12

Global Ecology & Biogeography Letters (in press)

final copy

Fish scale evidence for rapid post-glacial colonization of an Atlantic coastal pond

Robert A. Daniels, New York State Museum, CEC 3140, Albany, NY 12230, USA,
rdaniels@mail.nysed.gov

Dorothy Peteet, NASA/Goddard Institute for Space Studies, 2880 Broadway, NY 10025, USA
and Lamont-Doherty Earth Observatory, Room 204 New Core Laboratory, Palisades, NY
10964, USA, peteet@ldeo.columbia.edu

IN-48

024476

Running head: Evidence of colonization from fish scales

Address correspondence to R.A. Daniels at the above address

Abstract. Fish scales from the sediment of Allamuchy Pond, New Jersey, USA, indicate that fishes were present in the pond within 400 years of the time of the first deposition of organic material, at approximately 12,600 yrs BP. The earliest of the scales, from a white sucker, *Catostomus commersoni*, appears in sediment dated 12,260 ± 220 yrs BP. Presence of scales in sediment deposited before 10,000 yrs BP indicates that Atlantic salmon, *Salmo salar*, sunfish, *Lepomis* sp., and yellow perch, *Perca flavescens*, also were early inhabitants of the pond. The timing of the arrival of each of these fishes suggests that they migrated out from Atlantic coastal refugia. A minnow scale, referred to Phoxininae, was also retrieved; it could not be matched to any cyprinid currently found in northeastern North America. The species present historically in this pond are from five families found currently in ponds throughout the Northeast and suggest that the lentic palaeo-environment was similar to present mid-elevation or high-latitude lentic systems.

Key words. Allamuchy Pond, Atlantic coastal refugia, Atlantic salmon, fish scale, Phoxininae, post-glacial fish migration, sunfish, yellow perch, white sucker.

INTRODUCTION

Fish remains are rare from the portion of northeastern North America that was glaciated during the Pleistocene. Reports on the remains of fish from the Northeast are conspicuously absent from reviews of the Cenozoic fish fauna of North America (Uyeno & Miller, 1963). However, such remains are extremely important. The discovery of remains from the period immediately following deglaciation offers important clues to the identity and source of early colonists. Remains also establish the presence of species in the region. Use of fish remains, specifically fish scales, offers zoogeographers another tool that can be used to infer historic fish distributions along with insights drawn from the current distributions of fish, past changes in drainages patterns, and an examination of meristic, morphometric and genetic variation among current populations.

The earliest report on the identity of fish scales retrieved from lake sediment from the Northeast is that of Lagler & Vallentyne (1956). They reported the presence of scales of golden shiner, *Notemigonus crysoleucas* (Mitchill), and banded killifish, *Fundulus diaphanus* (Lesueur), from sediments of Linsley Pond, Connecticut, USA, dated at 7,500 yrs BP. We briefly reported on the presence of five additional taxa in an earlier publication (Peteet *et al.*,1993). Thus, of the 150 fish species regarded as native to the Northeast (Halliwell *et al.*, 1998), the palaeontological record includes scales from only seven species--five of them described in detail here for the first time.

These scales were recovered from sediments in Allamuchy Pond, northwestern New Jersey, USA, (40° 55' N, 74° 50' W). This pond is in the Delaware River drainage basin at an elevation of 218 m. It is about 20 ha in area and has a maximum depth of 8.2 m. It has three intermittent inlets and an outlet that drains north and flows into the Pequest River. It is approximately 25 stream km from the Delaware River. Allamuchy Pond is on the southern rim of the Great Valley section of the Valley and Ridge physiographic province. The Woodfordian terminal moraine position is south of the pond. The timing of the glacial retreat from this area of New Jersey is controversial, with estimates ranging from 18,000 yrs BP to 13,000 yrs BP (Peteet *et al.*,1993). The estimate of first organic deposition in Allamuchy Pond is 12,590 ± 430 yrs BP, based on AMS ^{14}C dates of plant remains (Peteet *et al.*, 1993). As the Pequest sublobe of the Hudson-Champlain lobe of the Laurentide ice sheet retreated, Allamuchy Pond and the Pequest River channel developed. The Pequest River, which joins the Delaware River, is, and has been, the only route available for migrating freshwater fish to reach Allamuchy Pond (Cotter *et al.*, 1986).

The fishes that would have had first access to this site would have been those residing in various Atlantic refugia, although previous reports indicate that fishes from Mississippian refugia may also have had access (e.g. Schmidt, 1986). All fishes present in the Northeast arrived after the retreat of the Wisconsinan glaciers. Some, such as diadromous or euryhaline species, would have had direct, early access to developing river systems. However, the majority of extant species in the Northeast are primary division freshwater species, i.e., they have a low tolerance for salinity. Thus, dispersal of these fishes required freshwater connections. Schmidt (1986) describes several Atlantic slope refugia that supported freshwater fishes: lowland coastal plain, upland coastal plain, and northeastern coastal refugia. The upland coastal plain refugium, postulated as being in the area currently drained by the Potomac River, is the refugium most closely linked geographically with this site. Schmidt (1986) suggests that stream capture was the most likely method of dispersal for fishes from this refugium. Fishes from the lowland coastal plain refugium (on the Atlantic slope off present-day Virginia and North Carolina) could have gained access to the Allamuchy Pond site through extensive interconnected deltas between 12,000 and 3,500 yrs BP (Strahler, 1966). Schmidt (1986) provided arguments supporting the presence of a northeastern coastal refugium isolated from the more southern refugia. This refugium existed on the Georges Bank and may have extended eastward to include the Sable Island and Grand Banks area. The dispersal of these fishes is mostly likely to have occurred through stream connections in what is now southern New England. Early workers (e.g., Flint, 1971) suggested that fish from Mississippian refugia could have gained access to Atlantic coastal drainages as early as 13,000 yrs BP through the Mohawk and Hudson Valleys. More recent work (articles in Cadwell, 1986) demonstrates that fishes from the western refugia did not have access to this site during this early time period.

METHODS

Sediment cores were taken from Allamuchy Pond during winter using a modified Livingstone piston corer (Wright, Mann & Glaser, 1984) and were refrigerated. Then, the lower portion of the core was sampled at 5- or 10-cm intervals. Samples were soaked in KOH overnight and washed through 0.5 and 0.1 mm mesh screens to retrieve fish macrofossils, including scales and bones (see: Peteet *et al.*, 1993). Scales were placed between microscope slides, viewed with transmitted light and compared to figures in Cockerell (1913), Cooper (1940), Daniels (1996), and Lagler (1947), and to scales from 140 fish species that inhabit inland waters of northeastern North America today.

Radiocarbon dates are accelerator mass spectrometry (AMS) dates on single identified plant macrofossils. The macrofossils used were soaked, screened through water, and picked following the same procedure described above for the fish remains. Then they were dried and sent for dating. Because the macrofossils are of terrestrial origin, they cannot be contaminated from hard-water effects. This method provides a more refined interpretation since the macrofossil is pinpointed within the pollen zones from which it is taken (Peteet *et al.*, 1990). Finally, since the macrofossil is identified, it substantiates the presence of the species during a specific time period and pollen zone (Peteet *et al.*, 1993).

LITHOLOGY, CHRONOLOGY AND VEGETATION

The basal sediments in Allamuchy Pond are clays and silts. The 9.3-m sediment core was taken in 7 m of water and was composed of soft gyttja from 0 to 7.0 m, dark brown consolidated gyttja from 7.0 to 9.0 m and olive-brown clay with some silt from 9.0 to 9.3 m. The deposits in the core from 7.0 to 9.0 m were laid down during an approximately 4500-yr period beginning at 12,260 ± 220 yrs BP. The vegetation common in the area for several thousand years after deglaciation was probably a mixture of shrubs, herbs and trees best labeled a park-tundra environment (Cotter *et al.*, 1986). The dominant forest component when the earliest fish macrofossils were deposited was *Picea* (Peteet *et al.*, 1993). Between 9,000 and 7,000 yrs BP, the dominant pollen was *Quercus* (Peteet *et al.*, 1993). Plant fossils suggest that the period between 12,000 to 10,800 yrs BP was one of continued warming, but nonetheless cool and mesic. A cooling period, a Younger Dryas equivalent, occurred between 10,800 and 10,000 yrs BP. This cooling period ended abruptly and was followed by a period of rapid warming leading to the loss of boreal conifers and replacement with a plant community dominated by thermophilous species (Peteet *et al.*, 1993).

SPECIES ACCOUNTS

Family Catostomidae

A partial sucker scale (Fig. 1) from the 9.0-9.1 m layer is the oldest fish macrofossil found at the site (Table 1). The fragment includes part of the anterior field, a lateral field and about half of the posterior field. The focus is central. There are radii in both the anterior and posterior fields and radii are conspicuously absent from the lateral field. Ridges surround the focus; ridges are approximately equal in number in the anterior and lateral fields and less abundant in the posterior field. The scale appears to be roughly oval with the longitudinal axis longer than the transverse axis. There are no ctenii. Based on these characteristics, this scale is that of a white sucker, *Catostomus commersoni* (Lacepède) (see: Daniels, 1996). The lack of radii in the lateral field precludes an identification of longnose sucker, *C. catostomus* (Forster) which is the only other catastomid currently present in the Northeast with scales with a longitudinal axis larger than the transverse.

A second fragment, from layer 8.9-9.0 m, may also be referred to a catostomid. The scale is cycloid. It consists of a lateral field and part of the posterior field. Both fields have radii. The ridges in the lateral field are more numerous than the ridges in the posterior field, characteristics consistent with those of the Catostomidae, but too little of the scale remains for reliable identification.

White sucker, a member of the Catostomini, a large group of primarily western North American catostomids, is one of the 26 currently recognized species within the tribe. It is one of three species found in drainages east of the Continental Divide. In fact, its range is more congruent with members of the tribe Moxostomatini, a group with no representatives in western North American. Smith (1992) noted that these tribes consisted of two types of fish. The species with more ancestral traits (e.g. *Chasmistes* and *Erimyzon*) tend to inhabit lentic systems or large rivers and those with more derived characteristics (e.g. mountain and torrent suckers) frequent upland and headwater creeks and brooks. In the Northeast, where torrent suckers are absent and chubsuckers rare, white sucker is typically found, not only in lakes and rivers, but also in creeks and brooks. In short, white sucker is widely distributed geographically and occupies a wide variety of habitats.

White sucker ranges from Hudson Bay to the drainages of the southern Appalachians in the east to the Mackenzie River and the drainages of the southern Rocky Mountains in the west (Lee *et al.*, 1980 *et seq.*). It is among the most ubiquitous fishes currently in the Northeast (Halliwell *et al.*, 1998) and is present in all major Atlantic slope drainages from the Peedee River system to the Saint Lawrence River, although it is confined to upland areas in the southern drainages. It tolerates a wide range of habitats as well. It is found in streams and lakes throughout its geographic range. It inhabits brooks, creeks, rivers, ponds and large lakes and tolerates clear and turbid, cool and cold, high- and low-flow systems and acidic waters.

Few workers have divided this species into subspecies and Bailey & Allum (1962) rejected the notion of subspecific designations. Based on morphometric and meristic characteristics, Metcalf (1966) suggested that three geographically distinct forms existed (or did exist) in the Mississippi basin: Teays-Mississippi, Plains, and Hudson Bay. However, this scheme does not include white suckers from the eastern slope of the Appalachians. Crossman and McAllister (1986) note the presence of white sucker in three Mississippian refugia and the possibility of its presence in Atlantic slope refugia during the late Wisconsinan. In the same volume, Underhill (1986), and Schmidt (1986) postulate the presence of white sucker in both Mississippian and Atlantic refugia.

It is difficult to assess the distribution of white sucker during the final stages of the Wisconsinan because currently it is widely distributed and seems to lack obvious subpopulations. Smith (1992) demonstrated that, within its genus, white sucker shows the fewest morphological changes from ancestral states, indicating a long-term residence in central North America that is also supported by fossil records (Smith, 1954,1958; Smith, 1963). The presence of this scale in 12,000-year-old deposits can be explained in two ways. White sucker was either an early migrant into Atlantic slope drainages, arriving from Mississippian refugia through the Mohawk and Hudson River valleys after deglaciation, or white sucker was a component of the Atlantic refugia.

White sucker has excellent dispersal capabilities as noted by Greene (1935) and Smith (1992). Fish of Mississippian origin could have used a Mohawk River outlet (Flint, 1971) or a Great Lakes connection to glacial Lake Vermont and its Hudson River outlet (Crossman & McAllister, 1986). Dineen (1986), Cadwell (1986) and Connally & Sirkin (1986) suggested that neither route was open early enough to allow fish to enter the Delaware River system ca. 12,000 yrs BP. The most likely explanation is that white sucker was a component of the upland Atlantic refugium. Its presence in Allamuchy Pond can be explained by a simple upstream migration of the species.

Family Cyprinidae

A scale from the 7.35-7.4 layer is refered to Cyprinidae (Fig. 2). This scale is cycloid, has radii in the posterior field only and a focus much closer to the anterior than to the posterior margin--scale characteristics associated with only this family of northeastern fishes (Daniels, 1996). The scale measures 3 by 1.9 mm and has a focus length: longitudinal length ratio of 0.33. It is shield-shaped with a rounded posterior margin, straight lateral margins, hypertrophied anterolateral corners and an anterior margin roughly the shape of an asymetrical arch. Ridges encompass the focus. They are about equally abundant in all four fields but greatly expanded (peaked) in the posterior field. Radii are parallel, relatively straight and include five primary radii and one, outer secondary radius.

The characteristics of this scale do not match any of those from species currently inhabiting northeastern waters. The shape differs from most northeastern minnows, which have scales with a transverse axis greater than the longitudinal one. No minnow currently known to inhabit northeastern streams or lakes has hypertrophied anterolateral corners. The primary radii count is low and no northeastern minnow has parallel radii. This scale shows a number of the plesiomorphic character states used by Coburn and Cavender (1992) to compare leuciscins (composed of Eurasian minnows and the North American *Notemigonus crysoleucas*) and phoxinins (all other North American minnows and some Eurasian forms). Plesiomorphic characters associated with leuciscins found on this scale include shield-shape; few, straight radii in the posterior field; and fine, evenly spaced ridges that peak in the center of the posterior field. It also possesses some of the more derived characters associated with phoxinin scales: the absence of radii in the anterior field and a subcentral focus. We cannot refer this scale to any genus or species of extant northeastern North American minnow.

Family Salmonidae

Two scales from the collection lack ctenii and radii. The first, from the 8.8-8.9 m layer, is teardrop-shaped with a pointed posterior margin and a rounded anterior margin. The second, from the 7.6-7.7 m layer, is round. Concentric ridges encompass the focus in both scales. Both scales are slightly eroded but these characteristics indicate that the scales belong to species in either the Salmonidae or Osmeridae.

The anterior of the older scale is slightly eroded, so ratios are approximate (Table 1). Despite this, the focus is subcentral, slightly closer to the anterior margin than to the posterior, open and surrounded by tightly spaced ridges. This scale is from a salmonin. Two native genera of Salmoninae are extant in northeastern North America: *Salmo* and *Salvelinus*. *Salmo* is represented by one species, *S. salar* L., Atlantic salmon; *Salvelinus* is represented by three species: *S. alpinus* (L.) Arctic charr, *S. fontinalis* (Mitchill), brook trout, and *S. namaycush* (Walbaum), lake trout. Atlantic salmon, Arctic charr and brook trout are postulated to have been present in Atlantic refugia (Schmidt, 1986; Underhill, 1986). However, since Atlantic salmon and Arctic charr are anadromous, they would not have been confined to refugia and would not have had to follow the routes used by primary division fishes. These species could have entered freshwater whenever habitat became suitable, although it is unclear how rapid this process may have been since salmon return to natal streams with a high degree of accuracy (Mills, 1989).

The scale is more *Salmo*-like. *Salvelinus* scales are ovoid with a longitudinal axis nearly twice that of the transverse axis. Ventral scales are even narrower than those found laterally on the body. The antero- and posterolateral corners are rounded and the lateral margins are typically straight and parallel. We found no scales with pointed posterior margins on any of the *Salvelinus* spp. examined. *Salmo* scales are also usually longer than they are wide, but the ratio is greater in *Salmo*, at 0.66 (Daniels, 1996). Typical scales have rounded antero- and posterolateral corners, but the lateral margins are also slightly rounded, giving the entire scale a more rounded appearance. Ventral scales, particularly interpelvic scales, often have pointed posterior margins.

We identify the teardrop scale as belonging to *Salmo salar,* Atlantic salmon. This is a ventral scale, most likely an interpelvic scale. Atlantic salmon is the only native member of this genus in North America and is indigenous to coastal streams from the Hudson River to Ungava Bay (MacCrimmon & Gots, 1979). The relative abundance of this species in these streams in early post-glacial times has recently been questioned (Carlson, 1992). However, the presence of this scale provides evidence that a member of the genus, most likely *S. salar*, invaded inland waters in the Northeast more than 10,000 years ago.

The scale from layer 7.6-7.7 is round. This is an atypical scale, but more *Salmo*-like than *Salvelinus*-like. If this is a salmonid scale, then the focus is very close to the posterior margin. The ridges surround the focus, but are loosely spaced in the anterior field and tightly spaced in the posterior field. There is an alternative explanation: the scale may belong to a member of the Osmeridae. Smelt scales have a loose focus relatively close to the anterior margin and ridges that are tightly spaced in the anterior field and expanded in the large posterior field (Daniels, 1996). Smelt scales also tend to have distinct corners and parallel lateral margins. This scale, unlike typical smelt scales, has a tight focus and is round. A definite identification of this scale is not possible.

Family Centrarchidae

Five of the scales retrieved are from Centrarchidae, sunfishes. Three scales are regenerated, but these scales are complete enough to allow identification. These scales are wider than they are long (Table 1), have 10-12 radii in the anterior field and have ctenii in the posterior field. The fact that the ctenii are whole is important since this characteristic is found in only one group of fishes currently living in northeastern North America, the Centrarchidae. The oldest sunfish scale, from layer 8.8-8.9 m, is the most complete (Fig. 3). It has 11 radii; five are primary and the six secondary radii are both peripheral and internal. Ctenii form a roughly triangular patch with the anterior apex separated from the well-defined focus by five ridges. Proximal and distal ctenii are whole, although they are slightly eroded. The tight focus is subcentral (Table 1). The scale is subquadrate with squared antero- and postero-lateral corners. The scale from layer 7.9-8.0 is small, rounded and broken (Fig. 4) but enough remains to allow identification. The ctenial patch and the radii count support the sunfish identification.

Centrarchidae is an endemic North American family with an ancestral range confined, with one exception, to freshwater east of the continental divide. Currently, 16 species in six genera are found in the Northeast. Despite the prevalence of sunfishes in northeastern freshwaters, their zoogeography is poorly known, in part due to their broad distribution and recent poorly-documented introductions into new drainage basins. Some species are recent introductions from southern or Mississippian assemblages that have expanded their ranges during the last two centuries. Other species were likely residents of one or more of the Atlantic refugia (Schmidt, 1986).

The scales from Allamuchy Pond are most likely *Lepomis* or *Enneacanthus*. *Acantharchus* scales have weak ctenii. *Ambloplites* and *Pomoxis* scales tend to have a higher radii count. *Micropterus* scales tend to have a lower radii count and are often longer than wide

(Daniels 1996). *Acantharchus* and *Enneacanthus* species have affinities with the Atlantic coastal plain and some *Lepomis* species are tentatively recognized as having affinities with the Georgian Banks refugium (Schmidt, 1986). As was true for white sucker, the most likely explanation for the presence of sunfish in Allamuchy Pond over 10,000 yrs BP is that it migrated out from Atlantic coastal refugia.

Family Percidae

Three scales belong to *Perca flavescens* (Mitchill), yellow perch. Yellow perch scales are ctenoid, distinctive, and share few characteristics with other species of the Northeast. The most distinctive feature is the large indentations on the anterior margin at the radii. Lateral scales have about seven primary radii and often lack secondary radii and have a ctenial patch with a straight edge anteriorly. Ctenial bases are longer than they are wide. The small scale from the 8.5-8.6 m layer (Fig.5) has three primary radii and one secondary radius, and a focus set in the posterior quarter of the scale. The posterior edge of the scale is eroded so the ctenii are missing. Ctenial bases form a patch in the posterior field with a straight anterior edge just posterior to the focus. Although this scale is not a typical yellow perch scale, it is consistent with scales found laterally in the caudal peduncle area of this species. Three scales were found in layer 8.6-8.7 m. One is a regenerated scale that is probably from a yellow perch. Like any regenerated scale, it lacks some of the characteristics necessary for positive identification. However, this scale has an anterior margin with deep indentations at the seven radii. The other two scales are yellow perch. Both have a strongly indented anterior margin, a straight anterior edge on the ctenial patch, ctenial bases that are longer than they are wide, and a focus in the posterior third of the scale.

McPhail & Lindsey (1970) suggested that *Perca* was distributed across northeastern

North America, Europe and Asia before the beginning of the Wisconsinan glaciation. As glaciers advanced in North America, populations were isolated in Mississippian and Atlantic refugia. *Perca* is well represented in the fossil record of the Mississippi River drainage (Smith, 1954; Smith, 1963). Crossman & McAllister (1986) and Underhill (1986) also recognized the presence of this species in Atlantic refugia. Others (e.g. George, 1981) suggested that yellow perch migrated into eastern North America from Mississippian refugia via the Mohawk system. A second type of data supports the presence of yellow perch in both Mississippian and Atlantic slope refugia. Differences in the distribution of polymorphic alleles in yellow perch suggest the presence of eastern and western populations with an overlap zone in western New York and Pennsylvania (Todd & Hatcher, 1993).

Dispersal capabilities of yellow perch are excellent. Yellow perch, although a primary-division fish, is tolerant of brackish water (Scott & Crossman, 1973) but its dispersal is apparently limited to cold temperatures (Ryder, Scott and Crossman, 1964). Tolerance of brackish water enhanced the dispersal capabilities of yellow perch during early post-glacial times; cold temperatures did not seem to hinder its early dispersal. Although usually a pond dweller, yellow perch is often found in streams and Bloomquist & Daniels (1996) suggested that suitable microhabitat is available for pond-dwelling fishes in the margins of riffles. This slow-water microhabitat in riffles provides a migration route that is constant and seasonably abundant. Although, as was the case for white sucker, a route through the Mohawk River is possible, the presence of yellow perch scales in Allamuchy Pond over 10,000 yrs BP supports the contention that yellow perch were present in Atlantic slope refugia.

DISCUSSION

Researchers explain the repatriation of the Northeast by aquatic fauna by the dispersal of these organisms from established ecosystems into newly available habitat following the retreat of the Wisconsinan glaciers (McAllister *et al.*, 1986). Most freshwater fish in North America have relatively good dispersal abilities (Jenkins & Burkhead, 1992). At the end of the Wisconsinan glaciation, as habitat became available on the margins of established ecosystems, successful migrants were those with the best dispersal mechanisms, subjected to an extrinsic event that promoted emigration, and those capable of surviving in new and often marginal habitat.

The discovery of these scales in the sediments of Allamuchy Pond is important. These specimens allow us to question some of the standard explanations of fish assemblage development. They also provide us with specific information on each of the five taxa represented, which allows a better understanding of the zoogeography of each.

The paucity of specimens and the time span between the deposition of the first white sucker scale and the final sunfish scale in this collection does not allow us to draw many conclusions on the assemblage composition of the pond. These specimens do indicate that the component species of this post-glaciation period were similar to those found in mid-elevation and, to some extent, upland and higher-latitude lakes today. The fishes represented are those typical of small, mid-elevation and upland lakes such as those found in the Adirondack Mountains in upstate New York today (George, 1981). These species are also included in the ichthyofauna of cold temperate lakes in Ontario (Keast, 1978). White sucker and Atlantic salmon, and certain minnows, are also typical of high-latitude lakes in northeastern North America as well (Scott & Crossman, 1973).

The fact that sucker, trout, sunfish, minnow and yellow perch scales were found in the pond within 2,000 years of the first organic deposition implies that conditions were right for emigration and that these species possessed the behaviours needed to effect this migration. It is interesting that these are the very taxa that exist in so many marginal or difficult-to-reach lakes today. For example, sucker, trout, sunfish and minnow species reside in, and are considered native to, many Adirondack lakes. Based on Mather (1890), yellow perch, are regarded as introduced in upland lakes (e.g. George, 1981). The ability of yellow perch to disperse through streams (Becker, 1992; Bloomquist & Daniels, 1995) is well documented. Given its ability to colonize available space rapidly, the absence of yellow perch from Adirondack lakes is suspect, and needs further examination.

In general, the identity of the scales offers few surprises. White sucker, Atlantic salmon, and yellow perch were regarded as residents of Atlantic refugia during the Wisconsinan glaciation (Schmidt, 1986). Physical evidence of their likely presence in these refugia is valuable, but does not alter the established viewpoint. Similarly, the identity of the sunfish scales as either *Enneacanthus* or *Lepomis* also follows current beliefs. These two genera are regarded as Atlantic slope residents. The other genera now found in the Northeast, *Ambloplites, Pomoxis* and *Micropterus*, are regarded as introduced in the Delaware and Hudson River drainages (Smith, 1985).

The most interesting scale, since it does not match the scales of any minnow now living in the Northeast, is the unidentified cyprinid scale. This is a phoxinin scale with no anterior radii and a focus in the anterior third of the scale. The unusual hypertrophied anterolateral corners and the low length-width ratio would seem to put this scale on a fish placed in the western clade of

Coburn & Cavender (1992). Although this clade comprises mostly fishes found west of the continental divide, it tentatively includes *Rhinichthys,* a genus that includes two species that are sympatric with the other species found in Allamuchy Pond. Furthermore, the two *Rhinichthys* spp. are believed to be residents of the Atlantic slope refugia. We have examined non-lateral scales from most extant fishes from the Northeast and have not found any that resemble this scale. Little more can be read into this lone scale. The possibility that this scale is from a form that is now extinct is a reasonable conclusion.

Based on the fishes present, the palaeo-environment of Allamuchy Pond was probably not unlike that of an oligotrophic, high-latitude or high-altitude lake today. The earliest residents, Atlantic salmon and white sucker, are tolerant of cool temperatures (Scott & Crossman, 1973). Although yellow perch and *Lepomis* are limited in distribution by very cold temperatures and are absent from or rare in high-latitude lakes today, both species maintain large populations in high-altitude lakes in the Northeast and elsewhere.

The discovery of these scales provides new information on the historic distribution of these five taxa, clues to the palaeo-environment of areas just after the retreat of the Wisconsinan glaciers, and information on the composition of Atlantic coast refugia.

ACKNOWLEDGMENTS

We thank R.E. Schmidt, C.J. George, and D.H. Cadwell for reviewing the draft manuscript. J. Yost photographed the scales. P. Kernan illustrated the figures. Contribution number 784 of the New York State Museum.

REFERENCES

Bailey, R.M. & Allum, O.M. (1962) *Fishes of South Dakota,* p. 131. Miscellaneous Publications of the Museum of Zoology 119. University of Michigan, Ann Arbor.

Becker, C.G. (1983) *Fishes of Wisconsin*, p. 1052. University of Wisconsin Press, Madison.

Bloomquist, D.A. & Daniels, R.A. (1995) Microhabitat use by fish of the riffle zone of Catskill Creek. *Final reports of the Tibor T. Polgar fellowship program 1994.* (ed. by W.C. Nieder, J.R. Waldman & E.A. Blair), pp. viii1-viii22. Hudson River Foundation, New York.

Cadwell, D.H. (1986) Late Wisconsinan stratigraphy of the Catskill Mountains. *The Wisconsinan stage of the First Geological District, eastern New York*, (ed. by D.H.Cadwell), pp. 73-88. New York State Museum Bulletin 455.

Carlson, C.C. (1992) *The Atlantic salmon in New England prehistory and history: social and environmental implications*, p. 198. Ph.D. dissertation. University of Massachusetts, Amherst.

Coburn, M.M. & Cavender, T.M. (1992) Interrelationships of North American cyprinid fishes. *Systematics, historical ecology, and North American freshwater fishes,* (ed. by R.L. Mayden), pp. 328-373. Stanford University Press, Stanford.

Cockerell, T.D.A. (1913) Observations on fish scales. *Bull. U.S. Bur. Fish.* **32**,117-174.

Connally, G.G. & Sirkin, L. (1986) Woodfordian ice margins, recessional events, and pollen stratigraphy of the mid-Hudson Valley. *The Wisconsinan stage of the First Geological District, eastern New York*, (ed. by D.H. Cadwell), pp. 50-72. New York State Museum Bulletin 455.

Cooper, G.P. (1940) A biological survey of the Rangely Lakes, with special reference to the trout and salmon. Maine Department of Inland Fisheries and Game, Report. **3**,1-182.

Cotter, J.F.P., Ridge, J.C., Evanson, E.B., Sevon, W.D., Sirkin, L., & Stuckenrath, R. (1986) The Wisconsinan history of the Great Valley, Pennsylvania and New Jersey, and the age of the "Terminal Moraine". *The Wisconsinan stage of the First Geological District, eastern New York,* (ed. by D.H. Cadwell), pp. 22-49. New York State Museum Bulletin 455.

Crossman, E.J. & McAllister,D.E. (1986) Zoogeography of freshwater fishers of the Hudson Bay drainage, Ungava Bay and the Arctic Archipelago. *The zoogeography of North American freshwater fishes,* (ed. by C.H. Hocutt & E.O. Wiley), pp. 53-104. John Wiley and Sons, New York.

Daniels, R.A. (1996) *Guide to the identification of scales of inland fishes of northeastern North America*, p.97. New York State Museum Bulletin 488.

Dineen, R.J. (1986) Deglaciation of the Hudson Valley between Hyde Park and Albany, New York. *The Wisconsinan Stage of the First Geological District, eastern New York,* (ed. by D.H. Cadwell), pp. 89-108. New York State Museum Bulletin 455.

Flint, R.F. (1971) *Glacial and Quaternary geology.* John Wiley and Sons, New York.

George, C.J. (1981) *The fishes of the Adirondack Park*, p. 94. New York State Department of Environmental Conservation, Lake Monograph Program, Albany.

Greene, C.W. (1935) *The distribution of Wisconsin fishes*, p. 235. State of Wisconsin Conservation Commission, Madison.

Halliwell, D.B., Langdon, R.W., Daniels, R.A., Kurtenbach, J.P., and Jacobson, R.A.. 1998 Classification of freshwater fishes of the northeastern Unites States for use in the development of indices of biological integrity, with regional applications. *Assessment approaches for estimating biological integrity using fish communities* (ed. by T.P.

Simon), pp. 301-337. CRC Press, LLC, Boca Raton, FL.

Keast, A. (1978) Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. *Environ. Biol. Fish.* **3**,7-31.

Lagler, K.F. (1947) Scale characters of the families of Great Lakes fishes. *Am. Microscopical Soc. Trans.* **66**,149-171.

Lagler, K.F. & Valentyne, J.R. (1956) Fish scales in a sediment core from Linsley Pond, Connecticut. *Science*, **124**, 368.

Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E., & Stauffer, Jr., J.R. (1980 *et seq.*) *Atlas of North American freshwater fishes*, p.854. North Carolina State Museum of Natural History, Raleigh.

MacCrimmon, H.R. & Gots, B.L. (1979) World distribution of Atlantic salmon, *Salmo salar*. *Jour. Fish. Bd. Can.* **36**, 422-457.

Mather, F. (1886*) Memoranda relating to Adirondack fishes with descriptions of new species from researches made in 1882*, p. 56. State of New York Adirondack Survey. Appendix to the twelfth report.

McAllister, D.E., Platania, S.P., Schueler, F.W., Baldwin, M.E., & Lee, D.S. (1986) Ichthyofaunal patterns on a geographic grid. *The zoogeography of North American freshwater fishes*, (ed. by C.H. Hocutt and E.O. Wiley), pp. 17-52. John Wiley and Sons, New York.

McPhail, J.D. & Lindsey,C.C. (1970) *Freshwater fishes of northwestern Canada and Alaska*, p. 381. Fisheries Research Board of Canada Bulletin 173, Ottawa.

Metcalf, A.L. (1966) Fishes of the Kansas River system. *Univ. Kan. Publ. Mus. Nat. Hist.* **17**, 23-189.

Mills, D. (1989) *Ecology and management of Atlantic salmon*, p. 351. Chapman and Hall, London.

Peteet, D.M., Vogel, J.S., Nelson, D.E., Southon, J.R., Nickman, J.R., & Heusser, L.E. (1990) Younger Dryas climatic reversal in northeastern USA? AMS ages for an old problem. *Quaternary Res.* **33**, 219-230.

Peteet, D.M., Daniels, R.A., Heusser, L.E., Vogel, J.S., Southon, J.R. & Nelson, D.E. (1993) Late-glacial pollen, macrofossils and fish remains in northeastern U.S.A.--the Younger Dryas oscillation. *Quaternary Sci. Rev.* **12**, 597-612.

Ryder, R.A., Scott, W.B. & Crossman, E.J. (1964) Fishes of northern Ontario, north of the Albany River. *Roy. Ontario Mus. (Life Science) Cont.* **60**, 1-30.

Schmidt, R.E. (1986) Zoogeography of the northern Applachians. *The zoogeography of North American freshwater fishes.* (ed. by C.H. Hocutt & E.O. Wiley), pp. 137-159. John Wiley and Sons, New York.

Scott, W.B. & Crossman, E.J. (1973) *Freshwater fishes of Canada*, p. 966. Fisheries Research Board of Canada Bulletin 184, Ottawa.

Smith, C.L. (1954) Pleistocene fishes of the Berends fauna of Beaver County, Oklahoma. *Copeia*, **1954,** 282-289.

Smith, C.L. (1958) Additional Pleistocene fishes from Kansas and Oklahoma. *Copeia*, **1958,** 176-180.

Smith, C.L. (1985) *Inland Fishes of New York State*, p. 522. Department of Environmental Conservation, Albany.

Smith, G.R. (1963) A late Illinoian fish fauna from southwestern Kansas and its climatic significance. *Copeia*, **1963**, 278-285.

Smith, G.R. (1992) Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia. *Systematics, historical ecology and North American freshwater fishes,* (ed. by R.L. Mayden), pp. 778-826. Stanford University Press, Stanford.

Strahler, A.N. (1966) *A geologist's view of Cape Cod.* The Natural History Press, Garden City.

Todd, T.N. & Hatcher, C.O. (1993) Genetic variability and glacial origins of yellow perch (*Perca flavescens*) in North America. *Can. Jour. Fish. Aq. Sci.* **50**, 1828-1834.

Underhill, J.C. (1986) The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland and Labrador. *The zoogeography of North American freshwater fishes.* (ed. by C.H. Hocutt & E.O. Wiley), pp. 105-136. John Wiley and Sons, New York.

Uyeno, T. & Miller, R.R. (1963) Summary of Late Cenozoic freshwater fish records for North America. *Occ. Pap. Mus. Zool., Univ. Mich.* 631.

Wright, H.E. Jr., Mann, D.H., & Glaser, P.H. (1984) Piston corers for peat and lake sediments. *Ecology*, **65**, 657-659.

Figure captions.

Fig. 1. Partial scale, referred to white sucker, *Catostomus commersoni,* from the 9.0-9.1 m layer, Allamuchy Pond, New Jersey. Lateral dimension 1.9 mm.

Fig. 2. Cyprinid scale from the 7.35-7.4 m layer, Allamuchy Pond, New Jersey. Lateral dimension 3.0 mm.

Fig. 3. Centrarchid scale from the 8.8-8.9 m layer, Allamuchy Pond, New Jersey. Lateral dimension 2.4 mm.

Fig. 4. Scale fragment, referred to Centrarchidae, from the 7.9-8.0 m layer, Allamuchy Pond, New Jersey. Transverse dimension 1.9 mm.

Fig. 5. Scale, referred to yellow perch, *Perca flavescens*, from the 8.5-8.6 m layer, Allamuchy Pond, New Jersey. Lateral dimension 1.6 mm.

Table 1. Characteristics of scales from sediment of Allamuchy Pond, New Jersey. Age refers to years before present determined by AMS ^{14}C dates of plant remains.

Depth (m)	Age	Identification	Length (mm)	Width (mm)	Length-Width Ratio	Length-Focus Ratio	Number of Radii	Remarks
7.0-7.05		Centrarchidae	3.0	2.8	0.93		12	regenerated
7.3-7.35		Centrarchidae	2.2	2.6	1.18		11	regenerated
		Centrarchidae	2.8	2.9	1.04		10	regenerated
7.35-7.4		Cyprinidae	3.0	1.9	0.66	0.34	6	
7.45-7.5		pieces						cycloid scales
7.6-7.7		*Salmo* sp. ?	1.4	1.5	1.07	0.80	0	
								fragment
7.9-8.0		Centrarchidae		1.9			11	fragment
8.0-8.05	9230±160	fragment						ctenoid
8.5-8.6	10740±420	*Perca flavescens*	1.6	1.3	0.81	0.78	4	
8.6-8.7								regenerated
		Perca flavescens	2.0	1.8	0.90	0.70	5	
		Perca flavescens	2.4	2.6	1.08	0.77	6	
8.8-8.9		Centrachidae	2.4	2.9	1.20	0.63	11	
		Salmo salar ?	1.9	0.8	0.42		0	
8.9-9.0								fragment
9.0-9.1	12260±220	*Catostomus commersoni*	3.9			0.46		fragment