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Status and Distribution of Fish in an Acid-impacted Watershed of the Northeastern United States (Hubbard Brook, NH)

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Abstract - Stream acidification across the northeastern US impacts fish abundance and fish communities. In this study, we document a fish community shift in the upper mainstem of Hubbard Brook (NH) from the presence of at least three species in the 1960s to the presence of only one species today. *Cottus cognatus* (Slimy Sculpin) and *Rhinichthys atratulus* (Blacknose Dace) are no longer present in this system, and we suggest that extirpation occurred during a period of chronic acidification during the early 1970s. Today, *Salvelinus fontinalis* (Brook Trout) is the only fish species present in the upper reaches of the Hubbard Brook Valley. The current upstream extent of Brook Trout is limited primarily by physical obstructions such as waterfalls or cascades. Acidification may lead to chemical barriers that limit upstream movement during high flow in a few streams. As recovery from acid deposition begins, and as regional climate changes, our observations demonstrate the value of periodic evaluations documenting shifts in the distribution and composition of fish communities in headwaters of the northeastern US.

Introduction

The ecological impacts of anthropogenic acidification (acid rain) on fish communities have been well documented in stream networks throughout the northeastern US (hereafter "Northeast") (Baker et al. 1996, Baldigo and Lawrence 2001, Baldigo et al. 2007, VanSickle et al. 1996). However, long-term observations of fish community changes, specifically changes in the upstream extent of fish in episodically acidified streams, are more limited. Both chronic and episodic acidification can reduce fish abundance and species richness in streams. At locations where refugia from acidification are available, some individuals can withstand episodic acidification and subsequently repopulate streams, yet population sizes still remain below levels expected in the absence of acidification (Baldigo and Lawrence 2001). Variability in fish susceptibility to acid pulses and variability in fish mobility together influence the community composition of streams that are episodically acidified. Variability in fish movement may also influence the upstream extent of fish in a stream network, as well as their recovery and recolonization following temporary extirpation caused by episodic acidification.

Bioassay studies have shown that adult *Salvelinus fontinalis* (Mitchill) (Brook Trout) and adult *Cottus cognatus* Richardson (Slimy Sculpin) are

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among the most acid-tolerant fishes found in North Temperate Zone streams and lakes (Gagen et al. 1993, VanSickle et al. 1996). Although Brook Trout often persist in acid-stressed systems (summer pH as low as 4.6; D.R. Warren, pers. observ.), Slimy Sculpin are frequently absent from episodically acidified systems (Kaeser and Sharpe 2001). This pattern could be a result of more limited movement by sculpin (and thus reduced access to refuges) as well as greater susceptibility of juvenile Slimy Sculpin to acidification. In Pennsylvania streams, Kaeser and Sharpe (2001) found that acid conditions in spring reduced Slimy Sculpin reproductive success such that even when adults survived episodic acidification, juvenile mortality could still lead to the eventual local extirpation of the species over time.

Brook Trout are often the only species found in the uppermost reaches of buffered and acidified streams in the Northeast. The upstream extent of Brook Trout distribution in headwater streams therefore often defines the boundary between the fish and fishless sections of a stream system. As an apex predator in these headwaters, the presence or absence of fish has the potential to influence a broad suite of ecological interactions. Studies in Rocky Mountain streams in the western US found that fishless streams have substantially different ecological conditions than streams containing fish (McIntosh and Peckarsky 1996, McIntosh et al. 2002). In northeastern streams, trout presence has been linked to reduced juvenile salamander abundances (Lowe and Bolger 2002). In addition to these influences on stream biotic interactions, many forest management regulations are designed to protect fish resources in streams within forested watersheds (Cole et al. 2006). Knowing the upstream extent of fish distribution can be important in determining biotic impacts from acid stress and in determining potential refuge provided by specific stream locations.

In well-buffered streams, Brook Trout colonization during invasions or following natural extirpation events can be rapid (Peterson and Fausch 2003, Roghair et al. 2002); however, in systems subject to episodic acidification the rate and extent of (re)colonization is limited. Under favorable pH conditions, Brook Trout tend to move upstream during periods of elevated discharge, when fish can circumvent barriers that are otherwise impassable during low flow conditions (Gowan and Fausch 1996). In acid-stressed systems, pH sometimes decreases during high flow, especially during spring snowmelt (Driscoll et al. 2001; Likens et al. 2002, 2004). In an episodically acidified stream in Pennsylvania, Gagen et al. (1994) found that fish moved downstream rather than upstream during a high-flow event with associated declines in stream pH. Thus, an acid pulse during high flow that would otherwise provide an opportunity for upstream fish movement beyond low-flow, physical barriers may restrict the upstream distribution of fish. In areas where acidification is not an issue (e.g., in western North America where Brook Trout are invasive) and in laboratory experiments, Brook Trout are able to recolonize upstream locations and pass large barriers during high flow (Adams et al. 2000, Kondratieff and Myrick 2006). By contrast, in many stream systems in the Northeast, fish distribution is likely to be limited by a combination of chemical barriers at high flow and physical barriers at low flow. Therefore, the geomorphic barriers that define the upstream extent of Brook Trout distributions may be smaller than anticipated based on research conducted in laboratories or in other regions.

In the Pacific Northwest, Latterell et al. (2003) and Cole et al. (2006) found that the upstream distributions of salmonids were primarily limited by steep gradients and waterfalls. Studies in the Northeast have suggested that both stream chemistry and physical barriers will limit upstream fish distribution in areas subject to acidification (Baldigo and Lawrence 2001, Kocovsky and Carline 2005). However, no previous studies have surveyed and documented the upstream extent of fish in headwater streams of eastern North America.

Sulfate deposition across the Northeast has declined over the last twenty-five years, and a concurrent but diminished decline in the amount of sulfate in stream water has also been observed (Likens et al. 2002). The reduction in stream sulfate concentrations has coincided with slight increases in stream pH and in the acid neutralizing capacity (ANC) of many streams across the region (Driscoll et al. 2001, Likens 2004, Yan et al. 2003). Reductions in acid deposition and increases in stream pH may allow fish to recolonize some areas from which they have been extirpated, especially if episodic acidification is reduced enough to allow previous barriers to become passable. While the impacts of acidification are expected to persist for many years, evaluations of the current upstream extent of fish in headwater streams are necessary if we are to determine future changes in fish distribution associated with the potential for increased habitat availability.

The Hubbard Brook Valley (HBV) in central New Hampshire has been widely used as a model system in documenting ecosystem impacts of acidification (Likens and Bormann 1995), but no studies to date have evaluated fish communities or fish distributions throughout the HBV. In this study, we (1) compile available historic information from field notes and limited early survey work on fish in the stream network of the HBV, (2) document current fish communities in this system, and (3) determine the upstream extent of fish in this system and evaluate stream features at the fish distributional limits. This information will allow us to determine the broader impacts of acidification on fish communities in this system. Surveys of the upstream extent of fish will also fill a knowledge gap regarding the features and limits to fish distribution in headwater stream networks of the Northeast. Further, documenting the current upstream extent of fish in this stream network will establish baseline information for future research evaluating changes to fish distribution in response to changing environmental conditions.

Study Site

The Hubbard Brook Valley is a fifth-order watershed located in the White Mountain Region of New Hampshire and drains to the Pemigewasset River. This study focuses on the portion of the watershed within the Experimental Forest boundary and excludes nearby Mirror Lake, its outlet, and areas of the watershed that have been subject to recent development. All streams except Norris Brook (Fig. 1) enter the mainstem Hubbard Brook within the Experimental Forest.

Detailed descriptions of the HBV can be found in Likens and Bormann (1995), and Likens and Buso (2006). The work by Likens and Buso (2006) is particularly relevant to this study because it documents low-flow water chemistry levels every 100 m for all streams in the HBV. Stream flow in this region is characterized by high discharge in the spring during snowmelt, low flow during the summer, and a slight recharge in the fall. The mainstem Hubbard Brook flows west to east and is dominated by large cobble and boulder substrates in the lower section. The upper section of this mainstem river has some boulder-dominated reaches, but also contains alluvial sections with smaller gravel and cobble and slightly lower gradients. Headwater streams are mid- to high gradient (5% to >20%), and substrates are dominated by boulders and cobble. The HBV is underlain by igneous and highly metamorphosed sedimentary bedrock, characterized by base-poor granites and schists. Glacial till is widespread and highly variable in thickness, and soils are generally thin, acidic spodosols. Forests are northern hardwood ecosystems, with the conifer component more common on the ridge tops and on the north-facing

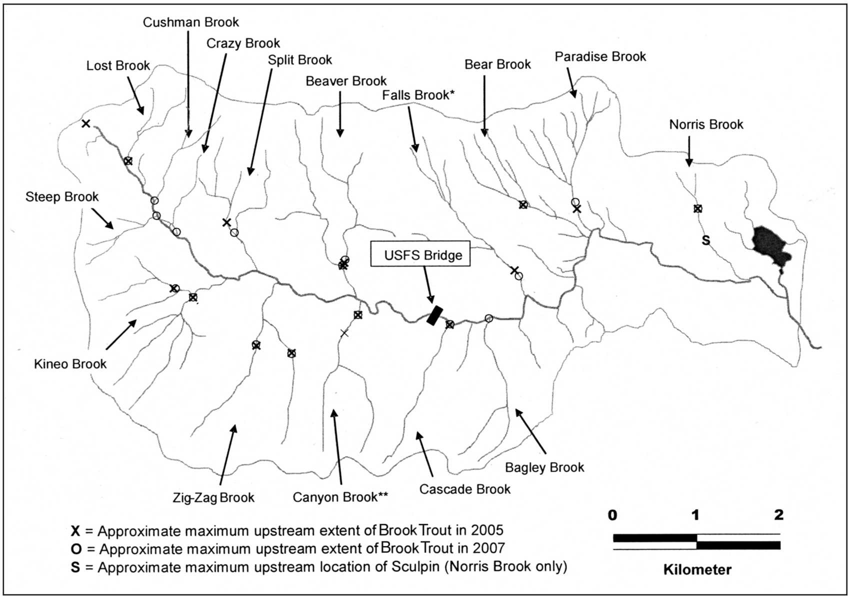

Figure 1. Map of the HBEF watershed indicating upstream extent of fish (only Brook Trout in all but Norris Brook) in late summer of 2005 and 2007. Prior to 2003, no fish were present in Falls Brook due to a physical barrier where the stream enters the mainstem, but fish were subsequently introduced in an experiment that year. New year classes were observed in 2005 and 2007 surveys. The upstream X on Canyon Brook also represents fish that were introduced in the 2003 cage experiment. There was no evidence of reproduction in this upper section in the 2005 survey.

slope of the HBV (Likens and Bormann 1995). Stream chemistry is variable among and within streams. As a rule, pH is lower in tributaries than the mainstem river, and the buffering capacity of tributaries declines in an upstream direction (Likens and Buso 2006). The mainstem maintains consistent pH relative to its tributaries (Likens and Buso 2006). Areas of groundwater discharge were apparent in the valley-wide survey in some streams and are characterized by increased pH, nitrate, and calcium (Likens and Buso 2006). Mean pH, acid neutralizing capacity (ANC), nitrate, sulfate, and monomeric aluminum for each tributary are reported in Table 1, as calculated from Likens and Buso (2006). Chemical characteristics change in these tributaries in an upstream direction from the mainstem to the headwaters. For example, pH declined with increasing elevation. Conversely, and logically, aluminum concentrations are generally lower near the mainstem than in the headwaters. Other chemical features such as nitrate exhibit stream-specific characteristics, with higher nitrate concentrations provided by groundwater inputs along a specific reach, and other sections having low nitrate due to strong in-stream uptake. Some ions such as sodium and chloride remain relatively constant across tributary elevational gradients.

Methods

We first document historic records on the fish species present in the HBV based on field notes by G. Likens in the late 1960s and a set of snorkel surveys conducted on the mainstem in the late 1980s. In 2005, 2006, and 2007, we conducted backpack electrofishing surveys to evaluate the presence or

Table 1. Mean water chemistry data from spring, summer, and fall water sampling efforts along tributary streams throughout the Hubbard Brook Valley from 1997 to 2003. Tributaries are listed in the order in which they enter the mainstem beginning downstream. The total number of samples used to calculate mean pH, ANC, [SO$_4^{-2}$] and [NO$_3^-$] ranged from 11 to 20. Mean monomeric Al^{+3} concentrations were calculated from two samples in each stream except Crazy Brook, where four samples were used.

Stream	ANC (μeq/L)	pH	SO$_4^{-2}$ (mg/L)	NO$_3^-$ (mg/L)	Al^{+3} (mg/L)	Ca^{+2} (mg/L)	Mg^{+2} (mg/L)	K$^+$ (mg/L)	Na$^+$ (mg/L)
Norris Brook	59	6.37	5.01	0.030	0.005	2.11	0.47	0.39	1.68
Paradise Brook	40	5.97	4.35	0.270	0.005	1.41	0.37	0.40	1.46
Bear Brook	27	6.05	4.10	0.050	0.005	1.02	0.31	0.26	1.29
Falls Brook	17	5.80	4.06	0.110	0.013	1.02	0.29	0.21	1.11
Bagley Brook	6	5.35	4.21	0.140	0.015	0.89	0.30	0.23	1.02
Cascade Brook	-27	4.61	4.35	0.180	0.190	0.73	0.24	0.20	0.82
Canyon Brook	21	5.68	4.04	0.210	0.015	1.04	0.34	0.19	0.98
Beaver Brook	9	5.42	3.92	0.140	0.035	1.04	0.29	0.20	0.91
Zig-Zag Brook	50	6.24	4.06	0.270	0.008	1.40	0.43	0.25	1.04
Split Brook	24	5.57	4.28	0.180	0.008	1.28	0.37	0.18	0.90
Kineo Brook	28	5.99	4.27	0.260	0.020	1.28	0.41	0.18	0.88
Crazy Brook	24	5.36	4.28	0.310	0.014	1.45	0.40	0.18	0.88
Steep Brook	7	5.49	4.25	0.340	0.020	1.07	0.35	0.14	0.64
Cushman Brook	-7	5.02	4.73	0.080	0.080	0.92	0.29	0.11	0.67
Lost Brook	3	5.23	4.57	0.260	0.020	1.09	0.33	0.15	0.69

absence of fish in Hubbard Brook and its tributaries during later summer/early fall. We documented the upstream extent of fish in each tributary and recorded habitat features at the location where fish were last observed.

Historic records

Early observations of fish in the Hubbard Brook watershed were made as visual assessments in the mainstem river and tributaries, primarily in Bear Brook. Beginning in 1963, anecdotal observations of fish and other wildlife (salamanders) were recorded in field notebooks. Given the nature of these field observations, the presence of fish can be reliably documented; however, without electrofishing or rotenone, the absence of fish, and therefore the absolute upstream distribution of fish, cannot be explicitly determined. Early fish surveys conducted by the State of New Hampshire in the White Mountains using more invasive methods did not include Hubbard Brook, but did encompass a number of comparable streams in the region (Hoover 1938; Seamans 1959a, b). We use data from these surveys to infer likely historic fish communities in our study-area streams.

In August 1988, a limited set of snorkel surveys were conducted to quantify salmonid densities in two sections of the mainstem of Hubbard Brook by two individuals counting fish either independently or together (Bryant 1989). The upstream survey reach extended from the confluence of Cascade Brook, upstream past the USFS bridge to the confluence of Kineo Brook (Fig. 1). The downstream reach encompassed the mainstem river from the USFS forest boundary upstream to the confluence of Falls Brook. A minimum of ten percent of the area within each reach was included in the snorkel surveys.

Electrofishing survey

Electrofishing surveys in 2005, 2006, and 2007 were conducted using a modified version of methods in Latterell et al. (2003). Fish presence/absence was recorded using a backpack electroshocker with a field crew of two people. Fish were either identified in the water or were captured briefly for identification when fishes could not be clearly identified while remaining in the water. Captured fish were returned to the water unharmed after identification. In 2005, each tributary was surveyed in an upstream direction from its confluence with the mainstem until fish were no longer observed. Surveys were conducted a minimum of 100 m past the last fish observed to be sure that fish were not present further upstream. The distance upstream from the mainstem was measured with a field tape to the nearest of the 100-m markers that were established during the 2001 valley-wide surveys (Likens and Buso 2006). The 2006 electrofishing surveys were initiated at least 150 m downstream from the furthest extent of fish found in that tributary during the previous year, then surveys were continued upstream using the same methods as in 2005. In all cases, fish were encountered when initiating surveys in 2006. The 2007 surveys were conducted beginning at the confluence with the mainstem for each stream. All major tributaries within the Hubbard Brook watershed were surveyed in 2007.

After we surveyed a minimum of 100 m past the last fish observed, we returned to the point where the last fish was observed and qualitatively evaluated stream characteristics at that point. We noted if there were cascades, waterfalls, stream sections with very steep gradients, a lack of water, or "unknown barriers." We noted an "unknown barrier" when fish were absent beyond a given point in the stream with no obvious physical limits to upstream distributions. This category included cases where the last fish was located below a cascade of a size comparable to other cascades in that system, which had clearly been passable for fish to reach that point. Potential physical barriers to fish movement were documented and included waterfalls or a series of two or three large cascades that reached heights of 2 m or more over a short distance and with no pools below from which fish could jump (e.g., Zig-Zag Brook). In some cases, individual barriers were not large but cascades or granite outcroppings were frequent, leading to a consistent high gradient reach (e.g., Falls Brook). In other streams, a lack of water was clearly limiting upstream distributions, and in these cases, we noted that "streambeds were dry."

Results

Historic and current fish communities

Historic field notes and anecdotal evidence indicate that Brook Trout, Slimy Sculpin, and at least one minnow species (*Rhinichthys atratulus* (Hemann) [Blacknose Dace]) were observed in the mainstem of Hubbard Book at least 7.4 km (4.6 miles) upstream from I-93 (near the USFS bridge) in the 1960s. Bear Brook is known to have contained both Brook Trout and Slimy Sculpin at this time, based on field observations. Historic surveys of fishing streams in the nearby Saco River watershed indicated that both sculpin and dace were commonly encountered and at times were found in high abundance (Seamans 1959a, b). In a survey of streams across the White Mountains, Hoover (1938) found community shifts in an upstream direction from mainstem rivers to headwater streams. In undisturbed (non-stocked, non-fished) high-elevation streams, both Brook Trout and Slimy Sculpin were present in seven of the eight streams sampled during these 1938 surveys.

Apart from a single *Salmo salar* L. (Atlantic Salmon), Brook Trout were the only fish documented in the Hubbard Brook mainstem snorkel surveys in 1988 (Bryant 1989). Atlantic Salmon fry were stocked into a few of the HBEF tributaries in the mid- to late 1980s, but survival was low. With regard to other fish species, Bryant (1989) specifically noted that "other species were not observed in Hubbard Brook"; yet that survey was focused on documenting the presence of salmonids, so few definitive conclusions can be derived from this work.

Streamside visual surveys by D. Buso in 2001 indicated the presence of Brook Trout in Norris Brook, Bear Brook, Zig-Zag Brook, and the mainstem river. Extensive fish surveys throughout the HBEF stream network conducted in late summer 2005 indicated that, with the exception of Norris Brook,

Brook Trout were the only fish present in HBEF tributaries. In all mainstem surveys above the Hubbard Brook gorge (a series of waterfalls and cascades up to 4-m in height), Brook Trout were the only fish present. Norris Brook also contains Slimy Sculpin, but this stream enters below the gorge.

Fish distributions

Fish were absent from five (Cascade Brook, the west branch of Beaver Brook, the tributary to the west branch of Kineo Brook, Steep Brook, and Cushman Brook) of the nineteen streams we surveyed. Brook Trout were the only fish found in the other streams, except for Norris Brook, which also contained Slimy Sculpin. In most cases, the upstream distribution of fish appeared to be constrained by a waterfall or other large physical barrier. In a few cases, the mechanism for the upstream loss of fish was not immediately apparent. Cascade Brook, which is a chronically acidified stream with a mean summer pH of 4.6 (Likens and Buso 2006), contained no fish.

Between 2005 and 2006, the upstream extent of Brook Trout decreased in most streams (the east branch of Zig-Zag Brook being the exception), but these changes in distribution were minor (<50 m). Similarly, the upstream extent of Brook Trout during late summer was relatively consistent from 2005 to 2007, with little change in most streams. The maximum increase in upstream extent was 48 m in Paradise Brook. The largest decrease in distribution (-162 m) occurred in Split Brook (Table 2, Fig. 1). Potential physical barriers to late-summer fish distributions were apparent in slightly more than half (11 of 19) of the surveyed streams. These potential physical barriers included both waterfalls/cascades and a lack of surface flow. In one stream, Canyon Brook, fish reached their upstream limit at a road culvert.

Table 2. Upstream extent of Brook Trout, change in distribution from 2005 to 2007 and presence of potential physical barrier in each Hubbard Brook tributary from 2005, 2006, and 2007 fish surveys. Tributaries are listed in the order in which they enter the mainstem beginning downstream ("-" = no data). For Canyon Brook, the first number represents the upstream extent of fish from an introduction of adults in summer 2003 via a failed caging experiment, and the second number represents the natural upstream extent of fish.

	Maximum upstream distance (m)			Change 2005 to	Potential
Stream	2005	2006	2007	2007 (m)	barrier?
Norris Brook	1383	1378	1379	-4	Yes
Paradise Brook	419	-	467	48	No
Bear Brook	962	959	960	-2	No
Falls Brook	479*	436*	433*	-46	Yes
Canyon Brook (W8)	430*/124	-*/125	-*/125	1	No**
Beaver Brook - East Branch	473	-	496	23	Yes
Zig-Zag Brook - East Branch (W7)	883	888	891	8	Yes
Zig-Zag Brook - West Branch	511	511	503	-8	Yes
Split Brook	720	-	558	-162	No**
Kineo East	521	515	522	1	Yes
Kineo West	719	700	711	-8	No
Crazy Brook	-	-	8	na	Yes
Lost Brook	25	-	25	0	Yes

*Fish introduced in an earlier experiment.

**Potential low-flow barrier.

This culvert was the only case where an anthropogenic feature was associated with upstream distributions. The pool below the culvert is quite large, and at high flows, the drop from the culvert to the pool is relatively small (<0.5 m). Evidence from other streams in the system suggest that Brook Trout are capable of passing a barrier of this size when there is an adequate pool below the barrier; however, Canyon Brook is episodically acidified, and as such, fish are likely to be moving downstream rather than upstream in this system during high flow, when the culvert is most likely to be passable (Gagen et al. 1994). Although identifying specific barriers to fish movement may be subjective during low-flow conditions, potential low-flow barriers can be clearly identified, as has been done in previous studies in the Pacific Northwest (e.g., Cole et al. 2006, Latterell et al. 2003).

The upper extent of fish distribution in Canyon and Falls brooks was artificially enhanced in 2005. During July 2003, adult Brook Trout >100 mm in length were held in cages placed in the upstream (and formerly fishless) sections of Canyon and Falls Brooks as part of a study conducted to evaluate the influence of trout on salamander behavior (B. Cosentino, University of Illinois, Urbana, IL, pers. comm.). During this study, a flood broke the cages in which fish were housed, and some escaped. Surveys in 2005 revealed that large adult fish were still present at locations upstream from the farthest upstream distribution observed in a brief preliminary survey conducted in 2003. No fish were found in Falls Brook in 2003, presumably resulting from the presence of a 100-m section of stream with a consistent gradient >25%. In our 2005, 2006, and 2007 surveys, we attributed the presence of large fish at these upstream sections to the cage study rather than to natural movement. In addition to the large adults, a distinct year-class of young-of-year trout was present in Falls Brook in the newly colonized upstream section. In Canyon Brook, only larger fish (>150 mm) were found in the area at which cages were placed. In documenting the upstream extent of fish in Falls Brook in 2005, 2006, and 2007, we included the introduced fish because recruitment had clearly occurred. In Canyon Brook, we focused the 2006 surveys only on the natural upstream extent of fish, and a survey upstream in 2007 did not reveal any fish remaining in the upstream section (Table 2).

Discussion

Recent surveys document that fish species have been extirpated from Hubbard Brook and its tributaries since the 1960s. Slimy Sculpin and Blacknose Dace have been lost from the mainstem of Hubbard Brook, and Slimy Sculpin are no longer found in at least one of its tributaries. Brook Trout are currently present in the mainstem of Hubbard Brook and in the lower reaches of most tributaries (Fig. 1). It is likely that the native fish community was still intact, although stressed, through the mid-1960s. In 1970, stream acidification at HBEF peaked, and for a period of about six years, streams in this region experienced chronic and acute acidification (Fig. 2). We suggest that sculpin and dace were extirpated during this period from tributaries in the HBV; based on historic surveys in the region, it is likely that Slimy Sculpin have also been lost from similar stream systems across the northeastern US. Calculations of acid neutralizing capacity (ANC) at this time indicated that the cations present in streams of the HBEF were not sufficient to balance anion loss (negative ANC's; Table 1, Fig. 2). Although inorganic monomeric aluminum was not measured directly, it was most likely the balancing cation at this time (Buso et

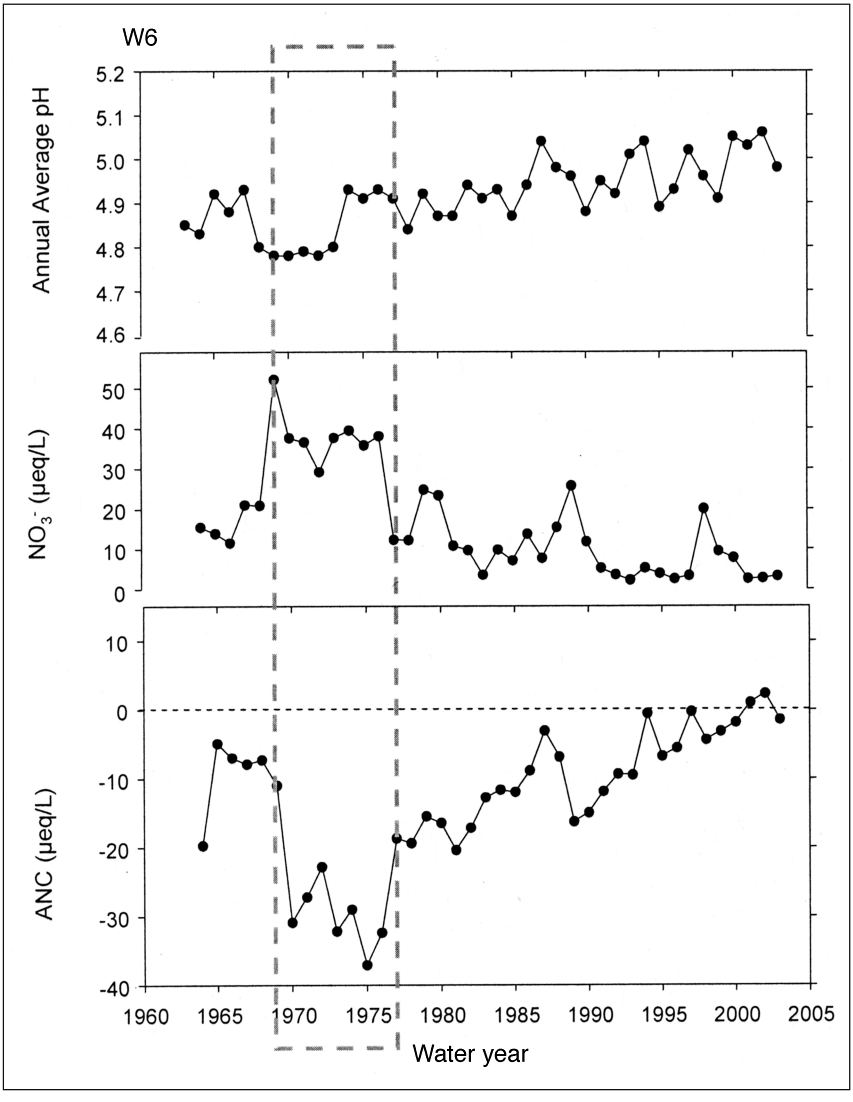

Figure 2. Average annual values for stream pH, nitrate concentration, and ANC over time in the reference watershed at Hubbard Brook (Watershed 6). The dashed box encloses the period over which we hypothesize dace and sculpin were extripated from the upper tributaries of the HBEF.

al. 2000). High inorganic monomeric aluminum concentrations are the primary cause of fish mortality during acidification (Baker et al. 1996, Booth et al. 1988, Dietrich and Schlatter 1989, VanSickle et al. 1996).

Brook Trout are currently present in most tributaries in the upper HBV, yet the upstream extent to which they are present varies. Along the north-facing slope of the HBV, fish generally occurred further upstream in tributaries that had greater buffering capacity (e.g., Zig-Zag and Kineo brooks vs. Canyon Brook vs. Cascade Brook; Table 1, Fig. 1). However, this trend was limited and was not constant across the south-facing slope of the HBV. Potential physical barriers such as waterfalls, cascades, and long, steep-gradient sections were the most common feature that appeared to limit upstream fish distributions in HBEF in late summer (Table 2). In one stream (Lost Brook), most of the streambed was dry during our late-summer surveys. A few fish were found in remnant isolated pools near the mainstem, but fish were absent from isolated pools at upstream locations. In a few cases, fish distributional limits were attributed to a combination of physical and chemical barriers. Kineo Brook and Bear Brook are all relatively well buffered for a substantial portion of their length (Table 1), but the pH and buffering capacity of these streams declines at higher elevations (Likens and Buso 2006). In both Kineo-West and Bear Brook during 2005, 2006, and 2007 and in Kineo-East during 2006, the location at which the last fish was present was not associated with a likely physical barrier. Although the fish observed farthest upstream were found below a small cascade in each of these three streams, the cascade upstream was the same size or smaller than those observed downstream. Therefore, cascades of this height could not be considered strictly physical barriers to fish movement in these streams. In these cases and in streams such as Split Brook and Cascade Brook where there was no obvious barrier present, we suggest that the limits to upstream fish distributions were a combination of physical and chemical barriers.

Latterell et al. (2003) found that (1) large shifts in stream gradient, (2) declines in pool frequency, and (3) channel constrictions with limited water were all key factors in limiting upstream distributions of *Oncorhynchus clarkii* (Richardson) (Cutthroat) and *Oncorhynchus mykiss* (Walbaum) (Rainbow Trout) in Cascade Mountain streams of the Pacific Northwest. Waterfalls were noted as the primary barrier to the upper extent of fish distributions in 14% of the 21 unlogged streams that were surveyed in that study. In a similar study, also in the Pacific Northwest, Cole et al. (2006) found that the dominant feature determining the upper boundary to fish distribution was most often an organic debris dam (48%), and the second-most common feature was a waterfall or a cascade (30%). The potential transient nature of debris dams could account for some year-to-year variability in fish distribution in their study. Within the HBV, organic debris dams were never noted as key features potentially limiting fish distributions. Although such dams become increasingly common in the headwaters of HBEF tributaries, they do not appear to influence fish distributions (Likens and Bilby 1982, Warren et al. 2007).

Knowing where headwater streams become fishless has important implications for current and future research on stream ecosystem ecology in the Northeast. In the western US, Brook Trout alter the behavior and life histories of aquatic macroinvertebrates, algal growth, and resource patch dynamics (McIntosh and Peckarsky 1996; McIntosh et al. 2002, 2004). In addition, across eastern North America, the presence or absence of fish can influence stream amphibian abundance and distribution (Lowe and Bolger 2002, Lowe et al. 2004). Fish can interact with salamanders at multiple trophic levels; they can be predators upon salamander larvae and competitors with some larger larvae and adults for invertebrate prey (Lowe and Bolger 2002, Lowe et al. 2004).

Given the potential for fish to influence stream communities, large changes in the upstream extent of fish distributions may have important ecological implications in some streams. Changes of this magnitude are most likely to occur when fish naturally or artificially expand beyond a previous barrier (chemical or physical). Cole et al. (2006) evaluated changes in the upstream extent of salmonids in 172 Pacific Northwest streams. When they observed a change in the upper extent of fish between 2001 and 2002, the distance difference between years (both upstream and downstream) was typically 50 m or less (94% of the study streams), but distribution shifts >200 m in extent were documented in eight of their streams (Cole et al. 2006). Changes in the upstream extent of fish in HBV were far less evident than those observed in the Pacific Northwest. In our surveys, shifts in the upper extent of fish distribution from 2005 to 2006 and 2005 to 2007 were relatively short.

Changes within the northern forest ecosystem including northern forest streams will influence the status of trout and other fish species in HBV and elsewhere across the region. The 2005, 2006, and 2007 surveys establish clear records that will allow future research documenting impacts of natural changes, such as continued forest development or periodic disturbances such as the 1998 ice storm, as well as changes caused by anthropogenic activities including forest management, fish stocking, climate change, and continued acidic deposition.

Forests in the Hubbard Brook watershed are at or near maturity, at least in terms of biomass accumulation (Fahey et al. 2005), but the streams may not yet be near a "mature" state. As forests in the HBV and across the northern forest region continue to progress toward old-growth status, wood loading, pools, and light dynamics in associated streams will increase (Keeton et al. 2007; D.R. Warren, unpubl. data). These changes have the potential to influence fish abundance (through increases in habitat) and primary production. Forest management and forest disturbances that slow or delay forest maturation can also influence fish abundance and productivity in headwater systems (Nislow and Lowe 2006). Logging by clear cutting can cause nitrate pulses in stream water (e.g., Likens et al. 1970) that are clearly lethal to fish in associated streams, and these would be expected to decrease both fish abundance and fish distribution (Baldigo et al. 2005). If fish were to survive or recolonize following these pulses, and if stream temperatures were to remain below lethal levels, production in the postharvest systems would increase well above levels observed in mature forest streams (Burton and Likens 1973, Nislow and Lowe 2006).

Climate projections for the Northeast indicate the potential for increased temperatures in the summer and decreased snowpack in the winter (Hayhoe et al. 2007). Current limitations to the upstream distribution of fish in the HBV appear to be driven primarily by physical barriers and episodic acidification, but increased anchor ice in winter (as a result of reduced snowpack) and greater areas of dry stream bed in summer are important factors to consider in evaluating future limitations to the distribution of fish in the Hubbard Brook ecosystem. A modeling study from the southern Appalachian Mountains also suggests that the downstream distribution of trout will also decline with increasing temperatures across eastern North America (Flebbe et al. 2006). Under these scenarios, trout distributions may be compressed with reductions in available habitat both upstream and downstream.

Streams in the HBV and across the northern forest region are experiencing increases in pH and ANC; however, recovery from acidification in headwater streams requires more than just an increase in mean pH. The re-establishment of natural fish communities is a key component of ecosystem recovery. The current water chemistry conditions in some of the HBEF tributaries and in the mainstem suggest that there may be potential for fish other than Brook Trout (e.g., Slimy Sculpin) to survive and reproduce if they were to be re-introduced to the system. It is important to recognize, however, that the streams in this watershed continue to be influenced by the effects of long-term base-cation loss, and pH and ANC have not yet returned to pre-disturbance conditions (Lawrence 2002, Likens et al. 1998, Palmer et al. 2004). With the loss of base cations from the soils of the HBEF (Likens et al. 1998), the chemical stability of watersheds has declined, and the dilute waters in these systems may be even more sensitive to acidic deposition as a result. Decreases in the capacity of the forest ecosystem to buffer episodic events will continue to result in episodic depressions in stream pH and associated spikes in monomeric aluminum during acidicification events. In addition, recolonization and establishment of the original fish community in the upper section of mainstem Hubbard Brook and its associated tributaries is unlikely to occur at locations upstream from large fish barriers, even with changes in chemical conditions in streams that would otherwise allow for fish survival. The recovery of native fish communities in headwater systems across the Northeast will likely take many years to occur and will rely not only upon adequate stream conditions but also upon chance recolonization events that move fish above otherwise impassable barriers.

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