Nontroglobitic Fishes in Caves: Their Abnormalities, Ecological Classification and Importance

WILLIAM J. POLY

Department of Zoology, Southern Illinois University, Carbondale 62901

AND

CHARLES E. BOUCHER

Ohio Environmental Protection Agency, 1685 Westbelt Drive, Columbus 43228

ABSTRACT.—A total of 190 individuals representing 14 fish species were discovered from surveys of four West Virginia caves. Cottus carolinae ssp. and Lepomis macrochirus were captured in Buckeye Creek Cave, while Semotilus atromaculatus, L. cyanellus, Oncorhynchus mykiss, Rhinichthys atratulus and Ambloplites rupestris were collected from Bruffey-Hills Creek Cave. Seven species were captured in Piercys Cave, including two species, Notropis photogenis and N. volucellus, never before recorded from caves. Six species, Cottus bairdi, Catostomus commersoni, Salvelinus fontinalis, A. rupestris, R. atratulus and S. atromaculatus were captured in Piercys Mill Cave. Many of the S. atromaculatus were depigmented upon initial inspection; however, exposure to light often returned normal coloration. Nontroglobitic fishes inhabiting caves are known to exhibit abnormalities such as depigmentation, skeletal deformities or reduced eye size. Little attention has been given to documenting occurrences of nontroglobitic fishes in caves, and most occurrences have been considered accidental. Correct classification of many populations is difficult since categories in the current system do not accommodate them adequately. Some fish occurrences may more accurately fit the trogloxene category, although, each case must be examined independently. The possible effects of cavernicolous, nontroglobitic fishes on other cave-dwelling organisms, especially endangered troglobites, rarely has been considered and should be studied.

INTRODUCTION

Although West Virginia has an extensive number of caves (3400 +) (R. Garton, pers. comm.), faunal investigations have been conducted in only a small number ($\approx 7\%$), resulting in a limited, but useful knowledge of the invertebrates and vertebrates in West Virginia caves (Holsinger et al., 1976; Williams and Howell, 1979; Garton et al., 1993). Only a few of the past investigators paid more than casual attention to fishes encountered in West Virginia caves. Holsinger et al.'s (1976) discussion of past explorations of West Virginia caves was devoted mainly to invertebrates. Reese (1933, 1934) collected fish specimens on his surveys, although only one museum record was found (UMMZ 64490, R. Bailey, pers. comm.). F. J. Schwartz (pers. comm.) conducted cave surveys while at West Virginia University and found fishes in only one cave, Sinks of Gandy, from which vouchers were taken. Hocutt et al. (1978) briefly discussed the karst region of the Greenbrier valley which includes the caves investigated herein. Hocutt et al. (1978:74) noted the lack of troglobitic fishes in West Virginia and mentioned that the karst area near Lewisburg was being investigated for such occurrences; however, no cave studies were undertaken (J. Stauffer, Jr., pers. comm.). Williams and Howell (1979) examined a unique, apparently albino sculpin from Buckeye Creek Cave. Garton et al. (1993) summarized some of the known occurrences of fishes in West Virginia caves; however, most of the fish sightings lack species identification and voucher documentation. The paucity of data for fishes in West Virginia caves and the possibility that unknown species occur in the caves prompted this investigation. The abundance, diversity and frequency of fishes encountered in West Virginia caves together with other records of nontroglobitic fishes in caves compelled us to question (1) the potential impacts of nontroglobitic fishes on cave organisms and communities and (2) the terminology applied to nontroglobitic fishes. Depigmentation and other abnormalities associated with living in darkness are also discussed since we, as well as other investigators, have observed such abnormalities in cavernicolous, nontroglobitic fishes.

MATERIALS AND METHODS

Surveys were conducted in four caves: Buckeye Creek Cave (BCC), Piercys Cave (PC), and Piercys Mill Cave (PMC) in Greenbrier County and Bruffey-Hills Creek Cave (BHCC) in Randolph County. The invertebrate and vertebrate cave faunas of BCC and PC have been documented (Holsinger *et al.*, 1976; Garton *et al.*, 1993; Poly and Noggle, 1996). The vertebrate fauna of BHCC has been reported, but the invertebrate fauna has not been examined thoroughly as reported by Holsinger *et al.* (1976:81). BCC has been completely mapped, and the stream level passage is 1767 m from the BCC entrance to the Spencer Cave entrance (outlet to Spring Creek); there are numerous other passages and small tributaries in this cave¹ (Dasher and Balfour, 1994). BHCC has also been mapped and contains 2156 m of surveyed passages (Storrick, 1992).

Fish surveys were conducted 3 September 1994 in BCC, 22 October 1994 in BCC and BHCC, 29 September 1995 in PC, 30 September 1995 in BHCC and 1 October 1995 in PMC. Fishes were collected with either small dipnets, a seine, or a battery-powered backpack electrofishing unit. Distance sampled and distance of capture or observation were measured to 0.1 m with a hip chain. Voucher specimens were preserved in 10% formalin and deposited in the Southern Illinois University at Carbondale Fish Collection (SIUC) and the Ohio State University Museum of Biological Diversity Fish Collection (OSUM). Fish nomenclature follows Robins *et al.* (1991).

RESULTS

The assortment of substrates within BCC is typical of a small stream and consists of gravel, mud, detritus, bedrock, cobble and boulder. Woody debris was sparse and scattered except in a few areas where small logiams were located. Stream channel development consisted of pools, runs, and shallow riffles. The total distance sampled was 850.0 m on 3 September 1994 and ≈200 m on 22 October 1994. Two species, Cottus carolinae (Gill) ssp. (Kanawha sculpin in Jenkins and Burkhead, 1994) and bluegill, Lepomis macrochirus Rafinesque, were captured (Table 1). Cottus carolinae ssp. has been collected previously from BCC (Williams and Howell, 1979). Additional information on BCC and the surrounding area can be found in Dasher and Balfour (1994). The stream in PC was dominated by sand substrate with minor amounts of silt and small gravel. The total distance surveyed was 414.2 m. Seven species were captured, and all are new records for this cave (Table 1). Notropis photogenis (Cope) and N. volucellus (Cope) have never been reported from a cave. The Semotilus atromaculatus (Mitchill) was somewhat depigmented even after exposure to light and preservation. One Pimephales notatus (Rafinesque) (65.4 mm SL) was fully tuberculate, which is unusual since this species breeds in late spring to late summer. In Virginia, Jenkins and Burkhead (1994) reported tuberculate males only in May and June. The stream substrate in PMC was composed of sand, gravel, cobbles and boulders. The total distance sampled was 299.1 m. Six species were captured, and all are new records for this cave (Table 1). The habitat of BHCC was similar to that of BCC, but differed in having more woody debris. In 1994, a distance of 479.0 m was sampled from the entrance of Bruffey Creek Cave to its junction with Hills Creek Cave and continuing by way of the North fork of Hills Creek Cave

TABLE 1	-Fish species, number ol	sserved or collected and distance of capture or observation in four	West Virginia	caves
Cave	Date	Species (size range, catalog number)	Number	Distance in cave§
BCC	3 Sept. 1994*	Cottus carolinae ssp. (21–87 mm, OSUM 77872)	16†	2.4 (1), 16.0 (2), 30.0 (1),
	æ			39.0(2), 47.0(1), 431.0
				(1), 850.0 (2)
	22 Oct. 1994*	Cottus carolinae ssp.	7	$\approx 20.0-200.0$
		Lepomis macrochirus (167 mm, OSUM 77873)	I	≈ 20.0
BHCC	22 Oct. 1994*	Semotitus atromaculatus (26–146 mm, $n = 11$, OSUM 77874)	46†	4.8-476.0
		Lepomis cyanellus (61 & 69 mm, OSUM 77875)	4+	45.8(1), 70.5(1), 476.0(1)
	30 Sept. 19951	Semotitus atromaculatus (39–167 mm, $n = 18$)	19	2.7-264.4
	«	Lepomis cyanellus (54–115 mm, $n = 14$)	14	2.7–198.5
		Ambloplites rupestris (68 & 104.6 mm, SIUC 24889)	2	2.7, 187.6
		Rhinichthys atratulus (73 mm)	1	35.8
		Oncorhynchus mykiss (275 mm)	1	35.8
PMC	1 Oct. 1995‡	Cottus bairdi (29.0 & 74.3 mm, SIUC 24843)	2	7.1, 8.0
		Cottus sp. (observed, probably C. bairdi)	3	14.8(2), 20.7(1)
		Rhinichthys atratulus (69.8 & 85.0 mm, SIUC 24844)	39	54.0, 160.9, 175.5
		Semotitus atromaculatus (101.3 mm, SIUC 24845)	17	16.3 - 255.3
		Catostomus commersoni (97.2 & 107.5 mm, SIUC 24846)	16	116.1 - 274.3
		Salvelinus fontinalis (one photographed)	2	154.2(1), 177.8(2), 190.7(1).

§ Distance in meters from cave entrance; number of fishes captured at each distance is in parentheses or a range of capture distances is given when numerous individuals were captured; in BHCC on 30 Sept. 1995, distance was measured at the center of a distinct pool or stream segment that was sampled

* Collecting with a seine and dipnets

[‡] Collecting with a battery-powered backpack electrofishing unit

† Distance not recorded for all fishes

[54.2 (1), 177.8 (2), 190.7 (1),

255.3 (1) 271.6 194.5, 355.2

3

17.2

257.2 303.9221.0 242.0265.5

85.2-355.2

 24

Pimephales notatus (39.8–65.4 mm, n = 15, SIUC 24853)

Semotilus atromaculatus (47.0 mm, SIUC 24857)

Notropis photogenis (87.2 mm, SIUC 24855) Notropis volucellus (41.1 mm, SIUC 24856)

Cottus carolinae ssp. (35.6 & 38.3 mm, SIUC 24859)

Ameiurus nebulosus (118.2 mm, SIUC 24854)

Ameirus sp. (observed)

Ambloplites rupestris (132.5 mm, SIUC 24847)

Cottus bairdi (49.7 mm, SIUC 24858)

29 Sept. 1995*

PC

Salvelinus fontinalis (one photographed)

Species	Hocutt et al. (1978)		BHCC	
	Bruffey Creek	Hills Creek	(10/22/94)	(09/30/95)
Campostoma anomalum (Rafinesque)	2	29		
Rhinichthys atratulus (Hermann)	11	29		1
Semotilus atromaculatus (Mitchill)	70	3	46	19
Oncorhynchus mykiss (Walbaum)			_	1
Salvelinus fontinalis (Mitchill)	<u> </u>	1		
Ambloplites rupestris (Rafinesque)	2		_	2
Lepomis cyanellus Rafinesque	1		4	14
Etheostoma flabellare Rafinesque		114	_	_
Species	5	5	2	5
Numbers	86	176	50	37

TABLE 2.—Fish species and number collected in Hills Creek and Bruffey Creek (which enter Bruffey-Hills Creek Cave, BHCC) by Hocutt *et al.* (1978) and in BHCC (this publication)

to the Hills Creek Cave entrance. The spring indicated on the Droop WV USGS 7.5' quadrangle map is actually the inflow and cave entrance (Storrick, 1992). Two species were captured in 1994, while in September 1995, 264.4 m were sampled in the Bruffey Creek segment of BHCC, resulting in the capture of five fish species and several new records (Table 1).

In a survey of fishes in the Greenbrier River basin, Hocutt *et al.* (1978) sampled both Hills Creek (at Lobelia) and Bruffey Creek (at confluence with Cave Run) and found the five species reported herein from BHCC plus three additional species (Table 2). Perhaps other species in Bruffey and Hills Creeks are unable to survive long after being washed into the cave. The sight feeding of a species such as *Etheostoma flabellare* Rafinesque would almost certainly be limited in the cave as would lack of food for a species such as *Campostoma anomalum* (Rafinesque). Garton *et al.* (1993) tentatively reported depigmented *Nocomis* sp. in BHCC. The presence of *Semotilus atromaculatus* likely accounts for the report of *Nocomis* sp. in BHCC. There was an abundance of pale *S. atromaculatus*; however, none were albino and exposure to light or preservation in formalin resulted in most individuals regaining normal coloration, but some maintained a depigmented state. The depigmented fishes did appear to differ from normally pigmented individuals; however, no specific counts or measurements were made. Depigmented *S. atromaculatus* were also captured in 1995.

DISCUSSION

Structural characteristics of nontroglobitic fishes in caves.—Nontroglobitic fishes inhabiting caves may be depigmented, small-eyed or blind and possess skeletal abnormalities. Williams and Howell (1979) analyzed characters of a 67-mm SL, male albino *Cottus carolinae* (captured in BCC on 3 September 1967 by Jack A. Stellmack) and compared the characters with those of 48 normally pigmented *C. carolinae* ssp. captured inside and outside BCC. The albino possessed several unique characteristics, including a frenum, which has not been found in any other cottids. The reduction in pelvic fin rays (4 to 3) in the albino also has occurred in cavernicolous *C. carolinae* in Missouri (Burr *et al.*, 1992; Paul *et al.*, 1993). No additional albino sculpins have been captured in BCC. The type of albinism expressed in the individual is not known. Albino threespine sticklebacks (*Gasterosteus aculeatus* Linnae-us) produced from laboratory matings always had a defective swimbladder even though broodstocks were obtained from both Canada and The Netherlands (Bakker *et al.*, 1988).

of the albino gene as suggested for the defective swimbladder in albino Gasterosteus aculea-

The unique characters of the BCC albino sculpin may have resulted from pleiotropic effects

tus (Bakker et al., 1988).
Some ichthyologists consider the albino cave sculpin a distinct species (Jenkins and Burkhead, 1994); however, additional specimens should be gathered (if possible) before that distinction is made. The surveys reported herein were, in part, an attempt to locate more of the albino Cottus carolinae, and future work in the caves of West Virginia may yield additional specimens. Apparently, only one other instance of albinism in Cottus has been published, *i.e.*, Bailey (1952) captured a 62-mm TL albino C. bairdi in Wolf Creek, Montana. The albino C. bairdi specimen has not yet been located by the authors. Albino Gyrinophilus porphyriticus (Green) larvae have been captured in an unspecified cave in Greenbrier Co., West Virginia (Brandon and Rutherford, 1967). The albinos resembled normally pigmented conspecifics in several meristic and morphological characters, and albino individuals may have comprised 2% to 3% of the population. This relatively high incidence of albinism in the cave may have been due to an unappreciable loss in fitness that may be a consequence of albinism in epigean organisms (Brandon and Rutherford, 1967).

A depigmented and unusual Semotilus atromaculatus has been collected from Lorenz Cave, Perry Co., Mo. (SIUC 23159). The snout was noticeably shorter, the mouth appeared almost subterminal (vs. terminal normally) and the isthmus was much wider in the hypogean S. atromaculatus as compared to epigean conspecifics, but these characters could be abnormalities associated with a hypogean existence. Cave-dwelling populations of yellow bullhead, Ameiurus natalis (Lesueur), in Florida were depigmented, and some individuals lacked pelvic fins or had deformed caudal fins (Relyea and Sutton, 1973). The cyprinid, Notropis harperi Fowler, also occurs in the same two caves as the A. natalis, but apparently has no obvious abnormalities (Relyea and Sutton, 1973). Skeletal abnormalities and associated morphological changes have been demonstrated in Astyanax mexicanus (Filippi) reared in darkness for many months; hormonal imbalance due to lack of light was considered the cause of the abnormalities (Rasquin and Rosenbloom, 1954) and also may explain the out-of-season tuberculation of one Pimephales notatus in PC. Cope (1864) described two supposedly blind ictalurids from a Pennsylvania cave as a new species, Gronias nigrilabris, but Taylor (1969) identified them as Ameiurus nebulosus (Lesueur) and noted that both possessed two eyes (although the eyes were asymmetrically developed). Even in A. nebulosus held in captivity under normal light/dark regimes, abnormalities and depigmentation were observed (Rasquin, 1949). After approximately 2 yr in captivity, two A. nebulosus became depigmented, although the eyes remained dark (Rasquin, 1949). Kosswig (in Hubbs, 1938) mentioned a depigmented Salmo trutta Linnaeus from a cave, and Kosswig (1937) discovered two extremely depigmented cyprinids, Leuciscus (Squalius) cephalus (Linnaeus) from a cave in Germany. Rasquin (1947) examined pigmentation in Astyanax mexicanus raised in total darkness for 2 yr and found the fishes to be depigmented due to a decrease in number of melanophores and the amount of melanin granules per melanophore. Whether these depigmented fishes could regain normal pigmentation over time with light exposure was not tested. Perhaps permanent depigmentation can occur within the lifespan of an individual fish living in darkness for an extended time. Epigean Astyanax mexicanus reared in total darkness have smaller eyes than those reared under normal light/dark regimes, while the blind cave form (formerly known as Anoptichthys jordani Hubbs and Innes) exhibits increased eye development when reared in a photic environment (Peters and Peters, 1973:187). Offspring of epigean \times hypogean A. mexicanus had intermediate eye development, indicating genetic control, probably by polygenes (Peters and Peters, 1973). Therefore, evidence exists for both genetic and environmental influences on eye structure, and

136(1)

the same may be true for pigmentation. Reduction or absence of light appears to be a major factor in the evolution of troglomorphisms as indicated by the parallelism between troglophilic and troglobitic fishes and fishes inhabiting large, muddy rivers (*e.g.*, Moore, 1950; Lundberg and Py-Daniel, 1994).

Banister (1984) examined characteristics of a hypogean population of the cyprinid, Garra barreimiae Fowler and Steinitz, and found the hypogean fishes to differ only in that they were depigmented, lacked externally visible eyes and had weak squamation. Smaller specimens (11-14 mm SL) had externally visible eyes, while larger (>24 mm SL) had tissue covering the eye. The optic lobes were reduced in hypogean fishes; however, examination of hypogean fishes that had been kept in a photic environment for 4 mo showed an enlargement of the optic lobes to approximately the size of epigean conspecifics as well as limited melanin production. The eyes displayed no evident changes. Cavernicolous Cottus carolinae from Mystery Cave and a few nearby caves in Missouri exhibit reductions in eyes, pelvic fin rays, and pigmentation and may be specifically distinct from epigean C. carolinae (Burr et al., 1992; Paul et al., 1993). Cavernicolous Poecilia sphenops (Cuvier and Valenciennes) from Tabasco, Mexico, were depigmented, had smaller eyes, slightly upturned caudal peduncle, different mouth morphology, and differed behaviorally in aquaria from epigean mollies with which the hypogean fishes apparently still interbred as indicated by clinal variation in characters from the deep cave to the surface stream (Gordon and Rosen, 1962). Future research on the effects of aphotic conditions on development and alterations of morphology and biochemistry may aid in our understanding of the evolution of troglobitic organisms.

Ecological classification of nontroglobitic fishes in caves.—According to Barr (1963), cavedwelling organisms are generally separated into four categories: (1) Troglobite (obligate cavernicole, usually specialized in various ways); (2) Troglophile (facultative cavernicole able to complete entire life cycle within caves, but can also be found in other similar habitats); (3) Trogloxene (habitually inhabit caves or other similar habitats but must return to the surface or near the cave entrance for food), or (4) Accidental (accidental entrants into caves surviving for a "relatively" short time). Debate exists over the ecological classification of nontroglobitic, cave-associated organisms but most has concerned invertebrates and amphibians (Brandon, 1962; Barr, 1963; Richards, 1971; Hamilton-Smith, 1972). Barr (1963) and Brandon (1962) have discussed the problem of proper classification for cavernicolous species. Barr (1960, 1963) suggested that a qualifying adjective be added to trogloxene to further clarify the nature of an organism's association with caves, e.g., threshold trogloxene. Hazelton and Glennie (in Barr, 1963) and Jefferson (1983) used the terms accidental trogloxene and habitual trogloxene. Accidental trogloxene appears to be a contradictory term, while habitual trogloxene is redundant since the definition of trogloxene indicates a close association with caves. Barr (1963:11) stated: "There seems no special advantage in calling an animal a trogloxene simply because it has occurred accidentally in a cave. The term trogloxene should be restricted to animals which are habitually found in caves, if it is to retain its ecological significance...." "Only the demonstration of habitual occurrence of this species [Plethodon richmondi Netting and Mittleman] in a large number of caves would justify its being called a trogloxene."

In contemplating the appropriate term for classifying a species' ecological cave association, one must not consider what the tendencies are for the species over its entire range, but rather, only the local population occurring within the cave. If, for example, *Semotilus atromaculatus* in BHCC fulfill the definition of trogloxene or troglophile, this small population should be so classified, even though *S. atromaculatus* (the species over its entire range) are generally not associated with caves. A focused study of the population must be undertaken to gather the data needed for classification (e.g., Resetarits, 1986). Barr (1963: 11) seemed to acknowledge the distinctiveness of different cave populations of the spider, *Meta americana* Marusik and Koponen, and the cricket, *Hadenoecus subterraneus* (Scudder): "Both *M. menardii* [=*americana*] and *H. subterraneus* are basically trogloxene. Under exceptional circumstances they can and do become (facultative) troglophiles." Initial transport of fishes into caves is likely "accidental" in that individuals are washed in during high flow; however, subsequent to this, survival for an extended period would not fit the accidental category. Such species seem to fall between trogloxene and troglophile, since returning to the entrance to feed (trogloxene) is almost certainly not possible when fishes are several hundred meters from the cave entrance, yet ability to reproduce in the caves (troglophile) has not been demonstrated. Several of the species reported herein may fulfill the definition of trogloxene. The most important point is that certain fish populations may not be accidentals in the strict sense and would be useful to study, rather than being absorbed with creating new categories or terminology, especially in the absence of appropriate data.

Since a species is not static, but a dynamic assemblage of populations and stocks, discriminating unique populations that are capable of hypogean survival is of great importance concerning evolution of cave-dwelling organisms. Dearolf (1956:204) stated: "Mentioning these fish from outside caves is worthwhile because it shows that outside forms enter caves, and in the case of sculpin, are capable of existence far within caves. These give us a group of vertebrates preadapted to cave life from which troglobites may develop." Greenwood (1967) and Poulson (1963) also noted that some epigean species seem to be preadapted to living in darkness and that many of these species have troglobitic relatives. Research on a potentially evolving cave-dweller could help our understanding of the origins of known troglobites, especially those with a closely related epigean species. Romero (1984, 1985) studied a small population of *Astyanax mexicanus* and *Brachyraphis rhabdophora* (Regan) that used both epigean and subterranean habitats over the course of the day. Both species entered the cave to avoid predation by fish-eating bats and often entered to consume food captured outside the cave. Romero (1984, 1985) suggested that such predator avoidance behavior may lead to the evolution of a cave-dwelling fish (troglophile or troglobite).

Most occurrences of epigean fishes in caves are considered accidental with some exceptions, e.g., Cottus spp. (Dearolf, 1956; Garton et al., 1993; Brown et al., 1994; Jenkins and Burkhead, 1994:94). Beck et al. (1976) reported Poecilia reticulata Peters in Aguas Buenas Caves, Puerto Rico. This guppy was common in shallow pools in the lower passage and was classified as a trogloxene. Brown et al. (1994) classified C. carolinae from Logan Cave, Arkansas, as troglophiles; however, they presented no evidence to support this classification. Ameiurus natalis and Notropis harperi from Florida caves were classified as troglophiles by Relyea and Sutton (1973) and as trogloxenes by Franz et al. (1994), but no specific data were presented to support either classification. These populations should be given further consideration, however, as they may be unique considering the information given by Relyea and Sutton (1973). Franz et al. (1994) also listed Anguilla rostrata (Lesueur), Aphredoderus sayanus (Gilliams), and Lepomis macrochirus as trogloxenes.

All specimens of fishes captured or observed in West Virginia caves, except *Notropis photogenis*, appeared to be quite healthy; although, the length of time the fishes had occupied the caves is unknown. The authors therefore hesitate to classify these species as accidental. These species, particularly, *Semotilus atromaculatus* and *Cottus carolinae*, may be trogloxenes or troglophiles, but supporting evidence is unavailable. If some individuals of a species are able to survive in good health for several months or years in a cave, but cannot reproduce, in which group would this species fit best? None of Barr's four groups seem to accommodate TABLE 3.—Nontroglobitic fish species reported from caves within the contiguous United States. Species name is followed by abbreviations for states in which found

Lampetra Bonnaterre sp., AL¹²; Anguilla rostrata (Lesueur), FL²¹; Campostoma anomalum[†] (Rafinesque), MO²⁶, WV⁷; Clinostomus funduloides Girard, VA⁸; Cyprinella spiloptera (Cope), KY¹⁰, TN¹¹; Cyprinus carpio Linnaeus, MO24; Margariscus margarita Cope, WV7; Nocomis micropogon (Cope), WV7; Notemigonus crysoleucas (Mitchill), MS¹⁶; Notropis atherinoides Rafinesque, KY^{4,8,10}; Notropis harperi Fowler, FL¹³; Notropis photogenis (Cope), WV²⁵; Notropis volucellus (Cope), WV²⁵; Phoxinus erythrogaster[‡] (Rafinesque), MO²⁶; Pimephales notatus (Rafinesque), IN²², WV²⁵, unspecified⁶; Rhinichthys atratulus (Hermann), TN²³, WV^{5,8,25}; Rhinichthys cataractae (Valenciennes), WV^{5,7,8}; R. cataractae \times N. micropogon, WV⁷; Semotilus atromaculatus (Mitchill), IL²⁴, KY¹⁰, MO²⁴, MS¹⁶, TN⁸, WV^{7,25}; Catostomus commersoni (Lacepède), KY¹⁰, TN^{2.8}, WV²⁵; Hypentelium nigricans (Lesueur), TN⁸, WV⁷; Ictiobus bubalus (Rafinesque), AL¹¹; Ameiurus melas (Rafinesque), MO²⁷; Ameiurus natalis (Lesueur), AL¹¹, FL^{13,21}, MS¹⁶; Ameiurus nebulosus (Lesueur), FL²¹, PA¹, WV²⁵; Ameiurus Rafinesque sp., IL²⁴, KY¹⁰, MO²⁴; Ictalurus lupus (Girard), TX²³; Ictalurus punctatus (Rafinesque), TX9; Noturus Rafinesque sp., unspecified8; Oncorhynchus mykiss (Walbaum), WV19,25; Salvelinus fontinalus (Mitchill), WV19,25; Aphredoderus sayanus (Gilliams), MS16, FL21; Chologaster agassizit Putnam, KY¹⁰, TN⁸; Gambusia holbrooki Girard, FL²¹; Cottus bairdi Girard, PA⁸, WV^{5,7,8,25}; Cottus carolinae (Gill), AL²³, AR^{8,20}, IL²⁴, IN^{6,8,22}, KY^{4,23}, MO^{6,8,17,18,22,24}, TN^{2,3,22,23}, VA^{8,22,23}, WV^{15,25}; Morone saxatilis (Walbaum), FL²¹; Ambloplites rupestris (Rafinesque), MO²⁴, WV²⁵; Lepomis cyanellus Rafinesque, AR¹⁴, MO²⁴, TX⁹, WV²⁵; Lepomis gulosus (Cuvier) MO²⁷; Lepomis macrochirus Rafinesque, FL²¹, MO²⁴, WV25; Lepomis marginatus (Holbrook), MS16; Lepomis Rafinesque sp., KY10; Pomoxis nigromaculatus (Lesueur), FL²¹; Etheostoma blennioides Rafinesque, WV7; Etheostoma parvipinne Gilbert & Swain, MS16; Etheostoma zonale (Cope), IN²²

Authors of genera follow Eschmeyer (1990). (‡) Reported as extremely emaciated and with empty intestinal tracts (Smith, 1948). (†) Now called *Forbesichthys agassizi* by some authors. Data from ¹Cope, 1864; ²Cope and Packard, 1881; ³Evermann and Hildebrand, 1914; ⁴Bailey, 1933; ⁵Reese, 1934; ⁶Hubbs, 1938; ⁷Frank J. Schwartz, unpubl. data collected in 1946 from Sinks of Gandy; ⁶Dearolf, 1956 (record of *Erimystax* sp. probably = *N. harperi*); ⁹Jones and Hettler, 1959; ¹⁰Kuehne, 1966; ¹¹Armstrong and Williams, 1971; ¹²Cooper and Iles, 1971; ¹³Relyea and Sutton, 1973; ¹⁴McDaniel and Gardner, 1977; ¹⁵Williams and Howell, 1979; ¹⁶Cliburn and Middleton, 1983; ¹⁷Pflieger, 1989; ¹⁸Burr *et al.*, 1992; ¹⁹Garton *et al.*, 1993; ²⁰Brown *et al.*, 1994; ²¹Franz *et al.*, 1994; ²²University of Michigan Museum of Zoology (UMMZ) records; ²³United States National Museum (USNM) records; ²⁴Southern Illinois University at Carbondale (SIUC) records; ²⁵this publication; ²⁶Smith, 1948; ²⁷Pembleton and Bake, 1967.

these fishes and a new category may be required. Alternatively, the accidental or trogloxene categories could be redefined to include such cases.

Table 3 contains reported occurrences of nontroglobitic fishes in U.S. caves. *Cottus* spp. seem to occur more frequently in caves than other surface-dwelling species (Hubbs, 1938: 262; Dearolf, 1956:204; Jenkins and Burkhead, 1994:36; Pflieger, 1989:39). *Cottus* generally rely upon the anterioventral lateral line system for prey detection (Hoekstra and Janssen, 1985; 1986; Janssen, 1990) and many species feed nocturnally (Hoekstra and Janssen, 1985; Greenberg and Holtzman, 1987; and references therein) making survival in caves feasible. Only the relatively limited food supply would affect fish survival. *Cottus* are opportunistic feeders and consume a wide variety of invertebrates and some vertebrates (Bailey, 1952; Northcote, 1954; Dewey, 1988; W. Poly, pers. observ.), while *S. atromaculatus* are omnivorous, and larger ones ($\geq \approx 80$ mm SL) are highly piscivorous (Barber and Minckley, 1971; Newsome and Gee, 1978).

In the past the occurrence of fishes in caves has been considered unimportant and little attention has been given to the role of fishes in cave ecology. In cases where a fish species is fairly common in a cave, its contribution concerning cave ecology should be considered, *e.g.*, Pruitt (*in* Franz *et al.*, 1994) counted over 100 *Ameiurus natalis* in

Firecracker Cave, Florida. How does predation by fishes affect a population of resident invertebrates? Brown et al. (1994) examined gut contents of three large Cottus carolinae from Logan Cave, Arkansas, and found remains of an endangered troglobitic crayfish, Cambarus aculabrum Hobbs and Brown, and a troglophilic crayfish, Orconectes neglectus (Faxon), in one stomach and a caddisfly head capsule in the second stomach, while the third stomach was empty. Predation on Amblyopsis rosae (Eigenmann) by C. carolinae was not observed (Brown et al., 1994). Both C. carolinae and Typhlichthys subterraneus Girard have been recorded in Lewis Cave, Ripley Co., Mo. (SIUC records). Relyea and Sutton (1973) found a troglobitic crayfish, Procambarus lucifugus (Hobbs), in the stomach of a cave-dwelling A. natalis, and Franz et al. (1994) reported a Procambarus pallidus (Hobbs) specimen in the USNM collection as having been recovered from an A. natalis stomach. Ameiurus spp. are omnivorous, feed nocturnally and therefore, could be formidable cave-dwelling predators. A Lepomis cyanellus Rafinesque was reported to have eaten a Mexican free-tail bat, Tadarida mexicana (Saussure), in a Texas cave (Jones and Hettler, 1959). Semotilus atromaculatus inhabiting caves with amblyopsids could have a serious impact on the population due to piscivory by the larger individuals (Barber and Minckley, 1971; Newsome and Gee, 1978; Keast, 1985); the same could also be said regarding C. carolinae and possibly salmonids, ictalurids or centrarchids even if accidentals. One S. atromaculatus observed at 422.9 m in BHCC in 1994 was > 200 mm SL (W. Poly, pers. observ.). Larger Cottus spp. (> $\approx 60 \text{ mm SL}$) also become piscivorous to some extent (Starnes and Starnes, 1985; Dewey, 1988; W. Poly, pers. observ.). Resetarits (1986) studied cave use by pickerel frogs, Rana palustris LeConte, in a Missouri cave and suggested that just the addition of organic material from the abundant frogs had an important impact on cave ecology, and the same may be suggested for fishes.

Jenkins and Burkhead (1994) discussed the absence of cave fishes in eastern Tennessee and western Virginia and noted that some speleologists have specifically looked for cave fishes in the region. Pollution may have affected subterranean fishes if any were formerly present (Hocutt et al., 1978). Reese (1933) also noted that blind cave fishes were absent from the West Virginia caves he investigated. Even though amblyopsids may not have entered the cave systems of West Virginia, Virginia or eastern Tennessee, sufficient time may have elapsed for unique forms to evolve. For example, a subspecies of longnose dace, Rhinichthys cataractae smithi Nichols, possibly arose within ≈ 9500 yr in the Cave and Basin Hotsprings of Banff National Park, Alberta, Canada; an alternative hypothesis was that it survived in a refugium and may be older in origin (Renaud and McAllister, 1988:110). A more thorough study may reveal new records for West Virginia, Tennessee and Virginia and perhaps undescribed forms as well. There have been rumors of cave fishes inhabiting caves in eastern Tennessee and northern/western Virginia, but no true cave fishes have yet been found (Etnier and Starnes, 1993; Jenkins and Burkhead, 1994). Jenkins and Burkhead (1994) discussed the relatively few reports of fishes in Virginia caves and advised spelunkers to take note of fishes, particularly Cottus spp., encountered in subterranean waters of Virginia. Investigations of other caves in the Greenbrier valley by the authors are ongoing and will likely result in additional species records in West Virginia caves. Studies cited above suggest that nomenclature has been applied somewhat indiscriminately to fishes occurring in caves. Classifications should be applied to specific populations that have been studied and for which data are available. Although relatively little information is currently available, the above discussion suggests that even accidentals may be an important component of cave communities. Only a few cases are known of epigean fishes consuming troglobitic organisms, although

such incidents are likely numerous. Further work is needed on the ecological contributions and impacts of "accidentals," particularly fishes, in caves.

Acknowledgments.—Many people contributed to this study. R. Noggle assisted with collecting in BCC. J. D. Williams provided information about BCC and the location and catalog numbers of preserved specimens. R. Garton provided information about BHCC and BCC. T. Hall provided information about PC and PMC and allowed access to PC. J. T. Williams provided collection data from USNM. F. Schwartz provided his unpublished data on fishes in Sinks of Gandy and other past cave work. R. Bailey and D. Nelson supplied UMMZ records. D. Cincotta informed us of the absence of voucher material in the WVDNR, Wildlife Resources Division Fish Museum. G. Turner allowed us access to and provided the exact location of BCC, H. Cole allowed access to Piercys Mill Cave, and A. White allowed access to and indicated the location of BHCC. WVACS provided lodging at their field station. J. Holsinger provided several reprints. D. Eisenhour informed us of the Moore (1950) paper. B. Burr provided abstracts concerning recent work on cave sculpins in Missouri, provided advice on Astyanax nomenclature, allowed the use of his personal library, and pointed out Taylor's (1969) treatment of Gronias nigrilabris. J. Krejca provided information on recent collections of fishes from Missouri and Illinois caves and informed us of the Meta americana description. J. Redell provided the Jones and Hettler (1959) reference. D. Claussen pointed out the paper by Resetarits (1986). R. Brandon provided reprints. H. Hobbs III and A. Wilson made comments on an earlier draft of the manuscript. This work was conducted under Scientific Collecting Permit #61-1994 and #26-1995 from the West Virginia Department of Natural Resources.

LITERATURE CITED

- ARMSTRONG, J. G. AND J. D. WILLIAMS. 1971. Cave and spring fishes of the southern bend of the Tennessee River. J. Tenn. Acad. Sci., 46:107–115.
- BAILEY, J. E. 1952. Life history and ecology of the sculpin, *Cottus bairdi punctulatus* in Southwestern Montana. *Copeia*, **1952**:243-255.
- BAILEY, V. 1933. Cave life of Kentucky: mainly in the Mammoth Cave region. The University Press, Notre Dame, Indiana. 256 p.
- BAKKER, TH. C. M., E. FEUTH-DEBRUIJN AND P. SEVENSTER. 1988. Albinism in the threespine stickleback, Gasterosteus aculeatus. Copeia, 1988:236–238.
- BANISTER, K. E. 1984. A subterranean population of *Garra barreimiae* (Teleostei: Cyprinidae) from Oman, with comments on the concept of regressive evolution. *J. Nat. Hist.*, 18:927–938.
- BARBER, W. E. AND W. L. MINCKLEY. 1971. Summer foods of the cyprinid fish Semotilus atromaculatus. Trans. Am. Fish. Soc., 100:283-289.
- BARR, T. C. 1960. Introduction (to symposium: speciation and raciation in cavernicoles). Am. Midl. Nat., 64:1–9.
- ------. 1963. Ecological classification of cavernicoles. Cave Notes, 5:9-12.
- BECK, B. F., M. FRAM AND J. R. CARVAJAL. 1976. The Aguas Buenas Caves, Puerto Rico: geology, hydrology, and ecology with special reference to the histoplasmosis fungus. *Natl. Speleol. Soc. Bull.*, 38:1–16.
- BRANDON, R. A. 1962. Comments on some terms used in ecological studies of cave-associated organisms. *Cave Notes*, 4:50-52.
- AND J. M. RUTHERFORD. 1967. Albinos in a cavernicolous population of the salamander Gyrinophilus porphyriticus in West Virginia. Am. Midl. Nat., 78:537-540.
- BROWN, A. V., W. K. PIERSON AND K. B. BROWN. 1994. Organic carbon resources and the payoff-risk relationship in cave ecosystems, p. 67–76. *In*: J. A. Stanford and H. M. Valett (eds.). Proceedings of the Second International Conference on Ground Water Ecology, American Water Resources Association, Herndon, Va.
- BURR, B. M., M. L. WARREN, JR. AND R. J. PAUL. 1992. Cavernicolous sculpins of the Cottus carolinae species group from Mystery Cave, Missouri. Abstract, 72nd Annu. Mtg. of the Am. Soc. of Ichthyologists and Herpetologists, 4–10 June 1992.
- CLIBURN, J. W. AND A. L. MIDDLETON, JR. 1983. The vertebrate fauna of Mississippi caves. Natl. Speleol. Soc. Bull., 45:45-48.

- COOPER, J. E. AND A. ILES. 1971. The southern cavefish, *Typhlichthys subterraneus*, at the southeastern periphery of its range. *Natl. Speleol. Soc. Bull.*, **33**:45–49.
- COPE, E. D. 1864. On a blind silurid, from Pennsylvania. Proc. Acad. Nat. Sci. Phila., 16:231–233. —— AND A. S. PACKARD, JR. 1881. The fauna of Nickajack Cave. Am. Nat., 15:877–882.
- DASHER, G. R. AND W. M. BALFOUR. 1994. The caves and karst of the Buckeye Creek basin, Greenbrier County, West Virginia. W. Va. Speleol. Surv. Bull., 12:1-238.
- DEAROLF, K. 1956. Survey of North American cave vertebrates. Proc. Penn. Acad. Sci., 30:201-210.
- DEWEY, S. L. 1988. Feeding relationships among four riffle-inhabiting stream fishes. *Trans. Ill. Acad.* Sci., **81**:171–184.
- ESCHMEYER, W. N. 1990. Catalog of the genera of recent fishes. California Academy of Sciences, San Diego, Calif. 697 p.
- ETNIER, D. A. AND W. C. STARNES. 1993. The fishes of Tennessee. The University of Tennessee Press, Knoxville. 681 p.
- EVERMANN, B. W. AND S. F. HILDEBRAND. 1914 (1916). Notes on the fishes of East Tennessee. Bull. U.S. Bur. Fish., 34:433-451.
- FRANZ, R., J. BAUER AND T. MORRIS. 1994. Review of biologically significant caves and their faunas in Florida and South Georgia. *Brimleyana*, 20:1–109.
- GARTON, E. R., F. GRADY AND S. D. CAREY. 1993. The vertebrate fauna of West Virginia caves. W. Va. Speleol. Surv. Bull., 11:1-107.
- GORDON, M. S. AND D. E. ROSEN. 1962. A cavernicolous form of the Poecilia fish *Poecilia sphenops* from Tabasco, Mexico. *Copeia*, **1962**:360–368.
- GREENBERG, L. A. AND D. A. HOLTZMAN. 1987. Microhabitat utilization, feeding periodicity, home range and population size of the banded sculpin, *Cottus carolinae. Copeia*, **1987**:19–25.
- GREENWOOD, P. H. 1967. Blind cave fishes. Stud. Speleol., 1:262-274.
- HAMILTON-SMITH, E. 1972. A reply to "The classification of Australian cavernicoles with particular reference to Rhaphidophoridae (Orthoptera)". Natl. Speleol. Soc. Bull., 34:27–28.
- HOCUTT, C. H., R. F. DENONCOURT AND J. R. STAUFFER, JR. 1978. Fishes of the Greenbrier River, West Virginia, with drainage history of the central Appalachians. J. Biogeogr, 5:59-80.
- HOEKSTRA, D. AND J. JANSSEN. 1985. Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. *Environ. Biol. Fish.*, 12:111-117.

- HOLSINGER, J. R., R. A. BAROODY AND D. C. CULVER. 1976. The invertebrate cave fauna of West Virginia. W. Va. Speleol. Surv. Bull., 7:1-82.
- HUBBS, C. L. 1938. Fishes from the caves of Yucatan. Carnegie Inst. Wash. Publ., 491:261-295.
- JANSSEN, J. 1990. Localization of substrate vibrations by the mottled sculpin (*Cottus bairdi*). Copeia, 1990:349-355.
- JEFFERSON, G. T. 1983. The threshold fauna. A neglected area of British cave biology. *Stud. Speleol.*, **1983**:53–58.
- JENKINS, R. E. AND N. M. BURKHEAD. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland. 1079 p.
- JONES, R. S. AND W. F. HETTLER. 1959. Bat feeding by green sunfish. Texas J. Sci., 11:48.
- KEAST, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. Environ. Biol. Fish., 12:119–129.
- Kosswig, C. 1937. Uber pigmentverlust wahrend des hohlenlebens. Beobachtungen an Squalius cephalus L. Zool. Anz., 117:37–43.
- KUEHNE, R. A. 1966. Depauperate fish faunas of sinking creeks near Mammoth Cave, Kentucky. *Copeia*, **1966**:306–311.
- LUNDBERG, J. G. AND L. R. PY-DANIEL. 1994. Bathycetopsis oliveirai, gen. et sp. nov., a blind and depigmented catfish (Siluriformes: Cetopsidae) from the Brazilian Amazon. Copeia, 1994:381– 390.
- McDANIEL, V. R. AND J. E. GARDNER. 1977. Cave fauna of Arkansas: vertebrate taxa. Proc. Ark. Acad. Sci., 31:68-71.

- MOORE, G. A. 1950. The cutaneous sense organs of barbeled minnows adapted to life in the muddy waters of the Great Plains region. *Trans. Am. Microsc. Soc.*, **69**:69–95.
- NEWSOME, G. E. (Buck) AND J. H. GEE. 1978. Preference and selection of prey by creek chub (Semotilus atromaculatus) inhabiting the Mink River, Manitoba. Can. J. Zool., 56:2486-2497.
- NORTHCOTE, T. G. 1954. Observations on the comparative ecology of two species of fish, *Cottus asper* and *Cottus rhotheus*, in British Columbia. *Copeia*, **1954**:25–28.
- PAUL, R. J., B. M. BURR AND M. L. WARREN, JR. 1993. Cavernicolous sculpins of the Cottus carolinae species group from Perry County, Missouri: cave-life phenomena or speciation? Abstract, 4th Annual Argonne Symposium for Undergraduates in Science, Engineering and Mathematics, Argonne National Laboratory, 5–6 November 1993.
- PEMBLETON, E. F. AND E. L. BAKE. 1967. The fauna of Maze Cave. Mo. Speleology, 9:8-13.
- PETERS, N. AND G. PETERS. 1973. Genetic problems in the regressive evolution of cavernicolous fish, p. 187–201. In: J. H. Schröder (ed.). Genetics and mutagenesis of fish. Springer-Verlag, New York.
- PFLIEGER, W. L. 1989. Aquatic community classification system for Missouri. Mo. Dep. Conserv. Aquatic Ser. No. 19. 70 p.
- POLY, W. J. AND R. A. NOGGLE. 1996. Natural history notes. Terrapene carolina carolina. Herpetol. Rev., 27, in press.
- POULSON, T. L. 1963. Cave adaptation in amblyopsid fishes. Am. Midl. Nat., 70:257-290.
- RASQUIN, P. 1947. Progressive pigmentary regression in fishes associated with cave environments. Zoologica, 32:35-42.
- ------. 1949. Spontaneous depigmentation in the catfish Ameiurus nebulosus. Copeia, 1949:246-251.
- AND L. ROSENBLOOM. 1954. Endocrine imbalance and tissue hyperplasia in teleosts maintained in darkness. *Bull. Am. Mus. Nat. Hist.*, **104**:359–426.
- REESE, A. M. 1933. Life of West Virginia caves (preliminary report). Proc. W. Va. Acad. Sci., 6:26.
- ------. 1934. The fauna of West Virginia caves. Proc. W. Va. Acad. Sci., 7:39-53.
- RELYEA, K. AND B. SUTTON. 1973. Cave dwelling yellow bullheads in Florida. Fla. Sci., 36:31-34.
- RENAUD, C. B. AND D. E. MCALLISTER. 1988. Taxonomic status of the extinct Banff longnose dace, *Rhinichthys cataractae smithi*, of Banff National Park, Alberta. *Environ. Biol. Fish.*, 23:95–113.
- RESETARITS, W. J., JR. 1986. Ecology of cave use by the frog, Rana palustris. Am. Midl. Nat., 116:256-265.
- RICHARDS, A. M. 1971. The classification of Australian cavernicoles with particular reference to Rhaphidophoridae (Orthoptera). *Natl. Speleol. Soc. Bull.*, **33**:135–139.
- ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKER, E. A. LACHNER, R. N. LEA AND W. B. SCOTT. 1991. Common and scientific names of fishes from the United States and Canada, 5th ed. Am. Fish. Soc. Spec. Publ., 20, 183 p.
- ROMERO, A. 1984. Behavior in an "intermediate" population of the subterranean-dwelling characid Astyanax fasciatus. Environ. Biol. Fish., 10:203–207.
 - -----. 1985. Cave colonization by fish: role of bat predation. Am. Midl. Nat., 113:7-12.
- SMITH, P. W. 1948. Food habits of cave dwelling amphibians. Herpetologica, 4:205-208.
- STARNES, L. B. AND W. C. STARNES. 1985. Ecology and life history of the mountain madtom, Noturus eleutherus (Pisces: Ictaluridae). Am. Midl. Nat., 114:331-341.
- STORRICK, G. D. 1992. Caves and karst hydrology of southern Pocahontas County and the upper Spring Creek valley. W. Va. Speleol. Surv. Bull., 10:1–214.
- TAYLOR, W. R. 1969. A revision of the catfish genus Noturus Rafinesque with an analysis of higher groups in the Ictaluridae. Bull. U.S. Natl. Mus., 282. 315 p.
- WILLIAMS, J. D. AND W. M. HOWELL. 1979. An albino sculpin from a cave in the New River Drainage of West Virginia (Pisces: Cottidae). *Brimleyana*, 1:141–146.

SUBMITTED 16 NOVEMBER 1995

Accepted 1 February 1996

STATEMENT OF OWNERSHIP MANAGEMENT AND CIRCULATION

The American Midland Naturalist (ISSN 0003 0031) is published quarterly by The University of Notre Dame, Notre Dame, IN 46556. The editor is Robert P. McIntosh of the same address. The owner is the University of Notre Dame.

The purpose, function and nonprofit status of this organization have not changed during the preceding 12 months.

The average number of copies printed is 1400, subscriptions 1126, exchanges 112 and free distribution 65.

I certify that the statements made by me are correct and complete.

Robert P. McIntosh Editor

ERRATUM

An error appeared in W. J. Poly and C. E. Boucher. Nontroglobitic Fishes in Caves: Their Abnormalities, Ecological Classification and Importance. Vol. 136: 187–198, 1996.

On page 190 the last sentence of results should read: The depigmented fishes did *not* (emphasis added) appear to differ from normally pigmented individuals, however no specific counts or measurements were made.

In Table 1 Ameirus sp. should read Ameiurus sp.