

FORAGING AND REPRODUCTION OF TWO CARIBBEAN REEF TOADFISHES (BATRACHOIDIDAE)

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ABSTRACT

Amphichthys cryptocentrus and *Sanopus barbatus* were studied in the San Blas Archipelago, off the Caribbean coast of Panama. Both species occupy burrows in sand areas in and immediately adjacent to coral reefs. Daily censuses of 9 tagged *A. cryptocentrus* and 24 tagged burrows in a 45 × 50 m study area showed that individuals vary in the duration of time spent in a particular burrow: most fish move to another burrow every 3 days but some fish remain in the same burrow for up to 6 months. Ten burrows that were never occupied during the survey were also tagged and censused daily; these burrows had been used by toadfish before our censusing began. An average of 58% of the 24 known burrows was unoccupied on any census day. A fish can excavate a new burrow in about 1 day although they do so only rarely.

Both toadfishes feed primarily on the abundant urchin, *Diadema antillarum*. The guts of 40 out of 48 fishes had at least one urchin bolus and contained little other food. Using predation rates and the population density of *A. cryptocentrus*, we estimate that this species may consume 20,000 urchins/ha/yr. However, the impact of toadfish predation on urchin populations in Panama remains undetermined. Live urchins were fewer in number near burrows occupied by *A. cryptocentrus* than near unoccupied burrows. This distribution may result from toadfish predation or the movement of urchins away from injured or preyed-upon conspecifics.

Free-swimming juveniles were found in the burrows of adult male *A. cryptocentrus*. This association is known in three other toadfishes but is uncommon in marine teleosts.

The toadfishes (Family Batrachoididae) are generally bottom-dwelling fishes with broad heads that are depressed anteriorly and a body that tapers rapidly behind the head to a long, slender tail. The natural history of only three species has been studied in any detail: *Opsanus tau* (Ryder, 1887; Gudger, 1908; Gray and Winn, 1961; Winn, 1967; Wilson et al., 1982), *O. beta* (Breder, 1941; Tavolga, 1958), and *Porichthys notatus* (Hubbs, 1920; Arora, 1948). The biology of Caribbean toadfishes remains largely unknown. We were led to study the Caribbean toadfish, *Amphichthys cryptocentrus* by two field observations taken in the San Blas Islands of Panama: (1) the fish ate the long-spined urchin, *Diadema antillarum*, by rapidly sucking in the echinoid, often in its entirety and (2) free-swimming juvenile toadfish were found in the burrows of adults. The first observation is of interest because it is a unique mode of feeding on the urchin (see below). The second finding is of interest because the association of free-swimming juveniles with a parent is rare among marine teleost fishes (Baylis, 1981, and references within).

We describe the use of burrows by *A. cryptocentrus* and the distribution and abundance of urchins around burrows. These results are related to other studies that deal with fish predation on *D. antillarum*, one of the most abundant Caribbean urchins. We document reproduction by describing the association of adults and juveniles and by analyzing gonad development.

The toadfish *Sanopus barbatus* co-occurs with *A. cryptocentrus* but the first species is not abundant in the San Blas Islands. We provide a few data on the biology of *S. barbatus* but mainly focus on *A. cryptocentrus*.

METHODS

Study Sites, Dates and Species

Most observations were made in an area adjacent to the Smithsonian field station in the San Blas Archipelago, Panama (Ogden and Buckman, 1973; Robertson and Hoffman, 1977). The study site was approximately 45 × 50 m and consisted of a shallow (<2 m depth), flat sand field covered with a short sparse turf of turtle grass (*Thalassia testudinum*), a few scattered coral heads (*Montastraea spp.*), and dead coral rubble. Only *A. cryptocentrus* was found in the study site. Some further observations on both species and all collections of specimens were made on reefs near San Blas Point, about 2 km from the main study area. *A. cryptocentrus* was identified using Greenfield and Greenfield (1973) and *S. barbatus* was identified using Collette (1974).

Stomach Content Analysis and Gonadal Activity

We collected 48 toadfishes by spear from 11 different reefs within 5 km of, but not in, the main study area. All fishes were collected between 0610–1705 h. One set of specimens (N = 21) was collected from 28 Aug–17 Nov 1977, and a second set (N = 27) from 2 Feb 1980–19 Jan 1981.

Species, standard length, weight, sex and types of food in the gut were recorded for each individual. The location of each food bolus was classified as (1) anterior—between the esophagus and the first third of the gut, (2) posterior—between the anus and the last third of the gut or (3) midgut—located between the anterior and posterior segments.

The gonads of females with ripe eggs were collected and fixed in 10% formalin. Ripe gonads contained eggs 5 mm or greater in diameter that were easily dislodged from ovarian tissue when the gonad was gently squeezed. Ovaries were weighed and dissected for an egg count.

Occupancy of Tagged Burrows

Toadfishes dig burrows under rock shelves in sand surrounding reefs as well as under coral heads, or on reefs themselves. We determined frequency of occupation by surveying all burrows within the study site for the presence or absence of *A. cryptocentrus*. The fish were easily censused because they generally placed themselves near the entrance of their burrows. Censuses were made daily from 26 Nov–22 Dec 1977, usually between 1200 and 1500 h. On the first census day a diver swam through the area in a criss-cross pattern, mapping the location of occupied burrows and tagging them with numbered aluminum strips.

We initially tagged 15 burrows and monitored these holes over the next 31 days. If a toadfish was subsequently observed in an unmarked burrow, the location was noted and the burrow was tagged and censused from that day onward. Additional burrows sampled included two burrows censused for 30 days, three censused for 28 days, and each of four others censused for 25, 23, 14 and 12 days, respectively.

Burrow Use by Tagged Toadfish

We determined how *A. cryptocentrus* used different burrows by tracking movements of nine tagged individuals. A fish was anesthetized in its burrow with quinaldine (Muench, 1956) and then tagged with three small, colored plastic beads on a loop of stainless surgical wire. The tag was located on the upper jaw at the dorsal midline. The fish was replaced in its burrow after being tagged.

Tagged fish were censused at irregular intervals over a 195-day period from 12 Jan–13 Aug 1978. All burrows in the study area were examined in each census. A fish was considered absent from the study area if it was not seen during a census. Each burrow that a tagged fish occupied was marked with a numbered aluminum strip and its location was mapped. Any change in the burrow location of a tagged fish was recorded on the map and the new burrow was tagged. When an adult fish was found with free-swimming juveniles in its burrow, the number of juveniles, their size and their location relative to the parent was recorded.

Urchins and Urchin Remains near Burrows

Each census day we recorded the number of live *D. antillarum* in four concentric areas centering on the mouth of tagged burrows as follows: A, 0 (touching the burrow)—24 cm; B, 25–49 cm; C, 50–74 cm; D, 75–100 cm. We also noted the location of any remnants of urchin tests and spines within 1 m of a burrow. On any particular day we only recorded those spines and test remnants that had not been counted in previous censuses.

Table 1. Location of food in sections of the gut according to the time of day in the toadfishes, *Amphichthys cryptocentrus* and *Sanopus barbatus*. Food location was not independent of time of day in *A. cryptocentrus* ($\chi^2 = 10.17$, $df = 2$, $P < 0.01$)

Species	Time of Day	Number of Toadfishes with Food Located in Different Parts of the Gut		
		Anterior	Midgut	Posterior
<i>Amphichthys cryptocentrus</i>	0600–1159	5	4	0
	1200–1800	1	5	8
<i>Sanopus barbatus</i>	0600–1159	3	1	0
	1200–1800	0	1	5

To assess whether toadfish affect the distribution of *D. antillarum* around their burrows we made daily counts around 10 holes in the study area that were never occupied during the survey, but which were used by toadfish before the survey began. We determined the distribution of urchins around these holes in the same way as for occupied burrows.

RESULTS

Stomach Contents and Gonadal Activity

During the day, a single *D. antillarum* placed by a diver at the entrance of an occupied burrow was typically attacked and consumed within a few seconds. Individuals of both fish species quickly ate up to three urchins presented to them during such a feeding session. A fish lunged out of its burrow about 10 cm and sucked in the entire urchin (test and spines). Urchins that were relatively large were taken in a series of gulps. Broken spines and, rarely, a piece of test remained in front of the burrow. The sucking action was performed too rapidly for us to be able to observe how ingestion was accomplished.

The stomach contents of 23 male and 5 female *A. cryptocentrus*, and 7 male and 5 female *S. barbatus* contained the urchin *D. antillarum*. The stomachs of three male and one female *A. cryptocentrus* and one male and one female *S. barbatus* contained two boluses of urchins; all other fish stomachs with urchins contained only one bolus. A female *A. cryptocentrus* had both urchin material and a prosobranch gastropod in its gut and a male of this species had both urchin material and the carapace of a decapod crab in its gut. Four *A. cryptocentrus* contained no urchin material: one male and one female each contained a single prosobranch gastropod, while another male and another female each contained only the parts of a crab. Fish with empty guts included one male and two female *A. cryptocentrus* and one male *S. barbatus*. The mean number of urchin boluses per individual was 0.9 (SE = 0.10) for *A. cryptocentrus* and 1.1 (SE = 0.14) for *S. barbatus*.

We investigated the relationship between time of day and the location of food in the gut by arbitrarily dividing the day into two, 6-hour periods starting with 0600 h (Table 1). Food location was not independent of time of day in *A. cryptocentrus*. Sample sizes in *S. barbatus* were insufficient for statistical analysis, but the distribution of food in the gut was similar to that found in *A. cryptocentrus*. The distribution data for both species indicated that food passed through the gut in about 12 h.

One *A. cryptocentrus* female (327 mm SL) and two *S. barbatus* females (347 and 380 mm SL) had ripe ovaries. The ovaries filled much of the body cavity and accounted for 3–4% of the fish's body weight. The *A. cryptocentrus* female had 307 eggs and the *S. barbatus* females had 245 and 499 ripe eggs, respectively,

in their ovaries. Twenty-five eggs taken from each female measured 5–7 mm diameter.

Burrow Excavation

Burrows found in sand habitats were usually located under a piece of flat dead coral or directly under overhanging cliffs of dead coral at the base of reefs. Twenty-one burrows in the study site had only one opening, while three burrows each had two entrances and two burrows each had three entrances. The average dimensions of the entrances were 24 cm width \times 11 cm height. The excavated tunnels ran 10–25 cm below the level of the sand substrate.

We observed only two *A. cryptocentrus* excavating burrows during the tagged-burrow census, and we induced another five individuals of that species to excavate burrows after filling in their holes with sand. In all seven cases, a toadfish initiated excavation by scooping up sand with its mouth, carrying it away and forcefully expelling the sand from its mouth. Most forward movements resulted from thrusts of the caudal fin, while lateral movements were performed by walking on the relatively large pectoral fins. After 40 min the hole was sufficiently deep for the toadfish to enter tail-first; excavation continued for up to 1 h when the fish was able to sit at the entrance with the rear half of its body inside the burrow. The initial burrow was enlarged by the next day and it extended under the sand more than 1 m.

Residency Time in Burrows

We determined the total number of days that a burrow was occupied without interruption from tagged-burrow censuses. We assumed that a tagged burrow was continuously occupied throughout the time period between any two recorded interruptions in burrow occupancy. The median duration of continuous occupancy was 2.8 days and the mode was 1 day, however two of the tagged burrows were occupied on all 32 census days (Fig. 1). We counted an average of 14 toadfish per day ($SD = 1.5$) in the study area. Thus an average of 58% of the known available burrows ($N = 24$) were occupied on any particular day.

The tagged *A. cryptocentrus* varied considerably in their tendency to remain in a given burrow (Fig. 2). One of the nine fish was found in the same hole in every census and it may have occupied the same hole for as much as 134 days. Six toadfish, whenever found in the study area, were in a particular tagged burrow; at other times they evidently used burrows outside the study area. Two toadfish used at least two burrows inside the study area and also lived outside the study area. Four fish were still tagged and used the study area on day 195. No tagged fish were present on day 213, although many burrows in the study area were occupied by toadfish.

Distribution of Live Urchins and Urchin Remains around Burrows

Live *D. antillarum* were present around never-occupied burrows more often than around variably-occupied burrows (burrows occupied at least once by a toadfish) (Table 2). More (62.4%) of the 2,066 urchins counted at both types of burrows were recorded around never-occupied sites than around variably-occupied burrows (Mann Whitney *U*-test, $P < 0.003$), even though the number of observations at never-occupied sites was less than one-half of that for variably-occupied burrows.

Urchins were generally absent around variably-occupied burrows, particularly when a toadfish was absent (Table 2). The distribution of urchins around variably-

occupied burrows did not differ depending upon whether a toadfish was present or absent (Fig. 3; $\chi^2 = 2.01$, $P > 0.5$, $df = 3$). However urchin distribution around variably-occupied burrows with toadfish absent was not different from urchin distribution around never-occupied burrows ($\chi^2 = 6.6$, $P > 0.09$, $df = 3$), while the distribution of urchins around variably-occupied burrows with toadfish present was different from urchin distributions around never-occupied burrows ($\chi^2 = 11.54$, $P < 0.01$, $df = 3$). There were significantly fewer urchins 0–24 cm from variably-occupied burrows than from never-occupied burrows ($\chi^2 = 7.40$, $P < 0.01$, $df = 1$) and significantly more urchins 50–74 cm from variably-occupied burrows than from never-occupied burrows ($\chi^2 = 10.68$, $P < 0.005$, $df = 1$; methods in Fleiss 1973: 17–19). The percentage of urchins surrounding variably-occupied and never-occupied burrows did not differ at 25–49 cm and at 75–100 cm.

Urchin remains were not observed around never-occupied holes ($N = 320$ observations). Urchin remains usually were absent (74.1% of 698 observations) around variably-occupied burrows, but a toadfish was found in a burrow in most instances when remains were present (Table 2). The remains almost always consisted of spines; pieces of test were recorded for only 8.3% of the 181 observations of remains around burrows. The pieces of test were usually one-half or more of an urchin and were estimated to come from individuals measuring 30–90 mm in test diameter. Urchin remains were present for 88 of the 206 counts recording live urchins around variably-occupied burrows, which was less than expected (Goodness-of-fit test, $\chi^2 = 4.37$, $P < 0.05$, $df = 1$; expected frequencies = 103 records of urchin remains when live urchins were present or absent). Among variably-occupied burrows, live urchins were located closer to an occupied burrow when urchins remains were absent than when remains were present ($\chi^2 = 16.86$, $P < 0.005$, $df = 3$).

Juveniles in Burrows with Adult Toadfishes

Three of the nine tagged *A. cryptocentrus* were observed with free-swimming juveniles in and around their burrows. One fish had at least three separate broods between Jan and May 1978. A brood of about 60 juveniles (25–30 mm SL) was first observed with the fish on 26 Jan. These juveniles were still in the burrow 7 days later but were gone 20 days after they were first observed. Juveniles were again seen in the burrow of this fish on 19 Mar and 26 May. Juveniles were found once in the burrows of two other tagged *A. cryptocentrus*. One fish had 25 juveniles (25–35 mm SL) in its burrow on 31 Jan and 2 days later, but none 10 days after they were first seen. The third tagged toadfish was observed with juveniles in its burrow on 13 Apr. Juveniles were also seen in the burrow of a male *A. cryptocentrus* on 1 Apr 1978 and with a male *S. barbatus* on 10 Jan 1981. A half-eaten urchin test was found once in front of a burrow containing juveniles; the tending adult was a male *A. cryptocentrus* and its stomach contents contained urchin material.

DISCUSSION

Predation on *Diadema antillarum*

Toadfishes outside of the Caribbean have been reported to consume a variety of foods including crustaceans, molluscs and fishes (Linton, 1901; Gudger, 1908; Hubbs, 1920; Chrobot, 1959; Schwartz and Dutcher, 1963; McDermott, 1965; Phillips and Swears, 1969; Wilson et al., 1982). Our analyses of stomach contents

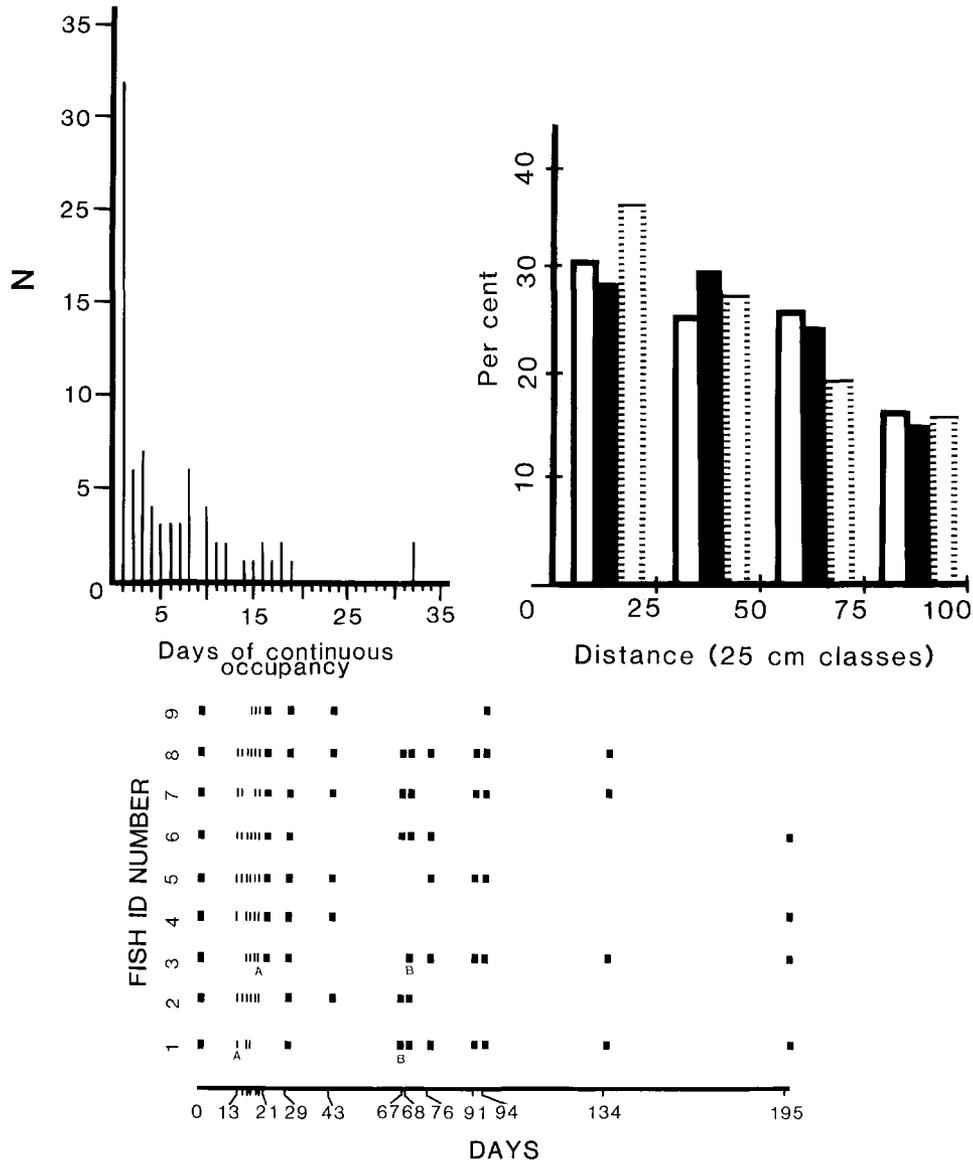


Figure 1. (Left) The number of days that a tagged burrow was occupied by a toadfish (*Amphichthyes cryptocentrus*). N is the frequency of observations; e.g., there were two instances of burrows continuously occupied for 32-day periods, one instance of a burrow occupied for 19 days, two instances of a burrow occupied for 18 days, etc. Data are based on a survey of 24 burrows over a time span of up to 32 days. It was assumed that a burrow was continuously occupied by a fish between any two consecutive vacancies.

Figure 2. (Lower) Censuses of nine tagged *Amphichthyes cryptocentrus* on 16 days over a 195-day time period. A fish absent from the study area during a census is represented by a blank space. All fish, except 1 and 3, were always found in the same burrow they were tagged in on day 0. Fish 1 and 3 were each found in different burrows on two occasions (the first change is indicated by the letter A and the next change by the letter B), but the fish consistently occupied the same burrow between the intervals marked by those letters. Censuses between day 13 and 21 were performed on days 15, 16, 17, 19 and 20.

Table 2. Presence or absence of *Amphichthys cryptocentrus* in tagged burrows relative to the presence or absence of live urchins (*Diadema antillarum*) or urchin remains near the burrow entrance. Variably-occupied burrows were occupied by a toadfish at least once during a 32-day census period

Type of Burrow	Number of Burrow Censuses in Which:	
	Live urchins present	Live urchins absent
Variably-occupied burrows	206	492
Never-occupied burrows	280	40
		$\chi^2 = 295.71, P < 0.001$
Variably-occupied burrows	Live urchins present	Live urchins absent
When toadfish present	150	298
When toadfish absent	56	194
		$\chi^2 = 9.47, P < 0.001$
Variably-occupied burrows	Urchin remains present	Urchin remains absent
When toadfish present	149	299
When toadfish absent	32	218
		$\chi^2 = 34.97, P < 0.001$

show that both *A. cryptocentrus* and *S. barbatus* feed primarily on the sea urchin *D. antillarum*. Urchin predation by toadfishes apparently has not been documented before this study. Some of the morphological traits of both species examined in this study indicate that they are well-suited to prey on a long-spined urchin by smashing through its test. These traits include fusion of the head bones to give a solid skull, a large head with a broad gape, a bony palate, large peg-like teeth closely set together and thick skin in the mouth. If *A. cryptocentrus* and *S. barbatus* are food specialists on *D. antillarum* they then differ in their feeding habits from other toadfishes who typically take the variety of foods listed above. The predominance of *D. antillarum* in the diet of San Blas toadfishes may result from the urchin being more abundant than any other suitable prey item.

It is important to establish how populations of *D. antillarum* in Panama are affected by predators because the urchin has been found to be an important herbivore on Caribbean reefs in terms of its effects on the rest of the community (Ogden et al., 1973; Lawrence, 1975). A toadfish takes about one urchin per day, and since we found an average of 14 *A. cryptocentrus* per day in the study site of 0.225 ha, a population of *A. cryptocentrus* at this density may take as many as 20,000 urchins/ha/yr. How such predation affects the population dynamics of *D. antillarum*, and thus secondarily affects the urchin's role in Panamanian reef communities remains an open question.

Distribution of Toadfish and Urchins

Some *A. cryptocentrus* stay in burrows for many months but the majority change burrows after approximately 3 days. The costs of switching burrows are not known,

Figure 3. (Right) The distribution of live urchins (*Diadema antillarum*) around the burrows of *Amphichthys cryptocentrus*. Data are expressed as percentage of the total number of urchins counted in four concentric zones around the mouth of the burrow. Open bar = variably-occupied burrows with a toadfish in the burrow (N = 529 urchins), dark bar = variably-occupied burrows when a toadfish was not in the burrow (N = 247 urchins), dashed bar = never-occupied burrows (N = 1,290 urchins). Data are based on daily censuses of 10 never-occupied burrows and 24 variably-occupied burrows taken over a 32-day period.

but the costs of building a new burrow are probably not minor, given the elaborate construction of the burrow and the time required for its completion. Unoccupied but suitable burrows do not appear to be limited: an average of 41% of the tagged burrows in the study area were unoccupied on any given day (this includes burrows that were never occupied during the census period).

A toadfish may move to another burrow or build a new burrow when the supply of live *D. antillarum* becomes reduced around its current burrow. The relative scarcity of live urchins around the burrows of *A. cryptocentrus* seems clearly due, in part, to predation by toadfish. But urchins tend to be relatively uncommon around variably-occupied burrows regardless of whether a toadfish is present or not, and urchins tend to be located further away from variably-occupied burrows (regardless of whether a toadfish is present or absent) than from never-occupied burrows. This distribution of urchins may be due to *D. antillarum* moving away from injured or preyed-upon conspecifics at night (Snyder and Snyder, 1970). Similarly, live urchins may avoid fresh urchin remains since live urchins are located closer to occupied burrows when urchin remains are absent than when they are present. The responses of live urchins to toadfish predation and the factors causing toadfish emigration to another burrow remain to be determined.

Reproduction

Egg size and number of eggs in the ovaries of the species examined here are similar to those of other toadfishes (Gudger, 1908; Breder, 1941; Arora, 1948; Collette and Russo, 1981). At least one male *A. cryptocentrus* was observed with young in its burrow on three separate occasions over a 5-month period; thus males may mate more than once a year. Males actively guarding free-swimming juveniles have been observed in other toadfishes including *O. tau*, *O. beta* and *P. notatus* (Ryder, 1887; Jordan and Starks, 1895; Clapp, 1899; Greene, 1899; Gudger, 1908; Hubbs, 1920; Breder, 1941; Arora, 1948; Gray and Winn, 1961), although such parental care of free-swimming juveniles is practically unknown among marine teleosts (Robertson, 1973; reviewed in Baylis, 1981).

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