A SUMMARY OF THE LIFE HISTORY AND DISTRIBUTION OF THE SPRING CAVEFISH, Chologaster agassizi, PUTNAM, WITH POPULATION ESTIMATES FOR THE SPECIES IN SOUTHERN ILLINOIS

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The genus Chologaster, which means mutilated belly in reference to the absence of pelvic fins, was proposed by Agassiz (1853:134) for a new fish found in ditches and rice fields of South Carolina and described by him as C. cornutus. Putnam (1872:30) described a second species of the genus found in a well at Lebanon, Tennessee, naming it C. agassizi for the author of the generic name. Forbes (1881:232) reported one specimen of Chologaster from a spring in western Union County, Illinois, and noted that it differed from known specimens of the two described species but did not assign a specific name to the Illinois population. After acquiring additional specimens, Forbes (1882:1) described it on the basis of color differences as a new species, C. papilliferus. Jordan & Gilbert (1883:325, 890) recognized all three species and noted that the two spring cavefishes (agassizi and papilliferus) occurred in Tennessee, Kentucky, and southern Illinois. Jordan & Evermann (1927:503) believed the different way of life between the epigean C. cornutus and the hypogean (subterranean) C. papilliferus warranted erection of a new genus for the latter and proposed Forbesella, but Jordan (1929:68) noted that Forbesella was preoccupied and suggested Forbesichthys as a substitute name.

Woods & Inger (1957) revised all species in the family Amblyopsidae and synonymized C. papilliferus under the earlier C. agassizi, although they pointed out that minor differences were observed from population to population. Their arrangement has been generally followed by subsequent authors, including Hill (1969b) who studied the effects of isolation upon meristic characters. Only Clay (1975:240) has maintained that C. agassizi and C. papilliferus are specifically distinct. Rosen (1962) discussed in detail the anatomy of amblyopsid fishes (including Chologaster) and their relationships to other fish families but did not concern himself with the validity of the described species.

Except for some studies of eye structure by Eigenmann (summarized in Eigenmann 1909), the nonsystematic literature on the spring cavefish consists mostly of new locality records and brief incidental accounts of behavior, habitat, food, and size classes (Forbes & Richardson 1908, 1920; Layne & Thompson 1952; Gunning & Lewis 1955). Weise (1957) summarized the prior work on the species and described in detail the habitat, phototaxis, thigmotaxis, rheotaxis, temperature tolerance, invertebrate and vertebrate species associates, and sexual dimorphism in a life-history study of the species at Pine Hills in Union County, Illinois. Poulsen (1963) discussed various adaptations and comparative metabolic rates of all known amblyopsids. The next major contribution to our knowledge was a series of papers by Hill, who worked with the Warren County, Kentucky, population of spring cavefish and described oxygen preferences (1968), food and feeding habits (1969a), effects of isolation upon meristic characters (1969b), and the development of squamation in the young (1971). Whittaker & Hill (1968) described a new species of cestode parasite, naming it Proteocephalus chologasteri.

In the early 1970's, H. E. McReynolds of the U. S. Forest Service, became concerned about the status of the cave fish and described oxygen preferences (1968), food and feeding habits (1969a), effects of isolation upon meristic characters (1969b), and the development of squamation in the young (1971). Whittaker & Hill (1968) described a new species of cestode parasite, naming it Proteocephalus chologasteri.

ACKNOWLEDGMENTS

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low took the photographs. Assistant Technical Editor Shirley McClellan edited the manuscript, and John E. Cooper of the North Carolina Museum of Natural History served as guest reviewer. Larry M. Page and Brooks M. Burr kindly copied records of spring cavefish in several museum collections that they visited, and officials in charge of these collections made their holdings freely available. David H. Snyder of Austin Peay University (Tennessee) advised us of several collections. The collections include the Illinois Natural History Survey (INHS), Eastern Kentucky University (EKU), Kentucky Fish and Wildlife Department (KFW), Murray State University (MSU), University of Michigan Museum of Zoology (UMMZ), U.S. National Museum of Natural History (USNM), University of Louisville (UL), University of Oklahoma (OU), University of Tennessee (UT), University of Tulsa (UTULSAC), University of Alabama (UA), and Northeastern Louisiana University (NLU). Jeffrey J. Webb of Anna, Illinois, supplied a population estimate for Cave Spring Cave, and Claude D. Baker of the University of Illinois Dixon Springs Agricultural Station performed some water chemistry analyses for us. Finally, the Illinois Department of Conservation Division of Fisheries granted permission to collect specimens for these studies.

HABITAT AND BEHAVIOR

The spring cavefish (Fig. 1) bridges the gap between an epigean and hypogean existence. It is known to occur in caves throughout most of its range, but it is much better known from springs, spring runs, and spring seeps (Fig. 2–4). It is subterranean, emerging at dusk and usually retreating underground an hour or two before dawn. It has eyes that appear functional but serve only to distinguish light and darkness (Hill 1969a). In southern Illinois its appearance above ground is strongly correlated with the amount of flow emerging from the springs and with the season. During dry seasons, some springs have no flow; others continue to flow but have only a few spring cavefish or none at all. Fish were found throughout the year in the LaRue-Pine Hills Ecological Area, but in fewer numbers in January, February, and March, and no gravid females were seen from January through May.

Fish from different springs were marked with various colors of tattoo ink so that when recaptured they could be identified with the spring in which they were initially found. The color coding was done deliberately to see if there was any mixing or exchange underground of individuals from adjacent springs. None was observed.

In tiles where spring water collected to form pools,
fish were usually not visible during daylight hours, and at night they usually disappeared into crevices and holes when the water was disturbed or when a strong light was directed at the fish. During the day, fish could be found in spring runs by turning over rocks, but they quickly buried in gravel interstices and under other stones when uncovered. Many of the localities from which the species has been found were discovered accidentally by collectors making minnow-seine sets in spring-fed headwaters and seeps.

The species also has been taken frequently over the years in the swamp at the base of the bluffs in the LaRue-Pine Hills Ecological Area, especially during the winter months. It was believed that the swamp has springs which feed it well away from the bluffs (this is a possibility), and that the cold water in the swamp during the winter permitted the survival of the fish for longer periods of time. It is now known that the greater frequency of fish in the swamp in winter is due in part to the greater output of all springs during that season, and some fish are unable to find their way back into the spring mouth for one reason or another as will be discussed subsequently. Moreover, Weise (1957:198) found that the species has evolved a remarkable ability to tolerate without acclimation a wide temperature range, and he believed this is an important adaptation for an animal frequently swept into surface waters of relatively high temperatures.

The well-developed negative phototaxis noted above is overshadowed by a strong thigmotaxis. Weise (1957:197) found that in the absence of other forms of concealment the fish would float at the surface with the tops of their heads in contact with floating corks, and that if only lighted places of concealment were present they would utilize them in order to have some kind of body contact. If no objects were in the tank, the fish would seek the darkest corners. Hill (1969a:111) found that laboratory fish were attracted to objects introduced into the tanks and that cotton swabs or even strands of wire or sticks were seized by the fish but rejected if not edible.

Fig. 3.—Big Spring in LaRue-Pine Hills Ecological Area, Union County, Illinois. Spring cavefish can usually be seen here, but quantitative sampling would have been impossible without destroying the character of the large spring pool. The surface is covered with duckweed.

The fish depend upon taste rather than sight or olfaction to determine edibility. The fish relies on the many neuromasts on the head (Fig. 5) to locate food objects

Fig. 4.—Ceramic tile at spring mouth in Union County, Illinois. When the water table is high, numerous spring cavefish can be seen at night in the tile.

The fish depend upon taste rather than sight or olfaction to determine edibility. The fish relies on the many neuromasts on the head (Fig. 5) to locate food objects

Fig. 5.—Head of spring cavefish, showing the clusters of neuromasts.

(Hill 1969a:111). Agitation of the water frightened the fish and they would dash about seeking concealment.

REPRODUCTION

Despite a careful search by Weise (1957) and Hill (1971), the details of reproduction in the spring cavefish remain almost unknown. Weise even attempted, but without success, stripping eggs and sperm from ripe adults into finger bowls. Our own efforts were equally unrewarding. Weise (1957:199) noted that external sexual characters were lacking, but that the fish could be sexed because the testes or ovaries could be seen through the nearly transparent body wall. We (Welch) found that
gravid females were easily recognized in the fall because the large eggs were evident through the body wall, and that live fish without eggs inside them were difficult to sex with any certainty because the centrally located gonads were not that clearly visible.

Although some fish can be found at any season when the springs are flowing, and occasional gravid females could be found “practically every month of the year” in nature (Weise 1957:200), the evidence suggests that most fish ready for spawning disappear in late winter, presumably going underground to spawn. Captive individuals held by Weise were unable to go underground and were in ripe condition from September to March. They refused to spawn in a simulated cave habitat in ice-cooled tanks or to exhibit any prespawning behavior. A 36.8-mm (standard length) female with eggs was found in June by us (Welch), and it is assumed that it had failed to go underground and would likely soon resorb its eggs. Hill (1971:13–14) found cave specimens barely over 4 mm in total length in mid-February and noted that the first fry appear above ground while the breeding adults are still underground.

Weise (1957:199) found that in five females over 43 mm (total length) the ripe ovaries contained 80, 95, 101, 202, and 285 eggs and that eggs averaged 0.25 mm in diameter in September but 1.5–2.0 mm at near maturity. Our own observations suggest that spawning probably takes place underground between January and April because this is the period when part of the population in the springs disappears.

Hill (1971:13–14) studied development of squamation and pigmentation and found that scale primordia first appear (on the sides of the caudal peduncle and a short distance forward in the lateral-line area) at approximately 6 weeks of age and that squamation and pattern are well developed by 11 or 12 weeks of age.

Growth in our recaptures was erratic and inconsistent, varying with the spring in which the fish were found. Some showed almost no growth during summer and fall, but in general the overall growth was estimated to be 10–20 mm per year. Most authors have assumed 3-year classes; young of the year, 1+ year old, and 2+ year old fish, and probably most individuals do not live more than 3 years. However, occasionally an individual is found that is strikingly larger than the average adult, and it is possible that a few live 3 years and attain standard lengths of more than 70 mm. The fish appeared to be sexually mature in their second year. The details of spawning are wholly unknown and, while some investigators suspect that the adult may carry eggs in its mouth as does the related Amblyopsis spelaea, they have avoided making the statement in the absence of evidence except for the anterior location of the genital pore.

FOOD HABITS

The spring cavefish in Union County, Illinois, feed almost exclusively on Gammarus according to Forbes & Richardson (1908:219), Layne & Thompson (1952:39), Weise (1957:198), and Gunning & Lewis (1955:556). Weise (1957) identified the species as G. troglophilus Hubricht & Mackin, an amphipod that is not known to occur at spring cavefish localities other than in south-western Illinois. Other items found in stomachs included insect remnants and detritus (Gunning & Lewis 1955) and one Asellus (Weise 1957), but Weise found that captive fish refused Asellus as well as everything but Gammarus.

In Kentucky the food habits are quite different, Hill (1969a), who examined nearly 4,000 specimens, compared stomach contents of surface-dwelling fish with those from within caves. He found that surface fish take mostly chironomids but also small numbers of copepods, oligochaetes, nematodes, and ostracods, whereas adult and half-grown fish from caves feed almost solely on other spring cavefish. The cannibalism thus provides a source of food supply in an environment where food is extremely limited, but a large proportion of the young in caves contained no food at all or at best small numbers of nematodes and copepods. Conceivably small fish may be forced to seek an epigean food source and thus be more frequently encountered in springs than in underground streams.

DISTRIBUTION

The spring cavefish occurs from south-central Tennessee (near the Alabama state line) northward into central and western Kentucky, and westward across the Shawnee Hills of southern Illinois to Scott County, Missouri (Fig. 6). Its range was long believed to be disjunct, consisting of Illinois, Kentucky, and Tennessee populations, but recent collections from geographically intermediate areas suggest that it is more likely continuous. The counties from which it is known and the documentation for the distributional data are tabulated below, although no attempt has been made to canvas all museum collections for their holdings of the spring cavefish. Weise (1957:196) attempted to introduce 36 individuals in a cold-water cave spring in Adams County, Illinois, nearly 200 miles northward. None was ever seen again and they were presumably washed out into the open.

Missouri

Scott County: 1 spring (Pflieger 1975:224 and personal communication)

Illinois

Jackson County: 1 spring (sight record, Welch)
Johnston County: 1 spring (INHS)
Hardin County: 2 springs (INHS), 1 cave (sight record, Webb)
Pope County: 1 cave (Forbes & Richardson 1908:219)
Union County: 1 cave, many springs (numerous museum collections)

Kentucky

Edmonson County: Mammoth Cave (Clay 1975:241), 2 springs (Woods & Inger 1957:240)
Livingston County: 2 springs (INHS)
Logan County: 2 springs (EKU)
Lyon County: 2 springs (KFW)
Todd County: 1 spring (INHS)
Trigg County: 2 springs (MSU)
Warren County: 1 cave (Hill 1971:13) and 7 springs (UMMZ), (UL)
Fig. 6.—Known distribution of the spring cavefish. Sometimes a symbol represents several different springs containing the species.

Tennessee

- Bedford County: 1 spring (UT)
- Coffee County: ? springs (UA), (UT), (UO), (UTULSAC)
- Davidson County: 2 springs (USNM)
- Dickson County: 1 cave (UMMZ)
- Franklin County: 1 spring (UA)
- Montgomery County: ? springs (UT), (NLU), (INHS)
- Stewart County: 4 springs (MSU), (UMMZ), (NLU), (INHS)
- Wilson County: 1 well (Putnam 1872:22, type-locality)

**POPULATION ESTIMATES**

Throughout most of its range the spring cavefish is rare to uncommon and easily overlooked because of its nocturnal and secretive habits. An exception is a large spring at Rich Pond near Bowling Green, Warren County, Kentucky, where it appears to be incredibly abundant. Many museum collections have specimens from this spring (one major museum has a series of more than 1,000 specimens), and staff and students at the University of Louisville and elsewhere have collected hundreds of specimens of the species at this locality.

Elsewhere in Kentucky and Tennessee, the species is erratic in distribution and represented by a few individuals to small series. In Missouri, it has recently been discovered by Eugene McDonald (Pflieger 1975:224), and it is almost certain that the Department of Conservation in that state will soon place the species on the list of protected species.

The species is well known from the LaRue-Pine Hills Area in southwestern Illinois, and many museum collections have holdings of a few specimens from that locality. In fact, it was the heavy collecting pressure that precipitated the concern over the status of the population and its chances for survival. The spring cavefish was known to occur in five different springs along the bluff, where it was generally quite vulnerable to dipnetting, as well as in the adjacent swamp. Outside the Ecological Area it was known from Cave Spring Cave, a cave in Pope County, and from springs near McClure on the Union-Alexander County line. A search for additional springs that might harbor the fish was begun and resulted in the discovery of three more springs that contained fish within the Ecological Area, one in adjacent Jackson County, one in Johnson County, and two springs and a cave in Hardin County.

A total of 180 fish from 10 springs in Union County was dipnetted and marked in 1973, and recaptures were made in 7 of the springs. Marking was accomplished by means of an injection technique utilizing different colors of printer's numbering ink. Fish were marked distinctively so that it would be known if they had emerged from a spring other than where initially found. Before
the fish were marked, they were anesthetized with 0.05 percent solution of MS222. Standard length was measured with a dial caliper. The fish were placed on a wet towel and marked by an injection at a combination of specific points along the back. The needle was inserted under the skin about 3 mm anteriad and the dot of ink placed in the subcutaneous fascia with care being taken to avoid muscle damage. A glass tuberculin syringe with a No. 23 or 25G needle was used. After marking, the fish were placed in a bowl of water and allowed to recover swimming ability before being returned to the spring. No ill effects of the marking were noted.

The marking technique was developed by Slack (1955) and has been variously modified by other workers, especially at Indiana University, for studies on crayfishes (Cooper & Cooper 1976:32 and in preparation). It consisted of using red and blue Bates and green and purple Carter’s numbering machine inks injected underneath the sternites and zinc white artists’ oil color to lighten colors as needed. Vegetable oil (Wesson) thinned the color to a consistency that would easily pass through the syringe needle. The method had been used previously by one of us (Welch) with good success on Amblyopis speleae. No marked fish showed any sign of infection and, although the colors faded after a period of several months, the marks remained unless blotted. The fish were placed in a bowl of water and allowed to return to the spring. Still no ill effects of the marking were noted.

A summary of the marking is presented for what it is worth. No ill effects of the marking were noted. Spring No. 7 is excluded from the total in Table 1 because many fish are stranded in the tile near the spring mouth and were recaptured more often than if they could have freely returned underground. Thus, the estimate for that spring may be based on stranded fish only.

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**Table 1.** Summary of mark-recapture data for eight springs in western Union County and Cave Springs Cave. Many of the standard errors are quite large because of the relatively small numbers used in the calculations.

<table>
<thead>
<tr>
<th>Spring</th>
<th>T = No. Fish Marked</th>
<th>Average N ± 1 S.E.</th>
<th>Percent Recaptured</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>1</td>
<td>15</td>
<td>63 ± 28</td>
<td>33</td>
</tr>
<tr>
<td>2</td>
<td>31</td>
<td>180 ± 123</td>
<td>30</td>
</tr>
<tr>
<td>3</td>
<td>46</td>
<td>302 ± 201</td>
<td>35</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>18 ± 16</td>
<td>29</td>
</tr>
<tr>
<td>6</td>
<td>12</td>
<td>250 ± 339</td>
<td>8</td>
</tr>
<tr>
<td>7*</td>
<td>56</td>
<td>75 ± 6</td>
<td>86</td>
</tr>
<tr>
<td>8</td>
<td>12</td>
<td>96 ± 180</td>
<td>17</td>
</tr>
</tbody>
</table>

**Overall, excluding No. 7 124**

785 ± 314 27

**Cave Springs Cave**

? 35-45 ± ?

*Extenuating circumstances because of physical nature of spring. See text for explanation.

b Estimate provided by Jeffrey J. Webb of Anna, Illinois.

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**CONSERVATION STATUS ON THE SHAWNEE NATIONAL FOREST**

In 1969 at the suggestion of one of us (Smith), the Illinois Department of Conservation nominated the spring cavefish and four other Illinois fish species as candidates for the list of protected species, and the Illinois General Assembly passed a bill affording some degree of protection from over collecting. It has since been so noted in the Illinois Fish Code. The U.S. Forest Service also placed the cavefish on the list of species that may not be taken in the Shawnee National Forest. The Illinois Fish Code. The U.S. Forest Service also placed the cavefish on the list of species that may not be taken in the Shawnee National Forest when the LaRue-Pine Hills Recreational Area was reclassified as an Ecological Area. Since that time, however, the species has been found in several new localities, including three southern Illinois counties, and thus does not appear to be in imminent danger of extinction in Illinois.

Nevertheless, in Union County the species is quite vulnerable to dipnetting at night by collectors, and a gene pool that may consist of fewer than a thousand individ-
uals should be watched carefully. The restrictions on taking specimens there by both the state and Forest Service are worth retaining. Even though the population is undoubtedly larger than the above estimates indicate (the largest spring in the Ecological Area could not be censused), it is still quite small compared to those of other badly decimated species.

In the highly unusual population at Rich Pond in Kentucky, natural predation on the species is seasonably heavy (J. E. Cooper, personal communication). Elsewhere in the range of the spring cavefish, it is likely slight because of its habits and habitat. Such is not surprising for a species living in a rather trophically deprived environment. Its numbers seem to be tightly regulated by the available food supply. Gunning & Lewis (1955:554) found that 2 of 30 central mudminnows, Umbra limi, examined at Pine Hills contained cavefish. In Illinois the spring cavefish is not known to be cannibalistic, but a few other fishes, water snakes, and aquatic birds and mammals may catch occasional cavefish. Several fish had small leeches (species not determined) attached to them, and mention has already been made of an endemic tapeworm parasite. Dr. George Garoian, parasitologist at Southern Illinois University, found that 71 percent of the fish he examined in the springs were parasitized by tapeworms and "other internal parasites" (personal communication to Welch).

The Ecological Area receives rigorous protection from the Forest Service, and there is now little danger of the springs and spring runs being physically destroyed. The Forest Service has been urged by us to cap the tiles with hinged lids of metal grating to further discourage the taking of fish by human collectors and natural predators.

Most of the springs tested in 1973 by us (Welch), through the courtesy of Dr. C. D. Baker at the University of Illinois Dixon Springs Agricultural Station, were relatively free of pollution, but two had elevated readings for ammonia and phosphate. These substances probably got into the groundwater from animal wastes and commercial fertilizers, and they pose some threat. Another potential threat is a periodically discussed reservoir on Clear Creek on the Mississippi River floodplain. The effects of such an impoundment could be disastrous to the cavefish population if the spring mouths were inundated by backflooding or if groundwater flows were disrupted and low-quality water recharge occurred.

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