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Relating fish biomass to habitat and chemistry in headwater streams of the northeastern United States

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Abstract Stream pH and stream habitat have both been identified as important environmental features influencing total fish biomass in streams, but few studies have evaluated the relative influence of habitat and pH together. We measured total fish biomass, stream habitat, and stream pH in sixteen sites from three tributary systems in the northeastern United States. The habitat metrics included total pool area, a cover score, large wood frequency, and stream temperature. We created and compared nine linear models relating total fish biomass in summer to stream pH and stream habitat using Akaike's Information Criterion (AIC) analysis. The best (most parsimonious) models included pool area and stream pH. These results and a separate comparison of three regressions (low-flow pH, pool area, and these two metrics together versus total fish biomass) suggest that both habitat and stream buffering capacity affect the total biomass of fish in northeastern US headwater streams. When stream pH is adequate (low-flow pH greater than at least 5.7), physical habitat is likely to be more important, but under lower pH conditions, habitat is likely to be less effective in accounting for the total biomass of fish in these streams. This work demonstrates the continued effects of stream acidification in the northeastern US and more generally, it illustrates the importance of considering both physical and chemical conditions of a stream when evaluating the factors influencing fish communities.

Keywords Stream pH · Pool habitat · Fish biomass · Headwaters · Brook Trout · Slimy Sculpin

Introduction

The total biomass of fish in a stream is influenced by biological, physical, and chemical characteristics of the system (Stoneman and Jones 2000; Nislow and Lowe 2003; Harvey et al. 2005), and understanding which aspects of the stream environment most strongly influence fish biomass is a key first step in assessing habitat and in developing restoration strategies. For example, in poorly buffered streams, episodic and chronic acidification are well established chemical perturbations that can limit the abundance and diversity of fish in headwaters (Sharpe et al. 1987). Alternatively, in well buffered streams, physical habitat features such

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as pools are more closely associated with fish biomass (Stichert et al. 2001). In environments that are affected by both acid deposition and habitat modifications such as the streams in eastern North America and northern Europe, measurements of acidification in conjunction with measurements of habitat may be the most effective overall method to account for variability in the biomass of fish in headwater systems (Baldigo and Lawrence 2001). In this study we develop a simple empirical model to estimate fish biomass in headwater streams in the northeastern US from a few easily measured metrics that reflect both stream habitat and stream buffering capacity. This information can be used to improve restoration and to help managers in determining which feature of a stream (acidity or habitat) may be limiting production in streams recovering from acidification and habitat degradation.

A number of studies have evaluated fish mortality during episodic acidification. Laboratory studies have found that low pH in combination with elevated inorganic monomeric aluminum (Al^{+3}) lead to increased fish mortality (Mount et al. 1990; Parkhurst et al. 1990; Cleveland et al. 1991). Similarly, under natural conditions, bioassay studies have demonstrated that low pH and high aluminum levels are the factors most closely associated with fish mortality during episodic acidification events (Simonin et al. 1993; Van Sickle et al. 1996; Baldigo and Murdoch 1997). Baldigo and Lawrence (2001) evaluated a large suite of stream characteristics and found that pH and aluminum concentrations during episodic acidification in streams of the Catskill Mountains explained a substantial proportion of the variability in fish abundance. In that study, habitat alone was rarely as important as chemistry alone, and the greatest proportion of the variation in Brook Trout abundance was accounted for when both chemical and physical factors were evaluated together (Baldigo and Lawrence 2001). In contrast to Baldigo and Lawrence (2001), who evaluated numerous aspects of stream habitat and water chemistry, we confine ourselves in this study to a few easily measured stream habitat features and a single measurement of stream chemistry (low-flow pH) that we use as a proxy for stream buffering capacity.

In systems that are not subject to acid deposition, or in studies that do not account for potential stream acidification, habitat is generally recognized as the dominant factor limiting fish in headwater streams (Rashleigh et al. 2005). Pool habitat (availability and quality) has been consistently identified as a key feature influencing the biomass of stream salmonids, a dominant fish in many headwaters. For example, in northwestern California streams trout biomass was positively related to both pool depth and cover (Harvey et al. 2005). Heggenes et al. (1991) found that Cutthroat Trout (*Oncorhynchus clarki*) occupied deep pool habitat in a much higher proportion than its relative availability, indicating preference for these habitats and that the fish holding in these pools were usually dominant individuals. Using snorkel surveys, Berg et al. (1998) also identified pools as key habitat for trout in headwater streams along with other cover items such as boulders, large wood, and undercut banks. Additional stream habitat metrics that are commonly associated with fish in streams include the amount of cover from predators (both terrestrial and aquatic) (e.g. Rashleigh et al. 2005), the amount of wood in the stream (e.g. Solazzi et al. 2000), and temperature regimes relative to the thermal tolerances of fish—in particular salmonids (e.g. Stoneman and Jones 2000).

As noted above, stream habitat and stream acidification have been independently identified as factors that influence fish biomass in streams. Recent studies are now increasingly recognizing the importance of evaluating the collective influence of habitat and pH together (Baldigo and Lawrence 2001). Nislow and Lowe (2003) evaluated the influence of low-flow pH and logging history on Brook Trout abundance in New England streams; however, their study did not address specific in-stream habitat factors that may have more directly influenced fish biomass. Similarly, in a recent analysis of landscape features influencing Brook Trout abundance in Pennsylvania, stream pH in summer was also found to be a key factor, but the relative influence of specific reach-scale habitat features were not evaluated (Kocovsky and Carline 2005). The current study assesses local habitat and relative stream buffering capacity both independently and together in evaluating factors associated with the variability in fish biomass in northeastern headwater streams.

The two dominant fish species in our study streams were Brook Trout (*Salvelinus fontinalis*) and Slimy Sculpin (*Cottus cognatus*). Brook Trout—the native salmonid in headwater streams of eastern North America—are considered to be an acid tolerant fish species. Brook Trout experience high mortality at low pH (<4.5) and are growth inhibited at pH levels below 6 (Baker et al. 1996). Limited research indicates that Slimy Sculpin are moderately tolerant of low pH conditions but episodic acidification has been found to increase sculpin mortality and decrease their spawning success (Kaeser and Sharpe 2001).

Our study was conducted in northeastern North American, an area where acid deposition and its ecosystem scale effects have been well documented (Driscoll et al. 2001). Recent studies have indicated the beginning of a recovery from acid stress in streams in North America and across regions of northern Europe (Stoddard et al. 1999; Driscoll et al. 2001; Yan et al. 2003; Simonin et al. 2005), suggesting that stream fish abundance and growth at these sites may begin to shift from chemical limitation to habitat limitations. Therefore both habitat quality and stream buffering capacity should provide a good indication of potential fish biomass within a given stream reach in this region. We hypothesized that stream buffering capacity (measured as low-flow pH) and the availability of pool habitat in particular would both influence total fish biomass during summer at the reach scale in headwater streams of the northeastern US.

Methods

Study sites

Surveys were conducted in a total of 16 headwater streams—defined as first through third order streams (Heard et al. 1997)—in two Adirondack watersheds and one watershed in northeastern Vermont (Fig. 1). The study streams encompassed a range of susceptibility to the effects of acid rain from chronically acidic to episodically acidic (Table 1). Streams in the Sleepers

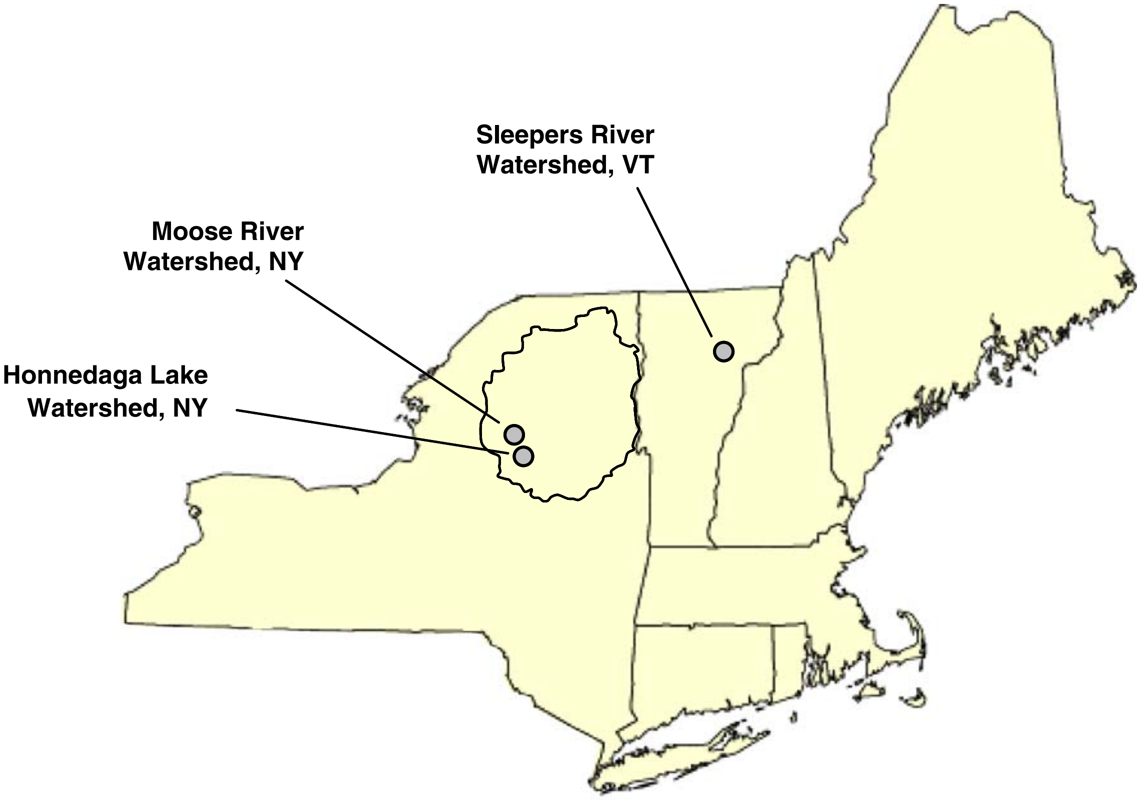

Fig. 1 Map of the Northeastern US noting approximate locations of each of the three basins in which stream surveys were conducted, Sleepers River, VT, Moose River, NY, and Honnedaga Lake, NY. The black outline in northern NY State represents the Adirondack park, in which two of the basins are located

Table 1 Site characteristics and mid-summer estimates of total fish biomass in each of 16 study streams from three different basins in the northeastern U.S. in 2004

Stream	Tributary system	Stream order	Number of reaches	Mean bankfull width (m)	Mean wetted width (m)	Mean reach length (m)	Pool area (m^2)	pH	Total fish biomass (g)
Anne's Run	Moose River	1	1	2.5	1.3	42.0	8.5	6.5	83.5
Beth's Brook	Moose River	1	3	3.4	2.2	22.6	11.0	5.7	77.0
Comb's Brook Trib	Moose River	1	2	2.7	1.8	22.7	3.8	7.0	105.0
Darby's Run	Moose River	1	2	2.7	1.6	27.0	10.6	5.1	59.4
Canachagala Trib	Moose River	1	1	2.7	1.1	35.0	7.2	6.6	100.7
LM Trib 3	Moose River	1	1	2.2	1.6	23.0	6.5	7.2	161.5
Otter Trib	Moose River	2	1	3.0	2.3	31.0	8.5	6.5	220.5
HAL T1	Honnedaga Lake	1	1	1.6	0.7	19.0	3.0	6.3	43.2
HALT2	Honnedaga Lake	1	1	3.0	2.6	18.0	3.0	4.4	0.0
HAL T6	Honnedaga Lake	1	1	3.2	3.1	21.0	9.1	4.6	49.2
HAL T9	Honnedaga Lake	1	1	3.1	1.1	25.5	3.8	6.2	20.3
Trail Bridge	Sleepers River	2	1	2.7	1.6	28.0	5.0	7.3	48.0
W16	Sleepers River	3	1	5.3	0.6	33.0	11.3	7.9	277.6
W3 Popes Brook	Sleepers River	3	1	5.3	1.5	36.0	13.3	7.7	301.9
W9-U	Sleepers River	2	2	2.1	2.5	25.8	3.4	7.6	62.0
W9-D	Sleepers River	3	2	2.8	1.7	42.5	11.6	7.2	294.8

River system in Vermont (five streams) are generally well buffered (Hornbeck et al. 1997), contrasting with the poorly buffered Adirondack streams. Study streams also encompassed a range of physical conditions for headwaters. Mean bankfull widths of study streams varied from 2.1 m to 5.3 m (Table 1). Gradient over the length of the study reaches ranged from 1% to 10% (measured using a clinometer). Riparian areas were dominated by northern hardwood forests that contained a mixture of both hardwood and conifer species. All streams experience a similar flow regime with peak flows in the spring associated with snowmelt and minimum discharge during the summer.

Field methods

Habitat and electrofishing surveys were conducted at all sites between June and July of 2004. Streams and electrofishing reaches within each stream were selected based on accessibility, the current or historical presence of Brook Trout, and consistency of gradient and riparian vegetation within the study reach. A minimum of one complete pool-riffle sequence was included in each study reach, and two or three replicate reaches were surveyed in five of the streams (Table 1). In these cases, replicate reaches were located within a distance of <100 m and mean values were used for analysis.

For fish surveys, the upstream and downstream ends of each reach were blocked and multiple pass depletions were conducted using a backpack electroshocker (Cowx and Lamarque 1990). A minimum of three passes were completed in each reach, and in the event of poor depletion, a fourth pass was conducted to ensure that accurate population estimates and capture probabilities could be determined. Total length (mm), wet weight (g), and species were recorded for each fish.

Stream habitat surveys were conducted in association with all electrofishing surveys. The following data were collected within each reach: number of pools; length, and width of each pool (from which we calculated total pool area for each reach); mean wetted width; reach length; number of pieces of large wood (dead wood >10 cm diameter and >1 m length); temperature when the surveys were conducted (between 10:00 and 16:00); and "cover score". The cover score ranged from 1 (low) to 5 (high) reflecting a subjective estimate of cover for fish that included: deep water, boulders, large wood, overhanging vegetation, and undercut banks. For tributaries of

Honnedega Lake and the Moose River, all pH measurements within the watershed were conducted in a single day to minimize temporal variability within the system. Water samples were collected from the Honnedaga study streams on 4 August 2004 and from the Moose River tributaries on 4 November 2004. Although these measurement dates occurred during summer and fall, all samples were collected during low flow and in the absence of prior rainfall events. Although water samples were collected after the electrofishing surveys were conducted along the Moose River, by sampling at low flow, the pH measurements at that time provide a robust estimate of the relative buffering capacity of these streams within our study year (Doug Burns, USGS, Troy NY—Personal Communication). Sleepers River streams pH measurements were conducted immediately before we conducted the fish and habitat surveys (between 7 and 9 July 2004). Seasonal biases in pH are not a concern at Sleepers River based on long term monitoring in this system where pH is known to remain circumneutral throughout the year (Hornbeck et al. 1997).

Analysis

Fish population estimates and capture probabilities were calculated using a weighted maximum likelihood population estimate for multiple pass depletions (Carle and Strub 1978). Because of variability in capture probabilities between Brook Trout and Slimy Sculpin, population estimates were calculated separately for each species when both species were present. For some of the streams, capture efficiency was high and the population estimate was equal to the number of individuals captured. In these cases the biomass estimate was simply the total weight of all fish captured in all passes with no estimate of error. When population estimates were larger than the total number of fish captured, fish biomass was estimated by multiplying the population estimate by the mean fish weight and error was estimated by multiplying the mean fish weight by the upper and lower bounds of the 95% confidence interval of the population estimate. When both Brook Trout and Slimy Sculpin were present, each species was analyzed separately and total biomass was determined by summing the estimates for each species.

Total fish biomass in summer was selected as the response variable in this study because biomass better represents the productive capacity of a stream than fish abundance, a concept central to fish habitat management (Stoneman and Jones 2000). Total biomass rather than biomass per square meter is used here because we were interested in evaluating the overall influence of pool area on the biomass of fish in a system independent of reach length or stream width, both features that influence biomass per unit area. Larger streams are expected to have more and larger fish, which should be accounted for by larger pool area. The covariates used in this study included: total pool area, large wood frequency, pH, temperature, and cover score. Total pool area, pH, temperature, and cover score data were all normally distributed based on an Anderson-Darling goodness-of-fit test ($\alpha > 0.05$) (MINITAB® Release 14.20, 2005). Large wood frequency data were natural log transformed to normalize the data. The largest correlation between covariates was between pool area and percent cover ($\rho = 0.46$, all others <0.33).

The nine linear models used here were created to evaluate habitat and pH influences on fish in our study streams. The first three models included individually each of the three metrics that we thought a priori might have the largest effect on fish biomass (stream pH, pool area, cover score). The next three evaluated a single stream habitat metric in conjunction with stream pH (pool area, cover score, and large wood abundance). Large wood is generally recognized as an important structural feature in streams but earlier work from this region suggested that its effects were variable (Warren and Kraft 2003), and for that reason it was considered only in conjunction with other metrics. Our seventh model included pH, pool area, and cover together. Our eighth model included temperature along with all three habitat metrics (pool area, cover score, and large wood) that are commonly included together in stream habitat assessments that do not include an estimate of stream buffering capacity. Given the location of the streams in this study (forested headwaters) and their limited species diversity, temperature was not expected to be a strong driver of fish biomass in this study; however, we made a point of including temperature with other metrics in some of the models because it is known to affect fish abundance and biomass in some streams (Stoneman and Jones 2000). Finally, we considered a global model, with all five covariates.

As a final covariate in all models, we considered the effect of tributary system (Moose River, Sleepers

River, and Honnedega). The sixteen streams used in this analysis are distributed among three basins; these streams may not represent completely independent observations, because fish biomass may be correlated among streams within a basin. We initially modeled fish biomass using nine mixed-effects models, with random effects included at the basin level ('lme' and 'lmer' in R). There may be no advantage in using random-effects, however, because the number of basins in our study is the minimum required for using mixed-effects ($n=3$). For comparison, we repeated the analysis of the same models, treating the basin effect as a 3-level factor variable.

We used Akaike's Information Criteria (AIC) as a model selection tool to determine separately which fixed or mixed effects model(s) were most supported by the data in explaining variability in total fish biomass across streams (Royall 1997; Burnham and Anderson 2004). Model selection with fixed effects is straightforward, because the number of parameters can be easily counted. With mixed-effects or hierarchical models, it is impossible to count the number of parameters. Further, likelihood calculations differ, depending on whether maximum likelihood (ML) or restricted maximum likelihood (REML) methods are used. To approximate AIC for our model selection analysis of mixed effects models, we combined the REML likelihood with the fixed-effects degrees of freedom as an estimate of complexity. Given the limited number of streams in the analysis ($n=16$), we used the small sample-size corrected version of AIC (AIC_c, Burnham and Anderson 2004). The most parsimonious model (lowest AIC score) represents the model that explains the greatest amount of variability with the fewest parameters. Subsequent models are ranked based on the difference in their value relative to the most parsimonious model (ΔAIC). The ΔAIC value then used to calculate the normalized AIC weight (Burnham and Anderson 2004).

In addition to the larger model selection comparisons, we conducted three separate regression analyses to evaluate the relationships between pool area and total fish biomass, low flow pH and total fish biomass, and these two metrics together relative to total fish biomass. These analyses were conducted separately from the AIC analysis because they do not account for basin as a mixed effect and instead focus only on the two metrics that we initially hypothesized would have the strongest relationships with fish biomass in these streams. The analysis of pool area and low-flow pH also allows us to compare the significance and explanatory ability of each of these two metrics that reflect stream physical habitat and stream chemistry, respectively.

Finally, to estimate a pH threshold (specific to these systems) at which a low-flow pH value would indicate that total fish biomass would be lower than expected for a given amount of pool habitat, we plotted the residuals from a linear model including pool area and stream basin (as a fixed effect in this case rather than a mixed effect as in the AIC analyses because of complications in estimating parameters in a mixed effect model) against the low-flow pH for each stream. Residuals were calculated by subtracting the predicted total fish biomass (determined from a regression analysis) from the actual total fish biomass values. Negative residuals indicate actual values are lower than expected for the total amount of pool habitat and positive residuals indicate that biomass values are greater than expected for the amount of pool habitat present.

Results

Fish communities

Total fish biomass in study stream reaches during summer ranged between 0 and 428.5 g (Table 1). Brook Trout were present in 15 of the 16 streams and were the most abundant fish, representing 72% of the total catch. Slimy Sculpin were present in six streams, and Central Mudminnow (*Umbra limi*) was found in one stream (within the Moose River watershed).

Model selection

The model selection results differ slightly, depending on whether basin is treated as a fixed or random effect. With basin as a random effect, the lowest AIC_c score is given to the model with pool area, cover, and pH (weight = 0.44, Table 2). Based on the differences in the AIC_c weight, this model was about 1.6 times more likely than the second-ranked model to be the best model in accounting for total fish biomass (Table 2). With basin as a fixed effect, the best model is one with just pool area and pH (weight = 0.56), which was also about 1.5 times more likely than the

Table 2 Model selection results for models of fish biomass in Northeastern US headwater streams in summer 2004. The effect of basin was treated as either a random effect (RE) or fixed effect (FE). The small sample AICc values cannot be compared between fixed and random effects, because the mixed-effects AICc is approximate, and uses restricted maximum likelihood (REML). The null model in both cases includes only the basin effect

	Random effect (RE)		Fixed effect (FE)	
Model	AICc	Weight	AICc	Weight
Null	178.78	<0.01	193.42	0.01
pH	179.84	<0.01	196.21	<0.01
Pool area	180.06	<0.01	189.97	0.06
Cover	164.09	0.12	192.03	0.02
pH + pool area	166.76	0.03	**185.37**	**0.56**
pH + cover	173.94	<0.01	197.51	<0.01
pH + large wood	179.13	<0.01	203.68	<0.01
pH + pool area + cover	**161.49**	**0.44**	186.30	0.35
Temperature + pool area + cover + large wood	162.42	0.28	203.97	<0.01
pH + temperature + pool area + cover + large wood	164.03	0.12	203.59	<0.01

second ranked model to be the “best” model among those tested. Including pool area and pH as covariates is supported by the data; however, neither covariate alone is strongly supported (Table 2).

Pool area and stream pH

The separate analyses comparing regressions of total pool area, low-flow pH and these two metrics together, also demonstrate the value of evaluating both habitat and stream buffering capacity together in accounting for variability in total fish biomass. Ignoring the effect of basin and other covariates, the relationship between total fish biomass and total pool area was significant (n=16, p=0.003; Fig. 2a) and total pool area accounted for almost 50% of the variability in total fish biomass (r^2=0.49). Stream low-flow pH was also positively related to total fish biomass and explained 39% of the variability in this metric (n=16, r^2=0.39, p=0.01; Fig. 2b). The multiple regression analysis with total pool area and low-flow pH together explained 78% of the

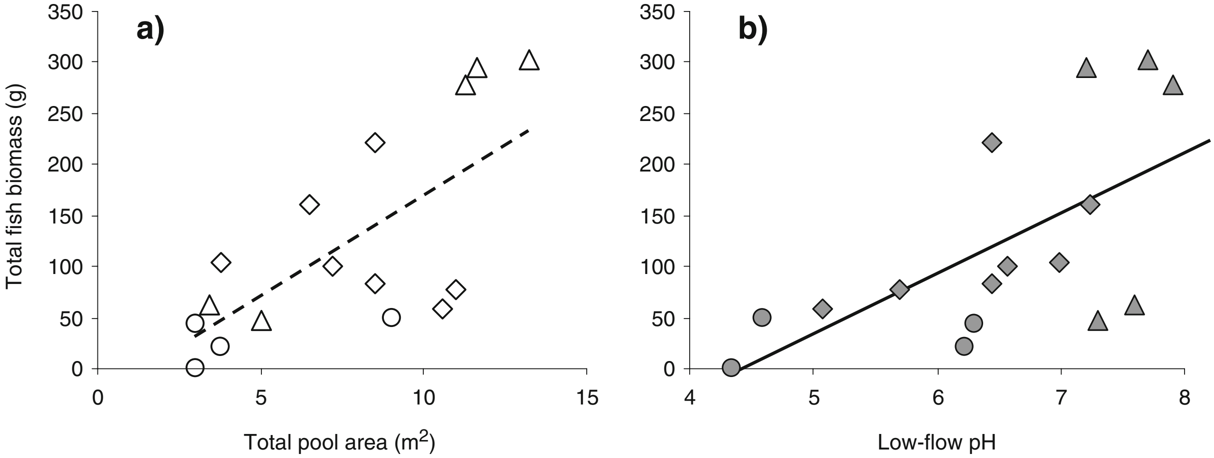

Fig. 2 Linear regressions of pool area (**a**) and pH (**b**) relative to total fish biomass in mid-summer 2004 (n=16 for both). Total pool area is significantly related to total fish biomass in summer (*open symbols*, *dashed line*) (n=16; r^2=0.49, p=0.003). Stream pH is also significantly related to total fish biomass in summer (*closed gray symbols*, *solid line*) (n=16, r^2=0.39, p=0.01). Streams from the Moose River drainage are represented by *diamonds*; streams from the Sleepers River drainage are represented by *triangles*, and streams in the Honnedaga Lake drainage are represented by *circles*

variability in the untransformed total fish biomass within the collective streams ($n=16$, $r^2=0.78$, $p<0.001$).

All streams with a low-flow pH of less than 6.25 had negative fish biomass residual values (lower total biomass than expected for a given amount of pool area) based on total fish biomass estimates calculated from parameters derived in the pool area and stream basin regression analysis. However, among the four streams with low-flow pH between 6.25 and 6.6 two had positive residuals and two had negative residuals. Given the limited number of streams and variability in residuals for streams with pH in between 6.2 and 6.6, we are reluctant to specifically suggest a low-flow pH threshold at 6.25. All four streams with low-flow pH values of 5.7 or less had total fish biomass values well below expectations for the total amount of pool habitat in those streams, so our data do suggest that a threshold for buffering capacity relative to habitat was likely passed in this study for streams with summer low flow rates somewhere between 6.3 and 5.7.

Discussion

Despite declines in acid deposition in the northeastern US, stream acidification remains an important consideration in headwater streams along with concerns over physical habitat degradation. This study clearly demonstrates the importance of accounting for both stream habitat and stream buffering capacity when considering factors related to the biomass of fish in northeastern US headwater streams. In steams with adequate buffering capacity, habitat alone can be a strong predictor of total fish biomass in summer; however, the amount and quality of habitat in a stream is likely to be relatively unimportant in accounting for total fish biomass when stream buffering capacity is low. These results illustrate the importance of considering multiple aspects (physical and chemical) of the environment when conducting stream assessments and before implementing management to improve the productivity of a target species.

The results from this study support the findings of Baldigo and Lawrence (2001), who considered a number of water chemistry and stream habitat characteristics to account for variability in the abundance and biomass of fish in Catskill Mountain streams. Although we measured fewer features, our models accounted for a substantial amount of variability in total fish biomass in summer. Variability accounted for by a mixed effects model is not easily assessed. However when basin is treated as a fixed effect, and only pH and pool area are included, our best model can account for up 72% of the variability in total fish biomass across study streams.

Stream low-flow pH alone was not among the top predictors of total fish biomass, however, the presence of pH in the top models and results from the regression comparisons clearly demonstrates the importance of pH in accounting for the biomass of fish in these streams. This study is consistent with results from other work evaluating pH in conjunction with other metrics in headwater streams from this region (Baldigo and Lawrence 2001; Nislow and Lowe 2003; Kocovsky and Carline 2005). The results presented here along with the recent literature suggest that despite slight increases in surface water pH across the region (Driscoll et al. 2001), acid deposition continues to influence fish abundance and production in many northeastern streams. Streams with a summer/fall pH of 6.3 or higher had greater fish biomass than systems with a pH below this value, but the actual low-flow pH threshold below which fish biomass was consistently lower than expected is likely to be closer to 6.0 or less. Brook Trout and sculpin are both reported to be highly tolerant of pH as low as 6.0, so this threshold value may seem high. However, stream pH in these systems can drop dramatically during snowmelt or other periods of intense precipitation throughout the year (Driscoll et al. 2001). Thus, the summer/fall low-flow pH represents the conditions of the system when additional acid inputs are low and as such our data provide a proxy measure of potential buffering capacity and associated effects of episodic acidification. Kocovsky and Carline (2005) also used baseflow pH as their metric to evaluate the effect of acidity on trout distribution in Pennsylvania, as did Nislow and Lowe (2003). Nislow and Lowe (2003) found that summer pH of 6.0 or less could be used as a rough threshold below which Brook Trout populations were substantially reduced relative to other streams with comparable riparian forest conditions. Kocovsky and Carline (2005) did not identify a specific threshold beyond which Brook Trout relative abundance or biomass declined. In evaluating the presence or absence of Brook Trout, however, they documented the lowest pH conditions in which trout were still present: streams with summer pH as low as 4.6 in the Appalachian Plateau province and 5.6 in the Ridge and Valley Province of Pennsylvania (Kocovsky and Carline 2005). In our study, the lowest pH conditions were found in tributaries to Honnedaga Lake. Brook Trout were present in one of these streams with a summer/fall pH of 4.6 but biomass and density were very low. The only fishless stream in our study was a Honnedaga tributary with a low-flow pH of 4.4.

Greater pool habitat has been linked to greater fish abundance and larger fish in various stream systems (Stichert et al. 2001; Binns 2004; Harvey et al. 2005; Young et al. 2005). Our results are consistent with these studies as evidenced by the importance of total pool area in the top models from the model selection exercise, and the results from the regression comparisons. Stream habitat management often focuses on creating and increasing pool area in streams and this work supports the importance of this feature in streams. However, this work also suggests that if the low-flow pH of a stream falls below a given threshold (likely between 5.7 and 6.3), improving the amount of pool habitat in a stream may have a limited effect on total fish biomass.

Cover score estimates provided a subjective measure of the cumulative amount of cover available to protect fish from avian, aquatic and terrestrial predators. Cover was clearly important in this analysis but there is some uncertainty in the degree of importance. As noted above, this metric is included in the top ranked model when basin is considered as a random effect, but not as a fixed effect. Although the quantification of the cover score was subjective, the criteria were based on a series of objective features that are considered relevant to fish: deep water, wood, boulders, undercut banks and overhanging vegetation (Berg et al. 1998; Rashleigh et al. 2005). One of the advantages of a cover score in conducting stream assessments is that it can be determined relatively quickly and easily. One of the disadvantages of such as metric is that even with specific criteria there is the potential for subjectivity in these scores, and variability among researchers is possible. All cover score surveys in the current study were conducted by the same individuals to maintain consistency and reduce estimate variability.

The influence of large wood on fish communities in boulder and cobble dominated streams is variable (Berg et al. 1998; Warren and Kraft 2003; Sweka and Hartman 2006). Large wood frequency, along with temperature, pool area and cover score, was included in second- and third-ranked models from the mixed-effects analysis, suggesting that it does account for some additional variability in total fish biomass. However, the absence of wood frequency from the best model in the mixed effects analysis and from any of the top models in the fixed-effects analysis suggests that the amount of additional variability accounted for by wood was low in this study. This should not necessarily be interpreted as a lack of importance for these structural elements in general. Berg et al. (1998) found that although wood was not the dominant cover item for trout in the Sierra Nevada Mountains, it was used for cover by fish in greater proportion than its availability. Similarly, Flebbe (1999) often found greater fish abundance in pools containing large wood, but large wood alone was not the dominant factor affecting the biomass of fish in the southern Appalachian streams evaluated in that study. The limited predictive power of our large wood assessment may also be a due in part to the measurement of all large wood rather than focusing on “functional” wood. Restricting ourselves to counting just wood within the wetted channel (rather than the full bankfull channel) may have yielded a stronger relationship of wood in our models. The season during which the fish surveys were conducted may also be a factor in a reduced influence of large wood in this study. Large wood may be particularly important during spring snowmelt and have limited influence during summer low-flow conditions (Warren and Kraft 2003). More specific criteria regarding wood function may improve its value as a predictor variable for summer fish biomass in future assessments.

Water temperature, like wood abundance, was included in the second- and third-ranked models from the random-effects analysis, but it was not as important a metric as pH, pool area, or cover in accounting for total fish biomass in this study. This result contrasts somewhat with Stoneman and Jones’ (2000) observation that temperature was the single best predictor of trout biomass in Southern Ontario streams. The relatively diminished importance of temperature in our study relative others is in part likely to be a result of our focus on headwater streams which often exhibit more limited variability in mid-summer water temperatures relative to larger streams. Indeed, none of the temperature measurements in this study are considered stressful for Brook Trout or Slimy Sculpin (range: 10.4°C to 14.7°C).

While most of the metrics assessed here are associated to some degree with total fish biomass in summer, they do not explain all of the variability. One of the primary factors likely to affect total fish biomass that our current study does not account for is food availability. Fish in these system feed primarily on invertebrates (most fish are well below 160 mm) but we have no measure of in-stream invertebrate production or the input of terrestrial invertebrates. Measurements accounting for invertebrate production and availability would most likely provide additional explanatory power to account for variability in total fish biomass.

We note two primary areas of caution in interpreting the results of this study. First, the specific stream features most closely associated with fish biomass in this study likely influence fish biomass in summer but may not necessarily reflect the importance or lack of importance of these features during other seasons. As noted above, in the spring, when flows are high, large wood may be more important as flow refuge habitat. Or, in the fall, when fish are spawning, areas of groundwater discharge are likely to be more important than pH, temperature, or pool habitat for larger fish. The "snap shot" nature of our pH, habitat, and fish biomass estimates allow for the possibility that other features, both measured and unmeasured, can account for more of the variability in overall fish production in a given system. Second, causation cannot be directly inferred from a correlation without a clear mechanism. For stream pH, numerous lab studies (Ingersoll et al 1990; Mount et al 1990; Cleveland et al. 1991; Jagoe and Haines 1997) and field bioassay studies (Gagen et al. 1993; Simonin et al. 1993; Baker et al 1996; Van Sickle et al. 1996; Baldigo and Murdoch 1997; Lachance et al. 2000) increase our confidence that low pH and associated dissolution of monomeric aluminum (Al^{+3}) influence fish biomass in headwater streams. As noted above, the association of pool habitat with fish biomass has been documented in other correlative studies (Stichert et al. 2001; Binns 2004; Harvey et al. 2005; Young et al. 2005). In addition, studies that manipulate streams to change the amount of pool area and cover have often documented changes in fish biomass (Gowan and Fausch 1996; Jones et al. 1996; Riley and Fausch 1995; Solazzi et al. 2000; Binns 2004), yet whether such changes are directly attributable to increased productivity or simply increased aggregation or increased immigration is unclear (Gowan and Fausch 1996; Riley and Fausch 1995).

Acid deposition continues to affect fish productivity in streams of the northeastern US where our study is focused, however, acid deposition and its associated effects are not restricted to northeastern North America. For example, in many areas of northern Europe, where the native salmonids (Brown Trout (*Salmo trutta*) and Atlantic Salmon (*Salmo salar*)) are less tolerant of stream acidification than the Brook Trout studied here, acid deposition rates were comparable to or greater than deposition rates in the eastern US (Stoddard et al. 1999; Laudon and Hemond 2002; Yan et al. 2003). And, in eastern Asia and in China in particular, coal fired power plants—a key contributor to acid deposition—are a widespread and rapidly increasing energy source. Although not historically highlighted as an environmental issue in this region, there may be an increasing need to consider both stream acidification with habitat when managing stream fisheries there and in other areas of in the developing world (Kuylenstierna 2001; Du 2007).

Our results have implications for stream management in headwaters in the northeastern US and elsewhere. Stream buffering capacity as well as habitat, affects fish biomass; consequently, conservation and restoration strategies that fail to account for both factors may be ineffective. These results in conjunction with other studies evaluating stream fish communities demonstrate that the factors limiting fish productivity are regionally and locally variable, and identifying whether fish are limited by pH, by habitat, or by some other factor is likely to be key in developing a successful management strategy in any system.

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References

Baker JP, VanSickle J, Gagen CJ, DeWalle DR, Sharpe WE, Carline RF et al (1996) Episodic acidification of small streams in the northeastern united states: effects on fish populations. Ecol Appl 6:422–437

Baldigo BP, Murdoch PS (1997) Effect of stream acidification and inorganic aluminum on mortality of Brook Trout (S*alvelinus fontinalis*) in the Catskill Mountains, New York. Can J Fish Aquat Sci 54:603–615

Baldigo BP, Lawrence GB (2001) Effects of stream acidification and habitat on fish populations of a North American river. Aquat Sci 63:196–222

Berg N, Carlson A, Azuma D (1998) Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Can J Fish Aquat Sci 55:1807–1820

Binns NA (2004) Effectiveness of habitat manipulation for wild salmonids in Wyoming streams. North Am J Fish Manage 24:911–921

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Carle FL, Strub MR (1978) A new method for estimating population size from removal data. Biometrics 34:621–630

Cleveland L, Buckler DR, Brumbaugh WG (1991) Residue dynamics and effects of aluminum on growth and mortality in Brook Trout. Environ Toxicol Chem 10:243–248

Cowx IG, Lamarque P (1990) Fishing with electricity, applications in freshwater fisheries management. Fishing News Books, Alden, Oxford

Driscoll CT, Lawrence GB, Bulger AJ, Butler TJ, Cronan CS, Eagar C et al (2001) Acidic deposition in the northeastern united states: sources and inputs, ecosystem effects, and management strategies. Bioscience 51:180–198

Du CY (2007) Input–output budgets for inorganic nitrogen under acid rain in a subtropical evergreen mixed forest in Central-South China. Water Air Soil Pollut

Flebbe PA (1999) Trout use of woody debris and habitat in Wine Spring Creek, North Carolina. Forest Ecology and Management 114:367–376

Gagen CJ, Sharpe WE, Carline RF (1993) Mortality of Brook Trout, mottled sculpins, and Slimy Sculpins during acidic episodes. Trans Am Fish Soc 122:616–628

Gowan C, Fausch KD (1996) Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecol Appl 6:931–946

Harvey BC, White JL, Nakamoto RJ (2005) Habitat-specific biomass, survival, and growth of rainbow trout (O*ncorhynchus mykiss*) during summer in a small coastal stream. Can J Fish Aquat Sci 62:650–658

Heard RM, Sharpe WE, Carline RF, Kimmel WG (1997) Episodic acidification and changes in fish diversity in Pennsylvania headwater streams. Trans Am Fish Soc 126:977–984

Heggenes J, Northcote TG, Peter A (1991) Spatial stability of cutthroat trout (O*ncorhynchus clarki*) in a small, coastal stream. Can J Fish Aquat Sci 48:757–762

Hornbeck JW, Bailey SW, Buso DC, Shanley JB (1997) Streamwater chemistry and nutrient budgets for forested watersheds in New England: variability and management implications. For Ecol Manag 93:73–89

Ingersoll CG, Mount DR, Gulley DD, La Point TW, Bergman HL (1990) Effects of pH aluminum and calcium on survival and growth of eggs and fry of Brook Trout S*alvelinus fontinalis*. Can J Fish Aquat Sci 47:1580–1592

Jagoe CH, Haines TA (1997) Changes in gill morphology of Atlantic salmon (S*almo salar*) smolts due to addition of acid and aluminum to stream water. Environ Pollut 97:137–146

Jones ML, Randall RG, Hayes D, Dunlop W, Imhof J, Lacroix G et al (1996) Assessing the ecological effects of habitat change: moving beyond productive capacity. Can J Fish Aquat Sci 53:446–457

Kaeser AJ, Sharpe WE (2001) The influence of acidic runoff episodes on Slimy Sculpin reproduction in stone run. Trans Am Fish Soc 130:1106–1115

Kocovsky PM, Carline RF (2005) Stream ph as an abiotic gradient influencing distributions of trout in Pennsylvania streams. Trans Am Fish Soc 134:1299–1312

Kuylenstierna, JCI (2001) Acidification in developing countries: ecosystem sensitivity and the critical load approach on a global scale. Ambio—J Human Env 30

Lachance S, Berube P, Lemieux M (2000) In situ survival and growth of three Brook Trout (S*alvelinus fontinalis*) strains subjected to acid conditions of anthropogenic origin at the egg and fingerling stages. Can J Fish Aquat Sci 57:1562–1573

Laudon H, Hemond HF (2002) Recovery of streams from episodic acidification in northern Sweden. Environ Sci Technol 36:921–928

Mount DR, Swanson MJ, Breck JE, Farag AM, Bergman HL (1990) Responses of Brook Trout (*Salvelinus fontinalis*) fry to fluctuating acid, aluminum, and low calcium exposure. Can J Fish Aquat Sci 47:1623–1630

Nislow KH, Lowe WH (2003) Influences of logging history and stream ph on Brook Trout abundance in first-order streams in New Hampshire. Trans Am Fish Soc 132:166–171

Parkhurst BR, Bergman HL, Fernandez J, Gulley DD, Hockett JR, Sanchez DA (1990) Inorganic monomeric aluminum and ph as predictors of acidic water toxicity to Brook Trout (S*alvelinus fontinalis*). Can J Fish Aquat Sci 47:1631–1640

Rashleigh B, Parmar R, Johnston JM, Barber MC (2005) Predictive habitat models for the occurrence of stream fishes in the mid-Atlantic highlands. North Am J Fish Manage 25:1353–1366

Riley SC, Fausch KD (1995) Trout population response to habitat enhancement in six northern colorado streams. Can J Fish Aquat Sci 52:34–53

Royall R (1997) Statistical evidence: a likelihood paradigm. Chapman and Hall/CRC, New York

Sharpe WE, Leibfried VG, Kimmel WG, DeWalle DR (1987) The relationship of water quality and fish occurrence to soils and geology in an area of high hydrogen and sulfate ion deposition. Water Resour Bull 23:37–46

Simonin HA, Kretser WA, Bath DW, Olson M, Gallagher J (1993) In-situ bioassays of Brook Trout (*Salvelinus fontinalis*) and blacknose dace (*Rhinichthys atratulus*) in Adirondack streams affected by episodic acidification. Can J Fish Aquat Sci 50:902–912

Simonin HA, Colquhoun JR, Paul EA, Symula J, Dean HJ (2005) Have Adirondack stream fish populations changed in response to decreases in sulfate deposition? Trans Am Fish Soc 134:338–345

Solazzi MF, Nickelson TE, Johnson SL, Rodgers JD (2000) Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Can J Fish Aquat Sci 57:906–914

Stichert ND, Hubert WA, Skinner QD (2001) A test of factors hypothesized to influence biomass of salmonids in rocky mountain streams. J Freshw Ecol 16:493–500

Stoddard JL, Jeffries DS, Ukewille A, Clair TA, Dillon PJ, Driscoll CT, Forsius M, Johannessen M, Kahl JS, Kellogg JH, Kemp A, Mannio J, Monteith DT, Murdoch PS, Patrick S, Rebsdorf A, Skjelkvale BL, Stainton MP, Traaen T, van Dam H, Webster KE, Wieting J, Wilander A (1999) Regional trends in aquatic recovery from acidification in North America and Europe. Nature 401:575–578

Stoneman CL, Jones ML (2000) The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonines. Trans Am Fish Soc 129:639–657

Sweka JA, Hartman KJ (2006) Effects of large woody debris addition on stream habitat and Brook Trout populations in Appalachian streams. Hydrobiologia 559:363–378

Van Sickle J, Baker JP, Simonin HA BPB, Krester WA, Sharpe WE (1996) Episodic acidification of small streams in the northeastern united states: fish mortality in field bioassays. Ecol Appl 6:408–421

Warren DW, Kraft CE (2003) Brook Trout (*Salvelinus fontinalis*) response to wood removal from high-gradient streams of the Adirondack Mountains (NY, USA). Can J Fish Aquat Sci 60:379–389

Yan ND, Leung B, Keller W, Arnott SE, Gunn JM, Raddum GG (2003) Developing conceptual frameworks for the recovery of aquatic biota from acidification. Ambio 32:165–169

Young MK, Guenther-Gloss PM, Ficke AD (2005) Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: revisiting a model of translocation success. Can J Fish Aquat Sci 62:2399–2408