8.—The biology and taxonomy of the cardinalfish, Sphaeramia orbicularis (Pisces; Apogonidae)

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Abstract

A study of the biology of *Sphaeramia orbicularis* (Cuvier) at the Palau Archipelago, Western Caroline Islands was conducted from November 1971 to March 1972. In order to clarify the taxonomic position of *S. orbicularis*, a review of the genus *Sphaeramia* is included in which an additional taxon (*S. nematoptera*) is recognised. The two species differ with regards to ecology, colour pattern, and counts for the gill rakers and soft anal rays. *S. orbicularis* were usually encountered in aggregations which number from a few to about 30 individuals. They prefer shallow water, usually near the shoreline, in which shade and shelter are provided by rocks, mangrove trees, or man-made constructions. The species is a carnivore which feeds on insects and a variety of small benthic and planktonic animals. Spawning and courtship activity occurred throughout the study period. Individuals spawned at average intervals which ranged from 19 to 33 days. The males incubate the egg masses orally. The estimated number of eggs per egg mass from three incubating males ranged from 6 100 to 11 700. The eggs hatch in approximately eight days at temperatures between 27 and 30°C. The fry are presumably pelagic and make their first appearance inshore at a total length of about 10.0 mm. The average growth rate for postlarval juveniles ranged from 3.3 to 6.4 mm per month.

Introduction

The present study was conducted while the author was stationed at the Palau Archipelago, Western Caroline Islands as a biologist for the Marine Resources Division of the U.S. Trust Territory Government. The author's residence (Fig. 1) was built on stilts over the sea, situated on the edge of a tranquil lagoon, bordered by the jungle-covered slopes of Malakal Island. Realising the tremendous potential of this setting I initiated a search for a species of fish which would readily lend itself to an intensive short-term biological investigation. The perfect subject was found in *Sphaeramia orbicularis* (Cuvier), a small species of cardinalfish (family Apogonidae). There was a permanent colony of approximately 60 individuals living directly under the house. These fish are particularly interesting from a behavioural standpoint as the males exhibit the unusual habit of oral egg incubation, a trait thus far recorded in only three families of marine fishes (Apogonidae, Ariidae, and Opisthognathidae). The study period extended from November 1971 to March 1972, during which time information was gathered on taxonomy, ecology, behaviour, reproductive biology, and growth.

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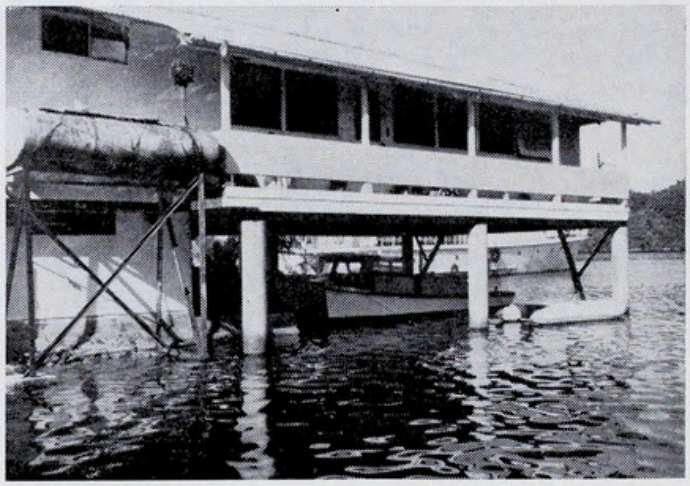

Figure 1.—The study area was located under the author's house at Malakal Island, Palau Archipelago (photographed at high tide).

Materials and Methods

Approximately two observation sessions per day of about ½ hour duration each were conducted during the study period. Standard skin-diving equipment (without SCUBA) was employed. Notes were usually recorded on a plastic sheet, but on some occasions they were taken by my wife or son, who sat nearby, as I dictated the observations.

The study population was composed of 33 adults (18 males and 15 females) and usually 20 to 31 subadults and juveniles. Recognition of individual fish and the study of their growth was facilitated by clipping the basal elements of certain fin rays. These incisions, if properly executed, inhibited normal fin regeneration and could be detected throughout the study period. A combination of different clips made it possible to differentiate fish of similar size. The growth subjects were periodically recaptured, measured, and released. Juveniles and small subadults were easily collected with dipnets, but quinaldine (a chemical anaesthetic) was necessary for the capture of larger individuals. Specimens were collected for stomach content analysis with a small Hawaiian-sling multiprong spear. The stomach contents were observed with a binocular dissecting microscope. The number of eggs in the egg masses of several incubating males was estimated by teasing the eggs from the mass, then counting the number of eggs which constituted a volume of 1.0 ml. The volume of the entire egg mass was then determined and multiplied by the number of eggs per ml.

Taxonomy

There has been some confusion concerning the synonymy of *Sphaeramia orbicularis*. For example, Weber and de Beaufort (1929), under their description of *Apogon nematopterus*, stated "this species is only a variety of *A. orbicularis* in which some rays of the soft dorsal are filamentous. The transverse band on the body is broader than in that species." Similarly, Munro (1967) suggested that *nematopterus* individuals were probably females of *orbicularis*. Fortunately, at Palau I had the opportunity to compare both forms, which were found to be clearly distinct. In order to clarify the systematic position of *S. orbicularis* a brief review of the genus *Sphaeramia* and a key to the species is presented below (see Fraser, 1972, for an analysis of generic characters).

Sphaeramia Fowler and Bean

Sphaeramia Fowler and Bean, 1930: 29 (type species, *Apogon nematoptera* Bleeker, by original designation).

KEY TO SPECIES

1a. Dark bar at middle of body about one scale wide; first few soft dorsal rays not produced into elongate filaments; gill rakers on first arch 24 to 27, soft anal rays 9 ..... *S. orbicularis*

1b. Dark bar at middle of body 3½ to 4 scales wide; first few soft dorsal rays produced into elongate filaments; gill rakers on first arch 32 to 37; soft anal rays 10 ..... *S. nematoptera*

Sphaeramia orbicularis (Cuvier)

Figs. 2, 3, 5, 6, and 7

Apogon orbicularis Cuvier, 1828: 155 (type locality, Java).

Apogon nigromaculatus Hombron and Jacquinot, 1853: 32 (type locality, New Guinea).

Diagnosis.—Dorsal rays usually VI-I, 9½ (fraction indicates last ray is bifurcate): anal rays II, 9; pectoral rays 12; lateral-line scales 26 including two scales on hypural); gill rakers on first arch 24 to 27; dark bar at middle of body about one scale wide.

Colour in alcohol: ground colour of head and body light tan; reddish-brown bar about one scale wide at level of first dorsal spine extending from dorsal fin base to abdomen; portion of head and body anterior to bar with numerous small spots especially concentrated on opercle and interorbital; posterior part of body with numerous, irregular shaped reddish-brown spots of variable size, those along the middle of the body largest and forming a broken stripe which terminates at the base of the tail; first dorsal fin pale reddish-brown with several dark spots on membranes; proximal half of pelvic fins translucent, distal half and spine dark reddish-brown; second dorsal, anal, and caudal fins generally pale, but membranes dusky; pectoral fins pale (slightly reddish) with diffuse reddish-brown spot at base.

Colour in life: ground colour of head and body pale grey with yellowish sheen; numerous small reddish-brown spots on snout, inter-orbital, and occipital; breast and abdomen slightly silvery; reddish-brown bar at middle of body; numerous reddish-brown spots and blotches on posterior portion of body; first dorsal spine reddish-brown, except creamy yellow at tip, remainder of first dorsal fin pale yellow with reddish suffusion; second dorsal, anal, pectoral, and caudal fins generally transparent; basal half of pelvic fins pale yellow, outer half dark reddish-brown except actual fin rays and distal tip of membrane between pelvic spine and first ray which are pale yellow.

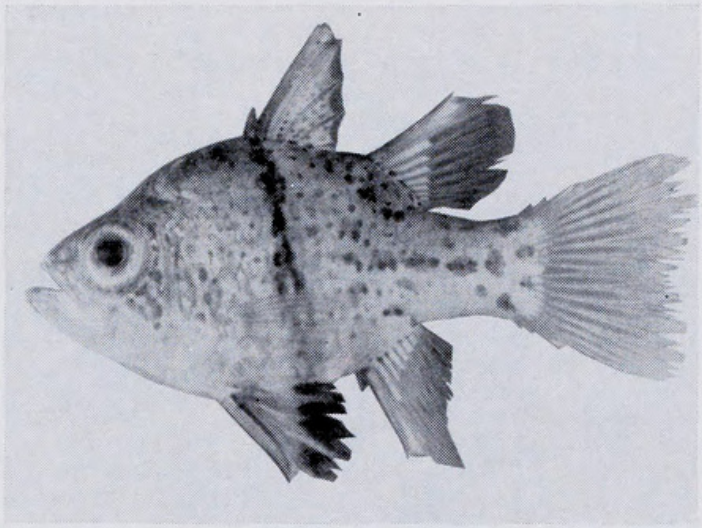

Figure 2.—*Sphaeramia orbicularis*, 55 mm SL, Palau Archipelago (photo by J. E. Randall).

Remarks.—The colour patterns of *S. orbicularis* and *S. nematoptera* are contrasted in Figs. 2 and 3. In addition, differences in counts for the anal fin and gill rakers are presented in Table 1. At Palau these two species are also ecologically separated. *S. orbicularis* generally occurs in small aggregations in extremely shallow water (0.1 to one metre) adjacent to the shoreline. It inhabits crevices and caves, and is frequently encountered among mangrove roots or in the vicinity of mangroves, breakwaters, piers, and wreckage (see section on ecology for further habitat information). *S. nematoptera*, however, is found away from the shoreline in 1.5 to six metres, usually in areas of rich coral growth. In addition, the two species appear to diffffer with regards to maximum size attained. The largest specimen of *S. orbicularis* which was collected at Palau was 89 mm standard length (SL), while the largest *S. nematoptera* measured 61 mm SL.

S. orbicularis has been recorded from the East African coast, Andaman Islands, Singapore, Indonesia, New Guinea, Philippine Islands, Hong Kong, Palau Archipelago, Truk, Ponape, and the Gilbert Islands.

Sphaeramia nematoptera (Bleeker)

Apogon nematoptera Bleeker, 1856: 35 (type locality, Manado, Celebes).

Amia nematophora Bleeker, 1873-76: pl. 313, fig. 1 (type locality, Celebes).

Table 1

Soft dorsal ray and gill raker counts for species of Sphaeramia

Species	Dorsal Rays		Gill Rakers												
	9	10	25	26	27	28	29	30	31	32	33	34	35	36	37
S. orbicularis	10	....	1	1	7	1	....	....	....	....	....	....	....	....	....
S. nematoptera	....	10	....	....	....	....	....	....	....	1	3	2	3	....	1

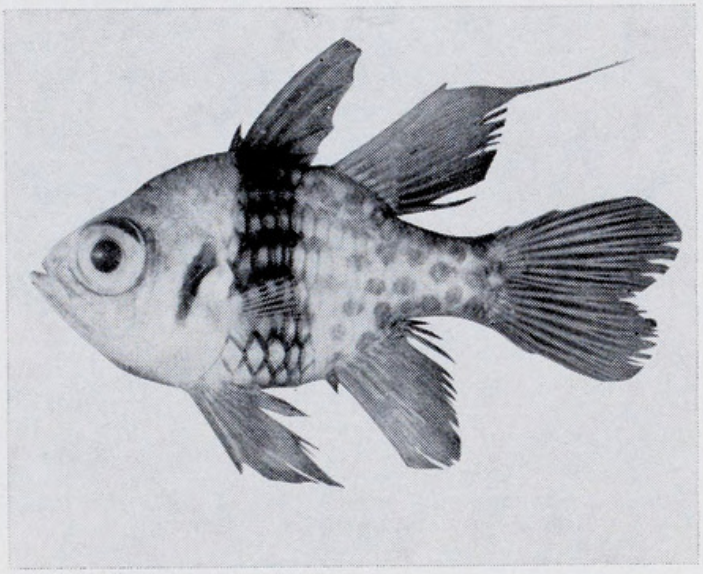

Figure 3.—*Sphaeramia nematoptera, 42 mm* SL, Palau Archipelago (photo by J. E. Randall).

Diagnosis.—Dorsal rays VI-I, 9½; anal rays II, 10; pectoral rays 12; lateral-line scales 26 (including two scales on hypural); gill rakers on first arch 32 to 37; dark bar at middle of body 3½ to 4 scales wide.

Colour in alcohol: ground colour of head and body light tan to greyish; dark reddish-brown bar 3½ to 4 scales wide at level of first dorsal fin extending from dorsal fin base to abdomen; portion of head and body anterior to bar mostly pale without spots (scales may have dusky edges); interorbital, cheek, and chin brownish; yellowish patch sometimes visible on upper portion of opercle; posterior part of body with about 25 to 30 round, reddish-brown spots of nearly uniform size (slightly smaller than pupil); first dorsal and pelvic fins dark reddish-brown; second dorsal, anal, and caudal fins generally pale, but membranes dusky; pectoral fins pale (slightly reddish); pectoral base pale.

Colour in life; head and anterior portion of body with yellowish sheen, peppered with numerous minute dark spots; reddish-brown bar at middle of body; posterior portion of body whitish to pink with maroon spots; first dorsal fin mostly reddish-brown; but membranes between last two spines whitish; second dorsal, anal, pectoral, and caudal fins generally translucent; pelvic fins reddish-brown suffused with yellow (yellowish suffusion more pronounced on basal portion of fin), edge of fin with narrow whitish margin.

Remarks.—This species appears to be restricted to the region which includes Indonesia, New Guinea, Philippine Islands, and Palau Archipelago.

Ecology of S. orbicularis at the Palau Archipelago

Habitat.—The Palau Archipelago is situated in the southwestern corner of the north Pacific Ocean, about 960 km east of the Philippine Islands and approximately the same distance north of New Guinea. The archipelago represents the extreme western end of the Caroline Islands and extends northeastward from about 6°53′N to about 8°06′N or over 112 km at a longitude of about 134°29′E. With the exception of two oceanic atolls at the extreme north tip of the chain, the northern half of the archipelago is volcanic in origin and is dominated by the island of Babelthaup which is about 40 km long and 13 km wide. This island rises to an elevation of about 200 metres and most of the shoreline is bordered by dense mangroves. The southern portion of the archipelago is remarkably scenic, characterised by a bewildering maze of limestone ridges and conical islets which extends for approximately 48 km. The main portion of the archipelago is surrounded by a barrier reef and there is a fairly well-developed lagoon in the southwest sector.

The limestone islands and islets of the south, including Malakal Island, rise up almost vertically from the ocean floor, forming a narrow complexity of canals some with depths greater than 30 metres. The islands are deeply undercut at the high-tide line, as much as two or three metres, forming deep notches above a submarine shelf of variable width.

Sphaeramia orbicularis is usually encountered in aggregations which number from a few to about 30 individuals in shallow, sometimes brackish water. Along the cosat of Babelthaup and to a lesser extent among the southern islands, it is found living among the submerged roots of mangrove trees. The preferred habitat among the limestone islands of the south appears to be the shallow submerged shelf immediately adjacent to the undercut shoreline. This area abounds with shady crevices and small caves which serve as diurnal retreats for the species. The shoreline is occasionally penetrated by relatively large caves, some of which are completely submerged. The fish are generally found around the

mouth of these or a short distance inside, but they rarely penetrate the inner depths which are perpetually dark. *S. orbicularis* is also found in the vicinity of piers, stone breakwaters, bridges, and wreckage. The substratum in these areas usually consists of mud or rock and is above the zone of live coral growth. Juveniles are sometimes found at the surface around piers, boat moorings, or floating debris. In summary, the basic habitat requirements appear to consist of shallow water, usually near the shoreline, in which shade and shelter are provided by rocks, mangrove trees, or man-made constructions. Because of the shallow depth and proximity to the land the habitat is subject to rather extreme fluctuations with regards to water depth and salinity. The daily tidal fluctuation at Palau is approximately 2.0 metres and subsequently *S. orbicularis* must make nearly constant adjustments to achieve optimum conditions of depth and shelter. Heavy rain showers are relatively frequent throughout the year. After a night of continuous heavy rain the salinity was measured with a refractometer at 21 ppt. This measurement was taken in the study area in 20 cm depth or at about the same level inhabited by the fish.

The study area proper (Fig. 1), which was located next to the boat-yard on Malakal Island, consisted of a rectangular pool-like enclosure with concrete walls on three sides. The pool had an area of approximately 24 square metres and was sometimes used for mooring small boats. It was situated directly under our residence, thus the floor of the house formed a roof which completely covered the area about 2.0 metres above the water surface at high tide. Water depth in the enclosure varied from only a few centimetres at low water to about 2.0 metres.

Food and Feeding.—The daily activity pattern of the study population can be summarised as follows: during most of the daylight hours (0900-1630) the fish were relatively inactive and remained in several aggregations directly under the house. They changed their position during the day to accomodate to changing conditions of tide and light, usually remaining in the shade, hovering at depths ranging from about 20 to 120 cm. During late afternoon the fish became more active and began to feed. It was not determined if feeding continued throughout the night, but on every occasion when nocturnal observations were made, the fish appeared to be active, ranging up to 20 metres from the house, usually in small groups of about two to 10 individuals.

S. orbicularis is a carnivore which feeds on insects and a variety of small benthic and planktonic animals. Crabs (mainly portunids and small grapsids and insects from a major portion of the ingested food items. The stomachs of 61 specimens (45 to 85 mm SL) were examined. Most of these were collected in the vicinity of the house, a short distance from the study population. Twenty-five stomachs were empty; however, seven of these were from incubating males, which do not feed during the brooding period. The results of the stomach content analysis of the 36 specimens containing food is presented in Table 2. The results are given as percentage volume of the different major groups of food organisms. The percentages were estimated visually for individual fish, and the total was computed from all the stations. The stomachs which were full usually contained either one or two small crabs, a small insect, or a variety of minute planktonic organisms. Specimens collected between 1700 and 1900 hours generally contained a high percentage of grapsid crabs and insects (beetles and crickets), while individuals taken later in the evening or during the predawn hours appeared to feed predominately on plankton. Most of the specimens collected during the middle of the day (1100 to 1430) had empty stomachs. The data indicates the fish feed actively at dusk, during the early evening and predawn hours (0500-0630). Unfortunately samples were not taken from 2230 to 0500.

Table 2

Percentage volume of major groups of food organisms in stomachs of Sphaeramia orbicularis

(10 stations ; 36 specimens—45 to 82 mm SL)

Food	Volume (%)
Crabs	28·8
Insects	22·9
Copepods	12·9
Sphaeramia eggs	5·6
Ostracods	5·0
Polychaetes	4·7
Amphipods	3·9
Zoea	3·7
Unidentified	3·4
Sergestids (Lucifer)	3·1
Unidentified crustacean fragments	1·4
Megalops	1·2
Small fishes	1·0
Mysids	0·8
Unidentified shrimps	0·8
Stomatopod larvae	0·4
Pleagic fish eggs	0·3
Gastropod fragments	0·1

S. orbicularis is probably opportunistic as far as food items and time of feeding are concerned. For example, fish in the vicinity of the house actively fed on plankton which was attracted to the household lights during the evening, while a collection made at the same time about one km away in total darkness indicated that crabs were the primary food taken. Resting aggregations exhibiting a minimum of feeding activity could be readily induced to feed on plankton by switching on a 75 watt lightbulb above the study area. Similarly, inactive fish during the middle of the day will eagerly take bits of bread and assorted table scraps. As mentioned previously the fish feed actively at dusk. However, on one occasion, a collection of nine individuals made at this time of day at the edge of a landlocked (except for a narrow submarine cave to the sea) saline lake yielded only empty stomachs.

It is interesting to note that insects are a major food item. This fact is clearly understandable if the habitat is considered. With the exception of fish living in the vicinity of man-made structures the preferred habitat of the species is either adjacent to the undercut shoreline or among mangrove roots. In both localities, the vegatative canopy overhangs the habitat of the fish. In areas of undercut shoreline, the lush growth of jungle stops at the high tide mark, but because of the undercutting phoenomena,

the vegetation extends a considerable distance out of the water, and at high tide the foliage is frequently adjacent to the sea surface. Thus, insects which fall from the trees or accidentally fly into the water are readily available as food.

Reproduction and early development

Courtship and spawning took place throughout the study period. Presumed courtship was observed around sunset on several occasions. During this activity pairs of *S. orbicularis* engaged in alternating patterns of chase and display. The most common display exhibited consisted of one fish confronting another in either parallel or lateral fashion while flicking the pelvic and first dorsal fin back and forth. The tips of these fins are relatively bright coloured which serves to enhance the display. Occasionally the fish chased each other for a distance of several cm and sometimes biting was observed, this activity usually being directed at either the sides or anal region. There was no evidence of sexual dimorphism except for the swollen mouth of egg brooding males (Fig. 4). Spawning was not observed and most likely takes place during the middle of the night.

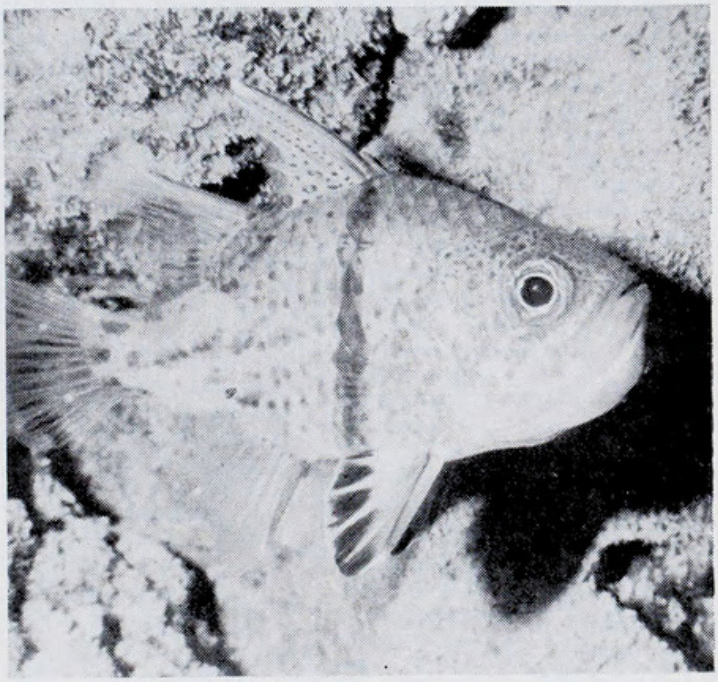

Figure 4.—Male *S. orbicularis* with egg mass in oral cavity.

Spawning occurred at more or less regular intervals with individuals spawning about once or twice monthly. Daily records were kept of the number of incubating males present, which served as an index of spawning activity. The graph in Fig. 5 represents the typical pattern which was observed during the study period. There appeared to be a correlation between the time of spawning and the phase of the moon. Spawning activity was at its highest peak each month at the period between first-quarter and full moon. Also there was a lesser peak between last-quarter and new moon. It is possible that the fish spawn at these times because of the tidal levels. During both of the monthly spawning peaks the high tide occurred within 1½ to two hours of midnight. If spawning occurred during these hours, as it suspected, there may be a requisite for high water. At low tide the fish are more or less driven temporarily away from their favoured habitat and might be reluctant to spawn.

The spawning record of several males as indicated by the presence of an egg mass in the oral cavity is indicated in Table 3. The spawning interval for these individuals ranged from 16 to 35 days with an average interval of 19 to 33 days between broods.

Table 3

Spawning Record of several male Sphaeramia orbicularis

Size (mm SL)	Spawning Dates			Average Interval (Days)
	First	Second	Third	
69	1/12/71	24/12/71	25/1/72	27
69	1/12/71	23/12/71	22/1/72	26
72	27/12/71	12/1/72	5/2/72	20
73	2/12/71	6/1/72	5/2/72	33
74	27/12/71	20/1/72	7/2/72	21
76	1/12/71	23/12/71	8/1/72	19
80	1/12/71	23/12/71	10/1/72	20

The spawning of this species is probably similar to that exhibited by *Apogon imberbis* (Linnaeus), which was observed by Garnaud (1950a and b). According to Breder and Rosen (1966), "Garnaud described the mating as a side-to-side affair in which the female placed her ventral under the male and he placed his anal under the female. In this position they performed the common teleost trembling movements. According to Garnaud, such behaviour did not take place when the eggs were finally extruded later. These eggs are cast in a single mass of material bound together by tendrils arising from one pole of the eggs. The male immediately takes them in in his mouth. These observations led Garnaud to postulate that this case was one of internal fertilisation." However, there is no experimental evidence to prove that internal fertilisation takes place in apogonids.

Many authors have stated that the male apogonid always incubates the eggs. However, Ebina (1932) reported that both sexes of *Apogon semilineatus* exhibit this habit. In the present study an examination of the gonads of many specimens indicated that only male *S. orbicularis* are oral incubators. Males which are incubating egg masses are easy for an observer to distinguish. The gular region is greatly enlarged which dramatically alters the lower profile of the head (Fig. 4). The incubation period lasts about eight days during which time the male periodically "juggles" or changes position of the mass in its mouth. As mentioned previously, the incubating males do not feed; however, *Sphaeramia* eggs are occasionally found in the stomachs of incubating males. Presumably, these are accidentally swallowed or, as in one case when the

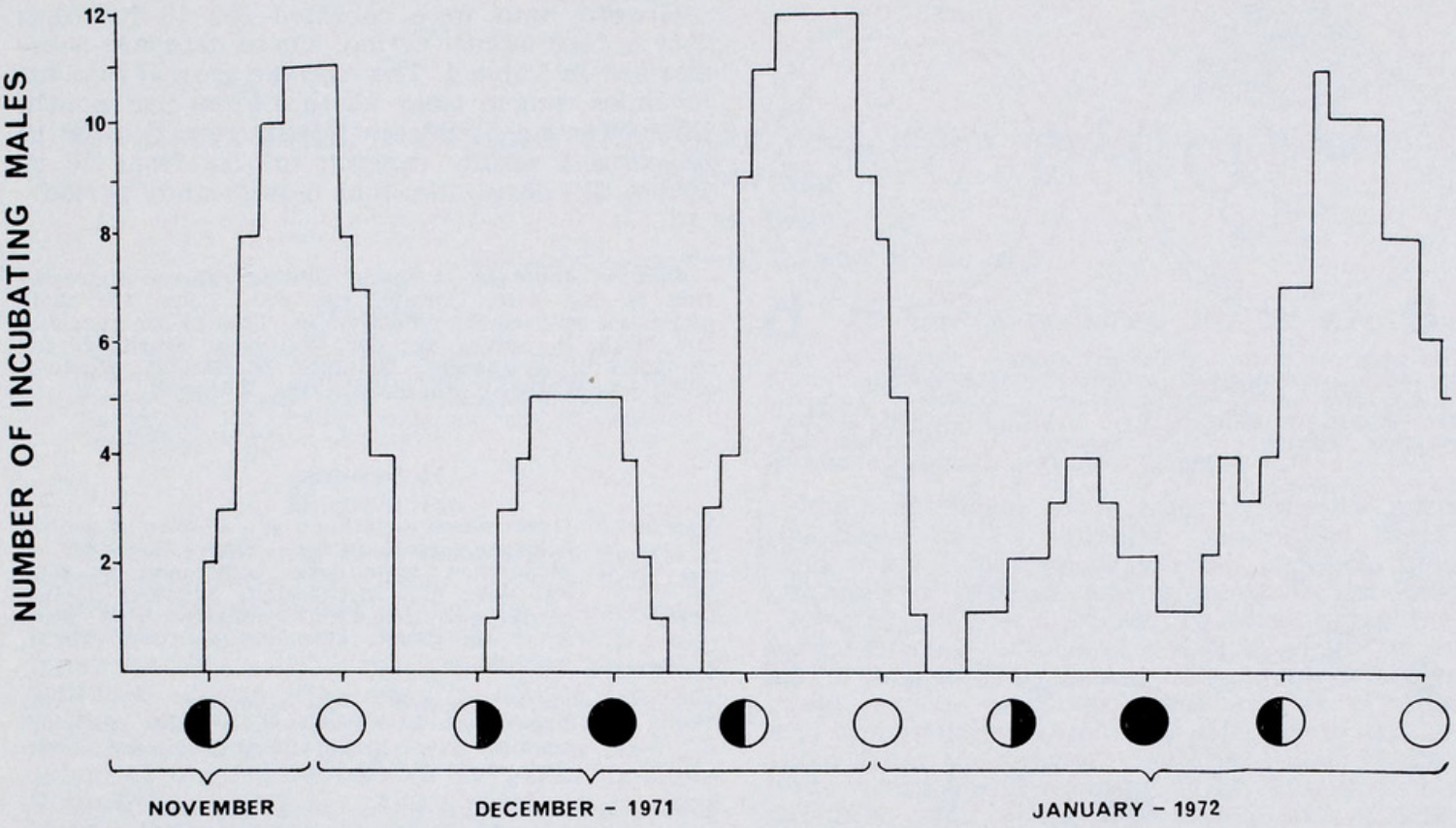

Figure 5.—Number of incubating males of *S. orbicularis* with relation to moon phase and time of month.

entire egg mass was found in the stomach, are ingested during periods of stress (specimen was captured with guinaldine). The egg masses are roughly spherical, although somewhat compressed, ranging in diameter from 14 to 20 mm. The estimated number of eggs per egg mass from three incubating males 72 to 89 mm SL, ranged from 6 100 to 11 700. The eggs are pinkish-orange when freshly spawned and as the embryos develop they gradually turn to purplish-brown. The smallest incubating male collected during the study was 69 mm SL; the smallest ripe female was 60 mm SL. The ovaries are elongate, compressed structures which are encapsulated in a silvery coloured sheath. One ovary of a 78 mm SL specimen was 11 mm x 26 mm and 7 mm thick.

Individual eggs are spherical and measure 0.6 to 0.7 mm in diameter. By approximately 24 hours the embryo has entered the blastula stage (Fig. 6a) and at approximately 40 hours gastulation is in progress (Fig. 6b). Up to this point the egg is characterised by the presence of two to five large oil globules. After about 70 hours the embryo is relatively well formed (Fig. 6c). The unpigmented eyes, otic vesicles, statoliths, and somites are clearly evident. The yolk is bilobed and there is a single large oil globule present. The heart which is positioned just under the head, pulsates at a rate of 120 to 140 beats per minute.

The 110 hour embryo (Fig. 6d) is similar to the previous stage except the yolk is further reduced, the eyes exhibit pigmentation, and the median fin folds have made their appearance. By about 160 hours (Fig. 6e) the pectoral fins are evident, the eyes are well formed and pigmentation is apparent in the form of two rows of stellar-like melanophores on the ventral surface. A full term embryo is shown in Fig. 6f. Hatching occurs in approximately eight days at temperatures ranging from 27 to 30°C.

The newly hatched, transparent fry (Fig. 7a) are apparently pelagic for at least a short period. The pelagic larval stage accounts for the wide geographic distribution of the species. The smallest post-larval forms which were collected inshore measured about 10.0 mm total length

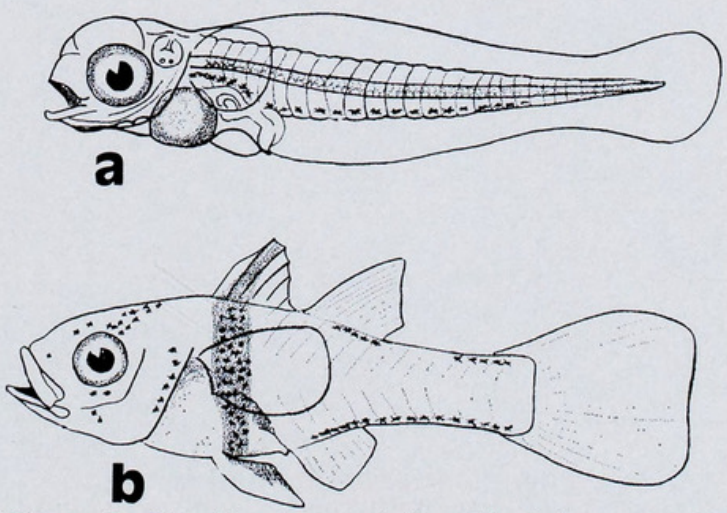

Figure 7.—Growth stages of *S. orbicularis*: a. newly hatched larva, 3.3 mm total length; b. postlarval juvenile, 10.0 mm total length.

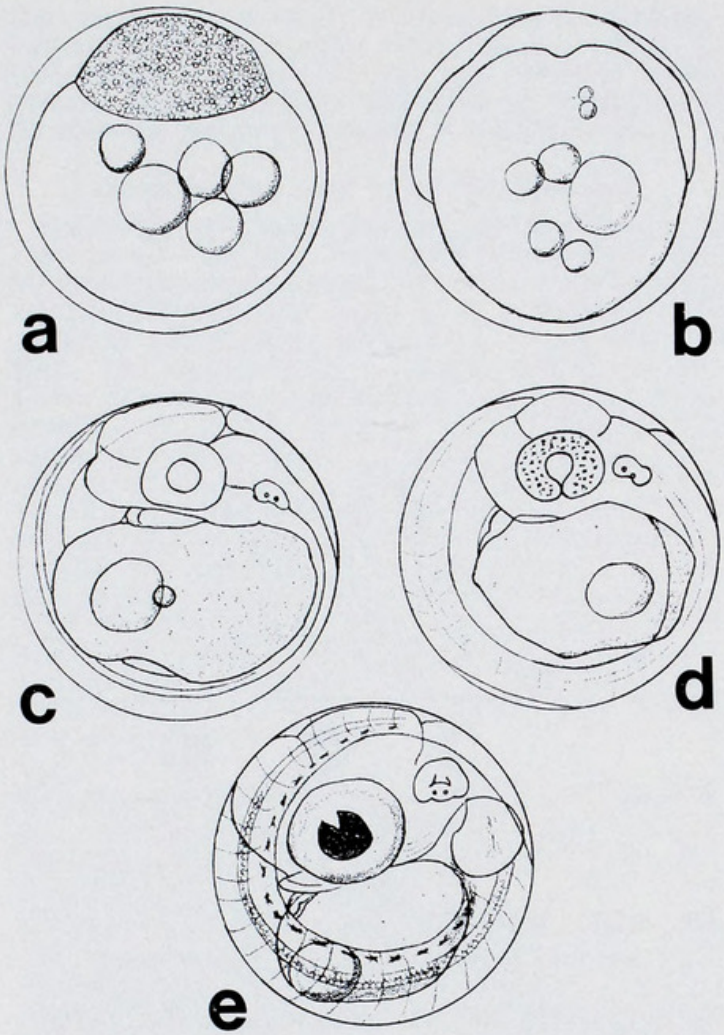

Figure 6.—Early development of *S. orbicularis*: a. 24 hours; b. 40 hours; c. 70 hours; d. 110 hours; e. 160 hours.

Table 4

Summary of growth data for juvenile Sphaeramia orbicularis

Initial Measurement Size	Initial Measurement Date	Final Measurement Size	Final Measurement Date	Total Increase	Growth Rate per month
(mm SL)		(mm SL)		(mm)	(mm)
12·0	6/12/71	22·0	29/2/72	10·0	3·6
12·0	6/12/71	23·0	29/2/72	11·0	4·0
12·0	6/12/71	28·0	29/2/72	16·0	5·8
13·0	8/11/71	32·0	29/2/72	19·0	5·1
13·0	6/12/71	22·0	29/2/72	9·0	3·3
13·0	6/12/71	30·0	29/2/72	17·0	6·2
13·5	6/12/71	24·0	29/2/72	10·4	3·8
13·5	6/12/71	28·0	29/2/72	14·5	5·3
13·5	6/12/71	28·0	29/2/72	14·5	5·3
14·0	6/12/71	30·0	29/2/72	16·0	5·8
14·0	6/12/71	29·0	29/2/72	15·0	5·5
14·5	6/12/71	29·0	29/2/72	14·5	5·3
15·0	6/12/71	30·0	29/2/72	15·0	5·5
15·0	6/12/71	30·0	29/2/72	15·0	5·5
16·0	6/12/71	30·0	29/2/72	14·0	5·1
18·0	11/8/71	36·0	29/2/72	18·0	4·8
18·0	11/8/71	41·0	29/2/72	21·5	5·7
19·5	11/8/71	42·0	29/2/72	24·0	6·4

(Fig. 7b). These tend to form small aggregations of about five to 20 individuals. They are found in the same habitat as the adults and feed on current-borne plankton.

Growth data were collected for 18 juveniles over a four month period. These data are summarised in Table 4. The average growth rate for juveniles ranged from 3.3 to 6.4 mm per month. There was no significant growth recorded for 17 fin-clipped adults, ranging in size from 70 to 89 mm SL, during the four month study period.

Acknowledgments.—I would like to express appreciation to my wife, Connie, and son, Tony, for their assistance in recording field notes. Thanks are also due Dr. James P. McVey and Dr. Walter A. Starck II for the loan of equipment. Dr. John E. Randall provided black and white photographs (Figs. 2 and 3).

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