

# Chemical and biological recovery from acid deposition within the Honnedaga Lake watershed, New York, USA

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**Abstract** Honnedaga Lake in the Adirondack region of New York has sustained a heritage brook trout population despite decades of atmospheric acid deposition. Detrimental impacts from acid deposition were observed from 1920 to 1960 with the sequential loss of acid-sensitive fishes, leaving only brook trout extant in the lake. Open-lake trap net catches of brook trout declined for two decades into the late 1970s, when brook trout were considered extirpated from the lake but persisted in tributary refuges. Amendments to the Clean Air Act in 1990 mandated reductions in sulfate and nitrogen oxide emissions. By 2000, brook trout had re-colonized the lake coincident with reductions in surface-water sulfate, nitrate, and inorganic monomeric aluminum. No changes have been observed in surface-water acid-neutralizing capacity (ANC) or calcium concentration. Observed increases in chlorophyll *a* and decreases in water clarity reflect an increase in phytoplankton abundance. The zooplankton community exhibits low species richness, with a scarcity of acid-

sensitive *Daphnia* and dominance by acid-tolerant copepods. Trap net surveys indicate that relative abundance of adult brook trout population has significantly increased since the 1970s. Brook trout are absent in 65 % of tributaries that are chronically acidified with ANC of <0 µeq/L and toxic aluminum levels (>2 µmol/L). Given the current conditions, a slow recovery of chemistry and biota is expected in Honnedaga Lake and its tributaries. We are exploring the potential to accelerate the recovery of brook trout abundance in Honnedaga Lake through lime applications to chronically and episodically acidified tributaries.

**Keywords** Acid deposition · Recovery · Chemistry · Fish · Zooplankton

## Introduction

Acid precipitation primarily originates from fossil fuel combustion and has negatively impacted aquatic and terrestrial ecosystems in eastern North America, Europe, and Asia for several decades (Driscoll et al. 2001; Tipping et al. 2002). The Adirondack Mountain region of New York State, USA is highly sensitive to acid precipitation due to the underlying bedrock geology characterized by low cation pools and weather patterns that deposit large amounts of acid-laden precipitation (Driscoll et al. 1991, 2003b). Acid precipitation has resulted in the chronic and episodic acidification of numerous lakes and streams in the Adirondack Mountain region (Baker et al. 1996; Driscoll et al.

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2001; Lawrence et al. 2008) with widespread loss of fish populations (Schofield 1976; Kretser et al. 1989; Baker and Christensen 1991) and altered zooplankton communities (Siegfried and Sutherland 1992; Nierzwicki-Bauer et al. 2010). Extensive research efforts over three decades (1960–1990) definitively identified anthropogenic sources of sulfur dioxide (SO<sub>2</sub>) and nitrogen oxide (NO<sub>x</sub>) emissions from burning of fossil fuels as the primary source of strong inorganic anions that produce acid precipitation (Driscoll et al. 2001; Jenkins et al. 2005).

The Clean Air Act Amendments (CAAA) of 1990 and Clean Air Interstate Rule (CAIR) of 2005 were implemented to reduce SO<sub>2</sub> and NO<sub>x</sub> emissions, which produce strong acids, and thereby reduce levels of acidic deposition to promote chemical and biological recovery in acid-impacted lakes and streams (Driscoll et al. 2001; Sullivan et al. 2007; Burns 2011). Since the implementation of CAAA and CAIR, SO<sub>2</sub> emissions in the USA have been reduced 64 % compared with 1990 levels and NO<sub>x</sub> emissions reduced 67 % compared with 1995 levels (Burns 2011). Consequently, significant changes in the surface-water chemistry of many Adirondack lakes have been documented including increased pH and reduced levels of inorganic monomeric aluminum toxic to fish and other aquatic biota (Driscoll et al. 2007). Few studies worldwide have documented biological changes coincident with chemical recovery in acidified surface waters since 1990, but those studies have indicated that the rate of biological recovery is lagging behind that of chemical recovery (Monteith et al. 2005; Momen et al. 2006; Burns 2011). Assessing changes in the chemistry and biota of acid-impacted watersheds is a high priority to determine if current acid emission controls have been adequate for targeted ecosystem recovery.

Honnedaga Lake is situated on the property of a private club in the southwest Adirondack Mountains of New York State, USA. The fishery of the lake has been managed and studied by this club and its various fishery consultants since the 1880s, though water chemistry and biota samples from Honnedaga Lake prior to 1950 are scarce. The historic environmental monitoring program on Honnedaga Lake allows for an assessment of its current state of chemical and biological recovery from acidification from atmospheric deposition.

Estimates of wet sulfate (SO<sub>4</sub>) and nitrate (NO<sub>3</sub>) deposition in the Adirondacks from the Syracuse Experimental Station at Huntington Forest in Newcomb, NY (Jenkins et al. 2005) and from Hubbard Brook Experimental Forest, NH (Driscoll et al. 2001) indicate progressive increases in acid deposition from 1850 until deposition peaked in this region in the mid-1970s. Historical changes in the Honnedaga Lake fish community coincident with increasing SO<sub>4</sub> and NO<sub>3</sub> wet deposition (and presumed increases in acidity), provide insights into the effects of acidic deposition on this watershed.

The historical fish community in Honnedaga Lake from 1880 to 1960 was described by Webster (1961) and Schofield (1965). Brook trout (*Salvelinus fontinalis*) is the only fish species indigenous to Honnedaga Lake. Circa 1890, four fish species including lake trout (*Salvelinus namaycush*), round whitefish (*Prosopium cylindraceum*), white sucker (*Catostomus commersonii*), and creek chub (*Semotilus atromaculatus*) were introduced and established reproducing populations. A thriving lake trout sport fishery existed between 1890 and 1930, with hundreds of fish caught by anglers. Round whitefish, white sucker, and creek chub disappeared from the lake by 1930, and lake trout disappeared by 1955. Brook trout are the only fish species currently existing in the lake. Nearly identical changes in the fish community of the nearby North Branch Moose River, which occurred from 1890 through 1985, were attributed to low pH and aluminum toxicity due to acid precipitation (Schofield and Driscoll 1987). Although not apparent at the time, the losses of fish species from Honnedaga Lake can now be attributed to acidification of the watershed by airborne pollutants. Beginning in the late 1950s, a more comprehensive chemical and biological monitoring program was established to better understand the Honnedaga Lake ecosystem.

The intent of this paper is to present an assessment of chemical and biological recovery from impacts of acid deposition within the Honnedaga Lake watershed since implementation of CAAA (1990) and CAIR (2005) to reduce acid emissions. Specifically, we investigate changes in surface-water chemistry over time, zooplankton community response to changes in water chemistry, variables controlling use of tributaries by young-of-year (YOY) brook trout, and changes in adult brook trout abundance in relation to surface water chemistry.

**Materials and methods**

**Study site description**

Honnedaga Lake is a 312-ha lake with a maximum depth of 55.8 m and is located at 701 m elevation in the southwestern Adirondack Mountain region of New York State (Fig. 1). Honnedaga Lake was historically called “Transparency Lake” owing to its high water clarity, with Secchi depth more than 23 m (Webster 1961). Honnedaga Lake supports one of the seven remaining heritage or original genetic strains of brook trout designated by the State of New York (Keller 1979) and brook trout is the only species of fish currently inhabiting the lake.

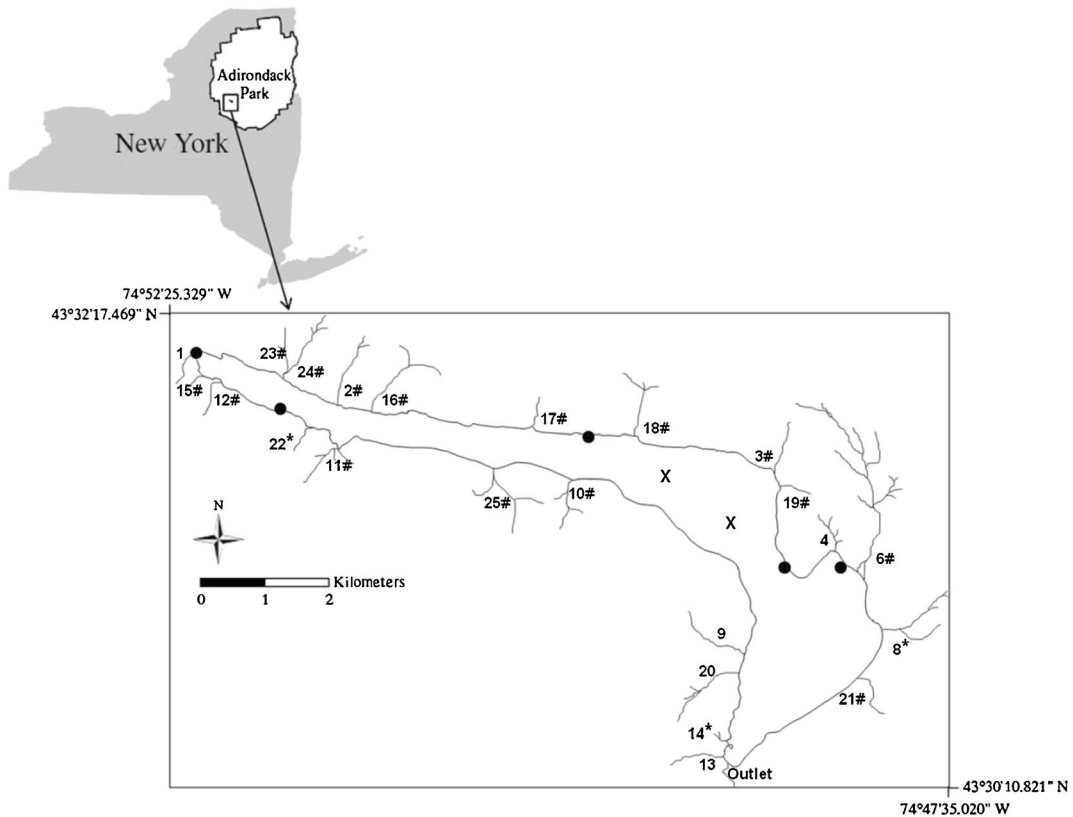
Honnedaga Lake is classified as a thin-till drainage lake with poorly buffered soils (Newton and Driscoll 1990). Considering its location and elevation in the southwestern Adirondacks, the Honnedaga Lake watershed receives some of the greatest amounts of acid

precipitation in the northeastern USA (Ito et al. 2002). The combination of a poorly buffered watershed and large amounts of acid deposition results in Honnedaga Lake being highly sensitive to the effects of acid deposition (Schofield 1965; Sullivan et al. 2007). The watershed is of glacial origin and dominated by thin till; however, some of its catchments are composed of thick glacial till and are better buffered than the thin-till catchments. Conditions observed within the Honnedaga Lake watershed are not unique in this region. Many watersheds in the southwestern Adirondacks are dominated by thin-till catchments with poorly buffered soils (Newton and Driscoll 1990).

**Water quality surveys**

*Lake surface*

Lake surface-water chemistry was analyzed for samples collected in summer (June through September) at



**Fig. 1** Honnedaga Lake and tributaries located in the southwestern Adirondack Mountain region of New York State, USA. Dock surface sample sites are denoted by *filled circles*. Deep lake sample sites are denoted by *error marks*. Tributaries with ANC > 50 µeq/L

denoted by plain numbers. Episodically acidified tributaries denoted by a *number and asterisk*. Chronically, acidified tributaries denoted by a *number and number sign*

established deep-water sites ( $n=2$ ) and several docks located around the lake perimeter ( $n=5$ ) (Fig. 1). Lake surface-water samples were collected sporadically, with many years not sampled from 1960 to 1999. More comprehensive summer sampling of lake surface water and major tributaries was initiated in 2001 to better characterize water chemistry within the entire Honnedaga Lake watershed. Surface-water samples and temperature data were collected weekly or monthly from June through September from 2001 through 2011. Secchi disk depth (m) and color were measured when deep lake sites were sampled from 1960 through 2011.

Measurements of pH and ANC were made on water samples collected from the lake surface at the Cornell University Little Moose Field Station in Old Forge, NY using US Environmental Protection Agency (1987) methods. From 2001 to 2011, water samples from the lake surface were analyzed for  $\text{SO}_4$ ,  $\text{NO}_3$ , calcium (Ca), chlorophyll *a* (chl $a$ ), dissolved organic carbon (DOC), total monomeric Al, and organic monomeric Al. Inorganic monomeric aluminum ( $\text{Al}_{\text{im}}$ ) was determined by subtracting concentrations of organic monomeric Al ( $\text{Al}_{\text{om}}$ ) from total monomeric Al ( $\text{Al}_{\text{tm}}$ ). Chemical analyses were conducted at the Darrin Fresh Water Institute Keck Water Quality Laboratory, RPI, Troy, NY from 2001 to 2010 following US Environmental Protection Agency methods (Stoddard et al. 2003), with the exception of total and organic monomeric Al, which were analyzed at the US Geological Survey Water Science Center, Troy, NY following methods described in Lawrence et al. (1995). All analyses other than ANC and pH were done at the USGS Troy laboratory from 2010 to 2011 following methods in Lawrence et al. (1995).

Simple linear regression models with year as the independent variable ( $\alpha=0.05$ ) were used to assess changes in surface-water pH and Secchi depth from 1960 to 2011 and all other parameters from 2001 to 2011. The difference between inorganic monomeric aluminum concentrations in the 1980s (1981–1983) and 2000s (2002–2011) was assessed using a *t* test ( $\alpha=0.05$ ). All data analyses in this paper were performed using program R (The R Foundation for Statistical Computing; <http://www.r-project.org/>).

### Tributaries

Tributaries were identified using a topographic index (TI) model to map and predict intensity of groundwater

inputs at the lake shoreline (Borwick et al. 2006; Stevens 2008). The TI map aided in the identification of 23 tributaries within the Honnedaga Lake watershed (Fig. 1). Water samples were collected weekly from June through August in 2008 to 2010 to characterize the summer chemistry of Honnedaga Lake tributaries. Tributary water samples were analyzed for pH, ANC, and  $\text{Al}_{\text{im}}$ . Analyses were conducted at the USGS New York Water Science Center, Troy, NY following standard methods in Lawrence et al. (1995).

Tributary water chemistry data were compiled, and 3-year (2008–2010) means and ranges were calculated for pH, ANC, and  $\text{Al}_{\text{im}}$  to characterize the summer chemistry, which represented base flow conditions. Based on 3-year means, the tributaries were classified as either: (1) chronically acidified with  $\text{ANC}<0$   $\mu\text{eq/L}$ , (2) susceptible to episodic acidification with  $0<\text{ANC}<50$   $\mu\text{eq/L}$ , or (3) relatively insensitive to inputs of acid deposition with  $\text{ANC}>50$   $\mu\text{eq/L}$  according to Driscoll et al. (2001). For ease of discussion, these categories are henceforth referred to as chronically acidified, episodically acidified, and not acidified, respectively.

### Biological surveys

#### Zooplankton

The mid-summer, pelagic, crustacean zooplankton community in Honnedaga Lake was assessed by analyzing zooplankton samples collected from a deep-water, mid-lake station in 1997, 1999, and 2001–2010 (Fig. 1). The analysis used samples collected in August for all years except 1997 and 2007 when August samples were not collected. Samples used from 1997 and 2007 were collected on 17 September 1997 and 30 July 2007, respectively. Zooplankton were sampled using a 153- $\mu\text{m}$  mesh nylon plankton net (0.5-m diameter) towed vertically from depths of 22.0–51.5 m to the water surface. Samples were preserved in 95 % ethanol.

One zooplankton sample was analyzed for each year except in 1999 when two samples were analyzed. Crustacean zooplankton were counted and measured using a dissecting microscope ( $\times 18$ –150 power) and a digitizing tablet. A 1-mL subsample was drawn from each sample with a Hensen–Stempel pipette, and all crustacean zooplankton were identified, counted, and measured for length. Subsamples were processed in this manner until a minimum of 100 organisms (range, 100–

213) were counted and measured from each sample. All subsamples were processed in their entirety.

Species richness, relative abundance of *Daphnia* spp., zooplankton density, and zooplankton size were determined for each sample. Densities (no./L) were calculated based on the number of 1-mL subsamples processed, tow depth of the sample, and net circumference, assuming 100 % filtering efficiency of the net. To assess the degree of within-sample variation, two additional replicate subsamples (for a total of three) were analyzed from the tow for 3 of the 12 years (2001, 2005, and 2009) in which zooplankton samples were available. Variability in the four parameters measured was quite low, so no additional replicates for other years were analyzed. Simple linear regression was used to test for a linear relationship ( $\alpha=0.05$ ) over time (1997–2010) for species richness, relative abundance of *Daphnia* spp., zooplankton density, and zooplankton size.

#### *Young-of-year brook trout*

Single-pass backpack electrofishing assessments were conducted in 23 tributaries of Honnedaga Lake during late July and early August of 2003, 2006, and 2008–2010 to determine occupancy and density (no./m<sup>2</sup>) of YOY brook trout. All 23 tributaries were not sampled each year. Eight of the tributaries were sampled all five years of the study, three tributaries were sampled 4 years, four tributaries were sampled 3 years, and eight tributaries were sampled only 2 years. Electrofishing reach lengths began at the tributary-lake confluence and continued upstream 10–29 m when natural migration barriers (i.e., waterfalls) were not present. When a barrier to migration was present within 25 m of the tributary-lake confluence, the electrofishing occurred throughout the entire stream reach up to the migration barrier.

Presence/absence of YOY brook trout was analyzed using multiple logistic regression to determine factors influencing occupancy. Fifteen models were developed based on biologically justifiable combinations of variables collected from each tributary. The variables included: a topographic index value (TI value),  $Al_{im}$  concentration, fall adult female brook trout CPUE (number/trap net night) from the previous year, and stream temperature (°C). The TI is a measure of groundwater influence (Stevens 2008). Increasing values represent areas of cooler water temperatures and the potential for mitigating undesirable surface water chemistry via

groundwater discharge (Borwick et al. 2006). The effect of  $Al_{im}$  on mortality of juvenile brook trout has been well studied (Van Sickle et al. 1996; Baldigo and Murdoch 1997; Baldigo et al. 2007) and  $Al_{im}$  concentrations above 2.0  $\mu\text{mol/L}$  are generally recognized to adversely affect aquatic biota (Driscoll et al. 2001). Levels of  $Al_{im}$  in 2003, 2006, and 2008 were predicted using a relationship between pH and  $Al_{im}$  concentrations collected in 2009 and 2010 ( $Al_{im} = 160,008(\text{pH})^{-7.125}$ ,  $r^2=0.78$ ). Female CPUE was included in the occupancy models to assess whether YOY distribution changes in response to changes in densities of females on the spawning grounds. The interactions  $Al_{im} \times \text{TI}$ ,  $Al_{im} \times \text{stream temperature}$ , and  $Al \times \text{female CPUE}$  were also included as variables in the candidate set of occupancy models.

As the same tributaries were sampled multiple years, we also tested whether presence/absence of YOY brook trout within each tributary were correlated due to repeated sampling, by adding a categorical tributary effect to each model in the occupancy analysis. No significant tributary effect was detected. Therefore, we did not retain the repeated measures component (i.e., tributary effect) in the occupancy analysis.

Data collected in 2006, 2008, and 2009 were used to assess the factors influencing the density of YOY brook trout. Only data collected from tributaries sampled in each of these years were used in the analysis. YOY brook trout density failed to meet the normality assumption associated with multiple linear regression due to the large numbers of zeros (absences) in the data set. Therefore, a likelihood ratio test was performed to determine whether a Poisson or negative binomial distribution better fit the data. Once a distribution was defined, a Vuong test was performed to determine whether the zero-inflated version of the distribution was more appropriate (Vuong 1989), resulting in the selection of the negative binomial distribution. A total of 51 models were developed based on biologically justified combinations of the variables collected from each tributary. Variables included in the candidate set of density models included all those mentioned above, in addition to the number of pieces of large woody debris (LWD) greater than 10 cm in width and 1 meter in length, volume of water sampled, dominant substrate size (fine material, sand, gravel, pebble, cobble, and boulder) determined through visual observation of the study reach, and a year effect. The interactions  $Al_{im} \times \text{volume}$ ,  $Al_{im} \times \text{substrate}$ , and  $Al_{im} \times \text{year}$  were also included as variables in the



candidate set of density models. The interaction between substrate and  $Al_{im}$  was identified as a possible predictor of YOY brook trout density. Substrate may influence YOY density (e.g., through higher spawning activity within tributaries); however the effect may ultimately be dependent upon the concentration of  $Al_{im}$ . At high concentrations of  $Al_{im}$ , YOY will be absent from tributaries, therefore substrate size will not affect density (Driscoll et al. 2001; Baldigo et al. 2007).

As the same tributaries were sampled multiple years, we also tested whether the within-tributary density of YOY brook trout were correlated due to repeated sampling, by adding a categorical tributary effect to each model in the density analysis. When a tributary effect was added, four of the eight tributaries were significant predictors of YOY brook trout density. In three of the tributaries YOY brook trout were present at low densities (mean=0.04; SD=0.06), and the fourth tributary contained a high density of brook trout (mean=0.32; SD=0.15). The mean  $Al_{im}$  value in the tributaries with low densities of brook trout was 2.70  $\mu\text{mol/L}$  (SD=0.89), which would be expected to negatively affect brook trout via aluminum toxicity (Driscoll et al. 2001). The mean  $Al_{im}$  value for the high density tributary was 0.96  $\mu\text{mol/L}$  (SD=0.59), which is within the range tolerated by brook trout (Baldigo et al. 2007). Based on these results, we conclude that the tributary effect observed in the density analysis was likely a direct result of  $Al_{im}$  concentration. Therefore we did not retain the repeated measures component (i.e., tributary effect) in the density analysis.

An information theoretic approach was used to compare the occupancy and density models. Models were ranked according to a bias corrected version of Akaike's Information Criterion ( $AIC_c$ ). Models were then compared using the difference between  $AIC_{c(i)}$  and  $AIC_{c(\min)}$  ( $\Delta AIC$ ) and  $AIC_c$  weights ( $AIC_{c(w)}$ ) (Burnham and Anderson 2002). The  $AIC_{c(w)}$  values were summed over all models to determine the importance of each parameter in the candidate models sets. The significance of individual parameters were tested by examining the change in deviance ( $-2\log(\text{likelihood})$ ) when parameters were added to candidate models and also by examining the confidence intervals (CI) of the regression coefficients. When the 95 % CI of an individual parameters regression coefficient did not contain zero (1.0 when transformed to the odds ratio scale) the parameter was considered to significantly predict the dependent variable (Anderson 2008). A model averaged estimate

of  $Al_{im}$  was calculated to determine the inflection point of  $Al_{im}$  where the probability of occupancy was 50 % (Anderson 2008). One of the most general models in each analysis was assessed for goodness of fit using a likelihood ratio test. The area under (AUC) the receiver operating characteristic (ROC) curve was calculated for each model in the multiple logistic regression candidate model set to assess model predictability. We assessed the predictive ability of AUC values according to the categories: poor (0.5–0.7), reasonable (0.7–0.9), and very good (0.9–1.0) (Swets 1988). Tolerance values ( $1-r^2$ ) were calculated for combinations of variables in all models to determine collinearity. A value less than 0.2 indicated high levels of collinearity and combinations of these variables were not included in the same model (Menard 2001).

#### *Adult brook trout*

Oneida-style trap net surveys were conducted in Honnedaga Lake to capture brook trout in 1960–1965, 1967, 1971–1974, 1976, 1979, and 2000–2011. These nets are particularly effective at capturing adult brook trout during the fall spawning season and provide an index of adult abundance. Two to six trap nets were set at six established sites located near spawning shoals and tributaries for two to four nights in late-October to mid-November. Total length (mm), weight (g), fin clips, sex, and maturity were recorded for all captured brook trout. Relative abundance of adult brook trout was represented as number caught per trap net night.

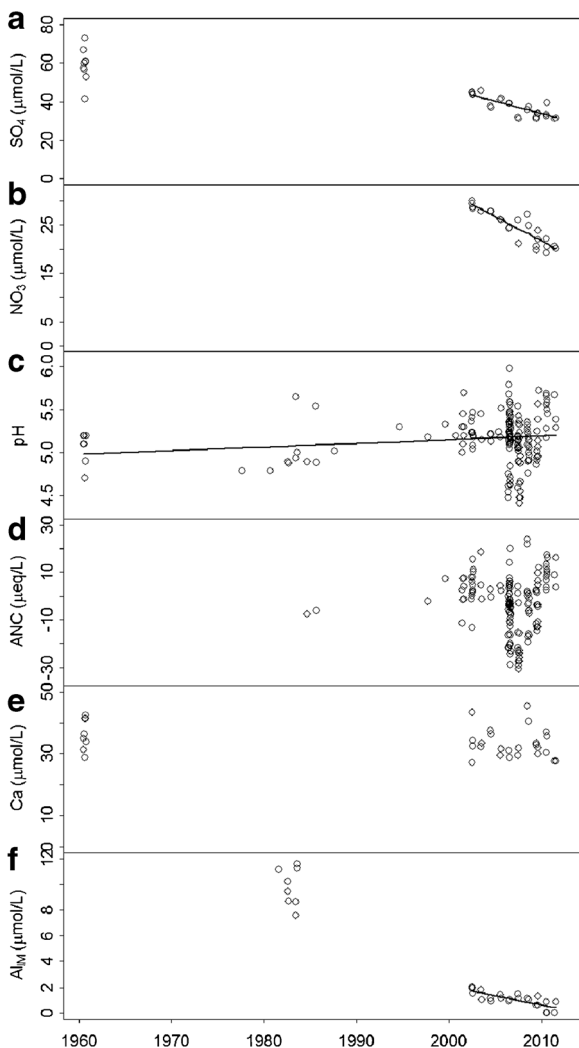
Honnedaga Lake-strain brook trout originating from eggs collected from spawning fish in the lake were stocked during two distinct periods: (1) 1952 to 1968 and (2) 2002 and 2003. Stocking from 1952 to 1968 included unmarked spring fry and marked fall fingerlings (age 0+). Fall fingerlings stocked in 2002 and 2003 were marked with unique fin clips. Stocking during these two periods was intended to supplement the wild brook trout population in Honnedaga Lake. The large number of unmarked fish stocked from 1952 to 1962 precluded distinguishing between stocked and wild fish in the fall trap net catch prior to 1970. Given this fact, only trap data from 1971–1973, 1976, 1979, 2000–2002, and 2007–2011 were used to assess annual relative abundance of adult wild brook trout. These trap net data were categorized as pre-implementation (1971–1973, 1976, and 1979) and post-implementation (2000–2002 and 2007–2011) of CAAA in 1990, and

differences in CPUE between those two periods were analyzed using a *t* test ( $\alpha=0.05$ ).

## Results

### Lake chemistry

The only  $\text{SO}_4$  data available prior to enactment of the CAAA are nine measurements from summer of 1960 (Schofield 1965) with a mean of  $58.7 \mu\text{mol/L}$  (range, 41.6 to  $72.8 \mu\text{mol/L}$ ) (Fig. 2a). Studies of



**Fig. 2** Surface-water chemistry in Honnedaga Lake (1960–2011) including  $\text{SO}_4$  (a),  $\text{NO}_3$  (b), pH (c), ANC (d), calcium (e), and inorganic monomeric aluminum (f). Significant trends were identified for  $\text{SO}_4$ ,  $\text{NO}_3$ , pH, and inorganic monomeric aluminum using simple linear regression

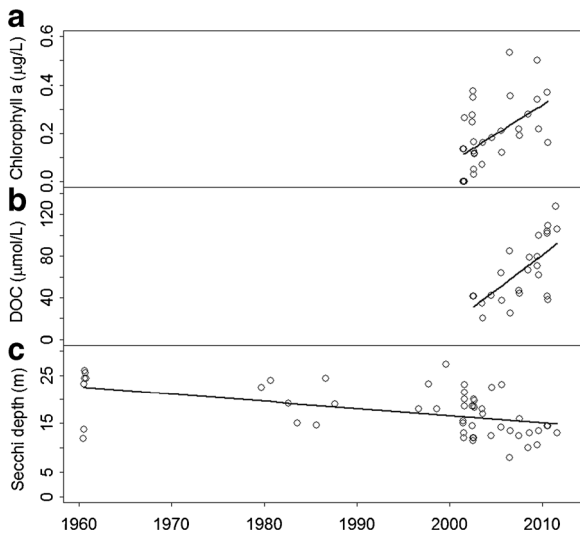
other regional waters indicate that wet  $\text{SO}_4$  deposition peaked in the mid-1970s (Driscoll et al. 2001). Given this regional trend, it is presumed that  $\text{SO}_4$  concentrations in Honnedaga Lake exceeded those of 1960. Honnedaga Lake surface-water  $\text{SO}_4$  concentrations declined significantly (from 45.1 to  $31.5 \mu\text{mol/L}$ ) from 2001 to 2011 ( $p<0.001$ ;  $R^2=0.64$ ) (Fig. 2a). The rate of decrease in  $\text{SO}_4$  concentrations was  $-1.4 \mu\text{mol L}^{-1} \text{ year}^{-1}$ . Similarly, since 2001, significant reductions in  $\text{NO}_3$  concentrations were observed in surface water from 29.1 to  $20.3 \mu\text{mol/L}$  ( $p<0.001$ ;  $R^2=0.82$ ) (Fig. 2b). The rate of decrease in  $\text{NO}_3$  concentrations was  $-0.88 \mu\text{mol L}^{-1} \text{ year}^{-1}$ .

Available pH data dating back to 1960 indicate a sustained period of summer surface pH  $<5$  from 1960 through 1990 (Fig. 2c). Summer surface pH has been consistently  $>5$  since the mid-1990s. Since 1960, there was an increase in mean lake surface-water pH from 4.8 to 5.5 (Fig. 2c). By contrast, ANC in lake surface water did not change significantly since 2001 (Fig. 2d) and calcium concentrations in lake surface water did not change significantly since 1960 (Fig. 2e).  $\text{Al}_{\text{im}}$  in lake surface waters showed significant reductions from 2001 to 2011 and ranged from 1.8 to  $0.4 \mu\text{mol/L}$  ( $p<0.001$ ;  $R^2=0.62$ ). The concentration of  $\text{Al}_{\text{im}}$  in lake surface water significantly declined from the 1980s (mean= $9.8 \mu\text{mol/L}$ ) to the 2000s (mean= $1.1 \mu\text{mol/L}$ ; *t* test,  $p<0.001$ ,  $df=30$ ) (Fig. 2f).

*Chla* concentrations in surface water increased significantly since 2001 ( $p<0.001$ ;  $R^2=0.31$ ) (Fig. 3a), with a rate of increase of  $0.02 \mu\text{g L}^{-1} \text{ year}^{-1}$ . Since 2001, there were significant increases in DOC concentrations in surface water ( $p<0.001$ ;  $R^2=0.49$ ) (Fig. 3b), changing at a rate of  $7.49 \mu\text{mol L}^{-1} \text{ year}^{-1}$ . Since 1960, water clarity measured by Secchi disk readings showed a significant decline ( $p<0.001$ ;  $R^2=0.23$ ) (Fig. 3c). Secchi water color was described as blue to light blue from 1960 to 2005 and as blue-green to light green since 2006.

### Tributary chemistry

Only five of the 23 tributaries were characterized as relatively unsusceptible to acid deposition inputs ( $\text{ANC}>50 \mu\text{eq/L}$ ) with thick glacial till, whereas three tributaries were characterized as susceptible to episodic acidification ( $0<\text{ANC}<50 \mu\text{eq/L}$ ), and 15 tributaries



**Fig. 3** Surface-water chemistry in Honnedaga Lake (1960–2011), including chl *a* (a), DOC (b), and Secchi depth (c). Significant trends were identified for chl *a*, DOC, and Secchi depth using simple linear regression

were characterized as chronically acidified with ANC < 0 µeq/L with thin glacial till (Table 1). Thus, 78 % of the tributaries within the Honnedaga Lake watershed are highly sensitive to acidic deposition and experience chronic or episodic acidification accompanied by chronic or episodic low pH (<5) and toxic levels of Al<sub>im</sub> (>2 µmol/L).

### Zooplankton

Six zooplankton species were identified from summer samples collected from 1997 through 2010 (Table 2). Annual species richness ranged from two to six taxa and showed no significant temporal trend (Fig. 4a). *Leptodiatomus minutus* (an acid-tolerant copepod) was the only species recorded in all 12 years and dominated the community, comprising 26.3–89.2 % of the community (Table 2). This dominance increased to 70.7–97.6 % when nauplii were excluded. *Daphnia pulicaria*, the only *Daphnia* species collected, was recorded in 9 of the 12 years sampled. *D. pulicaria* comprised 0.0–7.0 % of the community and showed no significant temporal trend (Fig. 4b). Zooplankton density ranged from 3.6 to 24.0 organisms/L (mean=12.6), and mean zooplankton size ranged from 0.45–0.75 mm (Fig. 4c, d). No significant temporal trend was observed for either of these measures.

### Young-of-year brook trout

Eighty-two backpack electrofishing assessments were conducted on tributaries of Honnedaga Lake over five years to determine the occupancy of YOY brook trout. The data set contained 37 sample events where YOY brook trout were present and 45 absences. The model that best explained the information in the tributary occupancy data included the variables Al<sub>im</sub> and female CPUE. However, seven of the other models evaluated also showed high support in the data (Table 3). All parameters in the top eight models were evaluated because no convincingly best model was identified. Evaluation of these parameters revealed Al<sub>im</sub> was the only significant predictor (model 1, CI=0.22, 0.57; coefficient=-1.03). Using the model averaged parameter estimates for Al<sub>im</sub> across all models, the predicted probability of presence decreased as Al<sub>im</sub> increased (Fig. 5). YOY brook trout were present in only one tributary when predicted Al<sub>im</sub> concentrations exceeded 3.55 µmol/L (Table 4). The AIC<sub>c</sub> weights summed across all models were 1.0 for Al<sub>im</sub>, 0.56 for female CPUE, 0.31 for stream temperature, and 0.21 for TI value. No collinearity was observed between variables in any of the models. Two models were assessed for goodness of fit using the likelihood ratio test, and for both models Al<sub>im</sub>, stream temperature, TI, female CPUE and the non-nested competing model Al<sub>im</sub>, year, Al<sub>im</sub> × year passed the likelihood ratio goodness of fit test ( $\chi^2=45.08$ ,  $p<0.001$ ;  $\chi^2=47.5$ ,  $p<0.001$ ), respectively. The AUC value for the top eight models ranged from 0.87 to 0.89 (Table 3).

Comparisons between the negative binomial and Poisson distributions using a likelihood ratio test revealed the negative binomial regression model was a better fit ( $\chi^2=11.24$ ,  $p<0.001$ ). Several of the candidate models were tested to compare the zero inflated versions of the negative binomial regression and ordinary negative binomial regression models. No difference was observed (Vuong test,  $p>0.05$ ), therefore the YOY brook trout density data was analyzed using a negative binomial distribution. Nine tributaries each sampled in 2006, 2008–2010 were included in the analysis totaling 36 YOY brook trout density estimates. Density estimates over the 3-year time period ranged from 0 to 0.56 YOY brook trout/m<sup>2</sup>, and a total of 37, 42, 57, and 63 YOY brook trout were captured during the years 2006 and 2008–2010, respectively. The model that best explained YOY brook trout density included the



**Table 1** Three-year means (1 SE) and ranges for temperature, pH, ANC, and inorganic monomeric aluminum in Honnedaga Lake tributaries (2008–2010) in order of decreasing mean ANC

Water	Temperature (°C)		pH		ANC (µeq/L)		Al <sub>im</sub> (µmol/L)	
	Mean (1 SE)	(Range)	Mean (1 SE)	(Range)	Mean (1 SE)	(Range)	Mean (1 SE)	(Range)
Not acidified (ANC, >50)								
Tributary 20	13.2 (0.2)	(13.0 to 13..5)	6.1 (0.3)	(5.4 to 6.8)	209.1 (97.5)	(77.7 to 457.1)	0.4 (0.1)	(0.3 to 0.5)
Tributary 1	13.3 (0.3)	(13.0 to 14.3)	6.1 (0.1)	(5.6 to 6.7)	161.9 (31.8)	(82.8 to 374.9)	0.7 (0.1)	(0.6 to 0.7)
Tributary 4	15.1 (0.7)	(12.5 to 17.0)	5.8 (0.1)	(5.2 to 6.4)	89.6 (18.1)	(24.6 to 213.6)	0.7 (0.1)	(0.5 to 1.1)
Tributary 9	14.5 (0.5)	(13.0 to 16.0)	5.7 (0.2)	(4.9 to 6.5)	55.0 (16.1)	(0.5 to 122.0)	0.5 (0.2)	(0.2 to 0.9)
Tributary 13	15.9 (1.1)	(14.0 to 20.3)	5.1 (0.3)	(4.2 to 6.4)	52.3 (43.0)	(50.0 to 257.6)	0.6 (0.3)	(0.1 to 1.1)
Episodically acidified (0<ANC<50)								
Tributary 14	18.7 (1.8)	(16.0 to 23.5)	5.5 (0.1)	(5.3 to 5.7)	40.5 (11.5)	(11.0 to 64.2)	0.6 (0.2)	(0.3 to 0.8)
Tributary 8	14.4 (0.5)	(12.5 to 16.5)	5.4 (0.2)	(4.6 to 6.4)	22.8 (7.8)	(16.4 to 59.8)	0.6 (0.2)	(0.2 to 1.3)
Tributary 22	14.1 (0.5)	(13.0 to 15.4)	5.1 (0.3)	(4.5 to 6.1)	6.7 (16.5)	(20.3 to 61.0)	1.9 (0.6)	(1.1 to 2.8)
Chronically acidified (ANC, <0)								
Tributary 21	14.2 (0.5)	(13.0 to 15.0)	4.7 (0.3)	(4.2 to 5.6)	-3.8 (21.1)	(µ43.3 to 61.7)	4.6 (0.9)	(3.3 to 5.9)
Tributary 3	13.7 (0.5)	(12.0 to 14.9)	5.0 (0.2)	(4.4 to 5.7)	µ3.9 (6.6)	(µ30.2 to 22.3)	2.6 (0.5)	(1.8 to 3.3)
Tributary 6	17.6 (1.0)	(15.0 to 20.5)	4.7 (0.1)	(4.4 to 5.2)	µ6.8 (6.2)	(µ30.9 to 16.2)	2.1 (0.1)	(2.1 to 2.2)
Tributary 15	14.1 (0.6)	(13.0 to 15.2)	4.8 (0.3)	(4.2 to 6.1)	µ7.1 (22.6)	(µ47.5 to 79.4)	1.8 (0.4)	(1.3 to 2.3)
Tributary 12	14.1 (0.7)	(13.0 to 15.8)	4.8 (0.1)	(4.5 to 5.2)	µ7.6 (5.7)	(-24.0 to 6.3)	3.1 (0.3)	(2.7 to 3.5)
Tributary 18	14.3 (0.3)	(13.5 to 15.1)	4.7 (0.2)	(4.4 to 5.1)	-9.7 (7.8)	(-23.5 to 14.0)	3.7 (0.7)	(2.6 to 4.8)
Tributary 11	12.7 (0.3)	(12.0 to 13.0)	4.6 (0.2)	(4.1 to 5.4)	-17.9 (13.9)	(-86.0 to 14.5)	3.5 (0.7)	(2.7 to 4.3)
Tributary 2	14.5 (0.1)	(14.2 to 14.8)	4.5 (0.3)	(4.1 to 5.6)	-23.8 (15.8)	(-60.7 to 32.8)	5.8 (0.2)	(5.3 to 6.4)
Tributary 25	15.5 (0.5)	(15.0 to 16.0)	4.5 (0.2)	(4.2 to 4.7)	-23.9 (9.6)	(-39.6 to -15.3)	3.4 (0.5)	(3.0 to 3.9)
Tributary 19	14.5 (0.4)	(14.0 to 15.6)	4.5 (0.1)	(4.2 to 4.9)	-24.3 (7.9)	(-41.1 to -1.2)	7.2 (1.1)	(5.7 to 8.7)
Tributary 24	15.2 (0.2)	(14.7 to 16.0)	4.4 (0.1)	(4.2 to 4.6)	-30.5 (6.3)	(-51.0 to -12.3)	7.5 (0.2)	(7.0 to 7.9)
Tributary 17	12.8 (0.3)	(12.4 to 13.5)	4.4 (0.2)	(3.9 to 5.9)	-31.0 (11.4)	(-58.6 to 44.8)	8.5 (1.0)	(7.1 to 9.9)
Tributary 23	14.3 (0.4)	(13.0 to 16.0)	4.4 (0.1)	(4.2 to 4.6)	-31.9 (6.0)	(-50.2 to -16.4)	7.5 (0.2)	(7.0 to 7.8)
Tributary 10	14.3 (0.7)	(13.0 to 15.3)	4.4 (0.2)	(4.0 to 4.7)	-35.2 (13.7)	(-67.3 to -10.8)	3.9 (0.5)	(3.3 to 4.4)
Tributary 16	14.4 (0.5)	(13.0 to 16.5)	4.2 (0.1)	(3.8 to 4.6)	-46.7 (6.0)	(-79.4 to -14.8)	5.1 (0.2)	(4.4 to 5.8)

Acidification classifications are based on mean ANC values

variables Al<sub>im</sub>, and volume (Table 3). The parameters in the top seven models were also evaluated. The variables Al<sub>im</sub> (model 2, CI=-1.01, -0.49; coefficient=-0.75), volume (model 2, CI=-0.078, -0.020; coefficient=-0.049), and the interaction Al<sub>im</sub>×volume (model 1, CI=-0.090, -0.005; coefficient=-0.048) were significant predictors of YOY brook trout density; no other parameters tested were significant predictors of YOY brook trout density. The AIC<sub>c</sub> weights summed across all models were 1.0 for Al<sub>im</sub>, 0.98 for volume, 0.15 for LWD, 0.09 for TI value, 0.07 for stream temperature, 0.07 for female CPUE, 0.03 for substrate, and <0.01 for all other variables. No collinearity was observed between variables in any of the models. The

model (Al<sub>im</sub>, female CPUE, substrate, volume, stream temperature, TI value, LWD, and year) passed the likelihood ratio goodness of fit test ( $\chi^2=50.70, p<0.001$ ).

#### Adult brook trout

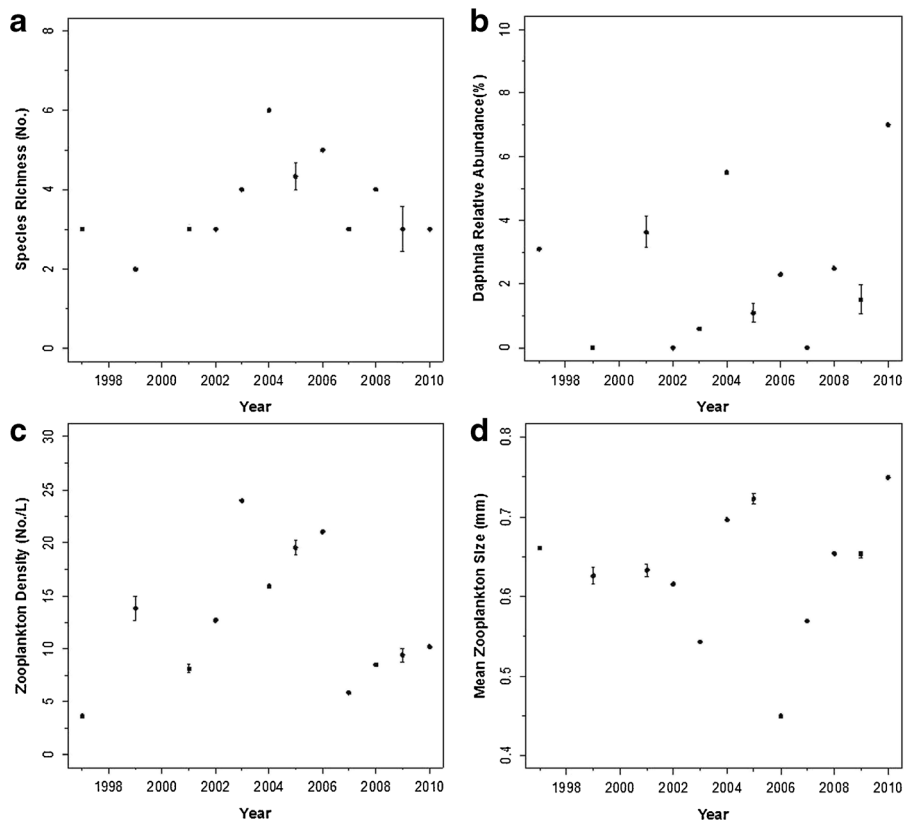
Fall trap net catches of brook trout were grouped into three periods: (1) from 1960 to 1966 when the origin of fish was unknown due to large numbers of unmarked brook trout stocked from 1952 to 1962, (2) the period from 1970 to 1980 when only wild fish were caught prior to CAAA in 1990, and (3) the period from 2000 to 2011 when wild and known stocked fish were caught after the CAAA was implemented (Fig. 6).

**Table 2** Relative abundance (% of community) of zooplankton species found in summer, deep-water tows from Honnedaga Lake, 1997, 1999, and 2001–2010

	Year											
	1997	1999	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Copepoda: Calanoida												
<i>Leptodiaptomus minutus</i>	89.2	81.6	78.7	65.0	82.1	86.2	82.4	26.3	80.3	76.9	95.9	79.0
Copepoda: Cyclopoida												
<i>Diacyclops thomasi</i>				2.0	2.5	0.6	8.5	1.9	2.0	1.9		
<i>Mesocyclops edax</i>						1.1			0.7			
Copepoda: Nauplii	3.28	0.3	6.6	8.0	13.5	1.7	6.4	67.1	17.0	1.9	1.8	2.0
Cladocera												
<i>Daphnia pulicaria</i>	3.1		2.7		0.6	5.5	0.5	2.3		2.5	2.4	7.0
<i>Eubosmina longispina</i>	3.8	18.2	12.0	25.0	1.2	4.4	2.1	1.4		16.9		12.0
<i>Polyphemus pediculus</i>						0.6		0.9				
Total taxa	3	2	3	3	4	6	4	5	3	4	2	3

Trap net catches from 1960 to 1966 were characterized by a mean CPUE of 60.8 fish/night (range, 16.0 to

131.3 fish/night) and were presumably heavily influenced by the stocking of thousands of marked and



**Fig. 4** Mid-summer, pelagic zooplankton species richness (a), *Daphnia* spp. relative abundance (b), zooplankton density (c), and mean zooplankton size (d) in Honnedaga Lake, 1997, 1999,

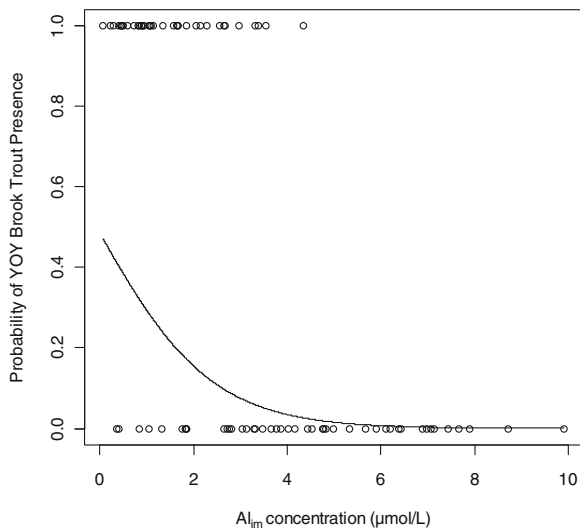
and 2001–2010. Error bars represent 1 standard error of the mean for years for which replicate samples were analyzed (1999, 2001, 2005, and 2009)

**Table 3** Candidate model set for the occupancy and density analysis ranked according to the corrected Akaike Information Criterion weight ( $AIC_{c(w)}$ )

Model	Variables	K	$AIC_c$	Log likelihood	$\Delta AIC$	Model likelihood	$AIC_c$ weight	AUC
Occupancy models								
Model 1	$Al_{im}$ , female CPUE	3	75.06	-34.37	0.00	1.00	0.25	0.88
Model 2	$Al_{im}$	2	75.93	-35.89	0.87	0.65	0.16	0.87
Model 3	$Al_{im}$ , female CPUE, $Al_{im} \times$ female CPUE	4	76.17	-33.82	1.11	0.57	0.14	0.89
Model 4	$Al_{im}$ , stream temperature, female CPUE	4	77.06	-34.27	2.00	0.37	0.09	0.88
Model 5	$Al_{im}$ , TI value	3	77.23	-35.46	2.17	0.34	0.08	0.87
Model 6	$Al_{im}$ , stream temperature	3	77.65	-35.67	2.59	0.27	0.07	0.87
Model 7	$Al_{im}$ , stream temperature, TI value, female CPUE	5	78.61	-33.91	3.55	0.17	0.04	0.88
Model 8	$Al_{im}$ , stream temperature, TI value	4	78.71	-35.09	3.65	0.16	0.04	0.87
Density models								
Model 1	$Al_{im}$ , volume, $Al_{im} \times$ volume	5	186.91	-87.46	0.00	1.00	0.44	
Model 2	$Al_{im}$ , volume	4	189.21	-89.96	2.30	0.32	0.14	
Model 3	$Al_{im}$ , volume, LWD, $Al_{im} \times$ volume	6	189.74	-87.42	2.83	0.24	0.11	
Model 4	$Al_{im}$ , TI value, volume	5	190.28	-89.14	3.37	0.19	0.08	
Model 5	$Al_{im}$ , female CPUE, volume	5	191.14	-89.57	4.23	0.12	0.05	
Model 6	$Al_{im}$ , stream temperature, volume	5	191.44	-89.72	4.53	0.10	0.05	
Model 7	$Al_{im}$ , LWD, volume	5	191.63	-89.81	4.72	0.09	0.04	
Model 8	$Al_{im}$ , stream temperature, volume, $Al_{im} \times$ stream temperature	6	193.12	-89.11	6.21	0.04	0.02	

The number of parameters (K), second-order bias correction Akaike Information Criterion ( $AIC_c$ ), log likelihood,  $\Delta AIC$  ( $AIC_{c(i)} - AIC_{c(min)}$ ), model likelihood, and area under the receiving operating characteristic curve (AUC) parameters are also shown

unmarked brook trout. During the 1970s, the mean CPUE of wild fish was 2.4 fish/night (range, 0.7 to 7.5 fish/night) representing low numbers of fish (Fig. 6).



**Fig. 5** The probability of YOY brook trout presence as it relates to the concentration of inorganic monomeric aluminum ( $Al_{im}$ )

The low catches in the 1970s, coupled with low pH and toxic aluminum conditions in the lake in the early 1980s, contributed to a decision to curtail trap net surveys throughout the 1980s and 1990s. Caged yearling brook trout bioassays were conducted in June 1983 when five groups of 25 brook trout were held in cages at various locations in Honnedaga Lake. Surface water pH was 4.93 and monomeric inorganic aluminum was 7.6  $\mu\text{mol/L}$  at the initiation of the bioassays. All groups experienced 100 % mortality within 15 days (unpublished data).

Beginning in the mid-1990s, lake property owners began to report sightings of brook trout in Honnedaga Lake and one angler caught several brook trout in September 2000 (personal communication). In response to these events, trap nets were set in fall 2000 and every year since through 2011. Two-year classes of hatchery-reared Honnedaga strain brook trout contributed substantially to the trap net catches from 2003 to 2006 (Fig. 6). During the 2000s (excluding 2003–2006), the mean CPUE of wild fish was 14.3 fish/night (range, 9.1 to 23.3 fish/night). Based on fall trap net CPUE,

**Table 4** The occupancy and density of young-of-year brook trout (2003, 2006, and 2008–2010) and mean summer  $Al_{im}$  concentrations (2008–2010) in Honnedaga Lake tributaries (in order of increasing  $Al_{im}$  concentrations)

Water	Occupancy Present/absent	Density (n/m <sup>2</sup> ) Mean (1 SE)	$Al_{im}$ (μmol/L) Mean (1.5E)
Not acidified (ANC, >50)			
Tributary 20	Present	0.49 (0.13)	0.4 (0.1)
Tributary 9	Present	0.32 (0.06)	0.5 (0.2)
Tributary 13	Present	0.13 (0.03)	0.6 (0.3)
Tributary 1	Present	0.23 (0.06)	0.7 (0.1)
Tributary 4	Present	0.40 (0.08)	0.7 (0.1)
Qisodically acidified (0<ANC<50)			
Tributary 14	Present	<0.01	0.6 (0.2)
Tributary 8	Present	0.20 (0.02)	0.6 (0.2)
Tributary 22	Present	0.00	1.9 (0.6)
Chronically acidified (ANC, <0)			
Tributary 15	Present	0.05 (0.03)	1.8 (0.4)
Tributary 6	Present	0.04 (0.03)	2.1 (0.1)
Tributary 3	Present	0.06 (0.04)	2.6 (0.5)
Tributary 12	Absent	0.00	3.1 (0.3)
Tributary 25	Present	<0.01	3.4 (0.5)
Tributary 11	Present	0.01 (0.01)	3.5 (0.7)
Tributary 18	Absent	0.00	3.7 (0.7)
Tributary 10	Absent	0.00	3.9 (0.5)
Tributary 21	Absent	0.00	4.6 (0.9)
Tributary 16	Absent	0.00	5.1 (0.2)
Tributary 2	Absent	0.00	5.8 (0.2)
Tributary 19	Absent	0.00	7.2 (1.1)
Tributary 24	Absent	0.00	7.5 (0.2)
Tributary 23	Absent	0.00	7.5 (0.2)
Tributary 17	Absent	0.00	8.5 (1.0)

significantly more brook trout inhabited Honnedaga Lake in the 2000s (mean CPUE=14.3 fish/night) compared with the 1970s (mean CPUE=2.4 fish/night; *t* test; *p*<0.001, *df*=11).

**Discussion**

During the past century, acid deposition has significantly altered water chemistry and biota within the Honnedaga Lake watershed. The first indication of the negative effects of acid deposition on the biota in Honnedaga Lake was the sequential loss of acid-sensitive fish populations from the 1930s through the

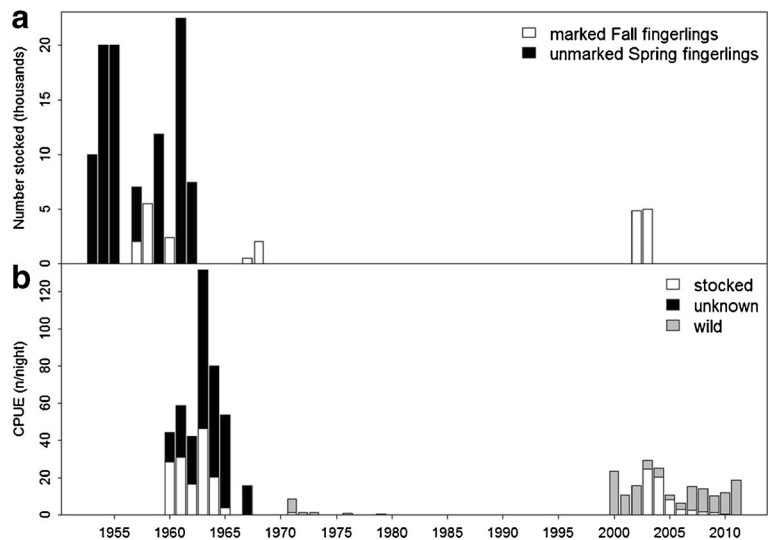
1950s. Schofield (1965) was the first to suggest that these losses might be due to low pH and resultant high concentrations of toxic metals resulting from acid deposition. Subsequently, numerous studies in the Adirondack Mountain region confirmed that airborne strong acids produced by combustion of fossil fuels were acidifying waters and altering chemistry and fish populations in lakes and streams (Schofield and Driscoll 1987; Kretser et al. 1989; Baker and Christensen 1991). The CAAA (1990) and CAIR (2005) were enacted to reduce emission of SO<sub>2</sub> and NO<sub>x</sub>, reduce the amount of acid deposition, and facilitate chemical and biological recovery in waters in the northeastern USA (Burns 2011). Our environmental monitoring program allowed for an assessment of the effectiveness of CAAA (1990) and CAIR (2005) to facilitate recovery of water chemistry and biota in the lake and tributary streams within the Honnedaga Lake watershed.

Low ANC (<25 μeq/L) waters like Honnedaga Lake are highly sensitive to acidic deposition and respond rapidly to reductions of SO<sub>4</sub> and NO<sub>3</sub> (Warby et al. 2005). Significant reductions of SO<sub>4</sub> and NO<sub>3</sub> in Honnedaga Lake surface-water have occurred in the past decade (2001 to 2011). The corresponding positive changes in lake surface-water chemistry have resulted in reduced aluminum toxicity to fish and other biota and possibly an increase in primary productivity. Similar improvements in surface-water chemistry have been observed in other Adirondacks lakes since 1990 (Warby et al. 2005; Momen et al. 2006; Driscoll et al. 2007).

The trend of increasing surface water pH has had the direct effect of reducing the concentration of  $Al_{im}$  which is toxic to brook trout at concentrations >2 μmol/L (Baldigo et al 2007). Toxic levels of  $Al_{im}$  in the early 1980s (9.2–11.1 μmol/L) significantly declined to non-toxic levels in the 2000s (0.4–1.8 μmol/L). The net effect is that aluminum toxicity to fish and other biota has been significantly reduced in Honnedaga Lake since implementation of CAAA (1990).

The reduced aluminum toxicity of lake surface waters has influenced primary productivity in Honnedaga Lake. Although not measured directly, the supporting evidence that primary productivity has increased is the significant increase in concentrations of chl<sub>a</sub> and decreases in water clarity (Secchi depth) over the past decade. Lake water color has gradually changed from blue to green blue which is also indicative of increasing amount of phytoplankton. The increase in phytoplankton is likely a direct

**Fig. 6** Number of brook trout stocked annually (a) and trap net catches (b) in Honnedaga Lake (1953–2011), including marked fish stocked, unmarked fish stocked, and wild fish



result of reduced aluminum toxicity, similar to responses observed in other Adirondack lakes (Siegfried and Sutherland 1992; Momen et al. 2006). The increase in phytoplankton density and coincident photosynthesis may also be affecting in-lake processes of  $\text{NO}_3$  reduction and increases in DOC.

Significant increases in lake surface-water DOC were observed over the past decade. Similar increases of DOC have been documented in many waters worldwide and have been attributed to reduced levels of  $\text{SO}_4$  deposition and increasing global temperatures, which accelerate decomposition of organic matter (Evans et al. 2005; Monteith et al. 2007). The increased level of DOC also has contributed to the reduced clarity of Honnedaga Lake.

The lack of historical chemical data for tributaries dictates the characterization of the current status of the tributaries to Honnedaga Lake. The majority of tributaries to Honnedaga Lake drain thin glacial till catchments and are either chronically (65 % of streams) or episodically (13 % of streams) acidified. These tributaries continue to be impaired and highly sensitive to acid deposition.  $\text{Al}_{\text{im}}$  levels are toxic to brook trout year round in chronically acidified tributaries and during high flow events (e.g., spring run-off) in episodically acidified tributaries (Lawrence 2002; Baldigo et al 2007). Those tributaries that are not acidified (22 % of streams) drain thicker glacial till catchments and have sufficient ANC to buffer acid inputs. Under summer base flows, the episodically acidified and nonacidified tributaries provide suitable conditions for brook trout survival.

Zooplankton communities in lakes experiencing acid stress exhibit reduced species richness, altered species dominance, reduced density, and altered size distributions due to the loss of larger grazers (primarily Daphnidae) and predators (e.g., *Leptodora kindtii* and *Epischura lacustris*) (Keller and Pitblado 1984; Marmorek and Korman 1993; Driscoll et al. 2003a). Direct impacts to zooplankton from acid stress stem from elevated levels of  $\text{H}^+$  ions and aluminum that cause osmoregulatory stress and physically interfere with gill function (Havas and Likens 1985; Havens and Heath 1989; Havas and Rosseland 1995). Particulate and ionic forms of Al can also negatively affect availability of phosphorus and indirectly affect plankton community structure (Vrba et al. 2006). Substantial recovery of acid-impaired zooplankton communities has been well-documented in lakes that have shown significant water quality improvements as a result of experimental neutralization or reduction of acidic atmospheric deposition (Frost et al. 1998; Keller and Yan 1998; Keller et al. 2002). Zooplankton show inter- and intra-specific variability in their response to acidic conditions (Price and Swift 1985; Havens et al. 1993), so the composition and relative abundance of the zooplankton community can provide insight into the level of biological recovery within a lake.

The summer, pelagic zooplankton community of Honnedaga Lake is characterized by low species richness (two to six species annually), a scarcity of *Daphnia* and lack of other acid-sensitive species, high dominance of an acid-tolerant species, low overall density, and



small zooplankton size. Keller and Pitblado (1984) sampled zooplankton communities from 249 north-eastern Ontario lakes and reported a mean of 4.5 species per lake in lakes with pH less than 5.0 (mean=4.7) versus 8.4–10.4 species per lake for less acidic lakes (mean pH=5.9–7.9). Similarly, Sprules (1975) reported one to seven species from lakes with pH less than 5.0 and 9–16 species from lakes with pH >5.0. Yan and Strus (1980) reported an average of 2.9–3.9 species per collection from four highly acidic (pH 4.1–4.4) Ontario lakes and 8.0–14.6 species per collection from seven less acidic (pH 5.7–6.4) Ontario lakes. Species richness in Honnedaga Lake is indicative of an acid-stressed community despite the observed improvements in lake water chemistry.

*Daphnia* spp. are among the more acid-intolerant zooplankton, being some of the first taxa to exhibit marked declines over a decreasing pH gradient (Confer et al. 1983; Keller and Pitblado 1984; Havens et al. 1993). Some species of daphnids show declines in abundance as pH drops below 6.5 (Havens et al. 1993), and daphnids as a whole are generally absent at pH less than 5.0 (Confer et al. 1983). *D. pulicaria* was the only daphnid found in Honnedaga Lake and is one of the more acid-tolerant daphnids, showing greater dominance as lakes acidify (Sprules 1975). *D. pulicaria* has shown a low-level presence in Honnedaga Lake since at least 1997, suggesting that pH is still occasionally depressed enough to limit significant expansion of the *D. pulicaria* population and establishment of other daphnids in the lake.

All of the non-daphnid species comprising the summer, pelagic zooplankton community in Honnedaga Lake also are considered acid-tolerant (present in lakes with pH of <5.0) as defined by Nierzwicki-Bauer et al. (2010). *L. minutus*, *Mesocyclops edax*, and *Polyphemus pediculus* have been reported from lakes with pH 4.7 or lower in the Adirondack Mountains (Nierzwicki-Bauer et al. 2010). *Eubosmina longispina* has been reported from waters in England with pH as low as 3.0 (Fryer 1993), and *Diacyclops thomasi* has been found to survive in lakes acidified to pH 4.7 if such lakes had a history of seasonal fluctuations in pH (Fischer et al. 2001). The lack of acid-resistant (present at pH of 5.0–5.6) or acid-sensitive (restricted to pH of >5.6) species in Honnedaga Lake further suggests that pH recovery in this lake has not reached the threshold at which a broader recovery of the zooplankton community can occur.

Zooplankton density has been shown to decline with decreasing pH, but the magnitude of decline is species and pH dependent (Roff and Kwiatowski 1977; Keller and Pitblado 1984; Fischer et al. 2001). Keller and Pitblado (1984) reported zooplankton densities from 249 northeastern Ontario lakes had a mean of 15 zooplankton/L in lakes with pH less than 5.0 (mean=4.7) versus 18–35/L for less acidic lakes (mean pH=5.9–7.9). Similarly, Yan and Strus (1980) reported an average of 0.6–36.0 zooplankton/L from four highly acidic (pH 4.1–4.4) Ontario lakes and 18.2–45.5 zooplankton/L from seven less acidic (pH 5.7–6.4) lakes. Honnedaga Lake zooplankton densities averaged 12.6 organisms/L (range=3.6–24.0), suggesting that densities in Honnedaga Lake are reflective of an acid-stressed condition.

Increasing lake acidity can indirectly reduce mean zooplankton size in a community by eliminating larger, more acid-sensitive species (Marmorek and Korman 1993). Zooplankton communities in acid-stressed lakes of northeastern North America are often numerically dominated by small species such as *L. minutus* and *Bosmina* spp. (Yan and Strus 1980; Confer et al. 1983; Keller and Pitblado 1984). Keller and Pitblado (1984) documented a substantial reduction in the importance of Daphnidae and a concomitant increase in the relative abundance of smaller grazers (particularly, *L. minutus*) in their study lakes. Mean zooplankton size in Honnedaga Lake is small (0.45–0.75 mm), reflecting the dominance of *L. minutus*, a relatively small, acid-tolerant calanoid copepod, and the scarcity of daphnids and other species that typically exceed 1.0 mm in length. The lack of any pattern of increase in mean zooplankton size in Honnedaga Lake from 1997 through 2010 reflects the relative stability of the community over this time despite the gradually increasing pH of the lake.

The concentration of  $Al_{im}$  was the only significant predictor of YOY brook trout occupancy in tributaries of Honnedaga Lake based on the parameters tested in this analysis. While there was no convincingly “best” model in our occupancy candidate model set, the predictive ability of the top seven models suggests the models were “reasonable” and approached “very good” when predicting the occurrence of YOY brook trout. Only one tributary contained YOY brook trout when the observed concentrations of  $Al_{im}$  exceeded  $3.55 \mu\text{mol L}^{-1}$ .  $Al_{im}$  concentrations in the summer often exceed this value in many tributaries of Honnedaga Lake, therefore these tributaries will likely not be utilized by YOY brook

trout. Based on the  $AIC_c$  weight of the other variables included in the candidate model set, only female CPUE had support in influencing the presence of YOY brook trout in tributaries to Honnedaga Lake. Although female CPUE was not a significant predictor in the analysis, a positive coefficient for this variable suggests the odds of YOY brook trout being present in a tributary increases as fall female CPUE increases in trap net catches the previous year. However, the same tributaries were not sampled each year, therefore this may be an artifact of only sampling tributaries with a high probability of finding fish in years of high female CPUE's. Overall, the impaired state of chronically and episodically acidified tributaries limits YOY abundance in those tributaries.

The concentration of  $Al_{im}$ , volume, and an  $Al_{im} \times$  volume interaction were all significant predictors of YOY brook trout density. While the decreasing densities of YOY brook trout associated with increases in  $Al_{im}$  concentrations were expected, the decreased densities of YOY brook trout when sampling larger volumes of water was not. Closer examination of the data revealed low densities of YOY brook trout in a tributary sampled in 2006 and 2008 containing large volumes of water. The mean  $Al_{im}$  concentration of this tributary was  $2.27 \mu\text{mol L}^{-1}$  (range, 1.83–3.03) over the years of the study. Volume and the  $Al_{im} \times$  volume interaction were no longer significant predictors after removing these data from the analysis, and the most parsimonious model in the candidate model set contained only the variable  $Al_{im}$ . Overall the density of YOY brook trout observed in the current study was low, suggesting that  $Al_{im}$  concentrations negatively influence YOY brook trout even in the highest quality tributaries of Honnedaga Lake.

Stream temperature was not supported as a variable that influenced the occupancy or density of YOY brook trout in the current study. This was likely a result of low water temperatures present throughout all tributaries sampled during summer (mean =  $14.5^\circ\text{C}$ ; range =  $10$ – $22^\circ\text{C}$ ). YOY brook trout during this time period distribute to areas that provide thermal refuge from water temperatures near the upper limit of their thermal tolerance ( $>20^\circ\text{C}$ ) (Venne and Magnan 1995; Curry et al. 1997; Biro 1998). Stream temperature exceeded  $20^\circ\text{C}$  in only three of 65 sampling events, indicating that water temperature in Honnedaga Lake tributaries is rarely limiting to YOY occurrence.

Historical changes in the fish community provide the best evidence of the effects of acid deposition on the

Honnedaga Lake ecosystem. The initial losses of round whitefish, white suckers, and creek chubs in the 1930s and the lake trout population in the 1950s coincided with increasing wet  $\text{SO}_4$  and  $\text{NO}_3$  deposition (Sullivan et al 2007), and Schofield and Driscoll (1987) showed the intolerance of these four species to acidity. By contrast, brook trout were able to survive and persist throughout the two decades (1970–1990) when lake surface-water pH was predominately  $<5.0$  and  $Al_{im}$  levels were likely toxic as observed in the early 1980s. Brook trout were able to carry out their entire life history throughout this period, likely persisting in a small number of relatively well-buffered tributaries that remained suitable for spawning, early life, and adult stages. Unlike the four fish species that declined, brook trout spawn at locations of upwelling groundwater and can therefore take advantage of less acidic groundwater sources that other fish species cannot utilize for spawning.

The Honnedaga Lake brook trout population has shown a substantial increase in relative abundance in the 2000s compared with the extremely low catch rates of the 1970s. This increase in population size coincided with significant improvements in surface-water chemistry, which became manifest following enactment of the CAAA (1990). It is important to note the stocking program in the 1950s was implemented to supplement declining natural recruitment. Unknown at the time, the underlying cause of declining natural reproduction by brook trout was likely the onset of chronic and episodic acidification of tributaries, therefore the fish stocking program masked the decline in recruitment. It was not until stocking ceased in the 1970s that the effects of increasing acidification were revealed by a declining wild brook trout population in Honnedaga Lake. The relatively large trap net catch rates of the 1960s suggest that lake conditions were still suitable for survival of fingerling and older life stages at that time, but ultimately, even older life stages disappeared from the lake.

## Conclusions

The state of the Honnedaga Lake ecosystem prior to the onset of acid deposition is largely unknown, and benchmarks for recovery must be based on existing knowledge of the chemistry and biota. We present evidence of partial and varying degrees of recovery of surface-water

chemistry, phytoplankton, zooplankton, and brook trout populations since implementation of CAAA (1990). All observed changes in the lake and tributary chemistry and associated biota during the past decade indicate that the Honnedaga Lake watershed remains an acid-stressed ecosystem and is highly vulnerable to future acid deposition. Under current levels of acid deposition, further recovery of chemistry and biota will likely be slow in Honnedaga Lake and its tributaries.

The trends in Honnedaga Lake water chemistry over the past two decades are similar to those of other lakes in the Adirondack Mountain region (Momen et al. 2006; Driscoll et al. 2007) and the northeastern USA (Warby et al. 2005; Burns 2011). Significant reductions in  $\text{SO}_4$  and  $\text{NO}_3$  deposition have led to increasing pH and decreasing concentrations of  $\text{Al}_{\text{im}}$  below levels toxic to brook trout and some zooplankton and phytoplankton in the lake. Mean surface pH, though improving since the early 1990s, still remains below 5.5 for much of the year, and seasonal episodic events during which pH drops below 5.0 have still occurred in recent years. ANC and concentrations of calcium in lake surface water have not changed significantly, indicating a weak chemical recovery. The presence of numerous chronically and episodically acidified tributaries draining thin glacial till catchments is indicative of little or no chemical recovery in this component of the Honnedaga Lake ecosystem. Overall, the chemical recovery within the Honnedaga Lake has been modest but sufficient to benefit some biota.

The lack of a significant recovery of the zooplankton community despite recent improvements in pH and  $\text{Al}_{\text{im}}$  levels is likely the result of pH remaining below levels at which significant changes in zooplankton community can occur. Doka et al. (2003) modeled biological recovery from acid stress of over 2,000 waters across southeastern Canada and identified pH 5.5–6.0 is an important threshold below which damage to aquatic biota, including zooplankton communities, will persist. Holt et al. (2003) modeled zooplankton community change across a pH gradient for 47 acid-stressed lakes in south-central Ontario and identified pH 6.0 as a threshold at which major change in community structure can be expected. Surface pH in Honnedaga Lake is currently consistently below thresholds at which significant zooplankton community recovery would be expected. Given that surface-water pH in Honnedaga Lake is

now commonly in the range (5.0–5.6) at which shifts toward more acid-resistant species might occur (Nierzwicki-Bauer et al. 2010), it is possible the zooplankton community will begin to show evidence of recovery in the near future. Substantial recovery of the Honnedaga Lake zooplankton community may not occur for many years because it can take up to 10 years for the reestablishment of most common, acid-sensitive, zooplankton species once pH remains above pH 6.0 (Keller and Yan 1998).

A considerable recovery in abundance of the Honnedaga Lake brook trout population has been observed since the 1970s; however, the relative abundance of adult fish in fall trap net catches has not increased since 2000. The current recovery of the brook trout population is directly related to the reduction in  $\text{Al}_{\text{im}}$  to nontoxic concentrations. Only a small number of tributaries within the Honnedaga Lake watershed drain catchments with thick glacial till that function as spawning sites and YOY summer brook trout habitat. The lack of a more robust recovery by adult brook trout in the lake can be explained by the large number of chronically acidified tributaries that are uninhabitable by YOY brook trout. Similar to many chronically acidified tributaries in the western Adirondacks, these tributaries will likely not recover from acidification under current levels of acidic deposition (Driscoll et al. 2001). Our findings strongly suggest that chronic and episodic acidification of numerous tributaries continues to limit YOY brook trout recruitment and consequently recovery of the adult brook trout population in Honnedaga Lake. We are currently exploring the potential to accelerate the recovery of brook trout abundance in Honnedaga Lake by conducting in-stream or watershed applications of lime to chronically and episodically acidified tributaries.

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