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Zoogeography and Characters of the American Cyprinid Fish *Notropis bifrenatus*

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ABSTRACT: Notropis bifrenatus, the bridle shiner, occurs from southeastern Canada along the Atlantic slope of the United States to the Neuse River drainage in North Carolina. First records from the Rappahannock, York, James, Chowan, and Neuse drainages are documented. This species inhabits lentic and moderate to low gradient lotic situations. Reports of its capture in waters of low salinity are only from the southern portion of its range.

This species apparently dispersed into northern sectors of its range relatively early during glacial recession. Its distribution on Long Island is evidence of its occupation during Wisconsin glaciation of an area that is now part of the continental shelf. Dispersal through the Chesapeake Bay region and southward was probably via extended main fivers during late Pleistocene, stream capture, and lateral meanders.

Analyses of certain meristic characters indicate an absence of significant geographic variation with the exception of lateral line pore development. Descriptions of nuptial tuberculation, pharyngeal arch, dorsal fin position, and lateralis system pores and canals are given.

Introduction

Notropis bifrenatus (Cope), the bridle shiner, is one of the better known American cyprinids. Its distribution, ecology, reproduction, and early development were treated by Harrington in six publications (1947-1951) and he figured and described the osteocranium (1955). Additional details on its biology are found in Harrington's (1946) thesis. Little, however, is published on the distribution and ecology of this species in the southern portion of its range and on its possible geographic variation. We review recent information and present new data on these topics, discuss aspects of its zoogeography, and describe its nuptial tuberculation, pharyngeal arch, dorsal fin position, and lateral line development. Only diagnostic characters or certain characters which may be important for future determination of phylogenetic relationships are treated. Some of these characters have previously been erroneously described, and it is our intent to rectify these circumstances.

Methods and Materials

The methods described by Hubbs and Lagler (1958) were followed where applicable. The lateral line system and nuptial tubercles were observed under a binocular microscope with aid of a gentle stream of compressed air. Lateralline scales with a canal and pore were included in pored-scale counts even if disjunct from other pored scales. The position of the dorsal fin insertion relative to the pelvic fin insertion was determined by spreading these fins, placing a clear plastic straightedge perpendicular to the longitudinal axis of the body over the apex of the angle formed by the extended pelvic, then noting where the apex of the dorsal angle fell in relation to the straightedge. Measurements were taken with dial calipers and read to the nearest .05 mm. The distance, dorsal fin insertion to occiput, was measured from the dorsal insertion to the mid-dorsal point between the most medial supratemporal canal pores. The terms used in describing pharyngeal arches and

dentition were defined and illustrated by Uyeno (1961).

Materials used are all at Cornell University (CU) except one series at the U.S. National Museum (USNM). Series that provided data on nuptial tuberculation have their catalog number preceded by an asterisk. Numbers in parentheses refer to the number of specimens from which meristic, morphometric and/or dental data were taken. E. Massachusetts-*20589 (5), 30512 (5). New York-upper Hudson drainage (dr.): *41517 (1); Oneida L. basin: *39395; Cayuga L. basin: *5932, *5988, 7903, *9077 (68), 44789 (54), *50497; Susquehanna dr.: 62533 (1). New Jersey-Passaic dr.: 5351 (1). 5358 (1); Green Brook, Somerset Co.: 5396 (5); L. Hopateony; 15461 (3). Delaware-Delaware dr.: *30778 (5). Maryland-Susquehanna dr. mouth: 14168 (2), 14204 (2); Swan Cr.: 43716 (1). Virginia-Rappahannock dr.: USNM 105319, Orange Co., Flat Run, trib. Rapidan R., near Wilderness, 28 May 1933, G. S. Myers and E. Reid; York dr.: 51933 (1), Spotsylvania Co., Matta R. at Jerrell Mill below dam and Rt. 1 bridge, 11 Nov. 1966, W. S. Woolcott and class; James dr.: *18399 (4), New Kent Co., east shore Chickahominy R. at Moyseneck Farm, 1 mi. E. Lanexa, 26 June 1949, R. Howell, E. C. Raney, N. D. Richmond; Chowan dr.: 52945 (33), Sussex Co., Stony Cr. at Rt. 301 bridge just E. town of Stony Creek, 30 Sept. 1967, Zorach and class. North Carolina-Neuse dr.: 52932 (1). Craven Co., Tucker Cr. 1 mi. upstream from mouth in Slocum Cr., about 3.0 airmi. ESE Croatan (Station 11 in Keup and Bayless, 1964: Fig. 1), 19 July 1960, N. C. Wildlife Resources Comm. crew.

ACKNOWLEDGMENTS

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Distribution and Ecology

Notropis bifrenatus is an Atlantic slope species, inhabiting a small portion of southeastern Canada and northeastern United States. Its range was indicated to be from southwestern Maine, eastern New Hampshire and northern New York westward to the southwestern Lake Ontario basin of New York, and south to the Potomac drainage of Maryland (Harrington, 1946; 1947 b:distrib. map). Cuerrier, Fry, and Prefontaine (1946) extended its range in the St. Lawrence drainage to the Montreal area and the lac Saint-Pierre area, about 60 miles downriver from Montreal. Scott (1967) included the eastern half of the Lake Ontario basin of Ontario within its limits. Schwartz (1963) reported it from Maryland streams entering the eastern shore of Chesapeake Bay. Hubbs and Raney (1947) and Moore (1957) gave its southern limit as the Potomac drainage, northern Virginia.

New records reported or confirmed herein extend its range southward to include the Rappahannock, York, James, and Chowan drainages of Virginia and the Neuse drainage of eastern North Carolina. Only one collection is known from each of these drainages; collection details are given in the materials section. The Neuse drainage record was first reported by Keup and Bayless (1964) and is confirmed by one specimen. This species may be expected from the Tar and Roanoke drainages, which are north of the Neuse in North Carolina and Virginia. Harrington (1946) mentioned regions in the northern portion of its range where it is uncommon, rare, or quite localized. The species apparently has similar patterns of distribution and abundance in the southern portion of its range.

The habitat of *N. bifrenatus*, summarized by Harrington (1947b), ranges from warm water small streams and ponds to large lakes and rivers, where shallows with still or slow flowing water are preferred. It is usually found over mud, silt, or detritus, and prefers areas of moderate to abundant vegetation. Records of its capture in waters of low salinity are all from the southern half of its range. De Sylva, Kalber, and Shuster (1962:22, Fig. 7) encountered *N*. bifrenatus only in the upper portion of the Delaware River estuary during May, at salinities of 0.05 to 2.0 o/oo. Hildebrand and Schroeder (1928) reported numerous specimens "... all taken in slightly brackish water" in the Chesapeake Bay region. Mansueti and Hardy (1967) recorded it from tidal and brackish tributaries of Chesapeake Bay and "along beaches in open, tidal rivers." Hildebrand and Schroeder (1928) and Schwartz (1964, apparently based on the former) noted its occurrence in Chesapeake Bay water of 11.8 o/oo. Keup and Bayless (1964) reported a salinity of 3.33 o/oo at the Neuse drainage N. bifrenatus locality. In the James drainage, N. bifrenatus was found in an area where the current was slow and the bottom was covered with fine sand, sporadically overlaid with silty mud and patches of Potamogeton and Nitella (Neil D. Richmond, pers. comm.). The river at this locality is usually fresh, becoming perceptibly brackish during prolonged dry weather (Richmond, 1940). The species probably was at least once common, based on U.S. National Museum collections, in tributaries of the tidal portion of the lower Potomac River, from Washington, D. C., downstream. The Rappahannock, York, and Chowan localities are in or near the Fall Line area where the water is fresh.

Dispersal

An extensive distribution in once-glaciated areas renders it probable that refugial populations of N. bifrenatus occupied the Chesapeake-lower Delaware region during at least the latter portion of Wisconsin glaciation. This would place it in proximity to northern drainage inter-connections established during glacial recession. Dispersal to favorable habitats in most of New York, including into the Lake Ontario-St. Lawrence drainage, could have been via routes discussed in detail by Cole (1967:37-39, 44-46). Radforth (1944) considered its limited distribution in Ontario as evidence that it entered that province fairly recently, and that insufficient time had elapsed for further spread down the St. Lawrence Valley. More recent range extensions for Quebec (Cuerrier, et al., 1946) indicate the latter limitation may not exist. An apparent absence of a significant dispersal north of the St. Lawrence River within Ontario and Quebec

may relate to low temperature intolerance (Radforth, 1944) and/or insufficient collecting.

To trace this minnow's probable postglacial movements through New England was somewhat more problematic. McCabe (1943) did not list N. bifrenatus among the 13 fishes in western Massachusetts whose present distribution there apparently resulted mainly from a relatively early postglacial entrance into the area and were dependent upon glacial flood waters for further spread. A primary criterion for thus classifying the 13 species was their occurrence upstream from all of a total of six waterfalls in central eastern New York and western Connecticut and Massachusetts. However, from the locality of each falls (McCabe, 1943) and the distribution maps (Harrington, 1947b; Whitworth, Berrien, and Keller, 1968) of N. bifrenatus, it was found that this species occurs above 4 of the 6 falls, indicating that it was a somewhat early penetrant of this southwestern New England region. The two falls above which it apparently is absent are Turners Falls on the Connecticut River and Salmon Falls on the Deerfield River. Bailey (1938) gave evidence supporting a hypothesis that there has been no major connection between the St. Lawrence and Merrimack drainages since early postglacial time, suggesting that the invasion of eastern New Hampshire and southeastern Maine was by a southwestern New England stock(s) of N. bifrenatus. Stream captures and major floods along the New England Atlantic coastal lowlands were invoked by Bailey as means for northeastward dispersal. Invasion of New England probably began from the lower and/or central Hudson drainage (across the low Hoosic River-Housatonic River divide), or via a Coastal Plain (now continental shelf) route, discussed below.

The distribution of *N. bifrenatus* and three other species on Long Island, southeastern New York, has direct bearing on the possibility that the adjacent continental shelf was once a Wisconsin glacial refugium and dispersal route for freshwater fishes. Long Island was well surveyed in 1938, when freshwater habitats in only its far western portion had been considerably modified; thus the survey results probably provide a good reflection of its native species distribution. Its fauna is depauperate even when compared to that of the lower Hudson drainage (Greeley, 1937) but certain aspects of species distribution are instructive. The few known bridle shiner populations were discovered well within the eastern half of Long Island (Greeley, 1939; recent CU series). The most western localities are in the eastward flowing Peconic River drainage and constitute a considerable distributional gap of about 70 airmiles to the lower Hudson area. Erimvzon o. oblongus and Enneacanthus obesus were found only in the Peconic drainage (Greeley, 1939) and Etheostoma f. fusiforme is apparently restricted to roughly the eastern half of Long Island (Collette, 1962: Fig. 8). The other presumably native, primary division species, all found in eastern and western areas of the island, are Esox a. americanus, Esox niger, Umbra pygmaea, Notemigonus crysoleucas, Ictalurus nebulosus, Aphredoderus savanus, Lepomis gibbosus, and Etheostoma olmstedi.

The majority of Long Island streams are short, coursing in a general north-south direction, and discharge relatively large volumes of cool to cold water directly into the South Bays and Long Island Sound. They were once excellent brook trout streams (some still are) for their entire or almost entire lengths. Thus they were apparently unfavorable for support of faunas rich in warmwater species of adjacent regions. However, personal (R.E.J.) familiarity with many of these streams indicates that N. bifrenatus and species with similar habits would not be ecologically excluded from portions of them. The Peconic River is the longest Long Island stream, has a naturally sluggish flow and higher temperatures (Moore, 1939) and, partly for these reasons, has the richest fauna.

Two hypotheses (or combination of the two) are offered relative to possible postglacial routes of all the above species onto Long Island: (1) dispersal from the area lying west and/or southwest of Long Island; (2) refugium within and dispersal from an area directly south of Long Island which was part of the Costal Plain during glaciation and is now part of the continental shelf.

Concerning the first hypothesis, all of the above species are known from the lower Hudson drainage and/or closely adjacent lowland regions southwest of Long Island. In particular, *N. bifrenatus* was reported from coves along the lower Hudson River (Greeley, 1937) and from Staten Island in the Hudson mouth (Harrington, 1947b). Possibly these

species moved eastward and/or northeastward onto Long Island after deglaciation, more likely when most glacial meltwater discharged through routes other than the Hudson Valley. Greeley (1939:31-32) gave evidence against this being an important pathway but apparently did not sufficiently consider the temporality of some dispersal routes and the brief period probably required to transit the lower Hudson. Eastward progression through the separate stream systems of the island would have been enhanced by temporary fresh or nearly fresh water conditions bridging stream mouths in bays and coves. In addition, headwater connections probably occurred since the stream divides on the island are very low, the soil largely easily-eroded gravel and other materials, and marginal swamps are common along streams. It is assumed that movement through western Long Island of the four species now limited to the eastern portion would have partly occurred during the Hypsithermal period when stream temperatures averaged higher. If once present in the western sector, N. bifrenatus probably was largely confined to more downstream, quieter, and warmer waters.

The second alternative derives evidence from the eastern confinement of the four species, which does not appear to have an entirely ecological basis. In addition, the distribution in Connecticut of two of these species, Enneacanthus obesus and Etheostoma fusiforme, clearly indicates that a route was taken from or around eastern Long Island and across a land and freshwater area that is now Long Island and Block Island Sounds (Whitworth, et al., 1968:124). This alternative is given credence since all Long Island species presently occur in eastern New Jersey (in part, Collette, 1962:168–169), indicating a likelihood of their having had access to the continental shelf. The past existence of freshwater species on the continental shelf is also implied by the record (Collette, 1962: Fig. 8) of E. fusiforme on Nantucket Island. This hypothesis was generally expressed by Greeley (1939:33) and elaborated upon by Cole (1967:36-39) to account for certain distributional relationships between two forms of E. olmstedi. It is favored to account for the present distribution on Long Island of the four species confined to its eastern portion.

The occurrence of *N. bifrenatus* in the Chowan drainage and southward is a significant

addition to our knowledge of the zoogeographic relations among the James, Chowan, and Roanoke drainages. The faunas of the western Chesapeake Bay drainages, from the Susquehanna to the James, are quite similar. The Roanoke, an Albermarle Sound tributary. is adjacent on the south to much of the montane portion of the James, but the distinct faunal break between the two mainly involves upland species. The faunal relations of the upper Chowan, draining regions between the lower James and Roanoke into Albemarle Sound, are much closer to the Roanoke than to the James. Species whose ranges terminate in the James or Roanoke were listed by Raney (1950). More recent work by the authors shows that the upper James and Roanoke faunas, while still markedly different, share more species than indicated by Raney and that the upper Chowan fauna is more similar to that of the upper Roanoke than previously realized. The faunas of the upper Tar and Neuse drainages, which flow into Pamlico Sound, are very similar to each other and less so to those of the upper Roanoke and Chowan drainages.

A means of dispersal among the several Chesapeake Bay drainages was the Greater Susquehanna River (Shattuck, 1906:134, pl. 31), the freshwater extension of the Susquehanna River during at least late Pleistocene. Also during late Pleistocene, the Chowan probably was a direct freshwater tributary of the Roanoke. Estuarine and at times freshwater conditions (Smith, 1893) now exist at their confluence. Since N. bifrenatus is an inhabitant of large rivers, it could feasibly have used these late Pleistocene routes for dispersal. Its occurrence on Kent Island (Hildebrand and Schroeder, 1928), just off the eastern shore of central Chesapeake Bay, Maryland, may be evidence that it used the Greater Susquehanna; this population may also have become established through a low salinity bridge furnished by the nearby Chester River. Although a lowland, large river exchange route between the Roanoke and Chowan would have been available, the distribution and ecology of several species shared by these two drainages indicate the past existence of an undetected higher Piedmont small stream avenue(s) of dispersal. Central eastern Coastal Plain and lower Piedmont species, such as N. bifrenatus, seem to

have had somewhat different histories and greater opportunities for spread than upland species; faunal breaks in the lowland areas of this region are relatively indistinct. In addition to stream capture and extended rivers, dispersal in central eastern lowlands has probably been facilitated by lateral meandering with water contact of adjacent base level streams and by the tolerance of some species to slightly brackish conditions.

Characters

The conditions of diagnostic characters in the specimens from the southern populations agree with those in northern populations. The pharyngeal teeth number 4-4 (5 of 5 specimens); a moderate to intense dark lateral body band of moderate to fairly narrow width, which continues over the operculum, and a discrete caudal spot conjoined with and usually darker than the band are present; the "bridle", a dark band from the orbits over the lachrymal bones, is confined anteriorly to the medial portion of the upper jaw and, occasionally and less distinctly, to the tip of the snout just above the upper jaw. Additional details of pigmentation were given and the head physiognomy illustrated in Hubbs and Raney (1947); the same figure was used by Moore (1957:123).

Geographic variation was not found in the following characters: lateral-line scales (pored and unpored) numbered 33 (in 19 specimens), 34 (45), 35 (22), 36 (2); body circumferential scales 22 (1), 23 (2), 24 (38), 25 (12), 26 (4), 27 (3); caudal peduncle circumferential scales 11 (1), 12 (66), 13 (1); anal fin rays 6 (2), 7 (98), 8 (3). Each drainage or state contributed approximately equal proportions to the modal count values and no clinal tendencies were evident. Circumferential body and caudal penduncle scales both above and below the lateral line, respectively, number 11-12 and 5. Bailey (1938) reported anal ray counts in 126 specimens, apparently from New Hampshire, to be 7 in 123 and 6 in 3.

The dorsal fin position is an important character for species identification and assessment of relationships within the Cyprinidae. The origin (insertion) of the dorsal fin of *N. bifrenatus* has been described as being anterior to or over the pelvic fin insertion (Hubbs, 1926:41-42). Miller (1963:24) stated that, in general, the dorsal fin is inserted more anterior in males than in females of American cyprinids. To ascertain the validity of these statements for N. bifrenatus, a sample of mature males and females from one collection was examined. The measurement, dorsal fin insertion to occiput, was obtained rather than dorsal insertion to snout tip or to caudal base since the former is more readily and accurately obtained. An absence of a sexual difference in dorsal position is indicated by Fig. 1. In all specimens studied from its geographic range, the dorsal origin was over the pelvic fin base, usually over the anterior portion of the pelvic base.

The pharyngeal arch is consistently stout but significant individual variation occurs in tooth form. Three or all four teeth of each arch often have a well-developed terminal hook. Long grinding surfaces and obsolescence or absence of a hook on some or all teeth of individual specimens are apparently the result of excessive wear. When the head is not greatly worn on teeth I–III, a low flange borders each edge of the incipient grinding surface; the anterior flange often bears a few small serrae.

Nuptial tuberculation of *N. bifrenatus* is not elaborate. In highly tuberculate males (e.g., CU 5988), which are generally the larger specimens, tubercles occur as a dense shagreen-like layer over the proximal three-fourths to four-fifths of pectoral fin rays 1 to 5 or 6; their density is greatest on the medial area of rays 2–4. On less highly tuberculate specimens, the tubercles are still multiserial on each ray segment in the

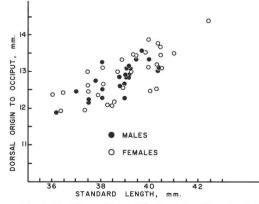


Fig. 1. Position of dorsal fin insertion (dorsal origin to occiput distance) in adults of N. bifrenatus (CU 9077) from the Cayuga Lake basin, New York.

medial area of rays 2-3. Females were not found with pectoral tubercles. On "high" males, tubercles were found on all dorsal and lateral areas of the head and on nape scales. They are largest and fairly closely spaced in the postero-dorsal area (more concentrated dorsolaterally than medially); slightly sparser on the operculum and very few in the suborbital area, over the lachrymal bone, and the mandibular rami. None were found over the branchiostegals. Nape tubercles are very sparse and generally scattered, but slightly more frequent along the posterior scale margins. Cephalic and nape tubercles are minute, the largest being slightly sub-equal in size to the average-sized pectoral fin tubercle. Many, generally smaller, males with tuberculate pectorals apparently lacked cephalic and nape tubercles. Widely scattered tubercles are found on the head and nape of only some females. Tuberculate individuals were collected only in or near the spawning period, which is during spring and early summer (Harrington, 1947b:188-9).

The "patches" and "bands" of tubercles described by Hubbs and Raney (1947:6) as being present on the head of N. bifrenatus may be clusters of superficial neuromasts, for the following reasons. We did not find well-defined patches and bands of tubercles. Hubbs and Raney did not report tubercles in some areas in which they were found during the present study. The distribution of tuberculate areas mentioned by Hubbs and Raney corresponds to that of well-developed patches of neuromasts. External portions of most neuromasts in N. bifrenatus are more obvious than its cephalic tubercles. Harrington (1948a:83) stated that N. bifrenatus does not develop tubercles. Tuberculate males were found in all collections examined which include mature males and ripe females, from Massachusetts, New York, Delaware and Virginia.

Sexual differences are developed in other characters, but on the whole the species does not show dimorphism as pronounced as in many American cyprinids. Larger nuptial males have thicker anterior pectoral fin rays than females with the medial portion of rays 2–4 usually slightly curved upward and the more sparsely tuberculate medial portion of the first ray bowed antero-ventrad. These conditions would permit the heaviest tuberculated rays of

the male to make more direct contact with the female during the spawning act. The roughened dorsal pectoral fin surface may also have a stimulatory function. Although considerable information from Harrington's works is available on reproduction in N. bifrenatus, the spawning act has not been clearly described. Hubbs and Raney (1947) and Raney (1947) mention other species of Notropis with and without the same or a very similar pectoral modification. It is interesting that males of N. bifrenatus perform considerable "nosing" of ripe females (Harrington, 1947b) although tubercles are minute or sometimes apparently absent on the anterior head. Other features of breeding adults mentioned or described by Harrington are the existence of sexual dimorphism in body depth and urogenital papillae (1950) and sexual dichromatism and functional dimorphism in body length, wherein the males court females larger than themselves (1947b; 1948a).

The cephalic lateral-line canal system of N. bifrenatus is considerably interrupted. In about 40 adults from much of its range, the preoperculomandibular canal was found to be uninterrupted in only about one-fourth and the infraorbital canal in fewer; the other cephalic canals were always interrupted. From 1 to 3 interruptions were found in each canal of most specimens; the greater numbers usually occurred in the infraorbital and supraorbital canals. Canal pore counts have the following ranges: supraorbital 5-11, infraorbital (including postocular commissure) 9–20, preoperculomandibular 6-11, supratemporal 0-8. These high ranges are partly due to loss or rudimentarity of canal sections. In no specimens were the supraorbital united with the postocular commissure nor the preoperculomandibular with the infraorbital. The courses of the canals are very similar to those of Notropis volucellus illustrated by Reno (1966). Harrington (1955) illustrated and described the canal bones of N. bifrenatus and discussed relations of some of these to underlying bones.

With apparent reduction in the cephalic lateralis canal system, there appears to have occurred a considerable development of superficial neuromasts on the head. Although these structures were not studied histologically, their identification seems certain. In external appearance they are very similar to those of *Notropis buchanani* and *N. volucellus* described by Reno (1966), which species we have examined. They are large and discrete depressions but whether they are actually tremognostic chambers (Reno, 1966:409) must be determined histologically. Their occurrence is generally in well-defined patches in the postoccipital, lateral interorbital, internasal, lachrymal, upper operculum, suborbital, and mandibular areas; most of these areas are coursed by lateralis canals.

The lateral line is typically incomplete. Hubbs and Raney (1947:4) stated that it "becomes nearly or quite complete at southern end of range", but they did not have material from south of the Potomac drainage. Apparently the lateral line is quite incomplete in most but not all populations in the southern portion of its range. Hildebrand and Schroeder (1928:127) examined 48 specimens from the Chesapeake Bay basin and found only one with a few pored scales posterior to the base of the dorsal fin and most with pores ending below this fin base. The Neuse, Chowan, and Rappahannock drainage specimens have pores developed on approximately only the anterior one-third to one-half of the lateral series scales. However, those from the James drainage and from a lower Delaware drainage collection have complete or nearly complete lateral lines. These specimens are also exceptional in their body length. Harrington (1947b) recorded the maximum known standard length of the species to be 48 mm. Two of the four specimens in the James drainage series are females of 48.1 and 47.5 mm S L; the others are males of 43.0 and 41.3 mm S L. Those from the Delaware series also average large, the largest being a 50.1 mm S L female. Fig. 2, based on a population with incomplete lateral lines, demonstrates a general increase in the number of pored scales with increase in standard length and considerable variation within size classes. It is assumed that the same or a similar pattern occurs in other populations whose members have markedly incomplete lateral lines. The James and Delaware specimens apparently had a greater rate of pore development than that in the other populations sampled. More numerous pores and larger body size seem to be correlated in these specimens, but

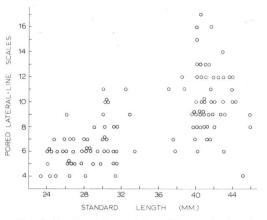


Fig. 2. Number of pored lateral-line scales in relation to standard length in N. *bifrenatus* from the Cayuga Lake basin, New York.

whether these differences are due to genetic or environmental effects or a combination of these was not determined.

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