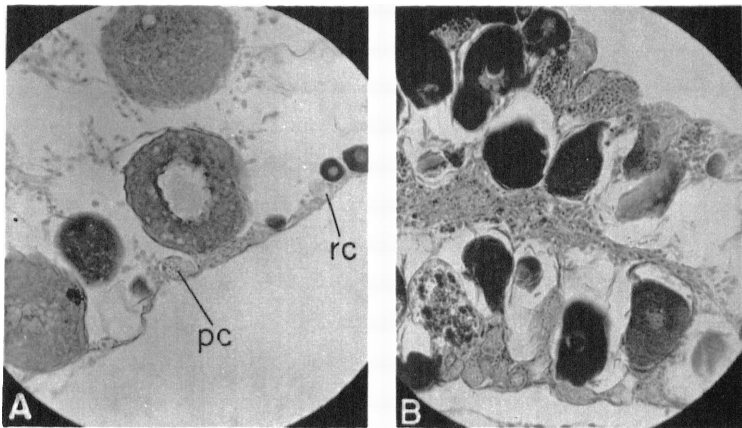


FIG. 10. Sperm crypts in *Cephalopholis fulva*. A. Female phase, showing a resting crypt and a precocious crypt. B. Proliferating crypts in a transforming individual. Abbreviations: pc, precocious crypt; rc, resting crypt.

as small groups of cells in the germinal epithelium of all the lamellae (fig. 10A). The spermatogonial crypts can easily be mistaken for groups of oogonia, but in general the oogonia develop singly and asynchronously within individual follicles, whereas the groups of spermatogonia are surrounded by a membrane and all develop simultaneously. Evidence that these crypts are testicular is provided by the observation that some of them develop precociously, and it is often possible to observe individual crypts containing fully ripe sperm even in females at the height of spawning (fig. 10A). These precocious sperm are probably non-functional, for there are only a few, and they appear to be confined by the crypt wall, with no access to the eggs. Precocious crypts appear to be more abundant in juveniles than in females, at least in *Petrometopon cruentatum*, which

suggests that there may be suppression of testicular activity during the female phase.

The presence of atretic bodies in many females indicates that these fishes spawn more than once as females before becoming males. Recently McErlean (1963) was able to determine age in *Mycteroperca microlepis*, using otoliths, and McErlean and Smith (1964) have suggested that these fish mature as females at age four or five, and then transform into males around age 10 or 11. Although based on small samples, these observations confirm the hypothesis that individual fish spend several seasons as females before becoming males.

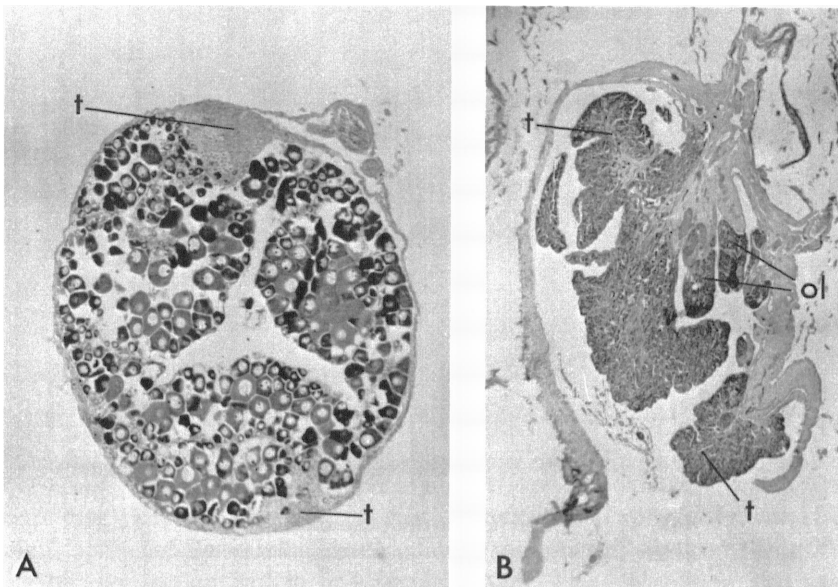


FIG. 11. Cross section of the gonads of *Rypticus*. A. *Rypticus arenatus* in the female phase. B. *Rypticus saponaceus* in the male phase.

Abbreviations: ol, remnants of ovarian lamellae; t, testicular tissue.

Transformation is achieved by proliferation of the seminiferous crypts and concomitant disappearance of the female elements (fig. 10B). First to disappear are stage-1 oocytes. Stage-2 oocytes remain for some time after the transformation. The atretic bodies resulting from the breakdown of oocytes in stages 3 and 4 persist; they can be seen in nearly all males long after the remains of other stages have disappeared.

As the seminiferous crypts proliferate to fill the lamellae, large sperm

sinuses develop in the bases of the lamellae and in the region of the genital artery and vein. These spaces are very extensive at full development and are reinforced by columns of connective tissue and smooth muscle fibers (fig. 6B).

Most of the mature, adult specimens collected at the time of spawning are either males or females; few are transitional. Conversely, during the non-breeding season there is a high percentage of recently transformed males. Apparently transformation to the male phase occurs soon after the

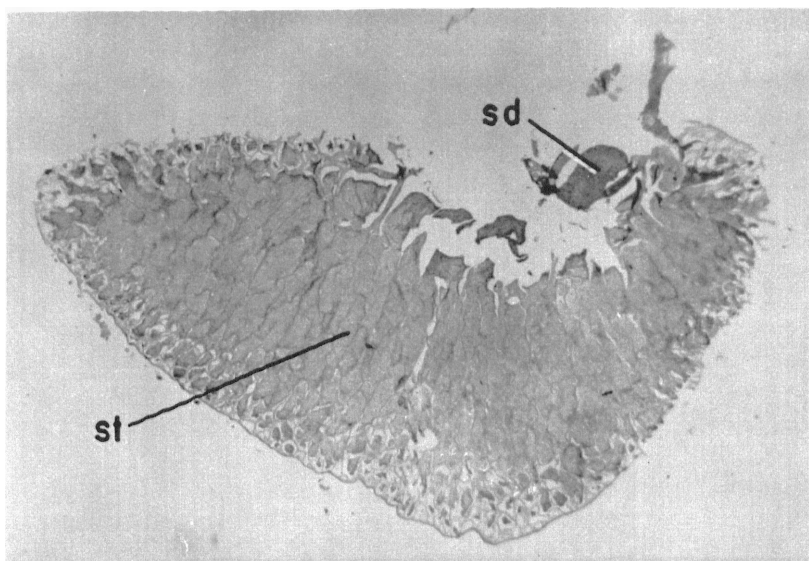


FIG. 12. Cross section of the testis of *Roccus chrysops*.
Abbreviations: sd, sperm duct; st, seminiferous tubules.

spawning season. There is no evidence that the transformation is seasonally reversible, i.e., that the males ever change back to females. None of the males or transitional individuals has any evidence of the development of early-stage oocytes that would have to precede a change from male to female.

Members of the genus *Rypticus* have a type of sexuality that is in some respects intermediate between the *Serranus* condition and the *Epinephelus* condition. This pattern was reported by Reinboth (1963) in *Sacura margaritacea* (Hilgendorf) and in *Pseudanthias elongatus* (Franz) and may be widespread among the *Anthias*-like serranids. These species are protogynous, but the testicular tissue is confined to two narrow bands at the

bases of the lamellae next to the alamellar sector. Here the testicular tissue is not well separated from the ovarian tissue, but developing oocytes are seen in the midst of the seminiferous crypts (fig. 11A). At transformation the male tissue hypertrophies, and the female lamellae atrophy. Figure 11B shows the final appearance in a fully transformed male. It is significant that the remnants of the ovigerous lamellae have vast amounts of atretic material, consisting of the remains of the many oocytes and other tissues of the lamellae.

The arrangement of the gonoducts in *Rypticus* is essentially the same as that of *Serranus*. Crypts in the testicular tissue open into large sinuses which lead in turn to the sperm duct in the posterior wall of the common oviduct.

In the protogynous *Rypticus*, testicular tissue is confined to a limited region (as in *Serranus*) but intermingled with ovarian tissue (as in *Epinephelus*). Although this reproductive mechanism would seem to be intermediate between the condition in *Serranus* and that in *Epinephelus*, it does not necessarily follow that *Rypticus* is phylogenetically intermediate. Most animals are mosaics of primitive and specialized characters, and *Rypticus* has so many other specialized features that it certainly could not be ancestral to the groupers allied to *Epinephelus*. Its interest therefore lies in the fact that it has apparently retained a mode of sexuality that could be transitional between that of *Serranus* and that of *Epinephelus*.

DISCUSSION

In my opinion, the forms allied to *Serranus* are the most primitive of the hermaphroditic Serranidae. They are small fishes (adults, 100 to 300 mm. long), comparable in size to the vast majority of perciforms, whereas many species of *Epinephelus* are very large (some over 2 meters in length). In this case size appears to be a specialization. The scales of *Serranus* and related forms are moderate in size (as in most perciforms), whereas those of *Epinephelus* are small and very closely imbricate. Close relatives of *Serranus* nearly always have 10 dorsal spines as do many other perciforms, but in *Epinephelus* only a few species have 10 spines; most have nine or 11. In *Serranus* the dorsal fins are usually without the elongate spines or filamentous rays that sometimes appear as specializations in *Mycteroperca* and some species of *Anthias*. The teeth of most species of *Serranus* are without specializations such as the anterior canines of some groupers or the hooked mid-lateral teeth of some anthiines.

Although these differences are small, they seem to indicate trends that assume considerable importance in view of the uniformity of these

generalized perciform fishes.

The genus *Rypticus*, along with *Grammistes*, *Pogonoperca*, *Grammistops*, and several other genera, was placed by Gosline (1960) in a separate family (Grammistidae) close to the Serranidae. The specializations of *Rypticus* are obvious and manifold. First there is the drastic reduction in fin spines; all the anal spines and all but two or three of the dorsal spines have been lost. In view of the constancy of the spines, especially the anal spines, throughout the order Perciformes, this is a significant specialization. The thick mucus-producing skin of these fishes is without parallel among the perciforms. *Rypticus* also has a distinctive cardiform tooth pattern, and Gosline has pointed out that the grammistids are distinguished by a modification of the olfactory rosette.

The serranids related to *Anthias* are also specialized in several respects. The lateral line runs high on the body, the fins often have filamentous rays, scales cover much of the head, and the tail varies from being emarginate to being deeply forked. The relationships within this complex of genera are not well known, and their classification is far from satisfactory. Apparently gonad structure has been studied only in the sexually dimorphic *Sacura margaritacea* and in *Pseudanthias elongatus*, in both of which the pattern is like that of *Rypticus* (Reinboth, 1963).

In view of these marked specializations, I believe it very unlikely that *Rypticus* or anything like *Rypticus* could be ancestral to the groupers, and it is also unlikely that *Anthias* or any of its near relatives, such as *Sacura*, could have given rise to the groupers. It is not, however, difficult to conceive of some ancestor like *Serranus scriba* (Linnaeus) that gave rise to an *Epinephelus*-like form. Evidence from sexual mechanisms, however, would suggest an intermediate having a mode of sexuality like that of *Rypticus*. Possibly the *Rypticus* sexual pattern can be retained only in animals with other, unrelated specializations to compensate for the relative inefficiency of its reproductive mechanism. In other words, if only reproductive structures are considered, perhaps the *Rypticus* pattern represents an adaptive valley between the *Serranus* and *Epinephelus* adaptive peaks.

I consider *Rypticus* and its allies to be an offshoot of some intermediate serranid stock. Whether it should stand as a separate family or a remote section of the Serranidae proper is a matter of the classifier's taste. For the moment I am content to follow Gosline's arrangement.

How the gonochoristic forms are related to the hermaphroditic forms is puzzling. Dr. W. A. Gosline (*in litt.*) has recently expressed the opinion that the forms allied to *Roccus* and *Acropoma* can be separated from other serranids on osteological grounds. All the serranids so far studied are either bisexual or hermaphroditic. No intermediates are known; that is

there are no known species that are sometimes hermaphroditic and sometimes bisexual.

The structure of the testis of the gonochorist *Roccus chrysops* is vastly different from that of any type of hermaphroditic serranid so far studied. In the fully developed testis of *Roccus*, irregular radial tubules conduct sperm to the sperm duct in the vicinity of the mesentery (fig. 12). There is no central lumen; the tubules make up the entire body of the organ. Spermatogonia line the outer ends of the tubules, and the sperm appear to be randomly oriented in the lumen of the tubules.

Felix (1906) noted that the developing testes of teleosts are of two types, the acinus type and the radial type. Apparently the hermaphroditic Serranidae have the former and the gonochoristic serranids have the latter type, but this distinction may not be entirely valid because, in the radial type of testis, spermatocytes develop in clusters within the tubules. Moreover, adjacent clusters in a single tubule may be in different stages of development.

Although it is unwise to attempt to generalize in this large and diverse family on the basis of gonad structure alone, the marine serranids appear to be more closely related to one another than they are to the fresh-water and anadromous genus *Roccus*.

SUMMARY

1. Serranid fishes exhibit several types of hermaphroditism.
2. Members of the genus *Serranus*, and its relatives *Hypoplectrus*, *Diplectrum*, and perhaps others, are synchronous hermaphrodites, with the gonad divided into separate male and female zones. There are separate ducts for the eggs and sperm.
3. Members of the genera *Epinephelus*, *Mycteroperca*, *Alphestes*, *Cephalopholis*, and *Petrometopon* are protogynous hermaphrodites in which the presumptive testicular tissue is scattered as crypts throughout the epithelial layer of the ovarian lamellae. Precocious sperm are formed in some crypts during the juvenile and female phases. Transformation to the male phase is accomplished by proliferation of these crypts, accompanied by the development of sperm sinuses in the gonad wall. The ovarian lumen remains in the male phase, but there is a separate sperm duct.
4. The genus *Rypticus* has a type of sexuality intermediate between that of *Epinephelus* and that of *Serranus*. *Rypticus* is a protogynous hermaphrodite, with male tissue confined to narrow bands on each side of the oviduct. Male and female elements are intermingled in this region.

5. Although the sexual pattern of *Rypticus* is intermediate between that of *Serranus* and that of *Epinephelus*, it is unlikely that it gave rise to *Epinephelus*. Rather, *Rypticus* must be regarded as a specialized derivative of an intermediate ancestor.

6. Hermaphroditic serranids have the acinus type of testes. Gonochoristic Serranidae of the genus *Roccus* have testes of the radial type. The spermatogonia line connective tissue tubules which radiate from the sperm duct. Their relationship to the marine Serranidae, on the basis of this evidence, does not seem to be particularly close.

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