

Influence of Spring Floods on Year-Class Strength of Fall- and Spring-Spawning Salmonids in Catskill Mountain Streams

DANA R. WARREN*¹

Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, New York 14853, USA

ANNE G. ERNST AND BARRY P. BALDIGO

U.S. Geological Survey, New York Water Science Center, 425 Jordan Road, Troy, New York 12180, USA

Abstract.—Climate change in northeastern North America has already led to earlier snowmelt and increases in the magnitude and frequency of large storms; associated changes are expected to intensify over the next several decades. Alterations in flooding regimes associated with climate change have the potential to negatively affect fish species with earlier fry emergence and alter the fish communities in tributary streams where fall- and spring-spawning salmonids coexist or where there may be invasion potential by a given species. This 6-year study (2002–2007) assessed the effects of the timing and magnitude of spring flood events on year-class strength in sympatric populations of fall-spawning brook trout *Salvelinus fontinalis*, fall-spawning brown trout *Salmo trutta*, and spring-spawning rainbow trout *Oncorhynchus mykiss*. The relative abundances of young-of-year (age-0) and age-1 fall- and spring-spawning salmonids were documented for 4 and 6 years in streams from two watersheds in the Catskill Mountains, New York. Fall-spawning age-0 fish dominated in all years except 2005. In spring 2005 a large flood occurred at nearly the same time of year as the 2004 snowmelt, but discharge was nearly an order of magnitude greater. The dominant salmonid for that year-class shifted to rainbow trout, but fall-spawned age-0 trout were again dominant in the following year. These results indicate that the timing and magnitude of spring high flows can increase the relative abundance of spring-spawning age-0 salmonids, decrease the abundance of fall-spawning age-0 salmonids, or both. The overall dominance of fall-spawned fish appears to be resilient as long as displacing floods occur a few years apart. If the trend toward larger, more frequent, and earlier spring floods continues, differential survival of age-0 fish of the three salmonid species will probably cause shifts in the dominant trout species in many Catskill Mountain streams.

Actual and projected changes in the magnitude, frequency, and timing of spring floods (Burns et al. 2007; Hayhoe et al. 2007) have amplified concerns over the effects that climate change may have on fish

assemblages in streams in the northeastern USA. The timing and magnitude of high-discharge events (floods) during spring can affect the structure of fish populations and resident fish communities (Pearsons et al. 1992; Poff et al. 1997; Lytle and Poff 2004), and several studies have related such events at the time of fry emergence to salmonid year-class strength (Seegrist and Gard 1972; Nehring and Anderson 1993; Latterell et al. 1998; Lobon-Cervia and Mortensen 2005). Salmonid fry are particularly vulnerable to washout for a period after their emergence, and floods during this critical period can cause the loss or severe depletion of a given year-class (Elliott 1994; Lobon-Cervia 2004; Nislow et al. 2004).

Potential displacement associated with high flow–high water velocity events is greatest as fry enter the swim-up stage (with yolk sacs fully absorbed) when salmonid fry can be displaced by flows between 0.1 and 0.25 m/s, depending on the species and water temperature (Heggnes and Traaen 1988). As fry grow their ability to hold their position increases. In a series of experimental stream channels, Heggnes and Traaen (1988) found that 2 weeks after emergence, critical velocities to displace salmonid fry were still relatively low (up to 0.27 m/s), but after 8 weeks, swimming ability had increased and many fish could hold their position at flows as high as 0.5 m/s. In the field, Jensen and Johnsen (1999) compared brown trout *Salmo trutta* and Atlantic salmon *S. salar* year-class strength across a range of spring discharges in Norway and found that extremely high flows during fry emergence adversely affected year-class strength in both species. This was consistent with studies by Elliott (1987) and Lobon-Cervia and Rincon (2004) who found that timing and magnitude of high discharge events relative to fry emergence affected salmonid year-class strength and subsequent population dynamics in streams in the United Kingdom and in northwestern Spain. Whether the mechanism for this relationship is density dependent, however, remains unresolved (see Einum 2005; Lobon-Cervia and Gutierrez 2006). In the Rocky Mountains of the western United States, Nehring and

* Corresponding author: dana.warren@noaa.gov

¹ Present address: National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA.

Received March 7, 2008; accepted October 6, 2008

Published online February 5, 2009

Anderson (1993) and Latterell et al. (1998) also found strong relationships between the year-class strength of fall-spawning salmonids and peak discharge in the spring.

Differences in the timing of spawning and associated emergence between species, combined with wide variability of high flows, may provide systematic, or occasionally random, advantages to one species over another in a given stream system. Strong relations between the presence of extremely high flows and the variable year-class strengths of brook trout *Salvelinus fontinalis* and rainbow trout *Oncorhynchus mykiss* in a California stream system were reported by Seegrist and Gard (1972) where rainbow trout are native and brook trout are invasive. The timing of salmonid spawning and subsequent emergence relative to the timing of peak flow may determine the success or failure of a salmonid stocking (Fausch et al. 2001), and the interaction of emergence with spring flooding has been suggested as a key factor in the success or failure of trout invasions (Strange and Foin 1999; Fausch 2008). Brook trout and brown trout spawn in the fall, whereas rainbow trout spawn in the spring, and this difference in life history is reflected in a difference in the timing of fry emergence in the spring–summer; rainbow trout consistently reach swim-up stage later in the year than brook trout or brown trout when populations occur sympatrically (Seegrist and Gard 1972; Nehring and Anderson 1993). Zorn and Nuhfer (2007) reported that in Michigan streams, brook trout and brown trout fry emerged at comparable times and that emergence within a given year was regionally synchronous.

Occasional recruitment failure by one species may allow inter- and intraspecific competitors to exploit available resources and thereby increase their ability to invade, occupy, and possibly dominate fish communities. This was observed in a Minnesota stream by Hanson and Waters (1974), who documented the invasion of rainbow trout into a formerly allopatric brook trout population after 2 years in which severe spring flooding had sharply decreased the brook trout population. The potential effect of flood timing on salmonid recruitment led Fausch et al. (2001) and Fausch (2008) to suggest that, at a global scale, the timing of spring high flows may determine the success or failure of rainbow trout invasions or introductions in a given region. This concept may be particularly relevant in predicting the success of rainbow trout invasions in streams where other salmonid species occur.

The Catskill Mountains were well suited as a study location for this research because three salmonid species (two fall spawning and one spring spawning) coexist in several watersheds. The Catskill Mountains

are located in southeastern New York State and include multiple forest types and stream habitats within a relatively small area, making them a good model for other systems across northeastern North America. Furthermore, the Catskill region is expected to experience many of the changes in precipitation regimes predicted by Hayhoe et al. (2007) and, as such, may function to exemplify potential ecosystem impacts associated with climate change. Shifts in the timing of spring snowmelt since 1952 have already been documented for this region (Burns et al. 2007), and current climate models suggest that conditions in the Catskill Mountains will become similar to those in areas of the southern Appalachian Mountains, where the invasion of brook trout habitat by rainbow trout is of particular concern (Hayhoe et al. 2007; Fausch 2008). This paper assesses fish community data from a 6-year study documenting winter and spring high flows and subsequent year-class strength for three sympatric salmonid species in two Catskill Mountain streams to illustrate the potential effects that climate change could have on dominant trout species in local fish communities.

Study Area

Sampling was done on two tributaries of Esopus Creek—Broadstreet Hollow Brook and Stony Clove Creek—in the central Catskill Mountains of southeastern New York (Figure 1). Annual stream discharge within this part of North America generally peaks during spring snowmelt, but large rainstorms can cause rapid increases in discharge of local streams throughout the year due to the steep slopes and thin soils of the Catskill Mountains. Both streams have south-facing basins and contain mixed hardwood–conifer riparian forests. Specific characteristics of each stream, including resident fish species, are outlined in Table 1. The reaches selected for study were the undisturbed reference reaches that had been previously selected and surveyed as part of a larger stream-restoration study (Baldigo et al. 2008a, 2008b). Stony Clove Creek and Broadstreet Hollow Brook study reaches were 370 and 430 m in elevation, respectively, and 7.8 and 4 km upstream from their confluence with Esopus Creek, respectively. Episodic acidification in the Catskill Mountains has had detrimental effects on fish (Baldigo and Lawrence 2001). However, no acidification events have been documented in these two streams that would be expected to affect salmonids. Esopus Creek is stocked with age-1 and age-2 brown trout in late April and again in May, and Stony Clove Creek is stocked with adult brook trout and brown trout just upstream from the study reach in May. The 1-year-old fish stocked into these streams are an average of 8 in (203

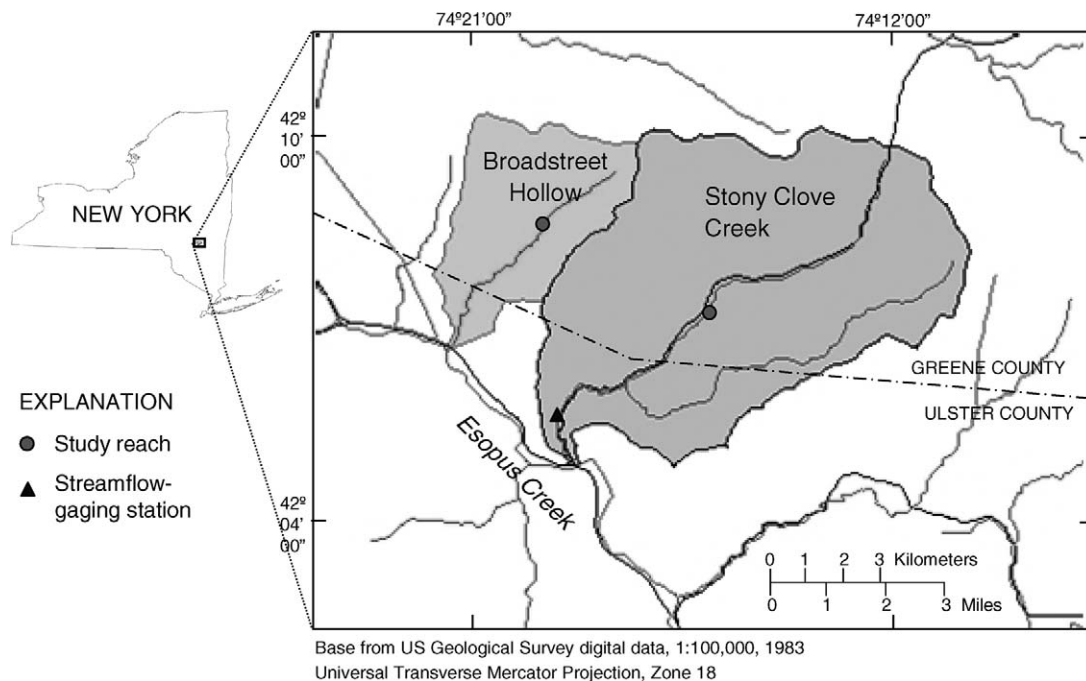


FIGURE 1.—The two tributaries of Esopus Creek in the central Catskill Mountains in which the effects of spring floods on the year-class strength of fall- and spring-spawning salmonids were studied. The shaded areas are the drainage basins of the tributaries.

mm) in length. Stocking could therefore potentially affect age-1 abundance estimates; however, based on our data in which the mean length of age-1 fish was well below 200 mm, it is not expected to substantially affect our abundance estimates and associated results (the mean length of age-1 salmonids, as inferred from length-frequency histograms, ranged from 126 to 167 mm and varied with year and species). Based on the stocking trends, fish targeted by anglers tend to be larger than 200 mm. Thus, angling predation is

expected to have limited influence on our fish abundance estimates. Data on wild age-0 and age-1 abundances in Stony Clove Creek were available for 2002–2007; no data for 2005 or 2007 were available for Broadstreet Hollow Brook. The U.S. Geological Survey maintains a streamflow-gauging station on Stony Clove Creek (gauge 01362380) that provides a continuous discharge record. The proximity and physiographic similarity of the two study reaches

TABLE 1.—Tributary and reach characteristics for the two study sites in the larger Esopus Creek 509 watershed in the Catskill Mountains, summer of 2002–2007.

Stream characteristic	Stony Clove Creek	Broadstreet Hollow Brook
Drainage area (km ²)	37.3	10.5
Average annual flow (m ³ /s)	1.39	0.37
Mean annual runoff (m ³ ·s ⁻¹ ·km ⁻²)	0.037	0.035
Elevation (m)	370	430
Distance upstream from Esopus Creek (km)	7.2	4.0
Gradient from site to Esopus Creek (m/m)	0.017	0.028
Average substrate size (mm)	174	241
Temperature during surveys (°C)	16.6	16.0
Resident fish species	Brook trout, brown trout, rainbow trout, slimy sculpin <i>Cottus cognatus</i> , blacknose dace <i>Rhinichthys atratulus</i> , and longnose dace <i>R. cataractae</i>	Brook trout, brown trout, rainbow trout, and slimy sculpin

allowed use of these records to infer streamflows in Broadstreet Hollow Brook.

Methods

Data collection.—Fish data were collected from both study streams under low flow conditions during July and August of 2002–2004 and 2006 as part of a larger study evaluating fish communities in Catskill Mountain streams (Baldigo et al. 2008a, 2008b). Data were also collected from Stony Clove Creek in early September 2005 and in August 2007. Fish were captured through multiple-pass depletion surveys in seine-blocked reaches in accordance with methods described in Baldigo et al. (2008a, 2008b). The same reach of stream was surveyed each year, and reaches in both systems were approximately 100 m in length. All salmonids were weighed to the nearest 0.1 g and measured (total length) to the nearest 1 mm. Year-classes were determined from length-frequency histograms for each species in each year. The backpack electrofisher was run by the same person in all surveys conducted for this study. The mean capture probabilities for brook trout, brown trout, and rainbow trout in Stony Clove Creek over the six survey years were 0.72, 0.54, and 0.52 respectively. Brook trout capture efficiency was particularly high at this site due to low abundance, which resulted in disproportionately high depletion rates. Brown trout capture probabilities were greater than rainbow trout capture probabilities in 2002, 2004, and 2005, and rainbow trout capture probabilities were greater than those of brown trout in 2003, 2006, and 2007. In 2005, when rainbow trout relative abundance was substantially greater than that of brown or brook trout, brown trout capture probability was 0.71 and rainbow trout capture probability was 0.58. At Broadstreet Hollow Brook, mean capture probabilities were 0.61, 0.62, and 0.55 for brook trout, brown trout, and rainbow trout, respectively. Total electrofishing crew size ranged from four to seven people. Electrofishing surveys have a tendency to collect large fish in the first pass and to miss smaller fish (Reynolds 1996; Peterson et al. 2004); therefore, we conducted population estimates separately for each year-class. We standardized fish population by area of wetted stream channel (reach length \times mean wetted width).

Data analysis.—The contributions of fall- and spring-spawning salmonids were assessed using both relative abundance (percentage) and estimated total abundance (number of fish per square meter of wetted channel). Analysis of total fish abundance relies on the assumption that the highest (and most influential) mortality occurs in spring and, as with analysis of relative abundance, that mortality rates for all three

salmonid species are fairly similar thereafter (an assumption supported by Elliott 1989). Total abundance estimates allow comparison among years; however, estimates of total abundance taken later in the year could introduce error owing to differential mortality through the summer. Measures of relative abundance address this issue to a large degree. Relative abundance data are also useful because high flows have the potential to indiscriminately remove a large percentage of all fish from a system and thereby skew results.

The lack of data from Broadstreet Hollow Brook in 2005 and 2007 prevented use of a single robust statistical analysis combining both sites across all 6 years. Year-to-year differences in the success of fall-spawning salmonids (brown trout and brook trout combined) and that of the spring-spawning rainbow trout were therefore assessed individually for each stream. Stony Clove Creek data on age-0 fish abundance and stream discharge were available for all 6 years of the study. Zorn and Nuhfer (2007) found that the emergence times for brook trout and brown trout were comparable in Michigan streams, so the age-0 abundances for both species of fall-spawning salmonids were combined for these analyses. Although fry swim-up usually begins in April, we included discharge from the entire first half of the year to encompass winter flows, which have the potential to scour redds and reduce year-class strength (Kondolf et al. 1991; Montgomery et al. 1999; Lapointe et al. 2000). Specific application of the models from Lapointe et al. (2000) could not be applied because the required data on spawning areas were not available.

The estimated abundances of fall-spawned age-0 and spring-spawned age-0 salmonids from both study streams were each regressed against the peak mean daily discharge in Stony Clove Creek between January 1 and June 30 each year. In addition, we conducted two multiple-regression analyses that incorporated timing of spring flood events or the presence of potential predators with peak discharge on year-to-year variability in age-0 abundance. Latterell et al. (1998) found that the abundance of potential predators (adult salmonids) influenced age-0 year-class strength in streams from the Pacific Northwest, and Lobon-Cervia (2004) found that in addition to the size of spring flood events, the timing of spring peak discharge events relative to the critical period for swim-up of age-0 fish was important. The first multiple-regression analysis included peak discharge and the timing of the peak discharge (the week during which the peak discharge event occurred) as the two independent variables. The second multiple-regression analysis included peak discharge and the estimated abundance of age-2 and older salmonids (potential predator abundance).

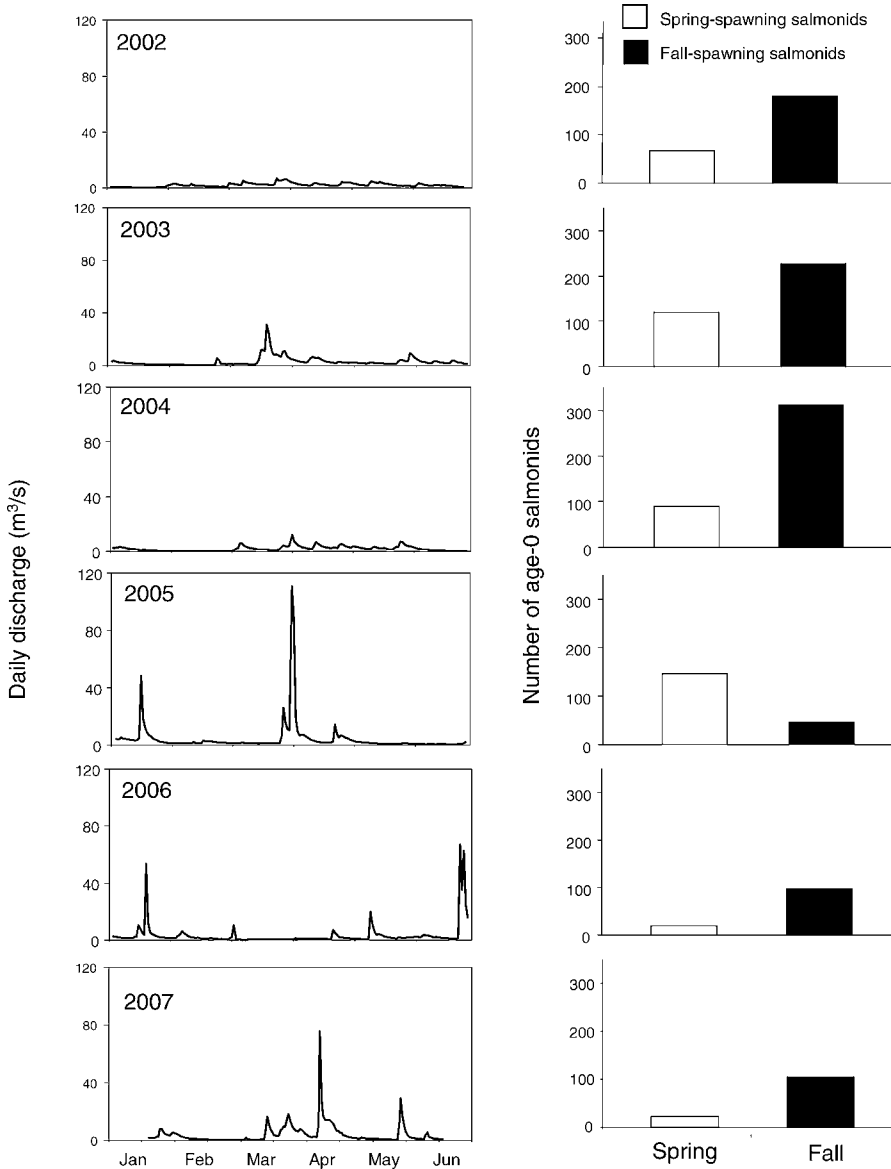


FIGURE 2.—Daily mean discharge of Stony Clove Creek (U.S. Geological Survey gauge 01362380) from January to June and the number of spring- and fall-spawning age-0 salmonids collected in the Stony Clove Creek study reach, by year.

Fall and spring age-0 abundance estimates from both study streams and Stony Clove Creek discharge values were all normally distributed ($P > 0.10$ for all data sets using an Anderson–Darling goodness-of-fit test; MINITAB release 14.20, 2005). A single-factor regression was conducted to evaluate the estimated total abundance and the relative abundance of age-0 salmonids for each spawning season versus the maximum mean daily discharge at the Stony Clove Creek gauge;

however, because Broadstreet Hollow Brook had only four data points and no data from the 2 years with the greatest mean daily discharge, the analysis at this site had low power and we did not expect to see strong results. As an additional evaluation on the influence of year-class strength on subsequent age-1 salmonid abundance, we regressed age-0 abundance against age-1 abundance to determine whether year-class strength carried through to subsequent age classes,

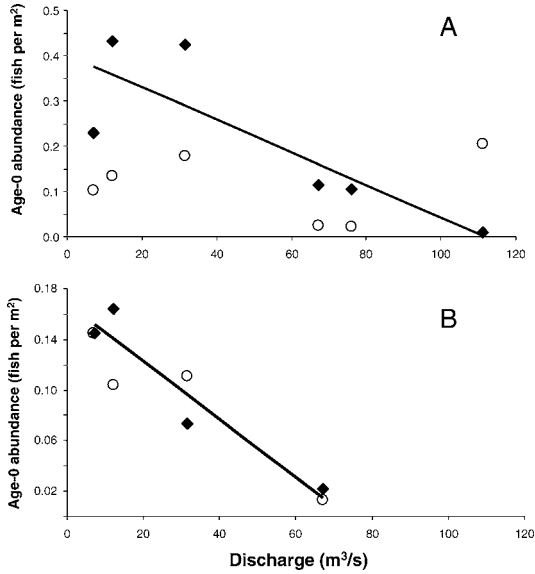


FIGURE 3.—Abundance of spring- (circles) and fall-spawned (diamonds) age-0 salmonids in (A) Stony Clove Creek and (B) Broadstreet Hollow Brook relative to the peak mean daily discharge in Stony Clove Creek between January 1 and June 30, 2002–2007. The relationship shown in panel (A) is significant ($P < 0.05$).

which would suggest that age-0 mortality would have a stronger influence than mortality in the fall or winter on fish abundance in the subsequent year.

Results

Peak Discharges

The maximum spring daily discharge of the gauged stream (Stony Clove Creek) was highly variable over the 6-year study ranging from 7.2 m³/s in 2002 to 111 m³/s in 2005 (Figure 2). The greatest mean daily discharge during the study occurred in spring 2005 (April 2). Discharge on this date was nearly an order of magnitude greater than the maximum daily discharge in spring 2004, 3.5 times that of spring 2003, and 15 times that of spring 2002. In both 2005 and 2006, a smaller, snowmelt-driven, high flow occurred in mid-January (daily discharge, 48.4 and 53.8 m³/s, respectively). No comparable January melt event occurred in the other 4 years of the study. Maximum daily discharge during the spring 2006 peak flow occurred considerably later in the year than in the previous 4 years or in the following year.

Year-Class Strength–Discharge Relations

In Stony Clove Creek, the total abundance of fall-spawning age-0 salmonids was negatively related to the

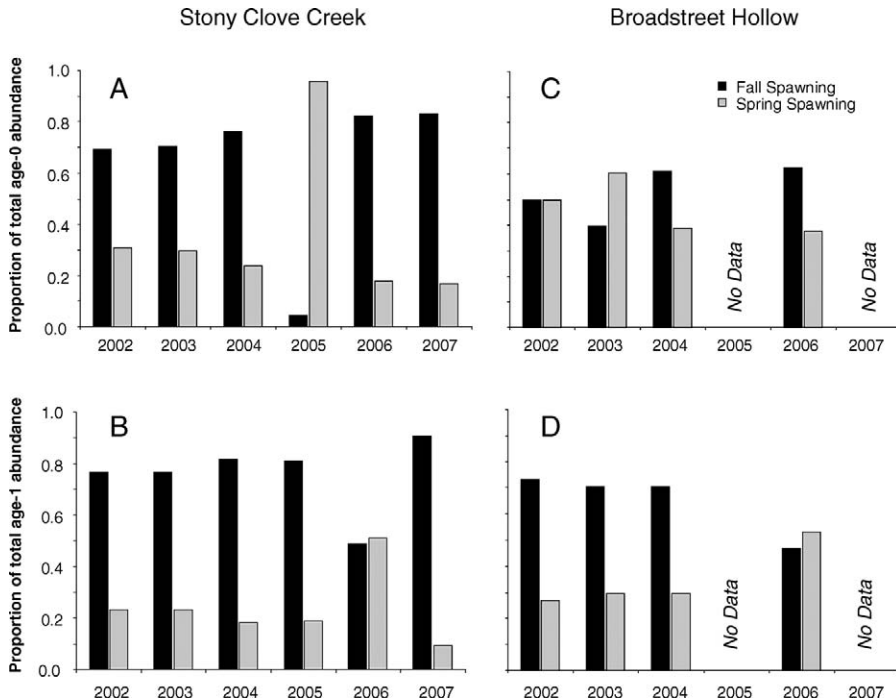


FIGURE 4.—Relative abundances of spring- and fall-spawning age-0 and age-1 salmonids in (A) and (B) the Stony Clove Creek and (C) and (D) the Broadstreet Hollow Brook study reaches, 2002–2007.

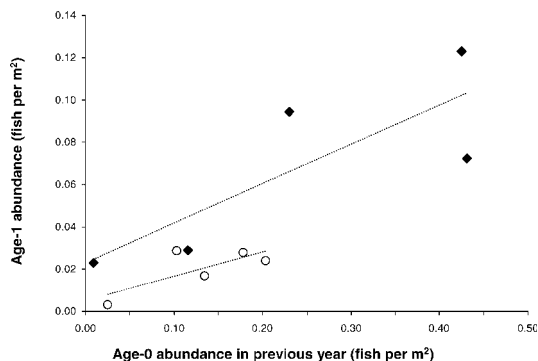


FIGURE 5.—Abundance of age-1 spring- (circles) and fall-spawned (diamonds) salmonids in Stony Clove Creek relative to the abundance of age-0 fish in the previous year. The dotted lines show trends, but regression analysis was not significant for either the fall- or spring-spawning salmonids ($P > 0.09$ and 0.16 , respectively).

peak mean daily discharge in the first half of the year ($P = 0.04$, $r^2 = 0.69$; Figure 3A). There was no comparable relation between year-class strength and discharge for the spring-spawning rainbow trout ($P = 0.99$, $r^2 < 0.01$; Figure 3A). In 2005, the year with the greatest peak discharge, the relative abundance of rainbow trout in Stony Clove Creek was substantially greater than the combined number of fall-spawning species (Figure 4A), and the strength of this cohort carried through to the following year's age-1 year-class (Figure 3B). Rainbow trout accounted for 16% to 34% of all age-0 salmonids captured in every year except 2005, when they accounted for 76% (Figure 4A); they

represented 9% to 20% of age-1 salmonids captured in every year except 2006, when they represented 68%.

Multiple-regression analysis with peak discharge and the total abundance of age-2 and older individuals as independent variables and the total abundance of fall-spawned age-0 fish as the response variable was not significant ($P = 0.17$, $r^2 = 0.70$). This measure of potential predation increased the explanatory power of the relationship by only 0.007%. Multiple-regression analysis of peak discharge on the timing of spring floods (week during which peak discharge occurred) also provided little additional explanatory power, and the overall multiple regression was not significant ($P = 0.15$, $r^2 = 0.71$). Multiple-regression analyses with rainbow trout year-class strength as the response variable also were not significant ($P > 0.20$ in both cases).

Overall, the total number of age-1 salmonids was positively related to the total number of age-0 fish in the previous year in Stony Clove Creek, but a simple linear fit of the data was not significant ($P = 0.11$, $r^2 = 0.63$). When the data were broken down into those for fall- and spring-spawning salmonids, the slope of the best-fit line was comparable between the two groups (slope = 0.19 for fall-spawning and 0.11 for spring-spawning salmonids; Figure 5) and age-0 abundance explained a substantial proportion of the variability in the abundance of age-1 individuals ($r^2 = 0.66$ and 0.53 , respectively), although the relationship was not significant for either group ($P = 0.09$ and 0.16).

The trends in the year-class strength and relative abundance of age-0 salmonids were comparable at Broadstreet Hollow Brook (Table 2). Abundance of

TABLE 2.—Population estimates of age-0 brook, brown, and rainbow trout in the two study reaches, summer 2002–2007. Reach lengths were approximately 100 m in both streams. The wetted widths in Stony Clove Creek were 8.6, 7.1, 8.3, 7.6, 9.2, and 9.7 m from 2002 to 2007, respectively; those in Broadstreet Hollow Brook were 3.7, 6.6, 5.4, and 6.7 m from 2002 to 2004 and 2006, respectively; na = not applicable.

Year	Spawning season	Species	Stony Clove Creek	Broadstreet Hollow Brook
2002	Fall	Brook trout	9	16
		Brown trout	189	41
2003	Spring	Rainbow trout	89	57
	Fall	Brook trout	2	20
2004	Spring	Rainbow trout	131	74
	Fall	Brook trout	3	17
2005	Spring	Rainbow trout	112	71
	Fall	Brook trout	0	na
2006	Spring	Rainbow trout	158	na
	Fall	Brook trout	0	3
2007	Spring	Rainbow trout	23	9
	Fall	Brook trout	2	na
		Brown trout	103	na
	Spring	Rainbow trout	21	na

fall-spawned age-0 fish was significantly related to peak discharge ($P = 0.05$, $r^2 = 0.90$; Figure 3B). There was a comparable trend with age-0 rainbow trout and spring peak discharge at Broadstreet Hollow Brook, but the relationship was not significant ($P = 0.06$, $r^2 = 0.88$; Figure 3B). Rainbow trout accounted for 32% to 51% of all age-0 salmonids captured during the 4 years in which surveys were conducted at Broadstreet Hollow Brook. Data were not collected from this stream during 2005 or 2007, so a direct comparison with data from Stony Clove Creek in 2005 was not possible; however, as in Stony Clove Creek, rainbow trout dominated the age-1 year-class in 2006, whereas in all other years the fall-spawning salmonids dominated this age-class (Figure 4D). The pattern seen in both systems suggests that a comparably large increase in relative abundance of age-0 rainbow trout probably also occurred in Broadstreet Hollow Brook in 2005.

Discussion

The results from this study suggest that the magnitude of spring floods can affect the relative abundance of age-0 fall- and spring-spawning salmonids by affecting the year-class strength of the fall-spawning species. The abundance of fall-spawning age-0 salmonids was significantly and inversely related to maximum winter–spring discharge, although the number of spring-spawning age-0 fish was not. The nearly threefold decrease in relative abundance of fall-spawning age-0 salmonids (brook and brown trout) in 2005 resulted largely from their low abundance that year; the numbers of spring-spawning age-0 rainbow trout were relatively constant from 2002 to 2005, but decreased in 2006 and 2007, whereas the absolute numbers of fall-spawning age-0 salmonids decreased sharply in 2005 and remained relatively low in the following 2 years. The relatively strong year-class of rainbow trout in 2005 allowed this species to dominate the age-1 cohort the following year in Stony Clove Creek, and this was most probably the mechanism for the dominance of rainbow trout in the age-1 cohort at Broadstreet Hollow Brook as well. This result is consistent with early work evaluating the relative influence of discharge on spring- versus fall-spawning salmonids. Seegrist and Gard (1972) found a substantial increase in rainbow trout recruitment after a winter flood that decreased brook trout recruitment in a California stream. Hanson and Waters (1974) noted that a single flood promoted the invasion and establishment of rainbow trout into a brook trout stream in Minnesota. In this study, we documented carryover in the dominance of the 2005 rainbow trout cohort, but the overall effect of this one particular year did not appear to lead to a substantial subsequent shift

in relative abundance at Stony Clove Creek. Frequent large floods in spring, however, could set the stage for increased relative abundance of rainbow trout in these stream reaches.

Although the exact range of emergence dates for stream salmonids in the Catskill Mountains of New York has not been documented, indirect evidence suggests that spring-spawning rainbow trout do indeed emerge after fall-spawning brook trout and brown trout. Rainbow trout in this system spawn from late March to the second week in April, followed by emergence three or more weeks later, depending on stream temperature (Smith 1985), whereas brook trout and brown trout in New York streams emerge from March through May (Smith 1985; M. Flaherty, New York State Department of Environmental Conservation, personal communication). Age-0 rainbow trout generally grow faster than age-0 brook trout or brown trout (Isely and Kempton 2000; Kocaman et al. 2006), yet the age-0 rainbow trout were consistently smaller than the age-0 brook or brown trout in our July surveys. We conclude, therefore, that the fry of the fall-spawning salmonids in these reaches emerge earlier than the fry of the spring rainbow trout. The available data were insufficient to differentiate between brown trout emergence time and that of brook trout.

Consistent stream temperature data are not available for either of our study streams, but data are available from a gauge on Esopus Creek, a site relatively close to our study streams, that can be used to evaluate regional trends in yearly stream temperature and identify potential extremes. Based on these data, mean daily water temperatures in summer were relatively consistent across years. Stream temperatures were greatest 2002 and 2006 and lowest in 2003 and 2004, with 2005 and 2007 exhibiting intermediate temperature trends. There was a short period of particularly high stream temperature in midsummer 2006 that may account for the loss of age-0 brook trout—the most thermally sensitive of the three resident salmonid species (Galbreath et al. 2004)—from Stony Clove Creek in that year. Overall, based on the available data, summer temperatures were unlikely to have substantially influenced the year-to-year variability in relative year-class strength of fall- versus spring-spawning salmonids in our study streams.

The decline in the total abundance of fall-spawning age-0 salmonids in 2005 and 2006 could also be a result of streambed scour during winter floods. Large flows have the potential to scour eggs from redds and thereby diminish year-class success for fall-spawning individuals by washing out eggs before hatching and emergence (Kondolf et al. 1991). In this study, however, winter floods of comparable magnitude

occurred in both 2005 and 2006, but spring-spawning salmonids were dominant only in 2005. In 2006, overall age-0 abundances for both spring-spawning and fall-spawning species were substantially lower than abundances of previous years. The January 2006 flood could not have directly affected age-0 spring-spawning rainbow trout. We suggest, therefore, that decreased abundance in the entire 2006 age-0 year-class instead resulted from the large flood that occurred at the end of June that year, before the fish data were collected in August. The June flood was substantial in both magnitude and duration, and prolonged high flows can still displace age-0 fish even when they occur after the likely critical period for both species. We suggest that the flood diminished age-0 abundances relatively equally; the relative dominance of fall-spawning age-0 salmonids over age-0 rainbow trout in 2006 is consistent with the expected age-0 fish distribution for this system in a year without a large early spring flood.

Many factors influence the abundance of fish in a stream, reach, or habitat unit. Physical habitat and stream conditions (Clarkson and Wilson 1995; Daney et al. 1998; Cote 2007; Deschenes and Rodriguez 2007), chemical conditions (Baker et al. 1996; Baldigo and Lawrence 2001; Nislow and Lowe 2003), and biological interactions (Einum 2005; Eby et al. 2006) can all act on a fish population or a fish community to influence fish abundance. Year-class strength for salmonids in streams has also been strongly correlated with the abundance of that cohort in subsequent years (Elliott 1994; Knapp et al. 1998; Lobon-Cervia 2004). Knapp et al. (1998) specifically note that following a period of high density-independent mortality early in development, the cohort strength of a given age-class of stream-dwelling California golden trout *O. mykiss aguabonita* was closely related to the strength of that cohort in the previous year (age-0, age-1, and age-2 of a given cohort are all correlated). Our results are consistent with previous studies indicating that year-class strength has a strong influence on abundance in the subsequent year for both fall- and spring-spawning species (Figures 4, 5). These results highlight the potential for differences in the year-class strength of spring- and fall-spawning salmonids to affect fish populations in subsequent years. A series of years with severe flooding may have the potential to shift the dominant salmonid in a stream.

Environmental changes throughout the northeastern United States are expected to result in earlier snowmelt and larger rain events across the region, including the Catskill Mountains (Burns et al. 2007; Hayhoe et al. 2007). These hydrologic shifts have the potential to favor the spring-spawning rainbow trout by decreasing

the probability of a snowmelt event occurring during the critical swim-up period for age-0 fish or even during the time when eggs are incubating and susceptible to bed scour. The spring 2005 flood, which coincided with a major decline in fall-spawning age-0 salmonids, was a combination snowmelt and rainfall event (Suro and Firda 2007). The peak discharge in 2006 was the result of a large rainstorm in June; snowmelt during the spring of 2006 was minimal. With the apparent greater susceptibility of fall-spawning salmonids to large floods in the first half of the year, we speculate that changes in climate will favor rainbow trout recruitment, especially if the anticipated increases in spring storms lead to large floods occurring two or more years in a row. Consequently, climate change over the coming decades could cause the composition of fish communities in Catskill Mountain streams specifically and in mid- to high-order streams across the northeastern USA in general to shift away from assemblages dominated by brown and brook trout towards those dominated by rainbow trout.

Acknowledgments

The authors extend their appreciation to Anne Finch, Rebecca Pratt Miller, Christiane Mulvihill, and Britt Westergard of the U.S. Geological Survey; Dan Davis, Phillip Eskeli, Christina Falk, Sarah Miller, Elizabeth Reichheld, and Mark Vian of the New York City Department of Environmental Protection; Cliff Kraft, Milo Richmond, Bethany Boisvert, Mike Compton, Matthew Horn, Walter Keller, Madeleine Mineau, Marshall Thomas, and Marissa Weiss of Cornell University; Douglas Dekoski, Joel DuBois, Jake Buchanan, and René VanShaack of the Green County Soil and Water Conservation District; Joe Benjamin of Idaho State University; three anonymous reviewers and numerous AmeriCorps and Ulster County Community College interns for technical support. This research was funded by the New York City Department of Environmental Protection, the Greene County Soil and Water Conservation District, the National Science Foundation IGERT program (NSF DGE-0221658), the U.S. Environmental Protection Agency STAR fellowship program, and the U.S. Geological Survey.

References

- Baker, J. P., J. VanSickle, C. J. Gagen, D. R. DeWalle, W. E. Sharpe, R. F. Carline, B. P. Baldigo, P. S. Murdoch, D. W. Bath, W. A. Kretser, H. A. Simonin, and P. J. Wigginton. 1996. Episodic acidification of small streams in the northeastern United States: effects on fish populations. *Ecological Applications* 6:422–437.
- Baldigo, B. P., A. Gallagher-Ernst, W. Keller, D. R. Warren, S. J. Miller, D. Davis, T. P. Baudanza, D. DeKoskie, and J. R. Buchanan. 2008a. Restoring geomorphic stability

- and biodiversity in streams of the Catskill Mountains, New York, USA. Pages 1777–1790 in J. L. Nielsen, J. J. Dodson, K. D. Friedland, T. R. Hamon, N. F. Hughes, J. A. Musick, and E. Verspoor, editors. Proceedings of the Fourth World Fisheries Congress: reconciling fisheries with conservation. American Fisheries Society, Symposium 49, Bethesda, Maryland.
- Baldigo, B. P., and G. B. Lawrence. 2001. Effects of stream acidification and habitat on fish populations of a North American river. *Aquatic Sciences* 63:196–222.
- Baldigo, B. P., D. R. Warren, A. G. Ernst, and C. I. Mulvihill. 2008b. Response of fish populations to natural-channel-design restoration in streams of the Catskill Mountains, New York. *North American Journal of Fisheries Management* 28:954–969.
- Burns, D. A., J. Klaus, and M. R. McHale. 2007. Recent climate trends and implications for water resources in the Catskill Mountain region, New York, USA. *Journal of Hydrology* 336:155–170.
- Clarkson, R. W., and J. R. Wilson. 1995. Trout biomass and stream habitat relationships in the White Mountains area, east-central Arizona. *Transactions of the American Fisheries Society* 124:599–612.
- Cote, D. 2007. Measurements of salmonid population performance in relation to habitat in eastern Newfoundland streams. *Journal of Fish Biology* 70:1134–1147.
- Danehy, R. J., N. H. Ringler, S. V. Stehman, and J. M. Hassett. 1998. Variability of fish densities in a small catchment. *Ecology of Freshwater Fish* 7:36–48.
- Deschenes, J., and M. A. Rodriguez. 2007. Hierarchical analysis of relationships between brook trout (*Salvelinus fontinalis*) density and stream habitat features. *Canadian Journal of Fisheries and Aquatic Sciences* 64:777–785.
- Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. *Trends in Ecology and Evolution* 21:576–584.
- Einum, S. 2005. Salmonid population dynamics: stability under weak density dependence? *Oikos* 110:630–633.
- Elliott, J. M. 1987. Population regulation in contrasting populations of trout *Salmo trutta* in two lake district streams. *Journal of Animal Ecology* 56:83–98.
- Elliott, J. M. 1989. The natural regulation of numbers and growth in contrasting populations of brown trout, *Salmo trutta*, in two Lake District streams. *Freshwater Biology* 21:7–19.
- Elliott, J. M. 1994. *Quantitative ecology and the brown trout*. Oxford University Press, Oxford, UK.
- Fausch, K. D. 2008. A paradox of trout invasions in North America. *Biological Invasions* 10:685–701.
- Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecological Applications* 11:1438–1455.
- Galbreath, P. F., N. D. Adams, and T. H. Martin. 2004. Influence of heating rate on measurement of time to thermal maximum in trout. *Aquaculture* 241:587–599.
- Hanson, D. L., and T. F. Waters. 1974. Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. *Transactions of the American Fisheries Society* 103:431–439.
- Hayhoe, K., C. Wake, T. G. Huntington, L. Luo, M. D. Schwartz, J. Sheffield, E. Wood, B. Anderson, J. Bradbury, A. DeGaetano, T. J. Troy, and D. Wolfe. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics* 28:381–407.
- Heggernes, J., and F. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology* 32:717–727.
- Isely, J. J., and C. Kempton. 2000. Influence of costocking on growth of young-of-year brook trout and rainbow trout. *Transactions of the American Fisheries Society* 129:613–617.
- Jensen, A. J., and B. O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology* 13:778–785.
- Knapp, R. A., V. T. Vredenburg, and K. R. Matthews. 1998. Effects of stream channel morphology on golden trout spawning habitat and recruitment. *Ecological Applications* 8:1104–1117.
- Kocaman, E. M., A. Bayir, A. N. Sirkecioglu, M. Cengiz-Bayir, and T. Yanik. 2006. Growth of trout juveniles (*Onchorhynchus mykiss*, *Salvelinus fontinalis*, and *Salmo trutta fario*) under uniform cultural conditions. *Journal of Applied Animal Research* 30:73–75.
- Kondolf, G. M., G. F. Cada, M. J. Sale, and T. Felando. 1991. Distribution and stability of potential salmonid spawning gravels in steep boulder-bed streams of the eastern Sierra Nevada. *Transactions of the American Fisheries Society* 120:177–188.
- Lapointe, M., B. Eaton, S. Driscoll, and C. Latulippe. 2000. Modeling the probability of salmonid egg pocket scour due to floods. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1120–1130.
- Latterell, J. J., K. D. Fausch, C. Gowan, and S. C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado Mountain streams. *Rivers* 6:240–250.
- Lobon-Cervia, J. 2004. Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1929–1939.
- Lobon-Cervia, J., and J. Gutierrez. 2006. Instability of stream salmonid population dynamics under strong environmental limitation: a reply. *Oikos* 114:376–380.
- Lobon-Cervia, J., and E. Mortensen. 2005. Population size in stream-living juveniles of lake-migratory brown trout *Salmo trutta* L.: the importance of stream discharge and temperature. *Ecology of Freshwater Fish* 14:394–401.
- Lobon-Cervia, J., and P. A. Rincon. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. *Oikos* 105:641–646.
- Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:94–100.
- Montgomery, D. R., E. M. Beamer, G. R. Pess, and T. P. Quinn. 1999. Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 56:377–387.
- Nehring, R. B., and R. M. Anderson. 1993. Determination of

- population-limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation system. *Rivers* 4:1–19.
- Nislow, K. H., S. Einum, and C. L. Folt. 2004. Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* 65:188–200.
- Nislow, K. H., and W. H. Lowe. 2003. Influences of logging history and stream pH on brook trout abundance in first-order streams in New Hampshire. *Transactions of the American Fisheries Society* 132:166–171.
- Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society* 121:427–436.
- Peterson, J. T., R. F. Thurow, and J. W. Guzevich. 2004. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. *Transactions of the American Fisheries Society* 133:462–475.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *Bioscience* 47:769–784.
- Reynolds, J. B. 1996. Electrofishing. Pages 221–253 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society* 101:478–482.
- Smith, C. L. 1985. *The inland fishes of New York*. New York State Department of Environmental Conservation, Albany.
- Strange, E. M., and T. C. Foin. 1999. Interaction of physical and biological processes in the assembly of stream fish communities. Pages 311–337 in E. Weiher and P. Keddy, editors. *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge, UK.
- Suro, T. P., and G. D. Firda. 2007. Flood of April 2–3, 2005, Esopus Creek basin, New York. U.S. Geological Survey, New York Water Science Center, OFR 2007-1036, Troy, New York.
- Zorn, T. G., and A. J. Nuhfer. 2007. Regional synchrony of brown trout and brook trout population dynamics among Michigan rivers. *Transactions of the American Fisheries Society* 136:706–717.