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A Three-Year Study of Ichthyoplankton in Coastal Plains Reaches of the
Savannah River and its Tributaries

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Introduction

Altering flow regimes of rivers has large effects on native floras and faunas because native species are adapted to the natural flow regime, many species require lateral connectivity with floodplain habitat for feeding or spawning, and the change in regime often makes it possible for invasive species to replace natives (Bunn & Arthington 2002). Floodplain backwaters, both permanent and temporary, are nursery areas for age 0+ fish and stable isotope studies indicate that much of the productivity that supports fish larvae is autochthonous to these habitats (Herwig et al. 2004). Limiting access by fish to floodplain habitat for feeding, spawning and nursery habitat is one of the problems noted with dams that regulate flow in rivers and is considered to be important as an argument to remove dams and other flow regulating structures from rivers (Shuman 1995; Bednarek 2001).

While there have been a number of studies in the literature about the use of floodplain habitat for fish reproduction (Copp 1989; Killgore & Baker 1996; Humphries, et al. 1999; Humphries and Lake 2000; Crain et al. 2004; King 2004) there have been only a few studies that examined this aspect of stream ecology in more than a cursory way. The study reported here was originally designed to determine whether the Department of Energy's (DOE) Savannah River Site was having a negative effect on fish reproduction in the Savannah River but its experimental design allowed examination of the interactions between the river, the floodplain and the tributaries entering the Savannah River across this floodplain. This study is larger in length of river covered than most in the literature and because of its landscape scale may be an important indicator of areas where further study is required.

Methods and Materials

Study area

The Savannah River watershed includes western South Carolina, eastern Georgia, and a small portion of southwestern North Carolina. It is formed by the confluence of the Tugaloo and Seneca Rivers in northeast Georgia and flows southeast through the Piedmont and Coastal Plain to the Atlantic Ocean. The Savannah River is broad with extensive floodplain swamps and numerous tributaries in its mid- and lower reaches. The substrate consists of various combinations of silt, sand, and clay. Water flow in the Savannah River is controlled by a system of reservoirs located upstream of the study area. Our study area stretched from just below the New Savannah Bluff Lock and Dam at RK (River Kilometer) 301 downstream to RK48.

Field methods

Sampling was conducted during 1983, 1984, and 1985 in the mid- and lower portion of the Savannah River located within the coastal plain physiographic province (Figure 1). During 1983 and 1984 there were 27 river stations between River Kilometer (RK) 47.6 and RK 301. The two most downriver stations were tidally influenced but the lowest one was more than 24 km above the salt wedge. The five most downriver stations were eliminated during 1985 leaving 23 stations between RK 144 (RM 89.3) and RK 301. Samples were also collected from the lower reaches of Savannah River tributary streams located within the study area (Table 1). The number of tributaries sampled each year varied depending upon water level and accessibility as explained below.

Ichthyoplankton were collected with paired 0.5 m plankton nets with 505 μm mesh. The nets were deployed for stationary sampling where the current was sufficient but were towed at creek stations with insufficient current for stationary deployment of the nets. Deployment time for both stationary and towed nets was adjusted to filter approximately 50 m^3 of water. Calibrated flow meters were mounted in the mouths of the nets to calculate actual volume filtered. Ichthyoplankton (eggs and larvae) collected in the nets were preserved in formalin and transported to the laboratory where they were sorted and identified under a stereomicroscope to the lowest practical taxa using taxonomic keys by Geen et al. (1966), Mansuetti and Hardy (1967), Hogue et al. (1976), Jones et al. (1978), and Wang and Kernehan (1979).

A minimum of three subsurface (0.5 m below surface) samples were collected from each river sample station: near the South Carolina shore, near the Georgia shore, and in mid-channel. A single subsurface sample was taken from each creek sample station in mid-channel near the creek mouth. Both river and creek stations were also sampled at approximately 0.5 m above bottom where the depth was greater than two meters. Weekly samples were taken during the day from February through July each year.

Tributary creeks that entered the river between RK 48 (RM 30.0) and RK 301 were sampled in 1983 and 1984 (Figure 2). Big Collis Creek (RK 48) was the only creek with measurable tidal influence but it had no detectable salinity. Creek stations were not sampled on dates when the river was so high that river water was flowing into the creek mouth or so low that the boat could not safely enter the creek mouth. Creeks samples stations that could not be sampled on half or more of the sampling dates were eliminated from the analysis. Data were analyzed from 22 creek sample stations in 1983 and 21 creek sample stations in 1984. In 1985 all creek stations below RK 149 (RM 92.6) were eliminated because the study area was reduced (as previously described) leaving 10 creek stations between RK 149 and RK 295 that were sampled consistently.

Several physical parameters were calculated for each station. Creek discharge was calculated based on field measurements of stream cross-section and current velocity data collected each week near the ichthyoplankton sampling stations.

River discharge was estimated based on USGS reported monthly discharge rates at three locations within the study area (RKs 191, 252, and 302) and interpolated to each sampling station location. Flood plain width was estimated using a combination of aerial photos, satellite images and USGS quadrangle maps.

Data analysis

Densities of fish eggs and larvae were calculated as number of organisms/1000 m³. Mean densities for each sample station each week were calculated by averaging densities for both nets from all samples taken at the station that week.

Although commonly reported in ichthyoplankton studies, density metrics were insufficient to evaluate the contribution of the tributary streams to the river because they provided no information on the number of ichthyoplankters that were exported from the streams (which is strongly affected by stream size). Similarly, density comparisons over time produced misleading estimates of ichthyoplankton abundance in the river because they did not account for large differences in water volume (i.e., discharge) among years. To avoid these limitations, we computed the number of ichthyoplankters transported past each sampling station from estimates of weekly station mean ichthyoplankton densities and station discharge rates. It was assumed that all larvae in the water column were carried past the station in question and no larvae remained in the station vicinity for this estimate. The number of ichthyoplankton transported over time at each sample station was calculated by averaging ichthyoplankton transport between each pair of consecutive sample dates, multiplying this mean by the elapsed time between sample dates, and summing the intervals. No effort was made to compensate for potential diel fluctuations in ichthyoplankton abundance (Robinson et al. 1998; Carter and Reader 2000; Copp et al. 2005)

The abundance and composition of ichthyoplankton at the creek and river sample stations was summarized using non-metric multidimensional scaling (NMS), a relatively assumption free ordination method (Clarke and Warwick 2001). The ordinations were based on the total ichthyoplankton transported from each sample station during each year of the study, $\log_{10}(x+1)$ transformed to prevent abundant taxa from dominating the analysis. The creek and river sample stations were ordinated separately. One hundred iterations were used to minimize stress (disagreement between similarities indicated by the Bray-Curtis coefficients and similarities indicated by distances in the ordination, Clarke and Warwick 2001). The number of significant dimensions (axes) was determined by a Monte Carlo procedure that compared the stress in the ordinations with the stress in randomized species arrangements (McCune and Mefford 1999). All ordinations were repeated with different random starting configurations to ensure a final solution with consistent and relatively low stress. Kendall correlation coefficients were used to assess the relationship between individual taxonomic variables and NMS ordination scores.

Common taxa as defined herein are taxa that were captured all three years, occurred at half or more of the stations at least in one year, and made up 10% or more of the captures at several stations during at least one year during the three year period (Table 2A). In order to avoid data matrices that were filled with non-occurrences, these taxa were the only ones used for analysis. Rare taxa are defined as taxa that had no captures at all in at least one year and never made up more than 1 or 2% of the captures for any given station (Table 2B).

Results

Anadromous species including striped bass *Morone saxatilis* (Walbaum), American shad *Alosa sapidissima* (Wilson), and blueback herring *Alosa aestivalis* (Mitchill) were common in the ichthyoplankton collections as were freshwater taxa within Centrarchidae, Clupeidae, Cyprinidae, Catostomidae, and Percidae (Table 2). A variety of less common taxa were also collected. Most taxa were collected from both river and creek sample stations, although some, including striped bass and American shad, were more common in the river.

Ordination (NMS) of the river ichthyoplankton transport data showed clear separation of years on axis 1, with 1985 receiving high scores, 1984 intermediate scores, and 1983 low scores (Figure 3). Nineteen eighty-three and 1984 were more similar to each other than either was to 1985. Axis 1 was inversely correlated with the transport of blueback herring, *Dorosoma* spp., Cyprinidae spp., and *Pomoxis* spp. (Kendall tau $r = -0.77$ to -0.54) indicating greater numbers of these taxa in 1983 and 1984 than in 1985 (Table 3). Axis 2 of the NMS reflected the segregation of sites based on spatial differences in the transport of striped bass ichthyoplankton, which may reflect spawning site preferences but whose exact cause is unknown.

Low transport in 1985 was associated with low average Savannah River discharge (reflected by symbol size in Figure 3). Because of this low discharge, the floodplain remained dry throughout the 1985 study period except briefly during early February before most fish spawned (Figure 4). In contrast, the floodplain was inundated during most of March and April 1983 and during March and late April through late May 1984. During these floods, extensive floodplain swamps associated with the river and lower reaches of the tributaries remained inundated for significant periods of time that corresponded with periods of peak ichthyoplankton abundance in the river.

Ordination of the creek transport data indicated annual patterns that were generally similar to those in the river, although there was greater scatter among the sample sites. Sample sites were again separated by year on axis 1, 1983 and 1985 were on opposite ends of the axis, and similarities in assemblage structure (as indicated by transport) were greater between 1983 and 1984 than between these years and 1985 (Figure 5). Axis 1 was correlated with the transport of all taxa included in the analysis except brook silverside (Kendall tau r

=0.52 to 0.75) indicating that ichthyoplankton abundance was greatest in 1983 and least in 1985 (Table 3). Discharge levels varied greatly among creeks (as indicated by symbol size in Figure 5) during all years, but the greatest creek discharges were in 1983 and 1984.

The annual transport of ichthyoplankton from each creek can be expressed as a percentage of the annual transport of ichthyoplankton in the Savannah River at the nearest downstream sample station (usually within 7 km, range 0.0 – 30.5 km) to provide a measure of the potential contribution of the ichthyoplankton from each creek to the river ichthyoplankton assemblage. Creek ichthyoplankton inputs to the river measured in this manner ranged from 10 - 40% for a number of creeks during 1983, indicating substantial contributions (Figure 6). Creek discharge was also high during 1983, ranging up to nearly 50% of the discharge at the nearest downstream sample station in the river. In 1983 ichthyoplankton transport from the creeks expressed as a percentage of river transport was strongly related to creek discharge (expressed as a percentage of river discharge) (Figure 6). In 1984 ichthyoplankton transport from the creeks remained relatively high, again up to nearly 40% of the transport in the river, although discharge from the creeks composed a lower percentage of the river discharge (up to 15%). The relationship between ichthyoplankton transport and creek discharge was again strong, although the R^2 of 0.68 in 1984 was slightly lower than in 1983 (0.80). In contrast to 1983 and 1984, there was hardly any ichthyoplankton transported to the river in 1985, and the regression of ichthyoplankton transport on creek discharge was much weaker ($R^2=0.36$, Figure 6).

The potential importance of floodplain inundation on ichthyoplankton abundance (as indicated by transport) was assessed by regressing ichthyoplankton transport at each sample station in the river on the width of the floodplain at that sample station (Figure 7). In 1983, the year of greatest flooding, this relationship was comparatively strong ($R^2=0.46$, $P<0.001$), in 1984 this relationship was weak but significant ($R^2=0.18$, $P=0.023$), and in 1985, the year of lowest discharge with no inundation of the floodplain, this relationship was nonexistent ($R^2=0.02$, $P=0.54$). Table 3 summarizes the regression analyses of larval transport versus floodplain width. For 1983 and 1984 total larval transport at both creek and river stations was significantly correlated with floodplain width while for 1985 neither creek nor river larval transport was significantly correlated with floodplain width.

Discussion

River flow has often been implicated as a controlling factor in riverine ecosystems (Bunn and Arthington 2002). Several mechanisms have been proposed for river flow to affect larval recruitment. Negative effects on larval recruitment have been hypothesized to include having reduced residence time in the nursery habitat portions of rivers due to washout at high flow rates (Meador, et al. 1984; Mion, et al. 1998) or increased turbidity from high flow events (Mion et al. 1998; Shoji et al 2005). Positive effects include having access to nursery

and spawning areas in floodplain pools and other inundated habitat (Sabo & Kelso 1991; Turner, et al. 1994; Fontenot, et al. 2001; King et al. 2003; Sommer et al. 2004; Walsh et al. 2005), having increased water mixing reduce floodplain pool anoxia (Fontenot, et al. 2001), and having flooded mouths of tributaries serve as backwater areas for those species that require backwaters for spawning and nursery areas (Holland 1986; Brown & Coon, 1994).

Some fish species that spawn in the main channels of rivers and larger creeks require relatively high flow rates for spawning and incubation. Blueback herring may not spawn at all in some streams during drought years (Loesch & Lund 1977). The main channel spawning species include species that are important commercially and as sport fish such as American shad and striped bass or species of special concern such as shortnose sturgeon *Acipenser brevirostrum* Lesueur, however, larval fish are normally more abundant near shore where stream velocities are lower. Some species that normally spawn in the main channel and have nursery areas in the margins of the main channel grow faster when they live in floodplain areas (Sommer et al. 2001)

Scheidegger and Bain (1995) report that 83% of the larval fish they caught in the Cahaba and Talapoosa rivers were captured in the shallow, low flow areas near shore. The taxa that they reported are similar to the ones encountered in this study so that it would not be surprising if our larval fish were also those that would benefit by having flooded creek mouths as backwater habitat as well as floodplain pools for nursery areas.

In our study almost all taxa were found both in the main river channel and in the tributaries (Table 2). Brown & Coon (1994) found the same pattern in the Missouri River and Turner et al. (1994) report this to be the case also for the Tallahatchie River of Mississippi.

We believe that river flow, both as mean spring discharge and as related to timing and period of pulses, is indeed the factor controlling larval recruitment in our study area. An examination of monthly river discharge at Augusta, GA for the three years 1983, 1984, and 1985, shows (Figure 7) that 1983 and 1984 had periods of flooding, while 1985 was a drought year and had much lower spring discharge with no flood pulse. In addition, 1983, the year with highest recruitment, had a significant flood pulse in April during the spring peak of spawning and larval fish densities. A flood pulse was also observed during 1984, except that it occurred later in the season (late April through May) and was likely too late to provide optimum benefits to early spawning species. During these pulses, fish had access to floodplain pools, flooded bottomland habitat and flooded mouths of tributaries that served as large backwater habitats. The timing of flood pulses has been reported to be important to reproductive success for several of the same taxa that we encountered (Fontenot, et al. 2001; Engel 2003).

Not all species responded similarly to the effects of flooding. Some, like blueback herring and crappie, clearly exhibited greater reproductive success during flood years. In contrast, the reproductive success of American shad and striped bass exhibited little relationship to water level (Table 3). The later two species typically spawn in river channels or the mouths of large tributaries rather than in backwaters (Marcy et al. 2005) and would not be expected to benefit from inundation of the floodplain to the same extent as species that spawn over vegetation or in shallow and still waters.

There is more than a century's worth of river stage and discharge data from the Augusta, GA, (RK 301) gauging station available at the U.S. Geological Survey website. Figure 8 is a scatter plot of annual discharge measurements as five year averages versus year of measurement. It is immediately obvious that over the last hundred years there appears to be a reduction in river discharge. While some of this may relate to the increased evaporation from having pooled water above the dams on the river, except for the small Stephens Creek Dam near Augusta which was completed in 1912, the other dams were completed in the 1950s and it appears that the loss in discharge trend was already started prior to the 1950s. This data set is shown primarily to indicate that, if we are correct that larval recruitment is controlled largely by spring flood pulses and the trend shown in Figure 8 is real, then we expect to see a future decrease in successful recruitment as these spring flood pulses become rarer.

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Table 1. Creeks sampled during this study with approximate river kilometer where creek enters the Savannah River and estimated floodplain width (km).

Creek	RK	FP Width	1983	1984	1985
Big Collis Creek	48	5.75	X	X	
Meyers Lake	57	5.76	X	X	
Coleman Run	65	4.11	X	X	
Lockner Creek	70	4.94	X	X	
Ebenezer Creek	72	5.33	X	X	
Seines Landing Creek	77	6.77	X	X	
Plank Creek	82	9.46	X	X	
Lake Palachucola Creek	103	14.86	X	X	
Black Creek	126	4.08	○	○	
Pike Creek	135	5.87	X	X	
Ware Creek	143	6.67	X	○	
Buck Creek	149	7.61	X	X	X
Briar Creek	157	8.71	X	X	X
Gaul Creek	175	4.53	○	X	○
Smith Lake Creek	204	3.33	X	X	X
Lower Three Runs	208	3.30	X	○	X
Sweetwater Creek	215	3.40	X	X	○
Boggy Gut Branch	227	4.49	○	○	
Steel Creek	228	3.59	X	X	X
Fourmile Branch ¹	242	4.66	○	X	X
Beaverdam Creek ²	245	3.56	X	X	X
Upper Three Runs	253	2.91	X	X	X
Boggy Gut Creek	261	5.72	○	○	
McBean Creek	264	3.60	X	X	○
High Bank Creek	276	0.56		○	
Hollow Creek	263	0	X	X	X
Pine Creek	290	0		○	
Spirit Creek	295	2.24	X	X	○
Butler Creek	301	0	○		

X = sampled

○ = sampled but dropped from analysis

¹Fourmile Branch received cooling water from a reactor and averaged 13-16 C above ambient

²Beaverdam Creek received cooling water from a reactor and averaged 7-9 C above ambient

Table 2. List of taxa of eggs and larvae captured during this study.

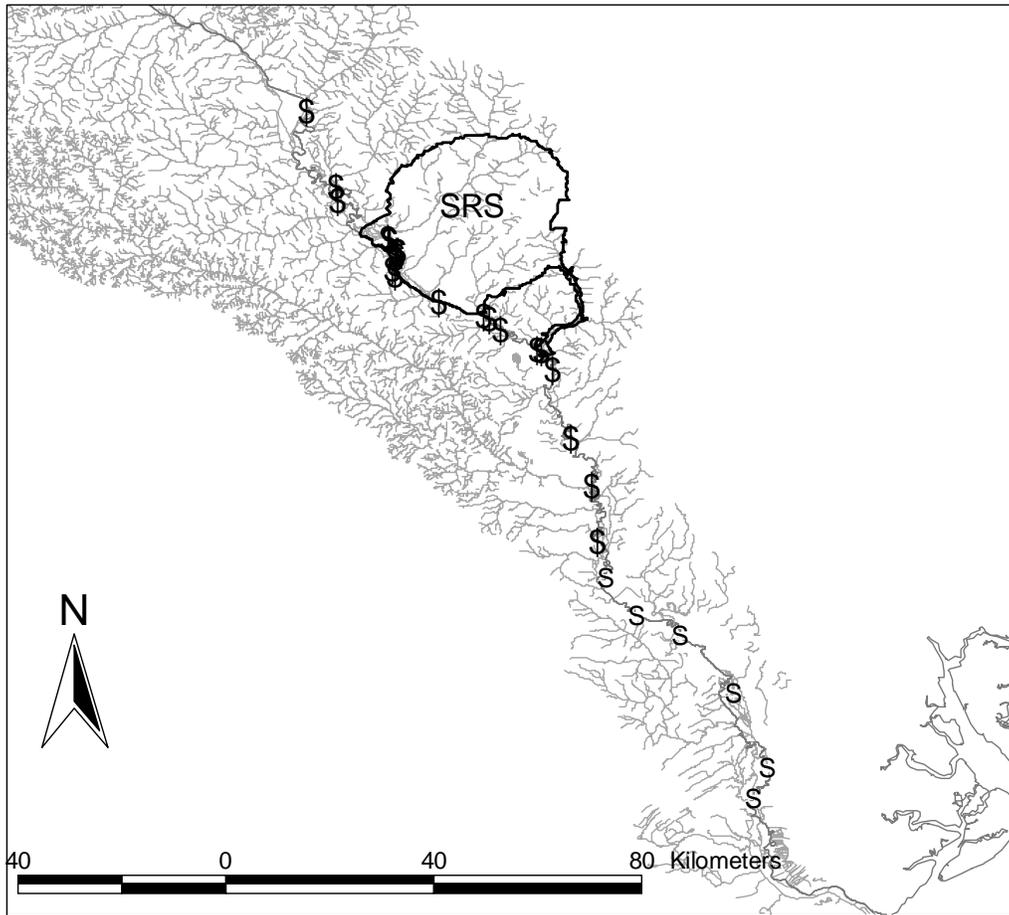
Table 2A: Common taxa captured			
Taxon	Common name	River	Creek
<i>Alosa aestivalis</i>	Blueback herring	X	X
<i>Alosa sapidissima</i>	American shad	X	X
<i>Dorosoma cepedianum/petenense</i>	Shad	X	X
Cyprinidae other than <i>Cyprinus</i>	Shiners	X	X
<i>Cyprinus carpio</i>	Common carp	X	X
<i>Minytrema melanops</i>	Spotted sucker	X	X
<i>Aphredoderus sayanus</i>	Pirate perch	X	X
<i>Labidesthes sicculus</i>	Brook silverside	X	X
<i>Morone saxatilis</i>	Striped bass	X	X
<i>Lepomis</i> spp.	Sunfishes	X	X
<i>Pomoxis nigromaculatus/annularis</i>	Crappies	X	X
<i>Etheostoma / Percina</i>	Darters	X	X
<i>Perca flavescens</i>	Yellow perch	X	X
Table 2B: Rare taxa			
<i>Acipenser brevirostrum/oxyrinchus</i>	Sturgeons	X	
<i>Lepisosteus osseus/platyrhincus</i>	Gars	X	X
<i>Amia calva</i>	Bowfin	X	X
<i>Esox americanus/niger</i>	Pickerels	X	X
<i>Umbra pygmaea</i>	Eastern mudminnow	X	X
<i>Ictalurus / Ameiurus</i>	Catfishes	X	X
<i>Chologaster cornuta</i>	Swampfish	X	
<i>Fundulus lineatus/chrysotus</i>	Killifishes	X	X
<i>Gambusia holbrooki</i>	Eastern mosquitofish	X	X
<i>Strongylura marina</i>	Atlantic needlefish	X	
<i>Micropterus salmoides</i>	Largemouth bass		X

Table 3. Average (standard deviation) number (x 1,000,000) of ichthyoplankton transported past sample stations in the Savannah River and from the mouths of Savannah River tributary creeks during February through July.

Taxa	1983	1984	1985
Savannah River			
American shad	58.2 (32.9)	30.3 (20.2)	91.0 (58.7)
Blueback herring	75.1 (86.7)	12.2 (8.4)	4.5 (2.5)
Striped bass	15.3 (20.6)	16.6 (18.7)	10.5 (14.2)
Yellow perch	17.7 (15.6)	0.0 (0.0)	0.0 (0.0)
Dorosoma spp.	117.6 (112.6)	25.7 (14.2)	18.8 (22.6)
Cyprinidae spp.	77.0 (32.3)	31.7 (17.0)	6.9 (3.8)
Lepoms spp.	17.7 (16.3)	26.5 (24.9)	17.5 (9.2)
Pomoxis spp.	89.5 (62.0)	34.0 (17.8)	1.9 (1.9)
Tributary creeks			
Blueback herring	17.2 (29.0)	0.3 (0.4)	0.3 (0.5)
American shad	2.3 (3.3)	1.2 (2.2)	0.2 (0.5)
Dorosoma spp.	10.3 (17.8)	3.3 (8.9)	<0.1 (0.1)
Spotted sucker	0.3 (0.6)	0.1 (0.3)	<0.1 (0.1)
Lepomis spp.	3.6 (5.6)	0.7 (1.9)	0.1 (0.1)
Pomoxis spp.	14.5 (23.3)	2.8 (5.6)	<0.1 (<0.1)
Darters spp.	0.8 (1.0)	5.2 (10.1)	<0.1 (<0.1)
Cyprinidae spp.	4.2 (6.6)	1.2 (4.1)	<0.1 (<0.1)
Brook silverside	0.3 (0.6)	0.1 (0.2)	0.4 (0.5)

Table 4. Results of regression of total larval transport at a given sampling station versus floodplain width at that station separated by year and river stations or creek stations.

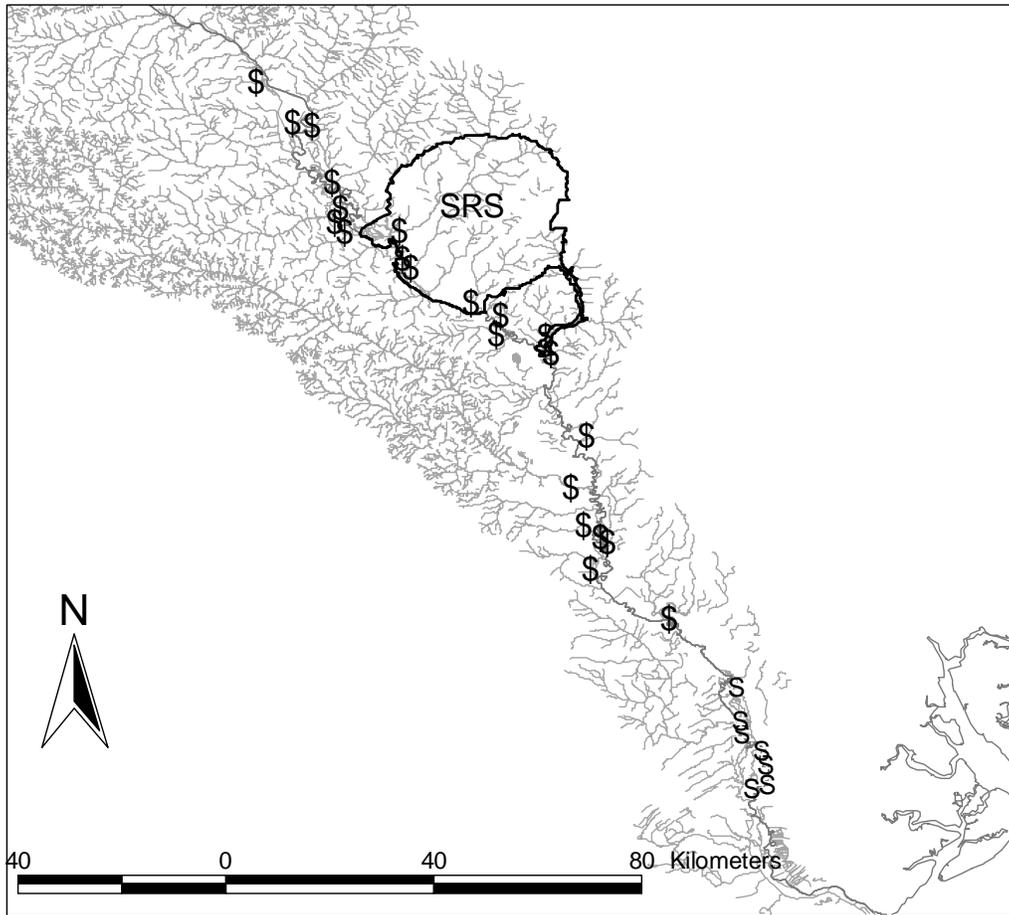
	R-square	Adjusted R-square	No. Observations	F	Significance
River 1983	0.4577	0.4368	28	21.9425	0.0001
Creek 1983	0.2063	0.1745	27	6.4967	0.0173
River 1984	0.1835	0.1521	28	5.8437	0.0229
Creek 1984	0.2369	0.2076	28	8.0716	0.0086
River 1985	0.0179	-0.0288	23	0.3831	0.5426
Creek 1985	0.0168	-0.0652	14	0.2045	0.6592



River Sampling Stations

- \$ Planned For All Years
- S Not Sampled in 1985
- SRS Boundaries
- ▾ Rivers and Streams

Figure 1. Locations of river sampling stations. See text for explanation of stations dropped in 1985.



Creek Sampling Stations

- \$ Planned For All Years
- S Not Sampled in 1985
- SRS Boundaries
- ▬ Rivers and Streams

Figure 2. Locations of creek sampling stations for all years. See Table 1 for details about which stations were dropped or otherwise not sampled in a given year.

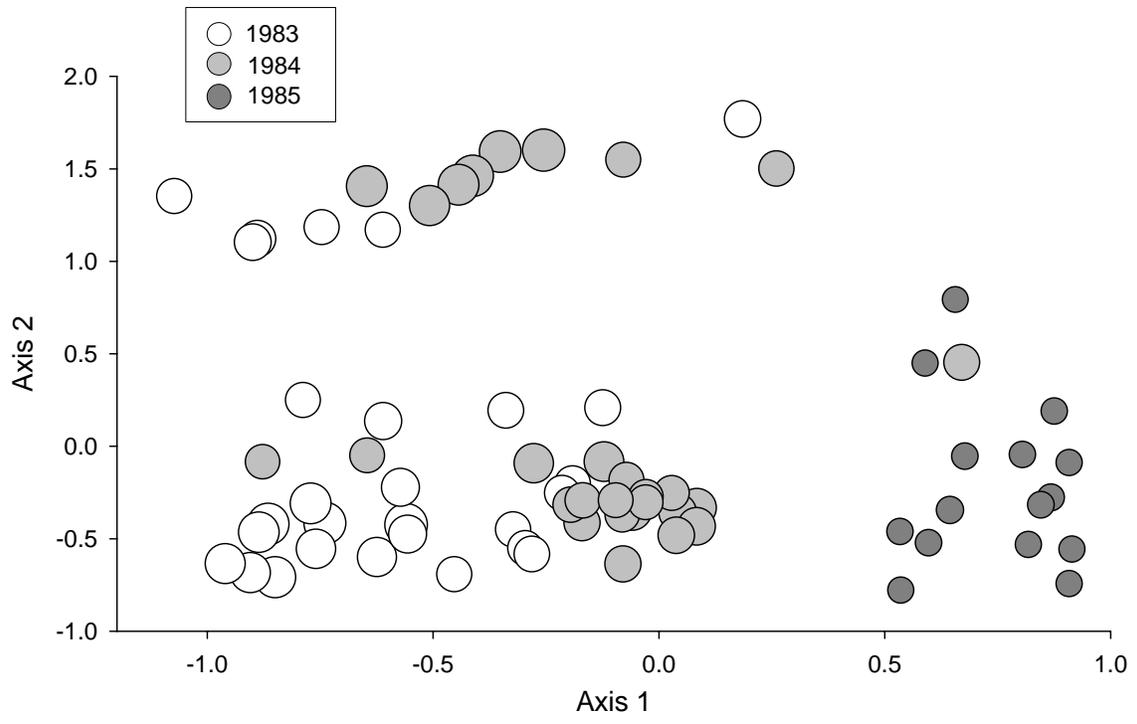


Figure 3. Multidimensional scaling based on larval composition of river samples. Symbol size is proportional to river discharge.

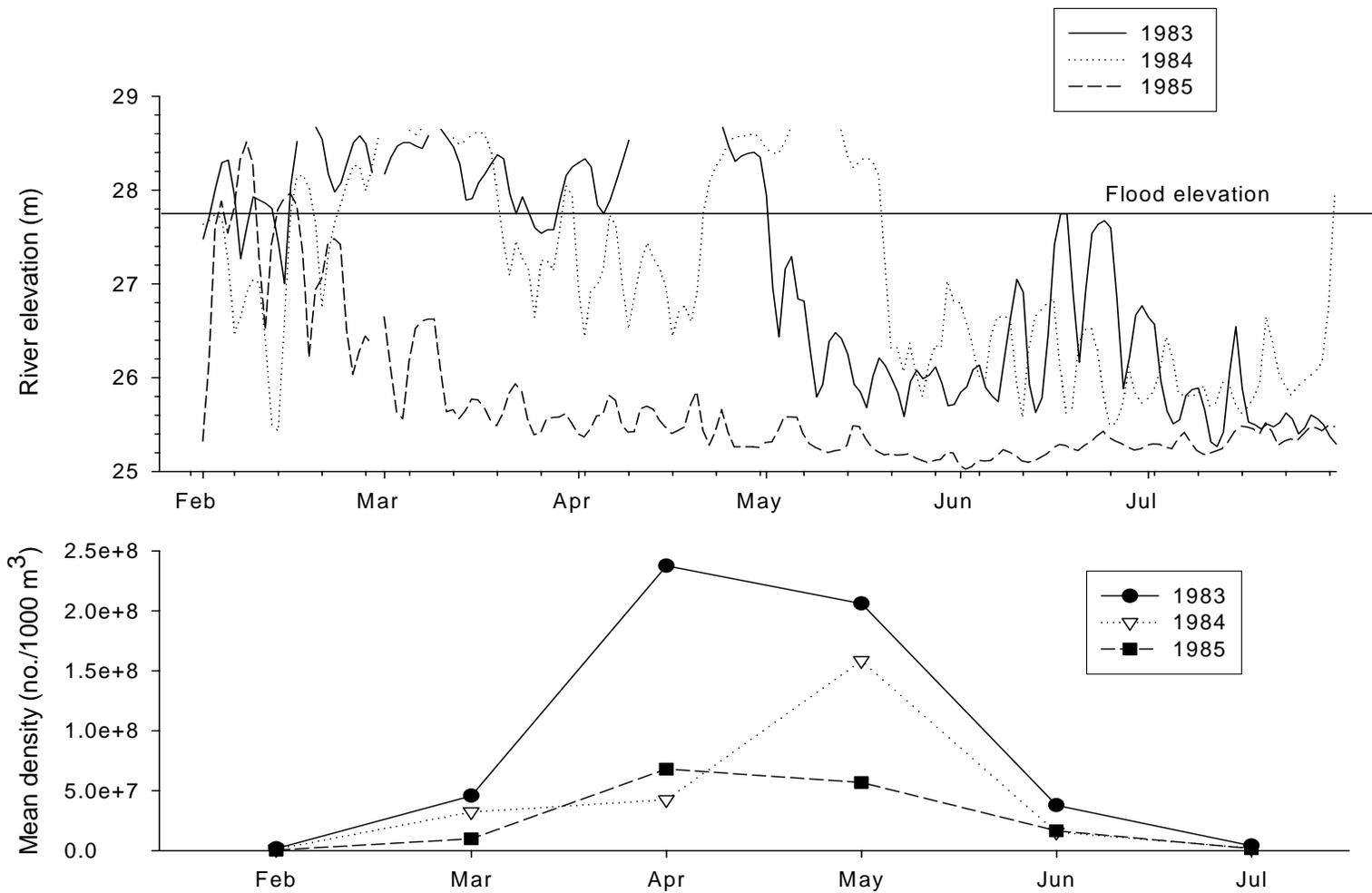


Figure 4. Water levels and average monthly ichthyoplankton density in the Savannah River. Flood elevation represents the minimum river stage at which extensive inundation of the floodplain swamps occurred.

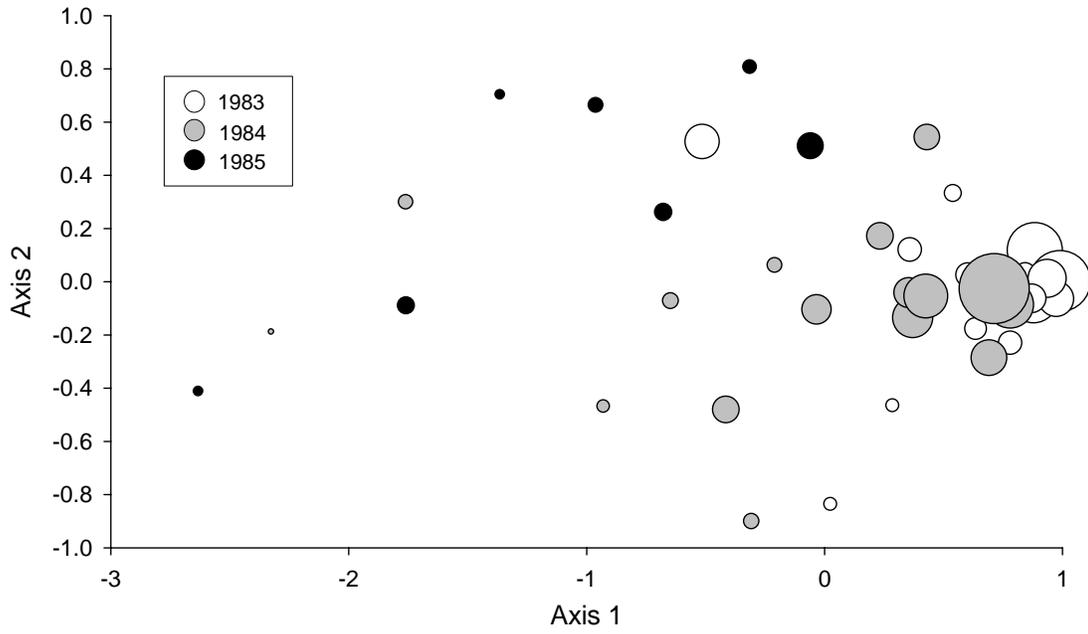


Figure 5. Multidimensional scaling based on larval composition of creek samples. Symbol size is proportional to creek discharge.

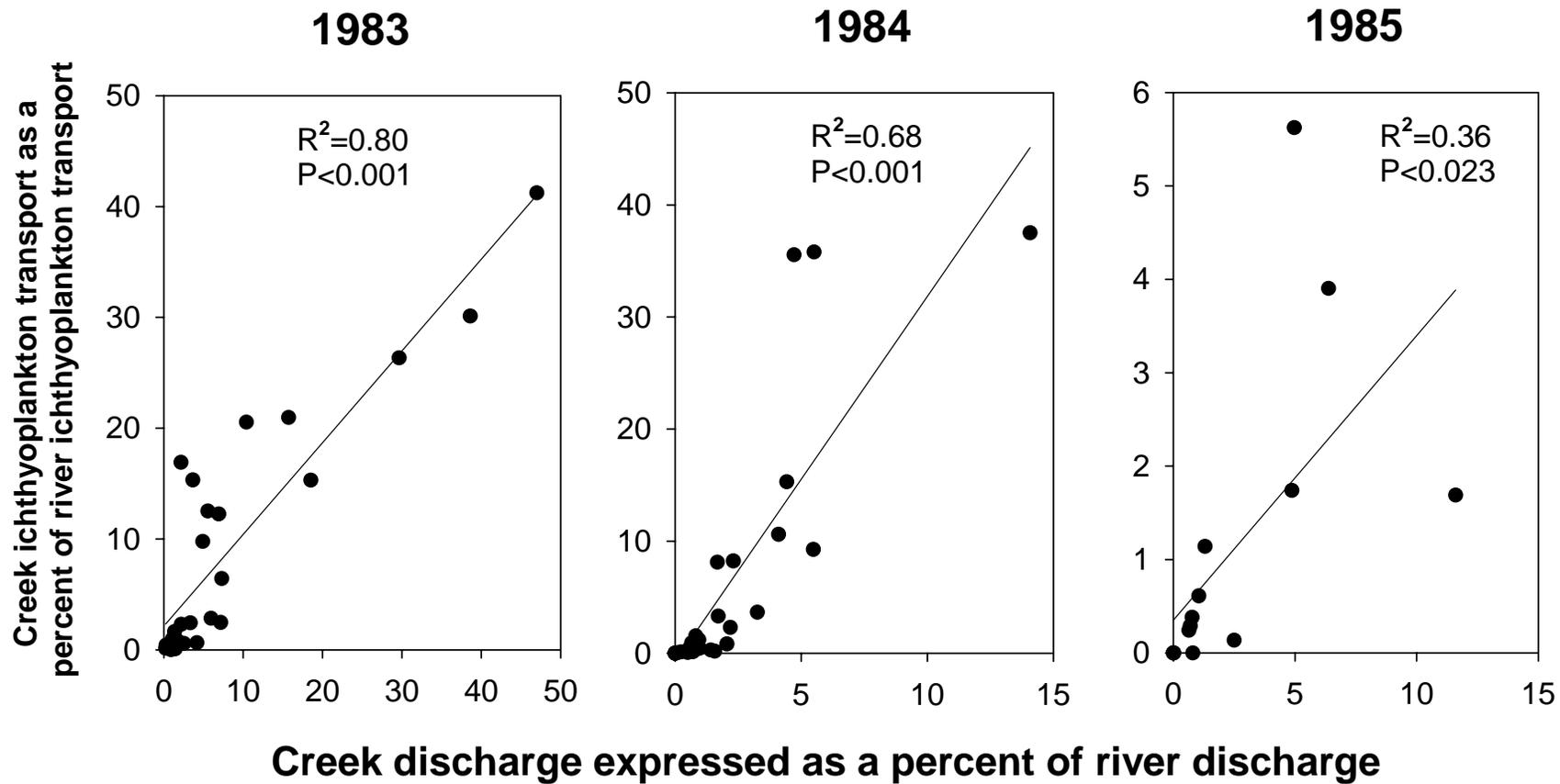


Figure 6. Proportional contributions of creeks to water discharge and larval transport.

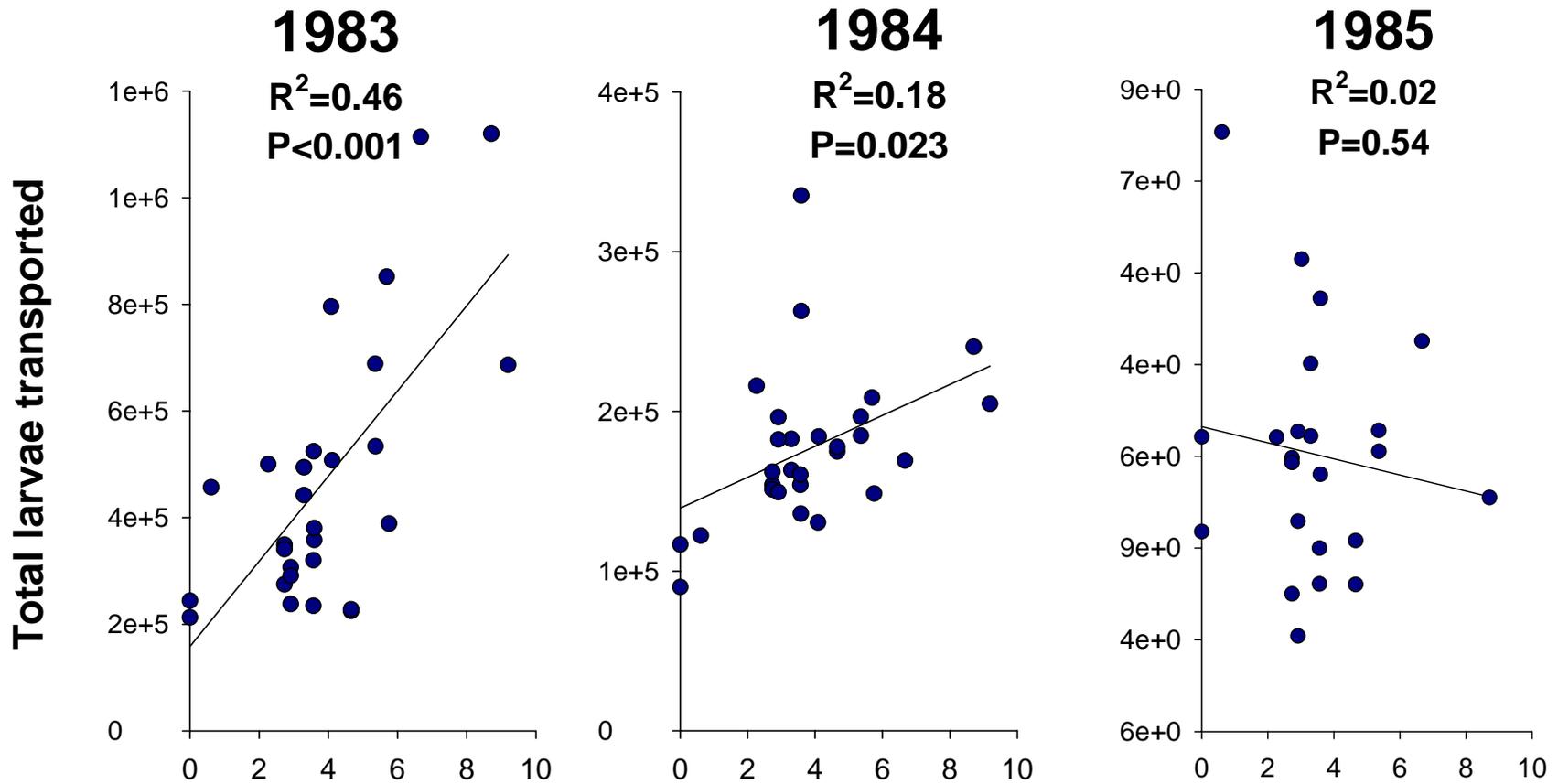


Figure 7. Larval transport (all species combined) at each river sampling station regressed against floodplain width at the sampling transect.

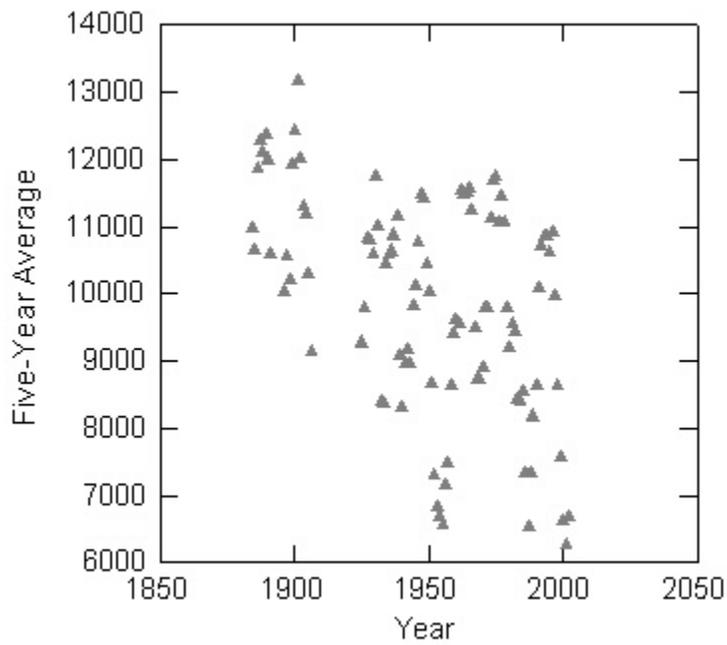


Figure 8. Plot of Savannah River annual discharge measured at Augusta, GA from 1884 to 2002 (data from USGS). Values are averages for given years and two years before and two years following to give a smoothing function.