Zoologica, Vol. XIX, No. 3.

THE REPRODUCTIVE HABITS OF THE COMMON CATFISH, *AMEIURUS NEBULOSUS* (LE SUEUR), WITH A DISCUSSION OF THEIR SIGNIFICANCE IN ONTOGENY AND PHYLOGENY.

C. M. Breder, Jr.
New York Aquarium.

(Figs. 12–23 incl.)

Introduction.

A considerable number of students have observed and described the reproductive habits of the common catfish, *Ameiurus nebulosus* (Le Sueur). They have in no case, however, attempted to analyze critically the possible ontogenetic and phylogenetic significance to be attached to the various details of the procreational behavior. It is the purpose of the present communication, therefore, to consider the biological import of the various items involved, especially in the light of detailed observations on four successive seasons of activity by two pairs of fish. These observations are supported by others in less detail, both in the laboratory and in the field, as well as by general agreement with the observations of Girard (1854), Eycleshymer (1901), Smith (1903), Smith and Harron (1904), Gill (1907 a and b), Hankinson (1908), Forbes and Richardson (1909), Wright and Allen (1913), McAtee and Weed (1915), Fowler (1917), and Adams and Hankinson (1928). A general account of the observations made the first year has already been published. (Breder 1932.)

Another reason for pursuing this study was to facilitate a comparison of reproductive habits between unrelated groups of fishes that have superficially similar behavior patterns. For example, the nest building habits of certain cichlids seem to be rather similar in the principal design. A study of one of these, *Aequidens latifrons*, has already been published, Breder (1934 a). In this the present study has been mentioned. The details of comparison, however, have been withheld for the present paper and are here treated in full. A further reason for making the present study involves the problem of the genesis of oral incubation in fishes. The mode of origin in the Cichlidae has already been discussed in the paper above referred to. (See also Breder 1933 b.). Details of its probable origin in the Nematognathi are discussed herein, while the origin of this habit in the labyrinth fishes will appear in a subsequent paper based on a similar study of the genus *Betta*.

All of the observations here described refer to studies made in the tanks of the New York Aquarium, unless mention is made to the contrary. The photographs of *Ameiurus* are all the work of S. C. Dunton of the Aquarium staff, whose intelligent efforts made possible these pictures of an intrinsically difficult subject. Appreciation is also expressed for the helpfulness of Mr. H. E. Dixon, in charge of temperate fresh water fishes at the Aquarium. The data concerning *Opladelus* were kindly supplied by Mr. W. H. Chute, director of the Shedd Aquarium, at which institution the observations were made. The photographs of this species were taken by L. Tutell.

Influence of Captivity.

Under the conditions in the exhibition tanks in which the catfish are displayed at the New York Aquarium, their health and activity appear to be entirely normal. Reproductive activity, however, was formerly unknown. This condition was under the author's personal observation from 1921 to 1930 inclusive, a period in which ten reproductive seasons passed with no such activity. The fishes usually numbered from eight to twelve mature specimens. They were confined in a glass-fronted aquarium measuring 44 inches deep, 51 inches long and 34 inches wide at the surface, the back sloping down to a width of 26 inches at the bottom. The water supply, New York City tap water, fluctuated with the season between an extreme winter low of 4.4° C. and a summer high of 23.3° C. Food consisted chiefly of fish flesh and beef heart. During the colder months little or no food was taken.

As the spawning season approached some of the specimens, presumably females, became larger in girth, seemingly with developing roe. Occasionally one or more fish made what appeared to be a desultory effort at fanning detritus from a corner. These two facts were the only ones that even suggested the passing of the spawning season. An effort to induce spawning, when such activity had been noted, was made on August 12, 1931. Breder (1932) wrote, "In order to encourage them as much as possible, two days later a few rocks were so arranged as to form a shelter to which they might retire. Almost at once they began to investigate the structure and apparently satisfied with it cleared away all the gravel under the most sheltered part down to the bare concrete base of the tank." Spawning occurred on August 18.

The attention of the parents was so largely occupied in defending the nest against the attempted depredations of their tank mates that the latter were removed and the breeding pair were left alone in the same aquarium until the next season, when they spawned twice in 1932. Two other fish, which appeared to be a male and female, were taken from the original group now housed in another tank, in the spring of 1932. These spawned almost immediately, under a similar rock structure, and a second spawning followed. They were left alone in their tank through the season of 1933, when spawning occurred once and twice in 1934. The original pair spawned twice in 1933. The data concerning these specimens are listed in Table I, with the pairs designated A and B, respectively. Other specimens, more than two to an aquarium, showed no spawning activity, nor did specimens of *Ameiurus natalis* (Le Sueur) or *A. catus* (Linnaeus) which could not be given exclusive quarters because of limitations in the number of available aquaria. It has been noted previously by Kendall (1910) that *A. nebulosus* may spawn more than once a season.

It would consequently appear that under such conditions the chief inhibition to the reproduction of *Ameiurus* is the lack of a suitable spawning site, and crowding. While it might well be supposed that spawning occurred every year, and that the products were simply immediately engulfed by the tank mates of the parents, there is reason to believe that no spawning took place in these relatively crowded tanks. Since the known spawnings took place in the early morning or forenoon, it is extremely unlikely that in ten years the keeper would have failed each time to find even a remnant of the egg mass or any other evidence of spawning. Further, the immediate collapse of the female's sides on spawning is very noticeable and not readily overlooked, while those fish distended in a crowded tank were noted to reduce slowly in girth over a period of about two months, as though the eggs were being resorbed.

If this interpretation can actually be shown to be the case then some reflex, operating through some neuro-endocrine mechanism, would have to be invoked. If such could be shown to be in operation it would have a significant bearing on many problems concerned with the effect of population density and its relation to the reproductive rate. At least this study has demonstrated that given two healthy *Ameiurus*, physiologically capable of reproduction, isolation in an aquarium provided with a rock or similar shelter will practically insure their spawning.

TABLE I. DATA ON THE SPAWNING OF *AMEIURUS NEBULOSUS*.

Spawning	Pair	Spawning Date	Hatching Date	Date young fish left bottom	Temp. ° C.[3]	Days to hatch	Days to swim	Refers to figure
1	A[1]	Aug. 18, 1931	Aug. 24	Sept. 3	21.1	6	10	20 and 21
2	A	July—1932	—	—	20.7 (mean)	—	—	18 and 19
3	B	July—1932	—	—	22.0 (mean)	—	—	—
4	A	Aug.—1932	—	—	21.1 (mean)	—	—	—
5	B	Aug.—1932	—	—	21.1 (mean)	—	—	—
6	A[2]	July 15, 1933	July 25	Aug. 10	21.1	10	16	12 and 13, 17
7	B	July 22, 1933	—	—	21.1	—	—	—
8	A	Aug. 13, 1933	Aug. 22	—	21.1	9	—	14 and 15, 16
9	B	July 5, 1934	July 11	July 18	23.3	6	7	—
10	B	Aug. 7, 1934	Aug. 15	—	23.3	—	—	—

[1] Other fishes present in the aquarium at this spawning.

[2] Eggs removed to laboratory, the dates of hatching et cetera, referring to the artificially incubated eggs.

[3] Temp. read at time of ovaposition except "means" which are for the current month.

Spawning.

The details of the reproductive act as here described are a composite of observation for four consecutive seasons compared with details given in the literature by others. The data covered by the spawnings studied are given in Table I.

On finding a spot to her liking, a gravid female catfish will proceed to modify it further to suit her purpose. The male will also partake in this activity, at least in some cases. In the aquarium studied, only a thin layer of sand and pebbles covered the concrete bottom. Consequently these fishes had little excavating work to do. The results of their labors may be seen in Figure 12 and in all subsequent pictures. The differences between the three successive years may be noted, as Figures 12 to 17 inclusive are of 1933, Figures

18–19 of 1932, and Figures 20–21 of 1931. The removal of the sand and gravel, so far as seen, was accomplished exclusively by pushing and exerting vigorous swimming motions close to the bottom. The size of the objects dislodged may be judged from the illustrations.

Others, with different conditions, made various observations; the difference probably represented merely the degree of adaptability, in the matter of nest building, that these fishes possess. Smith (1903) writes, "They made a nest on July 3, 1902, by removing in their mouths upwards of a gallon of gravel from one end of the tank leaving the slate bottom bare." Fowler (1917) remarks of this species, "It nests in various situations, or in water from several feet in depth to that of but a few inches. Though only a few nests were noticed in a restricted area, sometimes a dozen or more may be found on one shoal and close to one another. Frequently the fish take advantage of any objects, such as logs, rocks, et cetera, for sheltering the nest. There is always a great range of variation in many of these features, especially due to the individuals and conditions. No two nests were ever found exactly alike, and the same was true of the spawners." Gill's (1907a) drawing of an *Ameiurus* nest (ideal) is not like any described in the literature or seen by the author, but more nearly resembles a centrarchid nest.

Sex recognition is not understood in this species and there seems to be no fighting for mates. However, Kendall (1910) describes marks on males that suggest fighting. It would seem that when moved by the developing gonads, the fishes seek out holes and begin excavating. This is apparently the primary basis, but just how a male and a female come to occupy a single cavity, instead of two fish of the same sex, is not clear. Pearson and Miller (1935) describe large aggregations of mature and nearly ripe *Ameiurus natalis* in Florida on May 6 along the shore line. This would seem to be a preconnubium. Injuries were noted on the dorsal and caudal fins, as well as elsewhere. These, the writer suggests, may be due to the attacks of garfish, specimens of which were numerous. It would seem likely, however, that some of the injuries, at least, were due to the catfish mauling each other. It is suspected that tactile, olfactory and gustatory senses play a part, since a pair may be frequently seen going over one another with their highly sensitive barbels. Since *Ameiurus* is such a chemically sensitive fish, as is well-known, and since its optical apparatus is so poorly developed, this suspicion becomes not unlikely. If such is the case it is not remarkable that the detection of acts of sex recognition is difficult to humans. The transliteration of the impulses received, and the corresponding reactions of an animal living largely in a world of tactile and chemical stimuli to another living largely in a world of visual and auditory stimuli, is certainly apt to be difficult except in the simplest cases. That *Ameiurus* is capable of sound production is well known, as is the fact that most, if not all, Nematognathi are well marked in this respect. If the sounds that the common catfish produces have any significance in sex recognition, no evidence of it has yet been discovered.

After the nest has finally been completed the prospective spawners spend much time lying side by side with their tails to the opening of the nest, as shown in Figure 12. At such times they are usually in contact. This quietude is interrupted by swimming in a nearly circular path, the one fish following close to the other, as shown in Figure 13. Not infrequently at such times the tail of one fish, apparently accidentally, slips into the mouth of the other. If the latter closes down on the intruded tail, and it usually does, the bitten fish leaves the nest as though shot from a gun. After swimming about for a while it returns to resume the activities. This, so far as the present interpretations go, seems to be nothing more than a quite accidental byplay, caused by these circling movements and the large mouth of the species that is so frequently opened wide. As spawning becomes more imminent these circling movements occur with increasing frequency. Finally they flatten so as to merge into a simple quiescent side to side position, with the fish facing in opposite directions and with their bodies in close contact, as shown in Figure 14. In this position spawning takes place. A large number of "spawning acts" occur until the female is emptied of her eggs. The first few attempts produce few eggs, possibly not more than three or four with each effort. Figure 14 was photographed after a few spawning attempts had been made, and immediately in front of the fish two lone eggs may be seen. Finally the eggs begin to flow freely and hundreds are shed at a time. This condition is shown in Figure 15 where a conical pile of eggs just shed may be seen under the body of the female. They are of a pale cream color, and average about 3 mm. in diameter.

Between every spawning effort the fishes rest, the male in a seemingly exhausted state. The fishes separate slightly at this time, as is shown in Figure 16, sometimes the male half falling to one side. In this picture the eggs are entirely hidden by the anal and ventral fins of the female as she has settled down over them. The spawning here described occurred on August 13, 1933, but on the two days previous more or less continued efforts were indulged in. On August 12, about a dozen eggs were actually deposited but were eaten by the parents. Between 11:15 A. M. and 2:00 P. M. on that date, the fishes went through the motions of spawning six times.

While it is difficult to be certain about the identity of the sexes of these fish, it appears that the female does most of the actual incubating and the male most of the guarding, as has already been suggested by Kendall (1910). Both fishes were seen to defend their nest against other fishes, but unlike *Aequidens* (See Breder 1934a) showed little disposition to attack hands or other objects. Both parents were seen to incubate the eggs, although there was little of a regular exchange of labors. Occasionally both would incubate at the same time, as shown in Figure 20. This did not occur often. The efforts extended were directed more toward an actual manipulation of the eggs than the circulation of water over them, the latter being common in various other nest building fishes, *e. g. Lepomis, Cichlasoma, Pomacentrus* and *Gasterosteus.* Most commonly the parent fish would settle down on the eggs with the ventral fins widespread so as to cover the mass as well as possible. Then these fins would be paddled up and down alternately, actually striking the eggs with considerable force. In a few days, generally, this action was sufficient to loosen the mass entirely from its place of attachment, so that subsequent fanning caused the entire mass to slap up and down against the floor of the tank in rhythm with the fins. Sometimes this kind of motion was alternated with a swimming movement in which the long anal fin served to swirl the mass about, or even break it up. At other times the mass of eggs, or parts of it, would be taken into the mouth and "chewed" in such a fashion as to roll them over and over, after which they would be ejected with considerable violence. Rarely at such times would the cluster be swallowed. This has also been observed by Dean (1891).

Sometimes parts of the cluster, or the entire set of eggs, would be ejected from the nest. After a mass of eggs was thus evicted, apparently accidentally, the fish would frequently come out and go over them with her barbels, as is shown in Figure 17. This would be repeated again and again but it appeared that the fish had no clear set of responses invoked by this condition. Nevertheless, on several occasions the eggs were later seen to be back in the nest, with the parent incubating as before. Unfortunately we have no observations to show how they got there. It may be that they were transported orally, as has been observed by Smith (1903) in the matter of transporting gravel, or it may be that they were incubated in place, and again accidentally knocked back into the nest. The latter seems unlikely, for only once were the fish observed to incubate eggs out of the nest, although they continually returned to stroke them with their barbels. Both Eycleshymer (1901) and Kendall (1910) mention much variation in the attitude of the parent fishes to their eggs.

A typical brooding posture of *Ameiurus* is given in Figure 18. In this case the fish has an unusually large batch of eggs. During incubation prodigious yawns are frequent. At one time these were counted and found to occur about once every fifteen minutes or less. With the large mouth capacity that this species has, it may well be that the syringe action of this yawning aids in renewing the water in the immediate vicinity of the eggs. A typical yawn is illustrated by Figure 19. The continued and strong activity indulged in by *Ameiurus* in manipulating the eggs may be shown to have a distinct and necessary function. One of the batches of eggs was removed to the laboratory and the following results obtained: All eggs died in less than twenty-four hours in standing water (at the same temperature). All but the few outermost eggs of a cluster died in a flow of water at least equal to that used in trout culture. Eggs lived and hatched when placed in a flask with an inlet reaching to the bottom and with a flow strong enough to keep them in a constant state of violent tumbling. This, a remarkable condition in a fish marked by its ability to survive low oxygen concentrations, is well-known to fish culturists. Eycleshymer (1901) had similar difficulty with the eggs. It does, however, supply an adequate explanation of the violent activity of the parents. Possibly the heavy, gelatinous coating of these eggs serves to protect them from mechanical injury, on one hand, and on the other causes a demand for an unusual amount of aeration. These eggs were found to be as susceptible to daylight as trout eggs, possibly more so, which is certainly not to be unexpected considering the normal positions of catfish nests. No actual counts were made of the eggs, but their numbers were obviously close to those given by others, such as given in Table II.

The parents of those eggs removed for the preceding studies, continued for ten days to incubate the site from which the eggs had been taken. Their performance was identical, especially the ventral fin paddling, with that displayed toward the eggs themselves, and distinctly different from the earlier described cleaning activity. It is to be especially noted that incubation ceased the same day that the eggs hatched in the laboratory. It would seem that the spawning act "wound up" some mechanism that then simply ran down. The fresh cleaning of the nest for the second spawning did not begin until about two weeks later. Table I gives the details of the data here referred to, the spawning entered as item "6" being the one referred to above.

After the eggs hatch the activity of paddling stops and the parent fish are more gentle in their movements, confining themselves mostly to swimming about over the young that huddle in a compact mass encumbered by large yolk sacs. They keep up a constant beating of their colorless tails and as they advance manage to "skate" about on the bottom to a certain extent. By the time they are able to rise off the bottom they have attained most of their coal black coloration. When this time comes the young fish rise in a cloud that often has been described. The parents then endeavor to keep them in a compact school by swimming about, more or less in circles, as shown in Figure 21, and as described by Mellen (1926). The tropisms of the young *Ameiurus* themselves also tend to keep them together. These have been studied in much detail by Bowen (1930) and (1932) for *Ameiurus melas* (Rafinesque) who found they were almost entirely visual. As the present author has noted nothing at variance with those studies, the details of the features need not be discussed here. It may be pointed out, however, that the eye seems to become a much less important organ with age, as has already been indicated for the adults. A study of this change should be interesting. As the young fish grow and become more adventurous with the weakening of the early tropisms, the parents, in the aquarium at least, catch them in their mouths and return them to the school. Probably in a state of nature most of them escape parental solicitude about this time, but in confinement we found them all dying at this point. This is practically identical with the observations of Smith and Harron (1904). The conclusion that the young fish were victims of too much and continued handling by over-zealous parents could not be avoided, especially since on another spawning the removal of the parents allowed the young to develop with only nominal loss. An item of behavior valuable in a state of nature would thus have to be considered lethal in the relatively close confines of an aquarium.

The data concerning spawning, temperatures and related items, as found in the literature, are given in Table II for comparison with the present data. Although there is good general agreement throughout, it will be noted that the spawning dates of the New York Aquarium observations are considerably later than any of the others. This is apparently due to the fact that the water reaches a suitable temperature at a later date because of the extremely large, deep lakes serving New York City as reservoirs, and the depth in the ground of the water mains. The observations of others refer either to small ponds, the shallow margins of lakes, or aquaria with a normally warmer water supply. Further, the temperatures given by others are all actually higher than those found in the present case with one exception—Greeley (1930). A slow rise to about 21° evidently permits spawning which might otherwise take place at a relatively rapid rise to about 25.° Moreover, it is to be noted that Hildebrand and Towers (1929) examined a 235 mm. female from Greenwood, Tennessee, taken on August 27, that contained about 3,000 ovarian eggs of about 1.25 mm. in diameter. As they suggest, there may be a much larger spread to the spawning season than generally assumed. On the other hand, the single record of spawning in a lower temperature than found at the Aquarium is well to the north, in the cooler waters of the Lake Champlain region.

Comparison with Opladelus.

The literature contains no description of the reproductive habits of the related but much larger mud-cat *Opladelus olivaris* (Rafinesque). Presumably, they would be rather similar to those of *Ameiurus*. It is with considerable satisfaction, therefore, that it can be reported at this time that there is a great similarity. The following descriptive matter and pertinent illustrations have been made available through the kindness and generosity of Mr. Walter H. Chute, Director of the John G. Shedd Aquarium in Chicago. A

TABLE II. COMPARISON OF REPRODUCTIVE DATA ON *AMEIURUS NEBULOSUS.*

Reference	Locality	Spawning Date	Hatching Date	Free Swimming Date	Time of Spawning	Temp. ° C.	No. of Eggs	Size of Eggs	Water Depth
Dean (1891)	New York	April	—	—	—	—	—	1/8″	—
Eycleshymer (1901)	Mass. & Mich.	June 1–11	In one week	In a few days	—	—	—	—	6″ to 5′
Smith (1903) and Smith & Harron (1904)	Wash., D. C.	July 3	July 8	July 15	10–11 A.M.	25°	2,000 ±	—	1½′
Kendall (1904 & 1910)	General	May 8–July 6	In twenty hours	—	—	24.6°–25.7°	—	—	—
Hankinson (1908)	Mich.	—	—	Before June 28	—	—	—	—	—
Forbes and Richardson (1909)	Ill.	May	—	—	—	—	—	—	6″ to 2′
Wright and Allen (1913)	Ithaca	May 20–July 12	—	—	—	—	—	—	—
McAtee and Weed (1915)	Maryland	Spring	—	—	—	—	—	—	—
Fowler (1917)	Pa.	—	—	—	—	—	50–500 +	—	Few in. to several ft.
Evermann and Clark (1920)	Indiana	May–June	In five days	—	—	25°	—	—	—
Adams and Hankinson (1928)	Syracuse	May–June	May–June	June 19	—	—	—	—	—
Hildebrand and Towers (1929)	Miss.	Later than August?			—	—	30,000 ± ovarian	—	—
Greeley (1930)	Champlain Region	—		June 20	—	18.5°	—	—	4″
Original	New Jersey	July	July	Aug.[1]	—	25°	—	—	—
	N. Y. Aquarium	July 15–Aug. 18	July 25–Aug. 24	July 18–Sept. 3	11:15 A.M to 2:00 P.M.	20.7°–22.0°	500–2,000 ±	3 mm.	4′

[1] On Aug. 7, 1926 twenty young fish ranged from 15 to 20 mm. in standard length with a mode at 17 mm. and one fish of 58 mm.

pair of this species successfully spawned at that institution in 1934 and the following remarks are quoted directly from Mr. Chute's notes on the case. The photographs are the work of Mr. Loren Tutell of the Shedd Aquarium staff.

"July 6 & 7. Activity in the mud catfish tank was first noticed. This tank contains two mud catfish, each about four feet long, five large alligator gars, one blue catfish about the same size as the mud catfish, and five sturgeon ranging in size from two to six feet. The catfishes selected a corner of the tank close to the glass. Both of them used their tails and mouths to make a hollow in the sand down to the bare gravel and rock. The completed nest was approximately five feet in diameter.

"On the 7th they were seen several times in an embrace, suggestive of the embrace used by the Bettas, although the male fish was unable to completely encircle the female. I did not see this embrace but was told about it after the eggs had been laid.

"July 8. When the attendant came to work at eight o'clock in the morning he found the eggs in the nest. They apparently had been laid some time that morning.

They were adhesive and made a mass in the bottom of the nest approximately sixteen inches in diameter, six inches thick in the center tapering to the thickness of one egg on the outside edge of the mass.

"In appearance the egg mass suggested a tapioca pudding. The individual eggs were just about the size of boiled tapioca and the yolks of the eggs gave the entire mass a custard color which heightened the similarity. Both parents were hovering over the nest.

"July 10. Male only was guarding the nest. When one of the big gars swam close to the nest the male would swim under the gar and push upward until the gar was near the surface of the six foot deep tank. If one of the little sturgeon approached the nest the catfish would chase him clear to the other end of the tank, which is thirty feet long. When the female attempted to approach the nest the male bit her and chased her into a hole under a log in the background. It was interesting to note that he fought fishes of his own size or smaller and gently 'eased' the larger fishes away without starting an argument.

"We took out about four hundred of the eggs from the nest and measured one cubic inch, which counted 175 eggs. On this basis I estimated the total mass to be in the vicinity of 100,000 eggs. The few eggs that we took out were put into a glass bowl and hung under running water.

"In caring for the eggs, the male would settle over the mass and agitate the eggs strongly by using the ventral fins alternately. At the same time he repeatedly vibrated his anal fin, creating a current of water which washed away the dirt loosened by the beating of his ventral fins. The entire mass would shake like a bowl of jelly and at times he kneaded the eggs so hard that the edges of the egg mass would rise an inch or two above the bottom.

"In the later stages of development, when the eggs started to hatch, the young fishes would be swept away from the egg mass and lodged in the crevices around the edges of the nest.

"July 12. Some of the eggs in the bowl under running water started to hatch. The young fish were very tiny and weak. A number of egg shells were noticeable in the egg mass in the nest, but no young were visible.

"July 13. The young in the bowl were all dead and the remaining eggs in the bowl were turning white. The eggs in the nest were starting to hatch and the male was kept very busy between agitating the mass and chasing off the sturgeon, which apparently sensed the fact that food was near.

"July 15. Eggs were hatching very rapidly in the nest. Apparently the current caused by the agitation of the fins of the male carried off the young fish but left the adhesive shells still adhering to the mass. The largest sturgeon kept raiding the nest and eating all the young that were near the edge of the nest, so we removed a thousand or more young fishes. Some of these were put into a reserve tank with a depth of forty inches of water and about five hundred were put into an ordinary trout hatching box which had a layer of sand on the bottom.

"July 16. The egg mass had entirely disappeared. The male was still guarding several hundred of the young in a corner of the nest up against the wall. The young fish put in the reserve tank and the trout hatching trough had gathered in groups with all their tails rapidly vibrating in the same direction.

"July 18. Pigment beginning to develop in the young, Very prominent blood vessels, bright red in color, encircling the yolk, giving the entire mass of young a pinkish color.

"July 19. Male still guarding the nest with about two hundred young. The young fish in the reserve tank and trout trough much more active and showing signs of growth.

"July 20. Male still on the nest guarding a few young that are still in crevices among the rocks. The young fish under observation in the reserve tank and trough are becoming quite active, occasionally swimming short distances but always returning to the group. The head is exceptionally well developed and when viewed from above is as wide as the yolk sac. They are now recognizable as catfishes, as the maxillary barbels are about 1/16 inch long and easily discernible. Black pigment is starting to gather on the head, and on a saddle-like spot across the back and on the yolk, but the tails are still pale pink."

A comparison of the above remarks with the previous ones on *Ameiurus* reveals them to be nearly identical in their major aspects: the manner of working over the eggs; the failure of them to hatch successfully under ordinary running water; the matter of embracing several times before the eggs flow; the period of incubation, and time to free swimming. The items not in apparent agreement are discussed separately below.

The embrace as described for *Opladelus* would appear to be rather different, although Mr. Chute in a subsequent communication emphasized the fact that he did not personally see this act but based his description on the account of one of his employees. It may even be, however, that this is the normal silurid mating position, and that the position observed in *Ameiurus* at the New York Aquarium may be a distortion of it, because of the close confinement of the cavity which these fishes always choose for spawning purposes.

The spawning of *Opladelus* occurred in an aquarium containing other fishes, whereas we have had success only where pairs were isolated. It is to be noted, however, that only one pair of the spawning species was present. At this writing no attempt has yet been made to see if *Ameiurus* only resents its own kind. Although the *Opladelus* were large, "about four feet long," they were in a very large aquarium, 30 feet long, 6 feet deep and 10 feet wide. On the other hand the present studies were made for most part on fish one foot long in a tank 5 feet long, 4 feet deep and 3 feet wide. These proportions are not at great mathematical variance either as to bottom area or volume per length of fish. However, these matters do not usually correlate along a straight line, the factor for absolute size causing a considerable deflection in tanks so relatively small in relation to the fishes.

The rejection by the male of the services of the female is unlike the behavior of *Ameiurus* studied in detail by the author. It may be pointed out, however, that there is probably considerable individual variation in this matter. In spawning No. 10 of Table I, one of the fish drove and succeeded in keeping the other away from the nest. The driver was believed to be the male. This pair had both incubated the prior batch of eggs in the same site, No. 9 of Table I. It is noted, moreover, that in *Ictalurus,* according to Shira (1917a and b), only the male incubates.

COMPARISON WITH OTHER NEMATOGNATHI.

So far as known there are but four basic methods of reproduction employed in the entire order Nematognathi. There is the method involving the incubation of the eggs in a nest, as here described and illustrated for *Ameiurus nebulosus* and *Opladelus olivaris,* which may be taken as basically typical of the entire ameiurid aggregation. Other species are essentially the same, Ryder (1883), and Koller (1926), and Greeley (1929). The only other method known to be employed by the typical "naked" cats is that of oral incubation which seems to be confined to the ariids, and there is some reason to suppose that it may be true of nearly all those species. Semon (1899) describes the nesting of *Hexanematichthys australis* (Günther), which is the only apparent exception. This fish makes a circular nest as a cavitation in the gravel of rapidly flowing streams in which the eggs are deposited. They are then buried in a mound of gravel. *Tandanus tandanus* (Mitchell), one of the plotosids, also of Australia, Stead (1906) and Hale (1920), likewise builds a nest in the form of a mound. The other habits are apparently very similar to those of *Ameiurus,* including the oral transportation of gravel and the fanning movements to remove detritus. Also both sexes attend the nest. According to Bowers (1913) and Shira (1917a and b), the spawning of *Ictalurus punctatus* (Rafinesque) is essentially similar to that of *Ameiurus* except that only the male tends the eggs. With the exception of *Silurus glanis* which is discussed subsequently, the two other methods seem to be confined to the much more specialized and generally "armored" cats. One of these is that of sticking separate adhesive eggs on plants, and the other that of carrying the attached eggs to the ventral surface of one of the parents. Since the data on these various specializations are inadequate, as yet, to the making of truly significant comparisons, they are simply mentioned in passing. The literature is large and will not be fully discussed at this time, as for most part the descriptions are fragmentary. Gudger (1916), (1918) and (1919) gives all the important references on oral incubation in the ariids to that time. These are not included here. Since then many others have been mentioned as displaying oral incubation; *e. g.,* Pellegrin (1919), Mane (1929), Herre (1926), Aldaba (1931), Delsman and Hardenberg (1934) and Hardenberg (1935). See also Lee (1931). It has been shown that the Aspridinidae allow the eggs to become attached to the ventral surface, and certain of the Callichthyidae lay separate adhesive eggs. For abundant references to nematognath reproduction, see Dean (1916).

Oral incubators.

For present purposes it is sufficient to point out that the reproductive habits of *Ameiurus* involve both excavation of gravel by use of the mouth, and taking into the mouth the developing eggs, presumably for purposes of cleaning and aerating and possibly for returning dislodged eggs to the nest. This would clearly seem to be a necessary forerunner to the establishment of oral incubation. Gudger (1918), on a basis of the literature, has already indicated that such habits might well be expected to lead to oral incubation. After giving his evidence Gudger writes as follows: "It seems hardly necessary to argue the question as to the origin of the habit of oral gestation after the presentation of the facts above given. In the mind of the present writer there is no doubt that having begun by taking up the eggs and young for purposes of transportation, the fish have presently learned to retain them for longer periods of time; we have a record of at least one minute's retention; and as the fish that would retain their young even for short spaces of time and transport them to safer localities are more likely to leave descendants, through the action of natural selection, these fish and this habit will be perpetuated. Hence we may conjecture that as time has gone on the habit of retention has become more and more fixed until finally oral gestation has become an established habit." With the general idea expressed, this author of course concurs. The chief purpose in mentioning it here is for comparison with other habits also foreshadowed in ameiurid reproduction to be discussed later. It may also be mentioned at this place that there is need of a reconsideration of all the data concerning oral incubation and its origin, since the literature is full of inadequate and misleading statements, a considerable number of which are simply untrue. A single example may serve by way of illustration. Even Gudger (1918) mentions without criticism the description of Carbonnier (1874) of oral incubation in *Fundula cyprinodonta,* which fish Gill (1906) referred to *Umbra pygmaea.* Since all three species of *Umbra* stick their separate eggs securely on some object, such as a rock or plant, Carbonnier, it would seem, had some other fish, perhaps not even North American as he thought. Abbott (1874), (1890) was familiar with the breeding of *Umbra pygmaea;* Anon. (1918) and Gray (1923) described it in aquaria, and the present author robbed the nests of *Umbra* for developmental studies, Breder (1933a). With conditions of which the above serves as an example, it is clear that unsupported statements regarding oral incubation require more than the usual critical examination, and should be carefully checked before acceptance.

The development of oral incubation in the nematognaths would seem thus to be decidedly parallel to that found in the Cichlidae, as already discussed by Breder (1934a). In the present case the progress is clearly paralleled by unrelated structural changes, and change in habitat. The direction of evolution can scarcely be questioned in this case, with the curious chondocranium of the ariids that certainly was derived from some ameiurid-like ancestor. See Gregory (1933). Likewise the development of a marine habit is certainly secondary in the Nematognathi, and even yet their invasion of the sea can only be considered a weak one, since all the Ariidae are hardly more than estuarine. The building of the ameiurid type of nest in tidal and usually muddy waters could hardly be a successful method. The largely mud flat habitat described by Gudger (1918) for *Felichthys* certainly would be unfriendly to such a nest, as he clearly indicated. Furthermore, this catfish could scarcely be expected to defend its eggs successfully against marauding marine crustaceans, whereas possibly the worst that *Ameiurus* has to contend with is *Cambarus*. Marine fishes that do build nests somewhat comparable to those of *Ameiurus*, generally use a substantial retreat that renders protection relatively easy; *e. g.*, *Opsanus*, *Pholis* or *Pomacentrus leucostictus*. Other forms use other methods. For example, more numerous eggs may be produced; they may be pelagic or situated in some relatively inaccessible place. Such a situation might be up from the bottom on a smooth vertical surface, as in the case of *Pomacentrus leucoris*, Breder and Coates (1933). Furthermore, these latter do not live in mud flat environments. In this connection information on the reproduction of *Plotosus* should be valuable.

The eggs of orally incubating species are comparatively larger than those of related nest building species in cases studied by the author. These include the Cichlidae, Breder (1934), the Nematognathi and the Labyrinthidae; the orally incubating *Betta picta*

(Cuvier and Valenciennes) having larger eggs than the nesting *Betta splendens* Regan. Breder (1933b) and (1934b). This latter case will be discussed in a subsequent communication. The increased size of the egg of *Felichthys* is an extremely striking case. Gudger (1919) gives the average diameter as about 20 mm. The egg of *Ameiurus,* on the other hand, is about 3 mm. In the other two cases mentioned the orally incubating fishes have egg diameters about twice that of their nest building relatives, in species of comparable sizes. The problem of this shift to larger and proportionately fewer eggs is not readily explained. In each case the nest builders could hardly engulf all their eggs in a normal spawning. Gudger (1919) gives 55 eggs as the maximum he found for *Felichthys,* and certainly the ovaries of a female could hardly produce many more at one time. Compare this with the size of the egg masses of *Ameiurus* shown in the accompanying photographs. Figures 20 and 21 are especially pertinent. Semon (1899) states that *Arius australis* lays eggs about one-eighth of an inch in diameter. These are much smaller than any other known ariid eggs and this is the only species definitely known to be not an oral incubator.

It would seem that there is less wastage of eggs in the oral incubation method. Consequently, following the well-known reduction of young in proportion to the hazards of the species, it may be that the need for more numerous eggs has disappeared. Since there is no indication of a reduction in the size of the ovary, or any seemingly reasonable need of such, the potential ovarian activity would presumably remain about the same. This in turn might go to the production of eggs of increased size. This suggestion is the equivalent of saying that in some way the need of less numerous offspring is involved in not only the production of fewer but larger offspring. Certainly, in a broad phylogenetic sense at least, such is true of vertebrates generally.

Gudger (1918) takes the opposite view, *i. e.,* that the increased egg size has encouraged oral incubation. He writes: "Let it be recalled that these eggs are of enormous size (the average diameter of 327 eggs being 19.5 mm.) and that when in middle embryonic stages they are very attractive to the eye because of their blood-red vascular yolk investment. For these reasons, if laid like other fish eggs are, they could hardly be expected to escape the eyes of marauding fishes, but if any were so fortunate they would almost certainly be eaten by crabs, those scavengers from which practically nothing escapes. The result would be the inevitable extinction of the species. These catfish spawn and spend the hatching season on mud flats. If the eggs were discharged on such bottoms they would (because of their great weight, averaging 3.5 grams) sink into the mud and be smothered. To avoid these various dangers, these fish have to do one of two things to insure their perpetuity, *i. e.*, to practice mouth gestation or to lay eggs in nests which are guarded by one or both the parents. Some fresh-water catfishes have adopted the latter habit; the gaff-topsail the former." Since there is concurrence between Gudger and the present author, that the ariid type of reproduction was derived from some habit similar to the ameiurud type, his above quoted view must be able to explain away the following objections to be accepted as valid:

1. Since *Ameiurus* successfully defends its large mass of eggs against marauders, there is no particular reason why it could not equally defend eggs the size of *Felichthys* (if amounting to the same total bulk) in an identical environment. The color differences cannot be significant, since bright red eggs are not more visually evident than cream white ones, if as much, under such conditions. Then too, there is the question of the importance of the various receptors to the enemy species.

2. If *Ameiurus* attempted to reproduce in the environment of *Felichthys*, the relatively small size of its eggs would confer no immunity from suffocation on a mud flat not possessed by *Felichthys*. In other words, size of egg (of identical type) has little to do with suffocation in the same mud. Both types of eggs sink rapidly in sea water.

Stating it another way, while it is agreed that nest building is out of the question on mud flats, it is objected that an increased egg size may have led to the development of oral incubation. On the other hand the present view, which refers increased size to a need for fewer eggs because of better general protection, does not suffer from these same objections. This is given added support by the fact that other oral incubators have not resorted to mud flat environments, although in each case there is some size increase and number reduction.

Conorhynchus nelsoni Evermann and Goldsborough, an oral incubator of Mexico, has been referred to the Pimelodinae. At this writing we can see no reason for not considering it an ariid. The nares are as closely approximated as in many in that group (according to the type figure) and the adipose fin is too short for the former. Dr. G. S. Myers, of the U. S. National Museum, kindly examined the type specimen and stated in a personal communication that it "is an undoubted ariid, probably of a new genus." Dr. C. L. Hubbs, who has recently collected this species, also writes in a personal communication that he is of a like opinion.

Hardenberg (1935) describes and figures the hook-like thickening of the inner part of the female's ventral fins in *Arius maculatus* (Thunb.), and suggests that "this is a sexual character, which has something to do with spawning and mating. It is clear that the male is attached by these hooks and the fertilization of the eggs takes place perhaps inside the body of the female or more probably outside the body just at the moment when they leave the genital opening." However true this may be, it is certain that most of the ariids have some such secondary character. At the New York Aquarium the females of *Galeichthys milberti* (C. & V.) develop similar structures which are apparently resorbed every fall. Thus far we have been unable to induce reproduction, however, in this species. Dr. Hubbs found similar structures in "*Conorhynchus*" but could not find them in *Arius aqua-dulce* Meek. Occasionally a female *Ameiurus nebulosus* shows a slight ridge that may be an abortive form of this structure.

Alleged gastric incubation.

Devincenzi (1933) in a most interesting paper describes a condition in *Tachysurus barbus* (Lacépède) which he interprets as establishing what he terms "incubation gastrica." He found males with eggs in their stomachs in various stages of development. Histologic sections of the stomach walls showed an absence of the folds in the mucosa normal to non-breeding fish, and a general thinning of the stomach wall. This he interprets as representing a cessation of the digestive function while the eggs are so carried. He believes that this condition was responsible for the alleged viviparity in such fishes by early workers; *e. g.*, Schomburgk (1841). In this latter view we are in complete accord but cannot admit the fact of gastric incubation. The proper interpretation of the conditions that Dr. Devincenzi describes is believed to be as follows:

It is well known that various orally incubating fishes will frequently swallow their eggs when frightened. This is especially apt to be the case when such fishes are caught in a net or otherwise handled. In fact one of the greatest difficulties in the aquarium breeding of various orally incubating cichlids, and orally incubating species of the labyrinthine genus *Betta,* is their tendency to swallow their eggs on fright. It is consequently not surprising that some of Devincenzi's fishes swallowed their eggs. It is to be especially noted that he also describes oral incubation in the same species. Apparently not all of his specimens swallowed their eggs. One could hardly expect a single species to show two methods of incubation. Further, it is inconceivable that a single kind of egg could survive in the well aerated mouth cavity and also in the relatively anerobic stomachic pouch. In reference to the latter, a figure is given by Devincenzi which purports to show that the stomach has an unusual degree of vascularization. This is unconvincing, since many fish stomachs of diverse species possess an even greater supply of blood vessels and are found to contain nothing more unusual than a large amount of food. It is to be particularly noted that the first feeding after a fast in most fishes will induce a marked distention of the blood vessels in the stomach wall. The finding of eggs in various stages of development, in different individuals, interpreted as an accidental ingestion, indicates the advancement of the eggs at the time of swallowing and has no bearing on their time of entry. It may be noted that whole eggs are rather resistant but as the fish were either preserved and later studied, or examined fresh, the effects of digestion would be slight, especially in a stomach that has not contained food for some time.

The histological differences shown in the stomach walls are only those to be seen between a normal functioning fish stomach, and one which has been under starvation for some time and then stretched by cramming with food. A close examination of the photographs of the sections show all the cellular elements present in both. The functional stomach in a relaxed condition shows the folds normally present, while in the stomach filled with eggs these are flattened out and the sac itself, because of stretching, shows thinner walls. A remarkable feature of the fish stomach in this connection is the changes that it undergoes during starvation. A more or less bulky sac reduces typically to be almost cord-like in structure and stretches as a thin membrane on the first feeding, subsequently thickening to its original condition. At this time the vascularization is especially evident. It is just these features that Devincenzi shows in his figures but on which he places an interpretation with which we cannot agree.

The question might be raised as to whether it is possible for such fish to regurgitate the eggs after danger has passed, thus using the stomach temporarily for protection. While there is no observational or other data on such a possibility, there is certainly no reason to imagine that such might be the case. Other fishes of many kinds have never been known to regurgitate eggs once swallowed. These include all forms that have been personally observed in any way to manipulate their eggs with the mouth. They include *Ameiurus,* herein discussed, a variety of cichlids both nest building and orally incubating, a variety of labyrinth fishes both nest building and orally incubating, as well as a scattering variety of other forms, such as nandids, centrarchids and pomacentrids. Theoretically considered there is furthermore no likely reason why a fish carrying eggs in its mouth could escape any faster with them in its stomach. It of course could be imagined that respiration might be a little more free but, at this time, such a concept is pure speculation. It seems more likely that an involuntary gulp, on fright, places the eggs in a position beyond recall. At least this is the impression derived from other species of oral incubaters in aquaria, although obviously such a question is difficult of experimental verification.

Eggs adherent to abdomen.

While it might be straining a point to compare ameiurid reproduction with that of the nematognaths that attach their eggs to their ventral surface, such as *Aspredo,* (*Platystacus*) Cuvier and Valenciennes (1842), Green (1858), and Wyman (1859a and b), *Bunocephalus,* Bloch (1837), there are nevertheless certain suggestive features. It has been shown in this paper both by descriptions of detailed acts and by photographs, that *Ameiurus* literally lies on its eggs. See, especially, Figures 18 and 19. In addition this species strikes its eggs violently with its ventral fins as previously discussed. The eggs are of themselves distinctly adhesive. In the case of *Ameiurus* the integument is extremely slippery and no adhesion is possible. In the case of *Aspredo,* however, the mucus production is slighter, as is also true of the more fully armored loricariates. This statement is not meant to imply that this condition alone explains the egg carrying of *Aspredo*, as it has been shown that the specialized integument is structurally modified to accommodate the eggs. See the work of Vaillant (1898). However, the lack of excessive slime production must have preceded it, since it is difficult to see how any fish integument bathed in the particularly slippery mucus of the naked cats could function in the manner described for that of *Aspredo*.

The actual conditions in this case involve a structural change of the integument, and differ from the habit of oral incubation in that the development of the latter has so far not been shown to be accompanied by any functional change in structure. It may be, however, that the structural change in the integument may be induced by the adhesion of the eggs. If a means could be devised to cause the eggs of *Ameiurus* to adhere to the ventral surface of the fish, a study of the histological changes of the skin, if any, should be extremely illuminating.

It has been suggested by Eggert (1930) that *Macrones gulio* Ham. Buch. may carry its eggs on its ventral surface in folds on the abdomen. This is based on anatomical and histological data. Females with advanced ova were found to have these folds highly vascularized and large, whereas in unripe fish they were small. As Eggert suggests, these structures at the very least are probably associated with the reproductive habits, even if not as above indicated. They may represent the first step in this direction toward egg carrying, so highly developed in the aspridinids.

Eggs cast free.

Among the various specialized members of the Nematognathi there are several that are reported to deposit separate adhesive eggs. Such forms as *Astroblepus, Otocinclus* and *Corydoras* are known to breed in that fashion. This may be considered either as the retention of a primitive character, since it is typical of the generality of both the Heterognathi and Eventognathi, or as the secondary development of it. If the first possibility be considered, it follows that these fishes, not especially close to one another, all by-passed the ameiurid type of reproductive activity. Unfortunately, we do not know enough about the details of the reproductive habits of these fishes to find useful clews. However, since the nematognaths are all possessed of a highly specialized musculature of the pelvic appendages, we have some grounds for tentative speculation. The relatively primitive Ameiuridae make use of these ventral fins, as earlier described, in a distinctly definite manner in their reproductive activity. It so happens that both *Astroblepus* and *Otocinclus* have highly developed ventrals which they use for non-reproductive purposes. *Astroblepus marmoratus* is capable of scaling eighteen foot walls by means of its suctoral mouth and ventral fins, Johnson (1912), and *A. longifilis* is probably capable of similar performances. At least it was seen to use its ventrals to a considerable extent in climbing, Breder (1926). *Otocinclus* grasps more or less vertical plant stems between its ventrals in aquaria and rests for long periods, holding on in that fashion. *Corydoras,* on the other hand, with somewhat similar ventrals, so far as the author is aware, uses them as specialized organs in reproductive activity only, Carbonnier (1880a and b) and Vipan (1886). At such times they are cupped together to act as an inseminating basket for holding the eggs during fertilization, which eggs are then cast off to adhere separately to plants. *Hoplosternum,* according to Vipan (1886) and Hancock (1828), builds an elaborate nest of froth and plant fragments at the surface as does *Callichthys,* Devincenzi (1933). Carter and Beadle (1931) confirm this and give excellent illustration of the nest of *Hoplosternum.*

If the assumption is made that these fishes passed through some ameiurid-like breeding pattern and then discarded it, the above use of the specialized ventral musculature becomes understandable. They then take on a new useful function, differing in each group, when the original one is no longer applicable. The only other interpretation would be that the primitive nematognaths used their peculiar pelvic musculature for some purpose we know nothing about, and that it has simply been developed to a scattered variety of uses. This would be hard to establish, and it is rather difficult to imagine what type or use there might be, considered as a starting point, that would be simpler than the paddling movements of *Ameiurus.*

Floating nests of froth.

As has already been indicated, *Hoplosternum* constructs a floating nest of froth. The most recent and full description of this type of nesting has been given by Carter and Beadle (1931) for *H. litorale*

Hancock. This species spawns in the nearly anerobic waters of the Paraguayan Chaco. They write of the region: "Rain at the beginning of summer is the stimulus for the breeding of many of the fishes of these swamps (*Lepodisiren, Symbranchus, Hoplias,* etc.) and of many of the amphibia. After the rain the water is often cooler than usual, but rapidly heats in the following days. The amount of oxygen is not greatly altered by the rain except for a short time and at the surface. The most definite abnormality of the water at this time is the less amount of carbon dioxide in it, but this also passes rapidly. Possibly a combination of all these changes provides the stimulus for reproduction."

Under these conditions *Hoplosternum* constructs a raft about one foot in diameter of floating weeds and other aquatic plants. The mass of eggs is placed at the center of the underside of the raft and "the eggs are glued together and to the raft by a secretion which also prevents the materials of the raft from falling apart. Below the eggs and covering the whole of the underside of the nest is a mass of foam, probably made by the fish by taking air in at the mouth and bubbling it out again. The nest is guarded by the parent fish which is always to be found swimming below it, but it is readily deserted if the fish is disturbed in any way." Unfortunately, the sex of the guarding parent is not designated.

Little can be said regarding the possible evolution of this bubble blowing habit, but it may be pointed out that it also occurs in other fishes and a similar construction is made by several genera of frogs; *e. g., Eupemphix* and *Leptodactylus.* Of the fishes, only one belongs to the Ostariophysi, the African characin, *Hydrocyanoides odoe* (Bloch), which was first described by Budgett (1901). A variety of the entirely unrelated labyrinthine fishes, such as *Betta, Macropodus, Ctenops, Colisa,* et cetera, erect such constructions. An eel, *Fluta alba,* has also been credited with such a habit by Smith (1934) but needs confirmation. Living as it does in association with various froth-making labyrinth fishes, it seems likely, to the present author at least, that the observations may actually refer to a raid on such a labyrinth nest by a family of young *Fluta* still under the influence of their parent. This interpretation would imply parental care on the part of this eel, but not froth nest construction.

All these nests are to be found in waters of low oxygen content, and however they arose are apparently one solution to the problem of reproduction under such conditions. A remarkable feature of them is the essential similarity that they all bear one another.

Ancestral habits.

Thus far only the types of reproduction that the ameiurid habit may have led to have been considered. If we attempt to trace backward, to ascribe a point of origin to the breeding activity of *Ameiurus*, the evidence is very scant and unconvincing. Probably scattering loose non-adhesive eggs which sink, is the most primitive method of reproduction in the entire ostariophysid aggregation. Since they in turn lead back to isopondyles, in which the most primitive condition is probably that of scattering loose non-adhesive eggs which float, little in the way of clews can be found. The difference between floating and sinking of eggs in this case probably is simply the matter of relative specific gravity, since the isopondyles that lay floating eggs spawn at sea, and the Ostariophysi spawn in fresh water except for the orally incubating nematognaths. This, then, may be an almost purely environmental matter. It must be pointed out in this connection, however, that the eggs of both *Felichthys* and *Ameiurus* sink rapidly in sea water. Eggs of the latter were found to sink in sea water concentrated to the high specific gravity of 1.027. Since there is no known intermediate between casting eggs, adhesive or not, and incubating them with elaborate activity, except that of simply lying with them, as in *Schilbeodes*, Fowler (1917), on which further observation is needed, little can be adduced. We consequently can only guess what led to the origination of aerating activity in the nematognaths. Gill (1907a) discusses the nesting habits of *Parasilurus aristotelis* (Garman) based on Aristotle's description and the non-nesting of *Silurus glanis* Linnaeus, a relatively unspecialized silurid. In the latter the male simply mounts guard over the eggs, which are attached to plants.

The plotosid catfishes, representing the only other invasion of the sea found in this order, are little known in regard to their reproductive habits. *Plotosus* possesses a curious gland-like structure posterior to the genital pore which is present in both sexes. Broch (1887) suggested that it might form an egg receptacle. Hirota (1895) with more data indicated that it might be a gland of some unknown function. Eggert (1929) is of the opinion that whatever its function it probably would be found to be associated with the reproductive behavior. He suggested that it might be a scent organ. On this we can only speculate. The plotosids invading the fresh waters of Australia have developed at least one nest builder, *Tandanus,* which has already been mentioned. It may be that this is a secondary acquisition of the habit, for it would seem unlikely that such a habit would be found in the marine plotosids. They sometimes are found to inhabit environments similar to those of the marine ariids, and for the reasons set forth in the discussion of them could hardly be expected to build ordinary catfish nests. Otherwise they are apt to be associated with coral reefs, a type of habitat generally favorable to nesting.

If the various habits of the nematognath fishes are considered in reference to phylogenetic classification, the great gaps in our knowledge become apparent. So large are these that any attempt to trace the descent of habits becomes almost hopeless at this time. However, a consideration of the known facts may nevertheless have value in pointing to possibilities and indicating desiderata for further researches. Table III gives a list of families and subfamilies

TABLE III. REPRODUCTIVE HABITS OF THE NEMATOGNATHI.

Classification	Major Aspects of Reproduction	Genera Known
Diplomystidae	(?)	—
Aspridinidae	Eggs carried on ventral surface of female.	*Aspredo, Bunocephalus*
Siluridae		
Ariinae	Oral incubation by males in all marine forms? *Hexanemitichthys australis* builds a nest.	*Netuma, Arius, Osteogeniosus, Galeichthys, Hexanemitichthys, Felichthys*
Callophysinae	(?)	—
Pimelodinae	(?)	—
Silurinae	Eggs deposited on plants by *Silurus.* Nest built by *Parasilurus.*	*Silurus, Parasilurus*
Malopterurinae	Oral incubation has been suggested?	—
Plotosinae	Unknown in marine forms. *Tandanus* builds a nest.	*Tandanus*
Clariinae	(?)	—
Bagrinae	All build nests (?) except *Macrones* which may carry eggs on ventral surface.	*Ameiurus, Opladelus, Villarius, Schilbeodes, Ictalurus*
Doradinae	Builds a nest.	*Doras*
Hypopthalmidae	(?)	—
Trichomycteridae	(?)	—
Callichthyidae	Eggs deposited on plants by *Corydoras. Hoplosternum and Callichthys* build a floating froth nest.	*Corydoras, Hoplosternum, Callichthys*
Loricariidae		
Argiinae	Eggs deposited on plants.	*Astroblepus*
Plecostominae	Eggs laid in holes.	*Ancistrus*
Loricariinae	Eggs carried in folds of lip (male).	*Loricaria*
Hypoptopomatinae	*Otocinclus* may lay free eggs (?).	—

based chiefly on Eigenmann and Eigenmann (1890) and Boulenger (1904), which are used here chiefly for reasons of convenience. Opposite each group is given the major characteristic of the reproductive habits. All of these features have been mentioned in some detail in the foregoing discussion. Consequently, the suggestion of relationship of habit need only be indicated at this place. Of those forms of which there is anything known regarding reproduction, the following inferences would seem to follow.

The Aspridinidae, a highly specialized offshoot of the early stem, are uniform, so far as known, regarding the carrying of eggs on the ventral surface. This, now a highly developed integumentary involvement, may have arisen from the habit of lying on the eggs in a manner similar to that seen in *Ameiurus* today.

The Ariinae, generally considered a primitive form, although extending back to Eocene times, would nevertheless seem to have been derived from some ameiurid-like stock. This view is held by Gregory (1933), based chiefly on skull structure. Certainly at least the habit of oral incubation was derived from an ameiurid-like breeding habit at a time when they invaded estuarine waters. The nest building of the *Hexanemitichthys australis* would seem to be clearly associated with a secondary invasion of streams. This nest is a mound and to that extent differs from the excavations of the Bagrinae.

The Silurinae has both a nest building form, *Parasilurus*, and a non-nester, *Silurus*. On the latter there is not a great amount of data even today, which moves Long (1929) to call for more observation of the common European catfish.

Oral incubation has been reputed in the Malopterurinae, but the data are inadequate, Gill (1907a). Svensson (1933), studying Gambian fishes, states he could add nothing to the details of reproduction.

Nothing is known of all the marine Plotosinae except that they possess a curious gland-like organ which would seem to be associated with reproduction. *Tandanus*, an Australian invasion from the sea, of this group, constructs a mound. It is striking that the invasion of the fresh waters of Australia by two unrelated types of silurids should both be represented by mound-building forms.

All the Bagrinae build nests consisting of excavations, so far as known, with the possible exception of *Macrones* which it has been suggested may carry them on the under surface. This suggestion, however, needs further study for confirmation.

The Astroblepidae cast their eggs free, and from their relationships would seem to have lost rather than never had a brooding habit.

The Callichthyidae have nesting and non-nesting members *viz.: Callichthys, Hoplosternum,* and *Corydoras.*

The Loricariidae have some members, at least, which carry their eggs in labial folds, Steindachner (1879), Gill (1907a), Ribeiro (1918), Ihering (1928) and Devincenzi (1933): *Loricaria vetula* C. & V. and *L. anus* C. &. V. The carrying of eggs under the large everted lips of these fish may again be associated with the presumably ancestral habit of lying on the eggs. The males alone engage in this habit and have the posterior portion of the everted lips appropriately enlarged.

Many of the Loricariidae have a marked amount of sexual dimorphism. The males in some genera have enlarged bristles; *e. g., Oxyloricaria, Farlowella, Ancistrus.* In others the males possess dendritic appendages on the head; *e. g., Xenocara.* See Regan (1904). The males of the naked Argiinae possess an elongate genital papilla. The function of these structures is not understood.

Ancistrus anisitsi Eigenmann and Kennedy, according to Carter and Beadle (1931), lays its eggs in holes in banks at the edges of swamps. The eggs "are glued together by a secretion." This rather suggests the ameiurid type of reproduction, but it is to be noted that the eggs must have a much lower oxygen requirement, since the waters in which they are found are notable for their low oxygen content. Furthermore, Carter and Beadle write of the eggs that "they were found to live well in dishes" which, as previously indicated, is not true of ameiurid eggs.

Comparison with Certain Cichlids.

A study of the development of oral incubation in the Cichlidae, based on similar but more extensive data, has already been published by Breder (1934a). This has been referred to in the preceding section in passing, but a close comparison of the nest building habits of the two groups forms the basis of further consideration. In Table IV the chief items are listed in parallel columns for comparison. A consideration of this table will show at once that while the general pattern is fairly similar, not a single item is identical, from the details of courtship and spawning to the care of resulting young. It forms a splendid illustration of how superficially similar characters of habit may on critical examination actually be shown to be composed of distinctly different elements. Oral incubation can clearly be traced back to both of these reproductive types, with both involved in taking their eggs in their mouths but for entirely different reasons. Except for this there is no direct physical contact between eggs and parents in the cichlids, and no other habit but oral incubation has been found to develop in that family. In the ameiurids there is additional and close contact with the ventral surface and the ventral fins. In this group has also developed species that carry the eggs adherent to the ventral surface, and those that employ the ventral fins as holding organs for fertilization. It is difficult to believe that all this is merely coincidental.

It should be borne in mind that in Table IV the species compared receive their sensory impression by rather different channels. *Aequidens* is primarily a visual type and entirely diurnal in its habits, whereas *Ameiurus* is chiefly a tactile chemico-sensory type and to a considerable extent nocturnal. At least the first, third and ninth items may have to do with the different role that light plays in the lives of these two species. The second, seventh and ninth items, at least, are associated with the major receptors in each case.

TABLE IV. COMPARISON OF THE REPRODUCTIVE HABITS OF *AMEIURUS* WITH THOSE OF THE CICHLID, *AEQUIDENS LATIFRONS*.[1]

	Ameiurus	*Aequidens*
1. Sex recognition	Tactile or chemical?	Differential behavior.
2. Spawning position	Pair head in opposite directions in close contact.	Pair usually with male following female, but never in contact.
3. Location of nest	In a cavity.	*Not* in a cavity.
4. Nature of eggs	Slightly adhesive, adhere in a mass.	Strongly adhesive, no eggs in contact.
5. Need of aeration	Necessary for respiration of the eggs.	Not essential for respiration of the eggs. A protection from silting and enemies only.
6. Roles of parents	Female does most of the incubating, while male guards (sometimes both incubate).	Male does most of the incubating, while the female guards (sometimes both incubate).
7. Incubating method	Chiefly the ventral fins by means of a vertical motion aided by the anal.	Chiefly the pectoral fins aided by the anal, or swimming motions of the whole body.
8. Eggs taken in mouth	For churning, to insure adequate aeration (and cleaning?).	For removal of hatching young to the "nursery" only.
9. Care of young	Kept in or close to nest, but for which there is no special construction.	Removed to a shallow hole especially prepared.

[1] The details of behavior of *Aequidens* are set forth by Breder (1934a).

SUMMARY.

Breeding Behavior.

1. *Ameiurus nebulosus* may spawn at least twice a season after a temperature of 21° C. has been reached.

2. A natural, sheltered hollow is cleaned out by both sexes for the reception of the eggs. In the absence of such, a hole may be dug in gravel. The gravel may be transported by the mouthful.

3. Spawning occurs within the nest cavity. So far as known the fishes face in opposite directions during spawning.

4. The eggs are constantly attended, lain upon by either or both parents, violently agitated, beaten with the ventral fins, or taken into the mouth and ejected violently.

5. The young fish are guarded in a more gentle manner. When they are able to swim freely they are still guarded for a considerable time.

The Eggs and Young.

6. The eggs are large, about 3 mm., adhesive and covered with a soft, gelatinous covering, somewhat resembling frog eggs.

7. They will not hatch away from their parents unless continually agitated, in a manner approximating the activities of the parents. The oxygen requirement would seem to be unusually high, and the gelatinous envelope may account for it, while at the same time protecting the embryo from mechanical injury due to the necessary rough handling.

8. The young fish have a large yolk and are cream white in color. After about 12 days they are able to swim up from the bottom and are heavily pigmented by that time.

9. The young fish move in a dense school, kept together almost entirely by visual stimuli.

10. The reproductive habits of *Opladelus* are strikingly similar to those of *Ameiurus.*

Inferences.

11. The oral gestation of the Ariidae appears to be foreshadowed in the breeding behavior of the Ameiuridae, since the latter have already established the use of their mouths for churning their eggs about.

12. Neither viviparity nor gastric incubation has been satisfactorily established for the Nematognathi, both being apparently based on erroneous interpretations.

13. The adhesion of eggs to the ventral surface of the Aspredinidae is suggested by the position frequently assumed by the Ameiuridae in incubation. If they were not so slippery the eggs would undoubtedly adhere to their stomachs as may be the case in *Macrones*. This would seem to be a first step, leading to the advanced condition with modified integument, as found in *Aspredo*.

14. The well coordinated activity of the ventral fins of *Ameiurus* and *Opladelus* in working over the eggs, suggests a starting point possibly culminating in habits of those forms, such as *Corydoras*, that use the same fins as an inseminating basket.

15. The specialized nematognaths, such as *Astroblepus*, *Otocinclus* and *Corydoras*, that deposit separate adhesive eggs, would seem to have passed through some breeding habit similar to that of *Ameiurus* rather than have escaped it entirely. Since the specialized musculature of the nematognath pelvic appendages is clearly used for reproductive purposes in such relatively primitive forms as *Ameiurus*, it would seem to be a point of origin for such now used, in the three genera mentioned, for a distinctly different purpose.

16. It thus becomes apparent that, starting with *Ameiurus*, a clue to all of the reproductive habits of the more advanced nematognaths may be found. Further knowledge of the details of habits as yet unknown are necessary before it will be possible to trace the full history of any single mode of reproduction.

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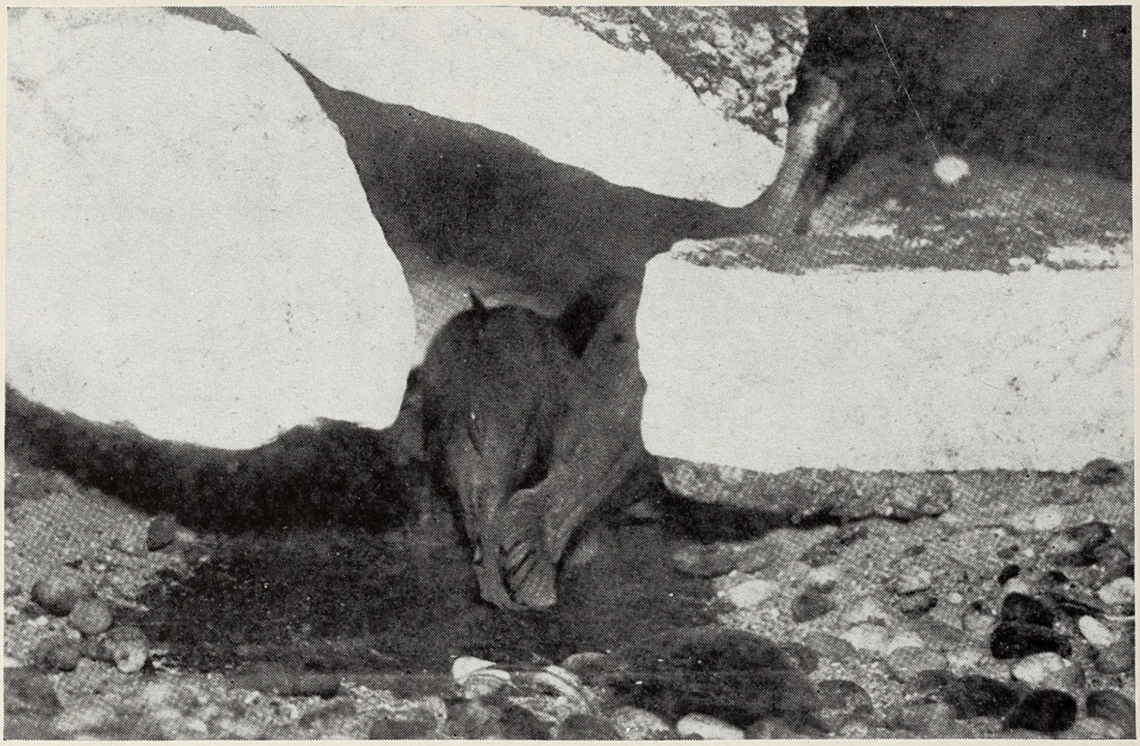


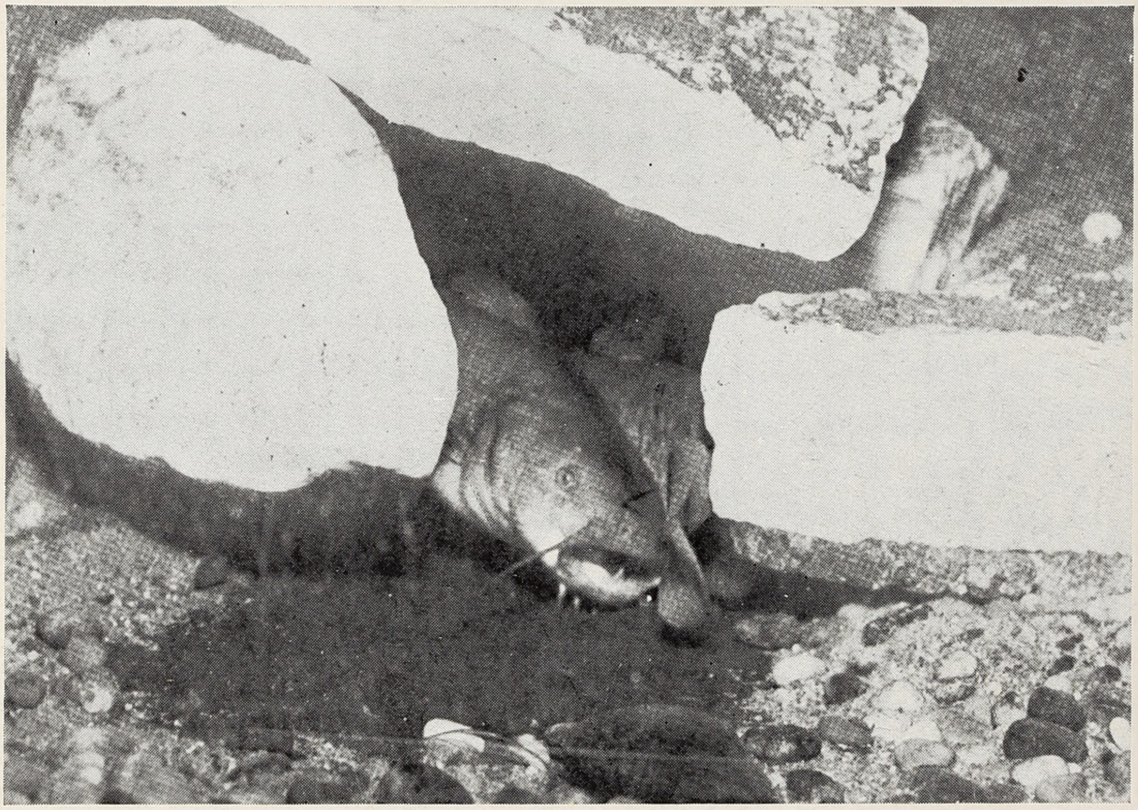
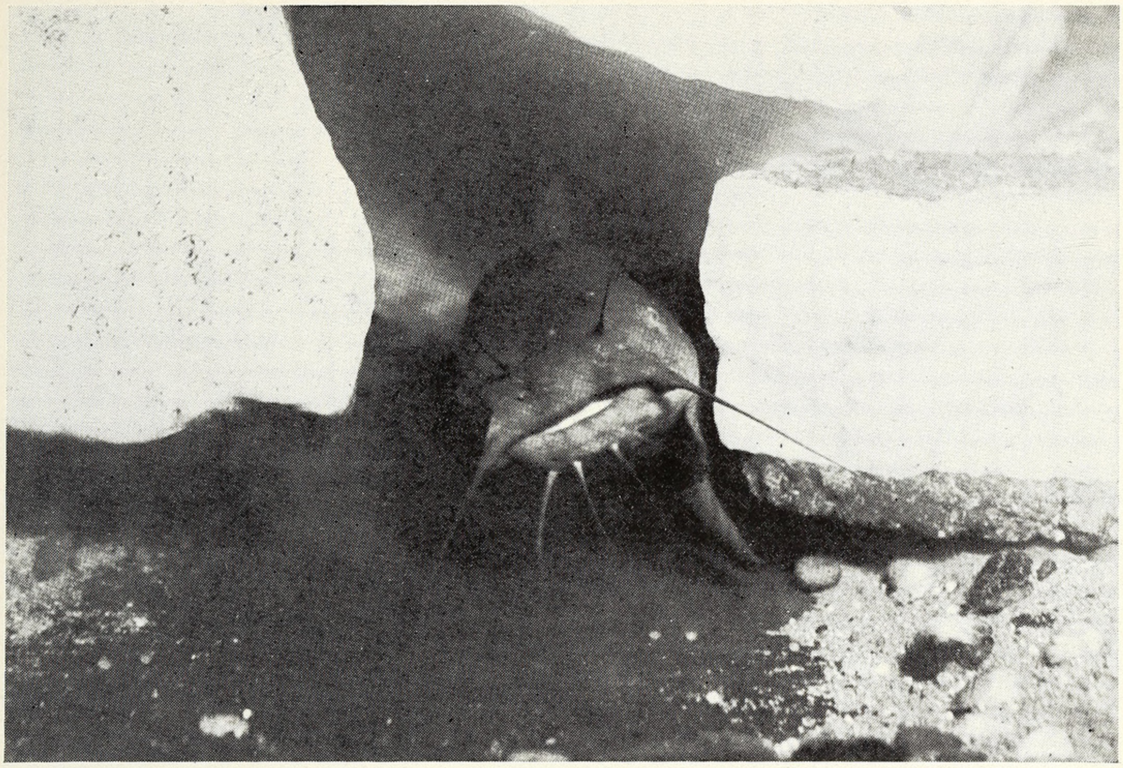


Fig. 12 (Upper). *Ameiurus nebulosus.* After a site for the nest is selected, the pair of catfishes spend much time resting quietly side by side with the tails pointing out. 1933.

Fig. 13 (Lower). As spawning becomes more imminent the fishes become active and circle continually in an agitated fashion. 1933.



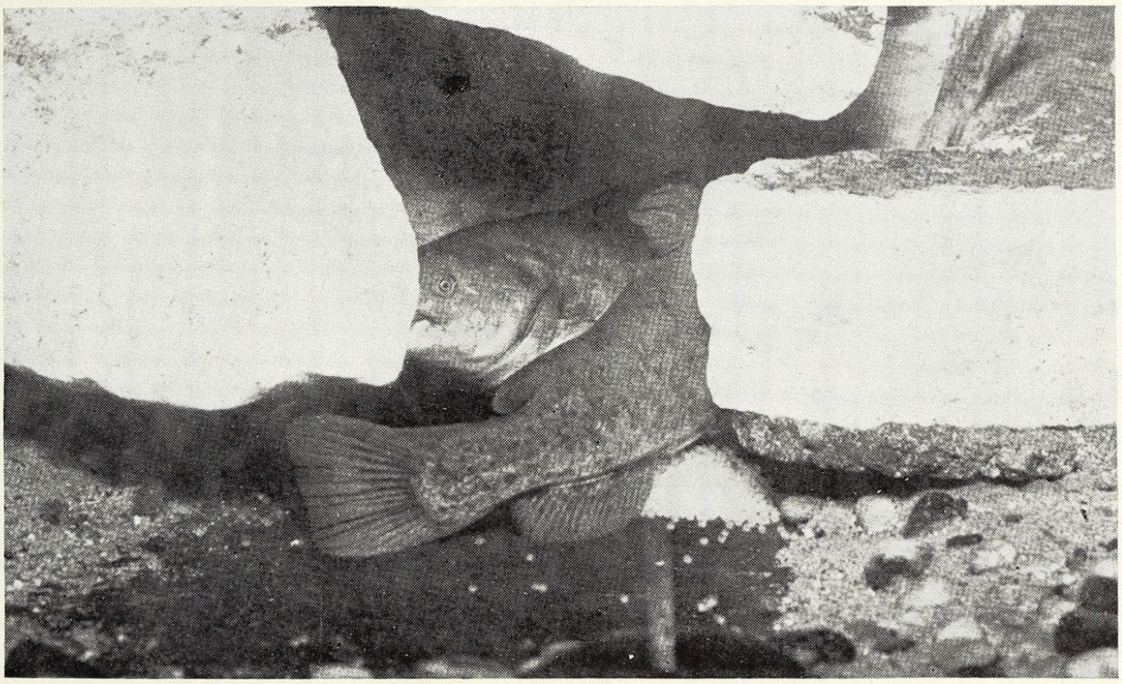
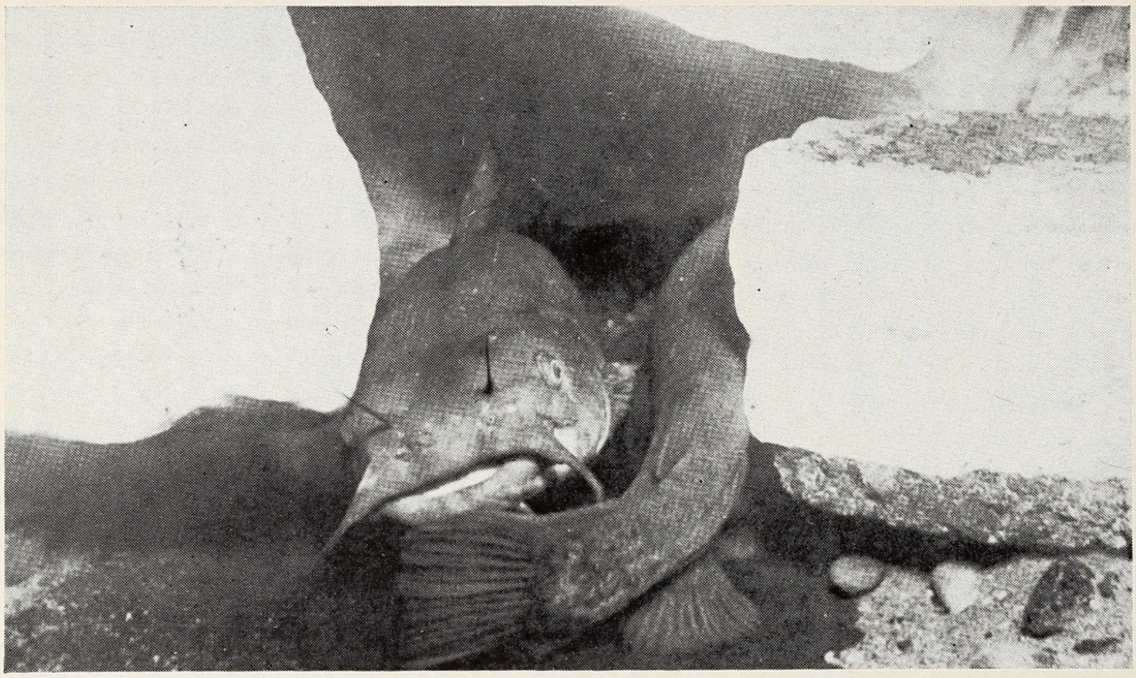


Fig. 14 (Upper). *Ameiurus nebulosus.* Just before spawning the circle that their two bodies form flattens so that the fish are in contact, head to tail. 1933.

Fig. 15 (Lower). At the moment of egg laying. The accumulating pile of large eggs may be seen under the female. Note that the head-to-tail position is retained. 1933.



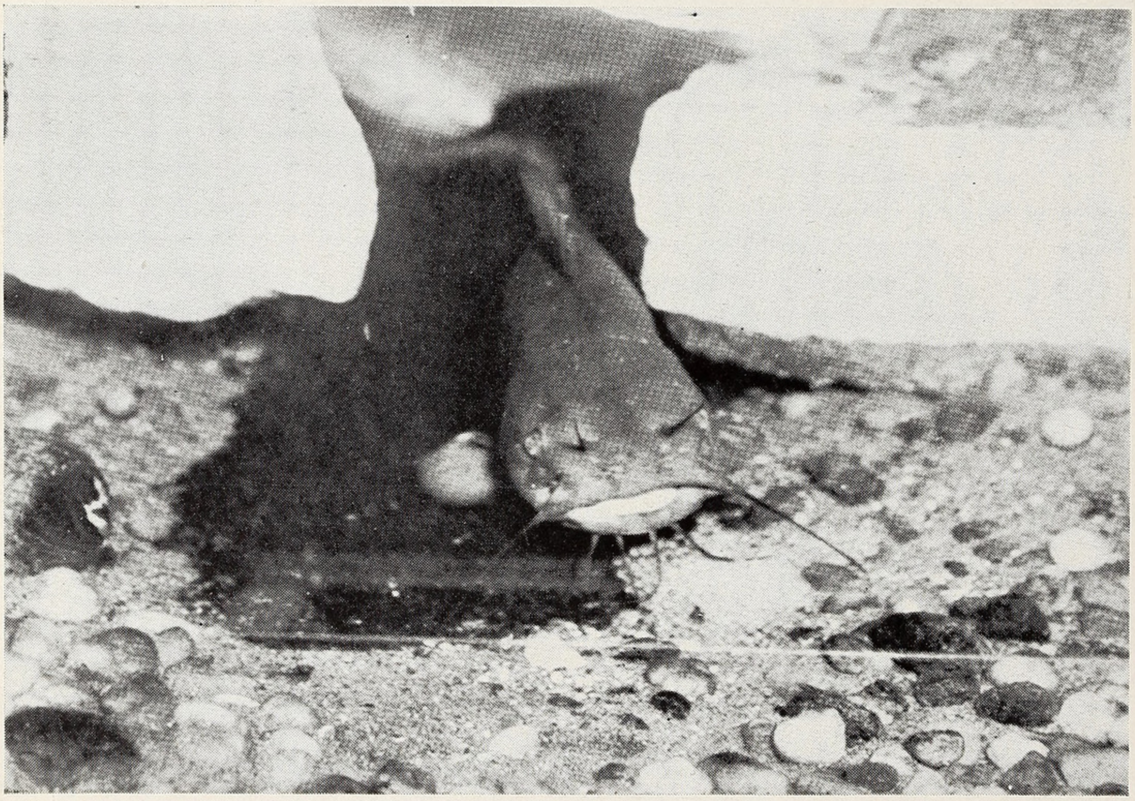
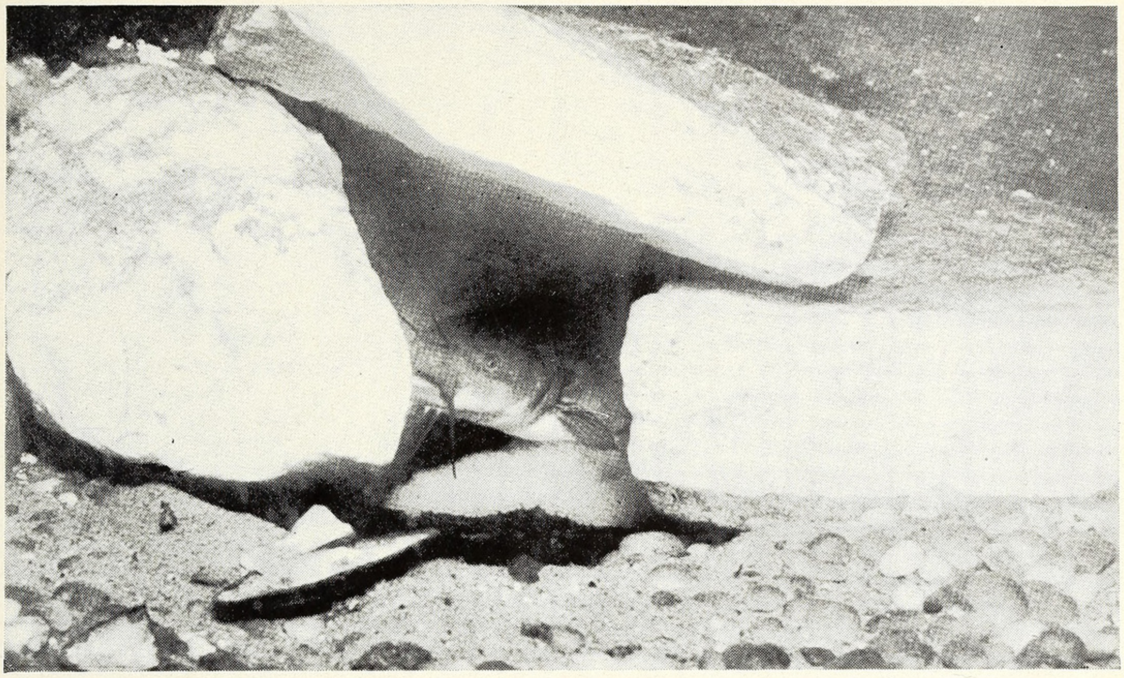


Fig. 16 (Upper). *Ameiurus nebulosus.* Immediately after spawning the fishes separate slightly and rest. In this photograph the ventral fins of the female entirely obscure the eggs. 1933.

Fig. 17 (Lower). Sometimes a clump of eggs is dislodged and knocked out of the nest. Here the female is feeling them with her barbels. 1933.



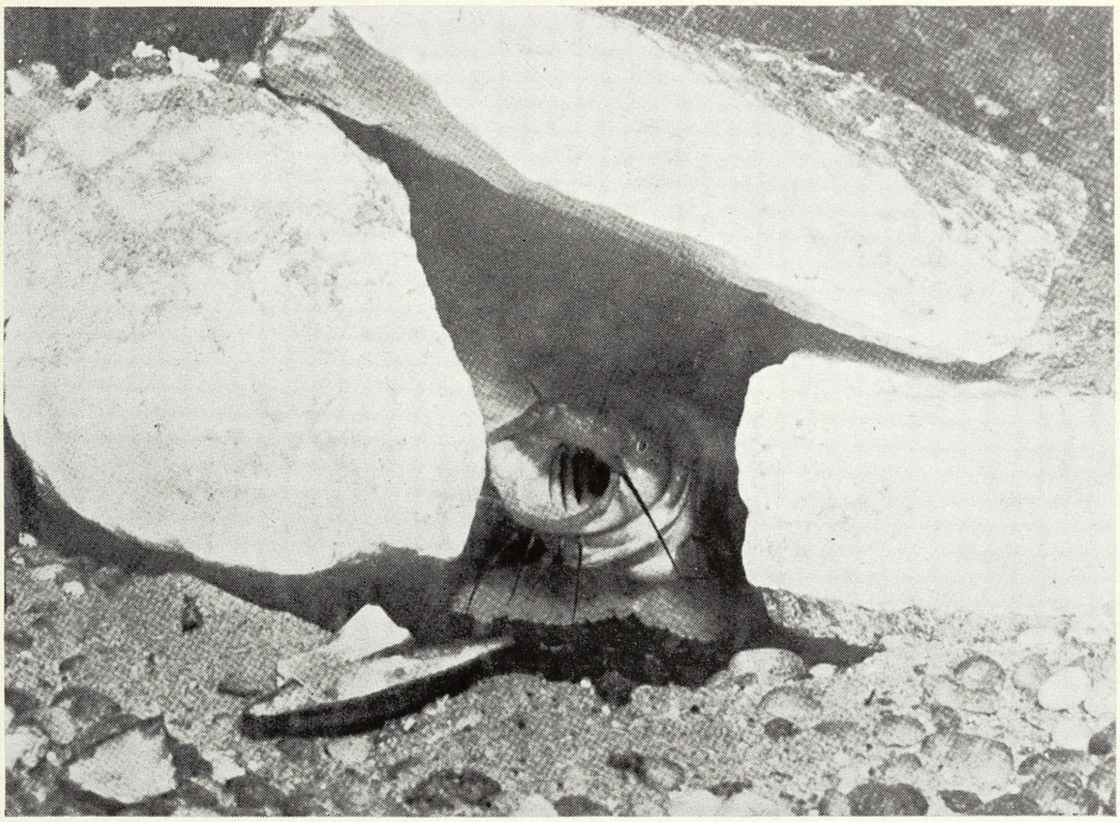
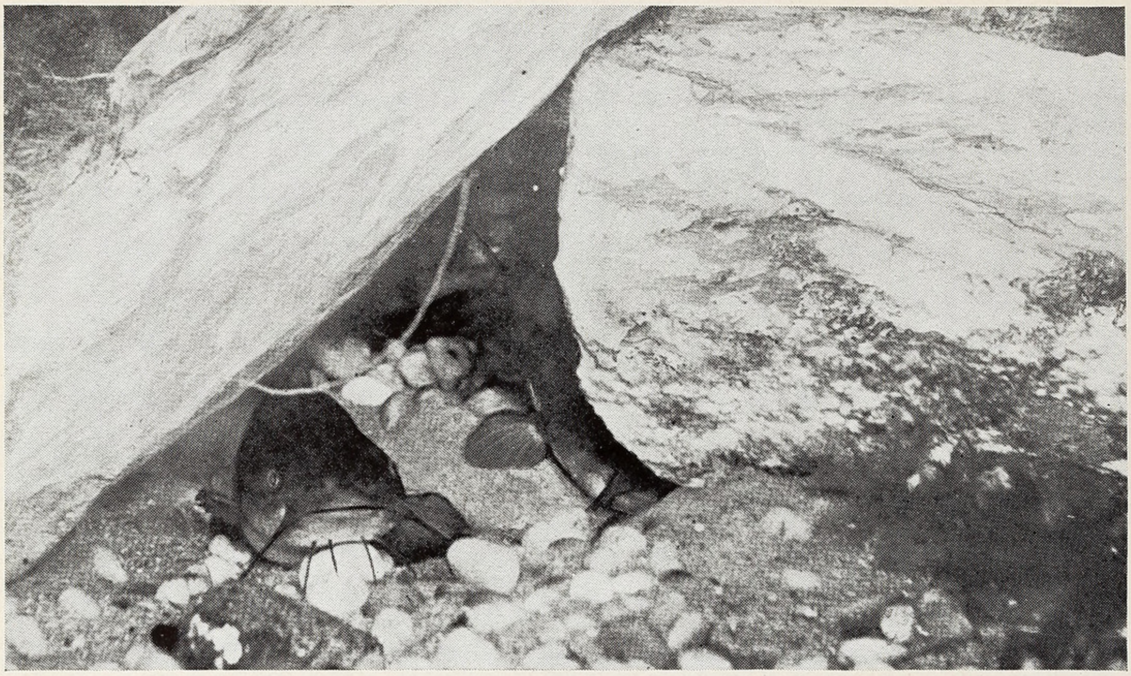


Fig. 18 (Upper). *Ameiurus nebulosus.* A typical pose of the female on her eggs. 1932.

Fig. 19 (Lower). The yawning of the brooding fish which is characteristic and may aid in aeration. 1932.



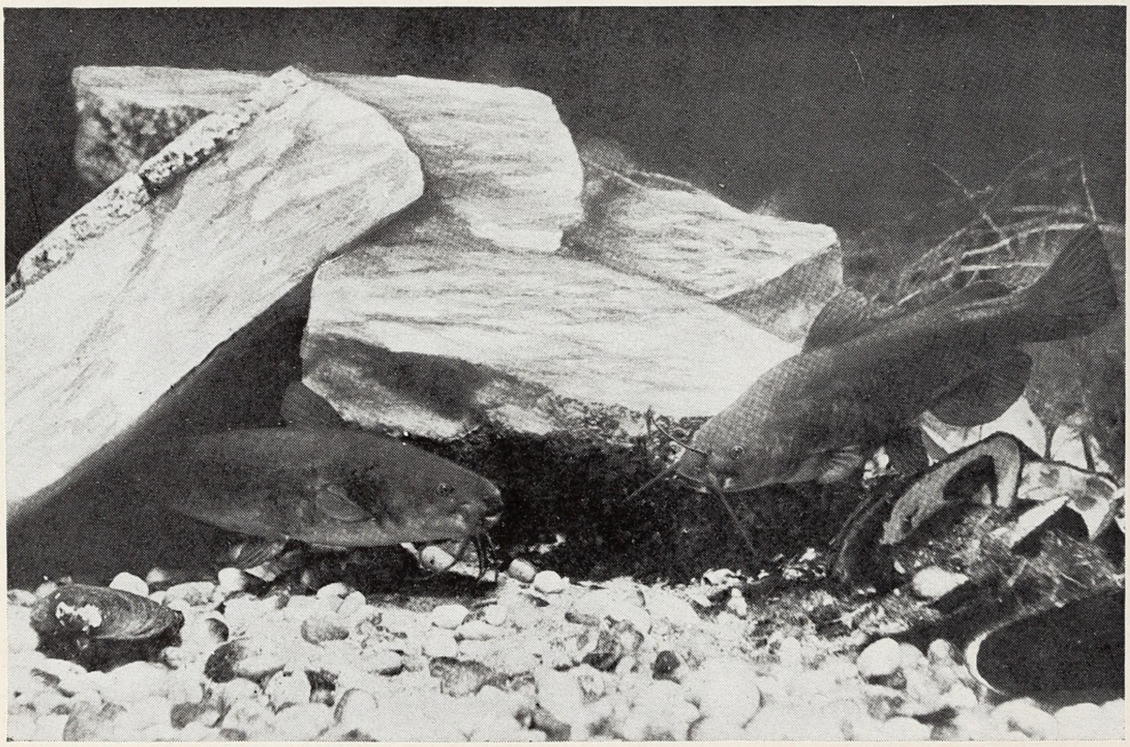
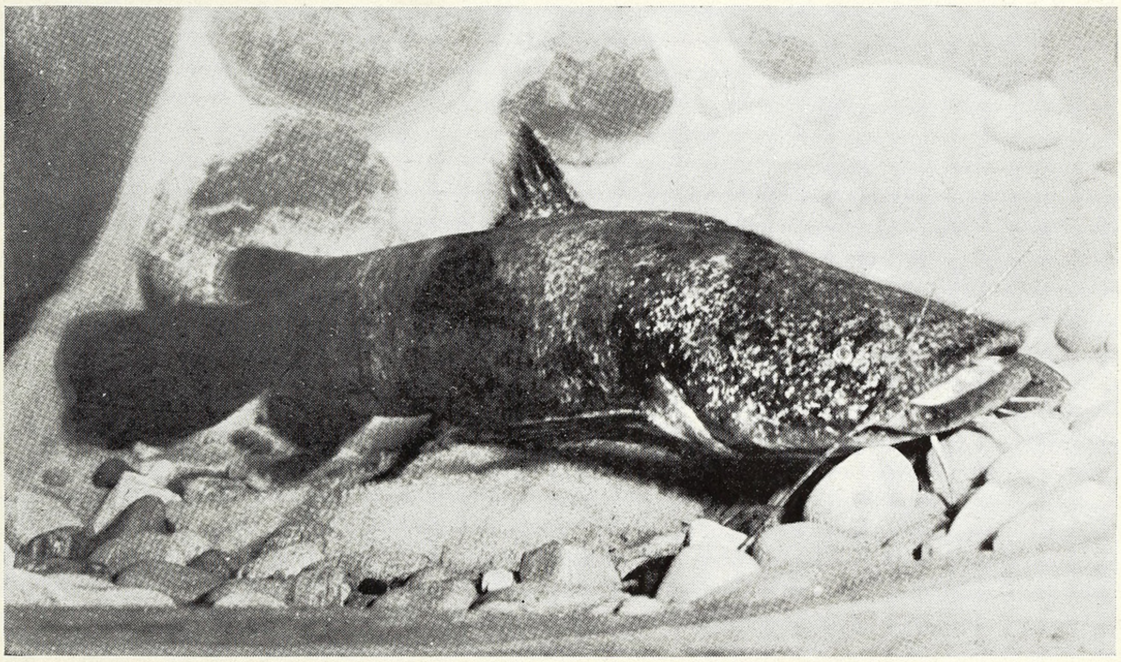


Fig. 20 (Upper). *Ameiurus nebulosus*. Both parents incubating at the same time. 1931.

Fig. 21 (Lower). Both parents "rounding up" the young fish, which may be seen as an oval black spot between them. 1931.



Figs. 22 and 23. *Opladelus olivaris*. Two typical postures of an incubating male. Note especially the application of the ventral fins to the egg mass.

These two photographs were taken at the John J. Shedd Aquarium in Chicago by Loren Tutell of the staff of that institution. The other photographs reproduced in this paper, of *Ameiurus nebulosus*, were taken at the New York Aquarium by S. C. Dunton of the Aquarium staff.