Effects of nutrients and zooplankton on an estuary’s phytoplankton: inferences from a synthesis of 30 years of data

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Abstract. Phytoplankton biomass is commonly used as a water quality metric in the management of anthropogenic nitrogen and phosphorus loading, yet interpretation of the long-term response of phytoplankton biomass to nutrient regulation may be confounded by changes in zooplankton grazing pressure. Zooplankton community structure may be affected by planktivorous fish whose populations are subject to losses through fishing and gains through restoration efforts. We investigated temporal changes in phytoplankton biomass, nitrogen and phosphorus concentrations, zooplankton, and planktivorous fish in the tidal fresh and oligohaline Chowan River, NC, over a 30-year period in order to compare long-term trends in these parameters and infer their relative influence on phytoplankton biomass. Data were compiled from the records of two state agencies and several academic studies and supplemented by our own two year monitoring of water quality and zooplankton in the Chowan River mainstem and two tributaries. Seasonal trend decomposition using locally weighted regression was applied to chlorophyll a (a proxy for phytoplankton biomass), nitrogen, and phosphorus, and showed that chlorophyll a declined more quickly than did nutrient concentrations over the 30-year period. Despite the long-term decline in nitrogen and to a lesser extent phosphorus, the long-term trend in phytoplankton growth rate (predicted using an empirical model involving irradiance and nutrients) remained relatively constant. Zooplankton abundance increased from the period 1981–1982 to 2008–2010, as did the predicted zooplankton community water clearance rate (a proxy for zooplankton grazing). River herring, historically the dominant planktivore, declined dramatically over the 30-year period. The data indicate that the most parsimonious explanation for the long term decrease in chlorophyll a is an increase in zooplankton and not a decrease in nutrients. This inference leads us to hypothesize that the historically large river herring population exerted a positive, indirect influence on phytoplankton biomass in the Chowan River system, and that the decline in river herring has lead to higher zooplankton abundance and subsequently lower phytoplankton biomass.

Key words: blackwater river; estuary; irradiance; nutrient limitation; phytoplankton; primary production; river herring; tidal freshwater river; trophic cascade; zooplankton; zooplankton grazing.

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INTRODUCTION

Syntheses of 3–4 decades of environmental data in estuaries is fostering an appreciation for the complexity of estuarine food webs and paving the way toward new hypotheses (Kemp and Boynton 2011). Prior conceptual models focusing only on nutrient enrichment as the driver of ecosystem change are being replaced by more sophisticated ecosystem based models that account for interactions between top-down and bottom-up processes (discussed by Cloern 2001, Daskalov et al. 2007). The emergent effects of trophic interactions and resource limitation are being discovered in analyses of long time-series data, where the importance of indirect trophic effects (e.g., Winder and Jassby 2010) and environmental chemistry (e.g., Glibert 2010) become apparent. These time-series data form the foundation for development of ecosystem-based models, which are being used to forecast the ecological effects of interacting management policy (e.g., Fulford et al. 2010). Ultimately, synthesis efforts can reveal patterns that are counter to expected ecological process and management action (e.g., Heffernan et al. 2010), and help explore new hypotheses in estuarine science.

One particular combination of ecological and management factors has co-occurred in many estuaries throughout the eastern US and Canada. Over the past 30 years, mandated limits on point source nutrient discharges have reduced nutrient inputs to river networks in an effort to control estuarine eutrophication (Howarth and Marino 2006). Over the same period, anadromous fish, particularly alosine planktivores, have declined within their natal freshwater ecosystems (Limburg and Waldman 2009). It is possible that long term declines in anadromous planktivores may indirectly suppress phytoplankton biomass, a phenomenon observed in lakes (Post et al. 2008). This indirect effect of zooplanktivorous fish on phytoplankton might obscure interpretation of phytoplankton trends that would otherwise be attributed to restrictions on nutrient inputs. Furthermore, restoration of anadromous fish populations may restore a trophic cascade that indirectly enhances phytoplankton biomass.

The Chowan River in North Carolina provides an example of an ecosystem simultaneously affected by eutrophication, nutrient regulation, and anadromous fish decline. Algal blooms, particularly of blue-green algae, plagued the Chowan River beginning in the 1970s, prompting environmental managers and scientists to investigate the cause of eutrophication in this system through a series of studies in the 1970s and 1980s. The first of these concluded that temperature and light were the dominant limiting factors on phytoplankton growth, except during summer when concentrations of inorganic nitrogen less than 50 µg N/L could limit growth (Stanley and Hobbie 1981). Subsequent studies also concluded that temperature, light, and residence time were the primary controls on phytoplankton growth, but that inorganic phosphorus potentially limits growth during summer periods when the N:P was greater than 20:1 and phosphorus concentration was less than 3 µg/L (Witherspoon et al. 1979, Kuenzler et al. 1982). Since nitrogen and phosphorus were both found to exceed the concentrations limiting phytoplankton growth, reductions in phosphate, ammonia, and nitrate of 28%, 27%, and 19%, respectively, were recommended to constrain phytoplankton growth (Witherspoon and Pearce 1982). In reaction to these studies, North Carolina designated the Chowan River basin as Nutrient Sensitive, mandating strict controls on nutrient inputs to the river. By 1990, nitrogen and phosphorus from point and non-point sources in the watershed were reduced 20% and 29%, and further reductions are currently being targeted by the North Carolina Division of Water Quality (NCDWQ; NCDWQ 2006).

Throughout this period of water quality management, anadromous fish populations plummeted. River herring (including blueback herring *Alosa aestivalis* and alewife *Alosa pseudoharengus*) declined to 1% of their historic abundance throughout the western Atlantic (Limburg and Waldman 2009). The Albemarle Sound and Chowan River once held the largest river herring fishery in North Carolina, but landings decreased precipitously at the end of the 20th century (Hightower et al. 1996). Despite harvest and gear restrictions at the turn of the century, the stock continued to decline, and in September 2007 the North Carolina Division of Marine Fisheries (NCDMF) declared a state-wide moratorium on river herring harvest (NCDMF 2007). Addition-
ally, the Atlantic States Marine Fisheries Commission (ASMFC) has instituted strict recovery and management requirements from Maine through Florida (ASMFC 2009).

River herring can have a dramatic effect on zooplankton abundance and community composition in lakes (Brooks and Dodson 1965, Hutchinson 1971, Palkovacs and Post 2008), rivers (Ning et al. 2010), and estuaries (Sellner et al. 1993). Despite the long-term changes in river herring in the Chowan River, their impact on zooplankton abundance in this ecosystem has not been examined. The only study of zooplankton abundance before the collapse of the river herring was conducted in 1982 and 1983 (Mozley 1984, Winslow et al. 1985), showing relatively low abundances in the tidal freshwater and oligohaline portion of the estuary during this time.

The goal of this study was to examine the relative importance of nutrients versus zooplankton grazing in the Chowan River by synthesizing 30 years of environmental data combined with our own two-year study of water quality and zooplankton. We take an inductive approach that relies on data synthesis, modeling, and comparison of long-term datasets. Our study addresses two questions: First, how has the change in anthropogenic nutrient inputs over the past 30 years affected phytoplankton growth in the Chowan River? We use an empirical model of phytoplankton growth parameterized with long-term data on nutrient concentrations and other environmental and physiological variables to answer this question. Second, how important is zooplankton grazing to phytoplankton biomass, and has it changed over the period that river herring have declined? We answer this question by comparing the recent zooplankton community with historical zooplankton data. Finally, we compare these long term trends with fish abundance data to explore the possibility that a trophic cascade may influence phytoplankton abundance in this river system.

**Materials and Methods**

**Study site**

The Chowan River drains a 12,600 km² watershed into the northwestern end of Albemarle Sound, North Carolina, USA. Our study sites encompassed the tidal freshwater portion of the Chowan River Estuary, with two sites on the mainstem Chowan River (36.36289° N, 76.78323° W; 36.277621° N, 76.695617° W) and two sites on each of two smaller tributaries of the Chowan, Bennetts Creek (36.35658° N, 76.721239° W; 36.318082° N, 76.705439° W) and Wiccacon River (36.313828° N, 76.792367° W; 36.349258° N, 76.764518° W) (Fig. 1). Bennetts Creek and Wiccacon River drain watersheds of approximately 200 km² and 666 km², respectively, and enter the Chowan River in between the two study sites on the mainstem Chowan River. The two sampling sites on the Chowan River and the two downstream locations on the tributaries were sampled monthly from April 2008 to May 2010 by boat, except that sampling frequency was every two weeks between March 2009 and May 2009. The upstream sites on the tributaries were sampled every two weeks from March 2009 to May 2009 and then monthly through May 2010. Upstream sites were accessed by a public dock on the Wiccacon and by canoe on Bennetts Creek. All sites were affected by tidal influence (a combination of lunar and wind influences; see Jackson 1968 for further details) and bi-directional flow was observed at all sites.

**Contemporary water quality and zooplankton**

Temperature, salinity, specific conductivity, and turbidity were measured at the surface and bottom of each site using a YSI 6800 multiparameter water quality sonde and 650 display (Yellow Springs Instruments, Yellow Springs, OH). Water transparency was estimated at each site with a Secchi Disk, and water column depth was measured with a SM-5 Depthmate portable sounder (Speedtech Instruments, Great Falls, VA). Underwater irradiance and light attenuation were measured with a 4pi quantum sensor (LI-COR Biosciences, Lincoln, NE).

Chlorophyll a concentration was measured as a proxy for phytoplankton biomass. Surface grab samples were collected in the field and stored on ice until analysis (<6 hr). Fifty milliliters of river water were then filtered through a Whatman GF/F glass fiber filter (0.7 µm pore size), and chlorophyll a in the retained phytoplankton cells was extracted in a 90% acetone solution for approximately 12 hours. Extracts were analyzed on a Turner Trilogy fluorometer (fitted with the
non-acidification chlorophyll module) (Turner Designs, Sunnyvale, CA).

Dissolved inorganic and organic nitrogen as well as dissolved inorganic phosphorus were measured on water samples filtered through Whatman GF/F filters (0.7 µm pore size). Samples were kept frozen until analyzed on a Lachat Quikchem 8000 autoanalyzer (Lachat Instruments, Milwaukee, WI).

Zooplankton were collected at 0.5 m from the water surface and 0.5 m from the river bottom using a hand operated bilge pump. Depending on the density of the zooplankton, 20–40 L of water was pumped through a 63-µm mesh plankton net. All zooplankton samples were immediately preserved in a 5% v/v buffered formalin. Duplicate samples were collected at both the surface and bottom of the water column. All collections were performed during the day between 1000 h and 1500 h.

In the laboratory, zooplankton were counted at 10–40× under a dissecting microscope. A 10-mL subsample of each replicate was placed in a Ward counting wheel and two replicate counts were made on each sample. Sample and count replicates were combined to calculate means and standard deviations. Rotifers and cladocerans were generally identified to genus while copepods were typically identified to family.

**Phytoplankton growth model**

Our objective in modeling phytoplankton growth was two-fold. First, the model allowed us to examine the effect of long-term changes in nutrient concentrations within the context of the irradiance and temperature regimes of the...
Chowan River. The model is intended as an empirical test of the relative importance of multi-decadal changes in nutrients and irradiance to a generalized phytoplankton community. Second, phytoplankton growth rate (d⁻¹) provides a common metric with which to evaluate the relative importance of zooplankton grazing (d⁻¹). The model was applied to both the 2008–2010 data we collected in the Chowan River, Bennetts Creek, and Wiccacon River as well as the historical data from 1980–2010 available for the Chowan River at Harrellsville (described below). Phytoplankton growth rate (G, d⁻¹) was predicted using the model of Geider et al. (1997), which is similar to other empirical models (e.g., Muyrla et al. 2005)

\[
G = D \frac{P^B}{P^m} [1 - \exp \left(-\frac{I/H}{P^m} \right)] \times \text{Chl:C}
\]

(1)

where D is daylength (hr), \(P^B\) is the biomass-specific photosynthetic rate (mg C·mg chl⁻¹·hr⁻¹), \(P^m\) is the maximum photosynthetic rate (mg C·mg chl⁻¹·hr⁻¹), I is the average water column irradiance (μmol photons PAR·m⁻²·hr⁻¹), \(\alpha\) is the initial slope of the photosynthesis-irradiance curve (mg C·mg chl⁻¹·m⁻²·μmol⁻¹ photons), and Chl:C is the chlorophyll a to carbon ratio. Daylength was obtained from the US Naval Oceanography Portal (www.usno.navy.mil/). Average daily irradiance was obtained from the NC Climate Office from the LEWS (36.1324° N, 77.17552° W) and PLYM (35.84887° N, 76.65058° W) sites near the Chowan River. \(P^m\) and \(\alpha\) were parameterized using data from assays conducted in the tidal freshwater Potomac River (Jones 1998). A mean and standard error of \(P^m\) and \(\alpha\) were reported for each month of the year in the Potomac River, and these monthly values and errors were matched with the corresponding month of measurement in the Chowan River. The biomass-specific photosynthetic rate \(P^B\) was calculated using the formula

\[
P^B = \frac{P^m \times n}{n + K_n}
\]

(2)

where \(P^m\) was the value reported in the Potomac River for the corresponding month of sampling, \(n\) is the concentration of limiting nutrient, and \(K_n\) is the half-saturation constant for the phytoplankton. We assumed that nitrogen was the limiting nutrient and used the NH₄ concentration (or the NO₃ concentration if NH₄ was <10 μg NH₄-N/L), and \(K_n\) was assumed to be 20 μg N/L (Stanley and Hobbie 1981). Phosphate was found to be limiting around 50 μg P/L, with a \(K_n\) of 5 μg P/L (Witherspoon et al. 1979, Balducci 1982, Stone 1982). Primary limitation by phosphorus was assumed when the N:P molar ratio was greater than 20:1 and the phosphate concentration was less than 5 μg P/L (Kuenzler et al. 1982).

The Chl:C was calculated using the regression formula of Cloern et al. (1995):

\[
\text{Chl:C} = 0.003 + 0.0154[\exp(0.05T)] \\
\times \left[ \exp \left( -0.059 \left( \frac{L_t}{kH} \right) \right) \times \left( 1 - \exp(-kH) \right) \right] \\
\times \frac{n}{K_n + n}
\]

(3)

where \(T\) is average water column temperature, \(L_t\) is the total daylight PAR averaged between the LEWS and PLYM sites (moles PAR·m⁻²·day⁻¹), \(k\) is the light attenuation coefficient (m⁻¹), \(H\) is water depth. Average water column irradiance was modeled as:

\[
l = \frac{L \times \left( 1 - \exp(-k \times H) \right)}{k \times H}
\]

(4)

where \(L\) is the observed average daylight PAR from the LEWS and PLYM sites (μmol PAR·m⁻²·s⁻¹). Historical data (see Historical data below) from the NCDWQ did not report irradiance or light attenuation, so these data had to be estimated based on Secchi depth. We developed linear regression models between Secchi depth and \(k\) from our data at the Chowan River upstream and downstream sites and used this model to predict \(k\) in historical data.

Uncertainty in several model parameters was incorporated in our analysis. First, the standard error of \(P^m\) and \(\alpha\) from Jones’ (1998) tidal freshwater Potomac River phytoplankton community study were used to adjust these parameters between ±1 SE of the monthly estimate. Second, the 95% confidence interval in regression of Secchi depth and light attenuation was incorporated into the model. An upper limit on uncertainty of phytoplankton growth rate was estimated using the \(P^m\) minus 1 SE, \(\alpha\) plus 1 SE, and \(k\) minus the 95% confidence interval; a lower limit on uncertainty of phytoplankton growth
rate was estimated using the $P^B_m$ plus 1 SE, $\alpha$ minus 1 SE, and $k$ plus the 95% confidence interval.

The phytoplankton growth model we used requires several assumptions. First, it assumed a single Chl:C ratio for the phytoplankton community, which ranges widely over time within individual phytoplankton cells and populations (discussed by Cloern et al. 1995, Geider et al. 1997). However, for the modeling scenario in the current study, the empirical relationship we use to define Chl:C may be an adequate representation of the community (Flynn 2003). Second, the model assumes a single $P^B_m$ and $\alpha$ representative of the entire phytoplankton community despite the fact that these parameters vary substantially between species and within species populations at different temperatures and nutrient concentrations (Coles and Jones 2000). To represent this heterogeneity within the phytoplankton community, we incorporated the seasonal range of these parameters to represent uncertainty in the model predictions.

**Zooplankton clearance model**

We calculated rates of water clearance by zooplankton to estimate their potential effect on the phytoplankton concentration. While water clearance rates (water volume-individual$^{-1}$-time$^{-1}$) differ from grazing rates (cells-individual$^{-1}$-time$^{-1}$, or mass-individual$^{-1}$-time$^{-1}$), clearance rates provide a relative measure of the potential impact of zooplankton grazing on phytoplankton communities. While clearance rate is not a measure of consumption, we assume that it represents the maximum effect zooplankton could have on phytoplankton in a volume of water if both feeding efficiency and selection for phytoplankton cells were optimized. Expression of the zooplankton community’s potential grazing impact as the product of clearance rate and abundance yields a clearance rate with a measurement unit of d$^{-1}$, permitting comparison with the potential growth of phytoplankton (d$^{-1}$) described previously. In other words, the fraction of a volume of water cleared by zooplankton grazing in a day was subtracted from the fractional increase in the phytoplankton concentration in that water volume over a day, yielding the potential net daily rate of increase in phytoplankton concentration.

Rates of zooplankton clearance were compiled from the literature (Appendix: Table A1). Various literature search engines were used to find studies that examined zooplankton clearance rates for the species, genus, or family of animals found in the current study. The mean (and maximum and minimum when available) clearance rates (water volume-individual$^{-1}$-day$^{-1}$) were recorded for each group if provided in a study. A maximum and minimum zooplankton clearance (d$^{-1}$) was calculated for each species, genus, or family as abundance (number of individuals/L) multiplied by clearance rate (µL water-individual$^{-1}$-d$^{-1}$), and summed to calculate a community-wide clearance (d$^{-1}$). This method of estimating zooplankton grazing has been performed elsewhere (e.g., Sellner et al. 1993). Our predictions of zooplankton clearance assume that grazing occurs on a 24-hr basis irrespective of light levels (Janssen 1978, Griffin and Rippingale 2001).

**Historical data**

The NCDWQ has a long-term water quality sampling site (D8356200) located half way between our upstream and downstream sites on the Chowan (Fig. 1). This site has the longest, most complete record of chlorophyll $a$ and nutrients of the neighboring NCDWQ monitoring sites on the Chowan River. Temperature, Secchi depth, nitrate + nitrite, ammonium, total phosphorus, and chlorophyll data for this site were downloaded from the EPA STORET database for the period January 1981 through November 2010. These parameters were input into the phytoplankton growth model described above.

Long term trends in chlorophyll $a$, ammonium, nitrate, and phosphate were analyzed using seasonal trend decomposition using locally weighted regression (Cleveland et al. 1990). This procedure is commonly used to examine seasonal and long-term trends in water quality data (e.g., Qian et al. 2000). In brief, this statistical procedure extracts the intra-annual and interannual trends from the time series of a parameter. The trends are estimated using an iterative process that minimizes the residual variation explained in the model. A locally weighted regression is performed on the extracted trends in order to smooth these time series. Missing data
in the original time series were estimated using the median polish technique (Tukey 1977; applications to time series data are discussed in Qian et al. 2000). Both seasonal trend decomposition using locally weighted regression and median polish were performed using the software package R (R Development Core Team 2011).

Zooplankton abundance and community composition were studied in the Chowan River from June 1982 through November 1983 (Mozley 1984, Winslow et al. 1985). This survey is the only one that we are aware of in the oligohaline and freshwater portion of the river prior to our own. The three farthest upstream sites reported by Mozley spanned a cross-section of the Chowan River approximately 3.5 km downstream from our Chowan downstream site (Fig. 1). A Schindler-Patalas trap with 70-μm mesh net was used in this previous study, with samples collected from the surface and 5 m at the mid-channel location, and at the surface at the two near-shore locations. Zooplankton counts from this study were summarized into cladoceran, copepods, ostracods, and rotifers, and the mean of all sites and depths was calculated for each sampling date (unpublished count data were obtained from Mozley, personal communication). Rotifers were not enumerated by Mozley in 1982 counts.

Long term changes in planktivorous fish abundance, including river herring, were examined in data collected by the NCDMF. A fisheries-independent sampling program is run by NCDMF that includes both shoreline seines and midwater trawls; the program is primary used by NCDMF to monitor anadromous fish, although all organisms caught are enumerated and synthesized in the current study. We examined data at four sites that bracket the region of the Chowan River examined in the current study (Fig. 1), including the upper Chowan River at Tuscarora Beach (NCDMF site 48S), the mouth of Bennetts Creek (NCDMF site 59), the Chowan River at Arrowhead Beach (NCDMF sites 56 and 56S). Data were obtained by request from the NCDMF office in Elizabeth City, NC (C. Godwin, personal communication). NCDMF sampling was performed monthly from June through October, except at the upstream site where year-round sampling was performed in 1972. Fish within the NCDMF database were classified as zooplanktivorous based on diet data reported in FishBase.org (www.fishbase.org); a list of the species included in this group is provided in Appendix: Table A2. The annual mean of zooplanktivorous fish and river herring where calculated for each of the four sites to allow examination of trends in relative fish abundance over the past three decades.

**RESULTS**

**Contemporary water quality**

Mean water temperature ranged from 17.3°C (Wiccacon Upstream) to 18.1°C (Bennetts Downstream) (Table 1). Wiccacon Upstream and Bennetts Upstream remained fresh throughout the sampling period, but all other sites experienced periodic intrusions of brackish water, most notably Chowan Upstream where a salt wedge developed that increased salinity to 7 psu. Mean turbidity ranged from 8 to 15 nephelometric turbidity units (NTU), with periodic values that exceeded the North Carolina state standard of 25 NTU for tidal waters at all sites except Bennetts Upstream. Mean $k$ ranged from 2.6 m$^{-1}$ to 4.9 m$^{-1}$, and Secchi depths ranging from 0.6 to 1.1 m. Concentrations of nitrogen and phosphorus were representative of a moderately productive system throughout most of the year (Wetzel 2001) (Table 2). Chlorophyll $a$ concentrations ranged from 0.25–55 μg/L with the highest mean concentration at Wiccacon downstream and lowest mean concentration at the Chowan downstream (Table 3).

**Contemporary zooplankton community composition**

Small-bodied rotifers were generally the dominant proportion of the community at all sites, particularly in the surface waters during the Spring and Summer months (Table 3; Appendix: Fig. A1). Over the course of the two-year study, rotifers represented 51% ± 30% and 45% ± 29% of total zooplankton in the surface waters of the main stem of the Chowan River downstream and upstream, respectively. Within the tributaries, rotifer community composition was often higher at the mouth than upstream. For example, rotifers comprised 63% ± 25% of the zooplankton community in the surface waters at Bennetts Creek downstream, yet only 31% ± 19% of the community at the upstream site. Rotifers comprised 49% ± 26% of the zooplankton commu-
nity at the Wiccacon River downstream and 32% ± 21% upstream. At all sites, *Keratella* spp., *Polyarthra* sp., and *Ploesoma* sp. were most frequently observed throughout the year. *Mono-styla* sp., *Notholca* sp., and *Trichocerca* sp. were observed primarily in the fall and winter months. *Asplanchna* sp. were most abundant in the spring. Other species were rarely seen at any sites throughout the year. Copepods were the second most abundant taxonomic group (Table 3; Appendix: Fig. A2). In the surface waters of the main stem of the

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Table 1. Physical properties of the Chowan River, Wiccacon River, and Bennetts Creek; data are shown as the mean, range, and sample size (n). Data collected from April 2008 through May 2010.

| Metric         | Temperature (ºC) | Salinity (psu) | Turbidity (NTU) | Light attenuation coefficient (m⁻¹) | Secchi depth (m) |
|----------------|------------------|----------------|-----------------|------------------------------------|-----------------|
| Chowan upstream |                  |                |                 |                                    |                 |
| Mean           | 17.9             | 0.2            | 9.2             | 3                                  | 1.0             |
| Range          | 4.2–30.1         | 0.0–7.0        | 0–35            | 1.7–4.7                            | 0.4–2.1         |
| n              | 61               | 61             | 44              | 22                                 | 27              |
| Chowan downstream |                |                |                 |                                    |                 |
| Mean           | 17.7             | 0.2            | 10.6            | 2.6                                | 1.1             |
| Range          | 4.4–30.8         | 0.0–2.5        | 0–100           | 1.5–3.9                            | 0.5–2.5         |
| n              | 61               | 61             | 44              | 22                                 | 26              |
| Wiccacon upstream |                |                |                 |                                    |                 |
| Mean           | 17.3             | 0.0            | 15              | 4.0                                | 0.7             |
| Range          | 6.1–27.9         | 0.0–0.1        | 2–55            | 1.9–6.3                            | 0.3–1.7         |
| n              | 39               | 39             | 39              | 19                                 | 19              |
| Wiccacon downstream |            |                |                 |                                    |                 |
| Mean           | 18.0             | 0.2            | 14              | 3.9                                | 0.8             |
| Range          | 4.4–31.4         | 0.0–4.7        | 0–62            | 2.1–6.2                            | 0.2–2.0         |
| n              | 61               | 61             | 44              | 22                                 | 27              |
| Bennetts upstream |                |                |                 |                                    |                 |
| Mean           | 17.8             | 0.0            | 8               | 4.9                                | 0.6             |
| Range          | 6.4–28.4         | 0.0–0.1        | 0–22            | 2.0–7.2                            | 0.4–1.3         |
| n              | 37               | 37             | 37              | 18                                 | 18              |
| Bennetts downstream |            |                |                 |                                    |                 |
| Mean           | 18.1             | 0.2            | 8               | 3.7                                | 0.8             |
| Range          | 4.5–31.2         | 0.0–2.1        | 0–46            | 2.2–7.1                            | 0.4–2.2         |
| n              | 61               | 61             | 44              | 22                                 | 26              |

Table 2. Chemical properties of the Chowan River, Wiccacon River, and Bennetts Creek; values are the mean, range, and sample size (n). Data collected from April 2008 through May 2010.

| Metric         | NH₄⁺ (µg N/L) | NO₃⁻ + NO₂ (µg N/L) | PO₄³⁻ (µg P/L) |
|----------------|---------------|---------------------|----------------|
| Chowan upstream |               |                     |                |
| Mean           | 60            | 146                 | 24             |
| Range          | 11–211        | 16–280              | 7–82           |
| n              | 22            | 22                  | 22             |
| Chowan downstream |             |                     |                |
| Mean           | 55            | 159                 | 24             |
| Range          | 9–140         | 5–419               | 10–66          |
| n              | 22            | 22                  | 22             |
| Wiccacon upstream |            |                     |                |
| Mean           | 64            | 105                 | 23             |
| Range          | 7–201         | 12–406              | 9–41           |
| n              | 20            | 20                  | 20             |
| Wiccacon downstream |         |                     |                |
| Mean           | 43            | 139                 | 22             |
| Range          | 3–106         | 4–624               | 10–41          |
| n              | 22            | 22                  | 22             |
| Bennetts upstream |             |                     |                |
| Mean           | 75            | 93                  | 25             |
| Range          | 6–256         | 4–623               | 11–43          |
| n              | 19            | 19                  | 19             |
| Bennetts downstream |           |                     |                |
| Mean           | 39            | 106                 | 18             |
| Range          | 4–119         | 1–629               | 8–38           |
| n              | 22            | 22                  | 22             |

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www.esajournals.org 8 July 2014 * Volume 5(7) * Article 89
Chowan River, copepods represented 44% ± 28% of the total zooplankton downstream and 47% ± 27% upstream. Unlike the rotifers, copepods generally comprised a greater percentage of the total zooplankton community upstream in the tributaries compared to downstream. Copepods represented 31% ± 21% and 41% ± 23% at Bennetts Creek downstream and the Wiccacon River downstream, respectively, compared to 40% ± 19% Bennetts Creek upstream and 50% ± 25% at Wiccacon River upstream. Copepods were overwhelmingly comprised by naupliar stages of cyclopoids and calanoids (~85–97% of total copepods). The nauplii of these two groups could not be reliably distinguished. However, adult cyclopoid species were typically observed in higher frequency than calanoid species at all sites. *Cyclops vernalis*, *Orthocyclops modestus* and *Paracyclops fimbriatuspoppei* were the dominant cyclopoid species while *Eurytemora affinis* was the dominant calanoid species. For both cyclopoids and calanoids, females were more abundant than males and were typically observed without egg sacs. Harapticoid species were rare at all sites throughout the study.

Cladocerans were the least dominant taxonomic group at all sites (Table 3; Appendix: Fig. A3). In the surface waters of the main stem Chowan River, cladocerans represented only 5% ± 9% of the total zooplankton downstream and 7% ± 11% upstream. At times, cladocerans were more prominent in the tributaries than the main stem. Within Bennetts Creek, cladocerans represented 5% ± 7% of the zooplankton community downstream but 26% ± 22% upstream. Cladocerans represented 9% ± 12% of the zooplankton community at Wiccacon River downstream and 15% ± 16% upstream. Small-bodied *Bosmina longirostris* and *Chydorus* sp. were the dominant species at all sites throughout the year followed by larger-bodied *Diaphanosoma brachyrum*. Large-bodied daphnids were observed in modest numbers in April, May, and December of all years. All other cladoceran species were rare.

**Historical nutrient trends**

The seasonal trend decomposition using locally weighted regression model indicated that chlorophyll *a* in the Chowan River above Holiday Island decreased between 1980 and 1990, but has remained similar since then (Fig. 2). A four year gap in this data record had to be filled using the median polish technique. Ammonium and nitrate+nitrite generally declined...
over this period from around 400 μg/L in the early 1980s to 200 μg/L in the late 2000s. Total phosphorus has been relatively constant in the Chowan River, with the exception of a subtle decline during the late 1990s. The predicted growth rate of phytoplankton, based on the model presented in Eq. 4, has been relatively constant throughout the 1980 through 2010 period. As with all of the parameters measured, there is substantial seasonal variation in the growth rate. However, the long-term decline in chlorophyll a and nitrogen are not reflected in the predicted growth rate during this period.

**Phytoplankton growth model**

At the sites monitored in the current study, mean phytoplankton growth ranged from <0.05 to <0.25 d⁻¹ (Figs. 3–5). Maximum growth rates

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**Fig. 2.** Observed and modeled chlorophyll a (A), observed and modeled NH₄⁺ (B), observed and modeled NO₃⁻ + NO₂⁻ (C), observed and modeled TP (D), and predicted phytoplankton growth and modeled trend (E). Red portions of each time series were predicted using the median polish technique. Orange background in panel E represents the uncertainty associated with the model parameters α, P₄⁰, and the Secchi versus light attenuation regression. The secondary y axis in each panel has a smaller range than the primary y axis to allow a more detailed display of the trend.
occurred in the tributary sites Wiccacon upstream (0.21 d⁻¹), Bennetts upstream (0.26 d⁻¹), and Bennetts Downstream (0.21 d⁻¹). Growth rates at Wiccacon Downstream were similar to the Chowan River sites, likely due to the greater depth of this site and proportionately lower average water column irradiance than the other tributary sites. Uncertainty in the predicted growth rates due to photosynthetic parameters $P_m^b$ and $\alpha$ was low relative to the seasonal changes in temperature and irradiance.

Historically, phytoplankton growth at the Chowan River downstream site was predicted to be generally less than 0.1 d⁻¹ with higher values during summer and lowest values during winter. As with contemporary phytoplankton growth rates, uncertainty in model predictions due to assumed photosynthetic parameters ($P_m^b$ and $\alpha$) and predicted light attenuation were small relative to the seasonal amplitude of changes due
Potential net phytoplankton growth was calculated using the minimum potential clearance rate. Given the uncertainty in both potential grazing rate and phytoplankton growth rate, calculated net growth is a simple estimate of whether the balance between growth and grazing is positive or negative. Generally, all sites except Wiccacon Downstream exhibited positive rates of phytoplankton growth during the late winter and spring, but negative rates during summer and fall.

Zooplankton clearance
During 2008–2010, zooplankton clearance was generally higher in the summer than winter at all sites (Figs. 3–5). In the Chowan River, minimum clearance rates ranged from <0.01 to >0.3, with maximum rates occurring at the downstream site. In Wiccacon River, clearance rates were generally higher at the downstream site, where minimum clearance rates exceeded 0.5 day\(^{-1}\). At Bennetts Creek, clearance rates were similar in range between the upstream and downstream sites, with minimum clearance rates exceeding 0.6 at both sites. Clearance rates calculated from Winslow et al. (1985) for the Chowan River downstream of Holiday Island were significantly less than the rates calculated for 2008–2010 in our study. Even maximum potential clearance rates during the early period were low relative to the 2008–2010 period.

Planktivorous fish abundance
Shoreline seine surveys of planktivorous fish at the upstream site show that the community was
dominated by river herring in the 1970s and early 1980s (Fig. 6). A decrease in mean catch occurred after 1983 and abundance remained low until 2005 when a high abundance of planktivorous fish (but not river herring) was found (Figs. 6 and 7). Trawl surveys at this site also show a planktivore community dominated by river herring in the 1970s and early 1980s. A dramatic decrease in all planktivorous fish occurred after 1980 in the trawl data, but no data were available to examine this trend from 1986 to 2003. Planktivorous fish abundance in trawls returned to pre-1980 levels by 2005, although river herring did not account for as great a percentage as during the pre-1980 period.

Seine data at the downstream site was available after 1984. River herring showed a decline in contribution to planktivorous fish community between the mid-1980s and 1990. There was no apparent trend in planktivore abundance over the period at this site in the seine data. However, trawl data show a dramatic decrease in both river herring and the overall planktivore community after 1980. Both seine and trawl data at the downstream site show a clear decrease in the contribution of river herring to the overall planktivore community throughout the 1980s.

Discussion

Nutrients and phytoplankton growth

The first question we sought to answer was how long-term changes in nutrient concentrations influenced phytoplankton growth in the Chowan River. Nitrogen (both NH$_4$ and NO$_3$) declined in the Chowan River between the mid-1980s through 2010, while phosphorus tempo-
rarily declined during the late 1990s. These declines in nutrients occurred more than five years after the decline in chlorophyll $a$ began, suggesting that the presumed reduction in phytoplankton biomass (indicated by the chlorophyll $a$ trend) was out of phase with the nutrient reductions. Furthermore, phytoplankton growth, predicted as a function of temperature, irradiance, and nitrogen concentration, remained constant throughout this 30 year period, again indicating that the reduction in nitrogen concentration in the Chowan River was not severe enough to over-ride the strong limitations of temperature and irradiance on growth rate predicted in previous studies of the Chowan River (Witherspoon et al. 1979, Stanley and Hobbie 1981, Sauer and Kuenzler 1981, Kuenzler et al. 1982). These two lines of evidence, first the decline in chlorophyll $a$ that preceded the decline in nutrients, and second the constant growth rate over the 30 year period, suggest that nutrient availability was not the primary cause of the decline in algal biomass in the oligohaline Chowan River.

If not due to a reduction in nutrient concentrations, what explains the reduction in chlorophyll $a$ during the early 1980s? One explanation for the decline in phytoplankton biomass in the Chowan River may be a shift in phytoplankton community away from highly productive, bloom-forming species with a high concentration of chlorophyll $a$ per unit biomass. During the 1970s and 1980s blue-green algal blooms were common during the summer months, providing

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**Fig. 6.** Mean annual zooplanktivorous fish and river herring caught by NCDMF anadromous fish surveys using beach seines at Tuscarora Beach on the Chowan River (A), mid-water trawl in Bennetts Creek near the confluence with the Chowan River (B), and by beach seine (C) and trawl (D) near Arrowhead Beach on the Chowan River.
the initial impetus for examining phytoplankton dynamics and water quality in the Chowan River (reviewed by Paerl 1982). While blue-green algal blooms still occur on the Chowan River (S. H. Ensign, personal observation of a surface blue-green bloom near the Chowan Downstream site in September 2009), their frequency and intensity have abated (NCDWQ 2006). It is possible that changes in nutrient species (e.g., NH₄ versus NO₃, sensu Glibert 2010) or nitrogen to phosphorus ratios (e.g., Pielhier et al. 2004) led to shifts of phytoplankton species assemblages. Unfortunately, there are no long-term records of phytoplankton community structure in the Chowan River with which to assess its role on chlorophyll a trends.

A second explanation for the reduction in chlorophyll a in the Chowan River is an increase in water column filtration by invertebrates. The invasive bivalve *Corbicula fluminea* is found throughout the tidal freshwater portion of the Chowan River, and occurs at densities high enough to filter the water column up to once per day during the summer (Lauritsen 1986). *Corbicula*’s high filtration rates have presumably influenced phytoplankton biomass in the Chowan River based on feeding trials by Lauritsen and Mozley (1983), and similar filtration studies in other estuaries indicate that *Corbicula* and other filter feeders can dramatically reduce phytoplankton biomass (e.g., *Corbicula* in the Potomac River, Cohen et al. 1984; *Dreissena polymorpha* in the Hudson River, Strayer et al. 2008). The *Corbicula* population throughout the Chowan River system was well established by 1980 (Lauritsen and Mozley 1983), prior to the beginning of the historical water quality or zooplankton records analyzed in the current study. However, records of *Corbicula* abundance over time are not available from the Chowan River to examine how they relate to long-term patterns in phytoplankton biomass. Zooplankton, the focus of the current study, may also explain changes in phytoplankton biomass in the Chowan River that cannot be attributed to changes in nutrient concentration.

**Zooplankton abundance and clearance**

The second question we addressed was whether zooplankton would be expected to have a large influence on phytoplankton biomass in the Chowan River system, and how this may have changed over time. Zooplankton were relatively abundant in the Chowan River system during the late 2000s, particularly the medium and smaller sized cladocerans and rotifers. The community composition in the mainstem of the Chowan River is similar to other large tidal rivers such as the Potomac (Buchanan and Schloss 1983) where few large bodied cladocerans (e.g., *Daphnia* spp.) are found. The zooplankton community in the oligohaline portion of the Chowan River differs from the mesohaline portion of the Chowan, Albemarle Sound, and other large estuaries (e.g., Chesapeake Bay) where calanoid copepods become more dominant (Kimmel and Roman 2004, Binion et al. 2012). Relative to the large estuarine portion of the Chowan, there are few published studies of zooplankton in small, blackwater coastal plain streams such as the Bennetts Creek and Wiccacon River (see Herlong and Mallin 1985 for one example of zooplankton in blackwater streams).

Summer zooplankton communities at all sites resulted in the prediction that grazing can have a significant impact on phytoplankton, with clearance rates exceeding 0.5 d⁻¹. Clearance was predicted to be particularly heavy in Wiccacon River and Bennetts Creek, where residence times may have been longer allowing for greater zooplankton population growth. During the summer at all sites net phytoplankton growth was predicted to be negative, indicating that these areas were sinks for phytoplankton growth. While our method of predicting zooplankton clearance incorporated a wide range in individual clearance rates in order to represent the high degree of uncertainty, our minimum clearance estimates are comparable to grazing rates measured in the oligohaline portion of other estuaries. In the oligohaline reach of the Schelde estuary, for example, rotifers exhibited community grazing rates of 41–183% d⁻¹, while mesozooplankton had no discernable impact on phytoplankton (Lionard et al. 2005). In the upper Potomac River, Buchanan and Schloss estimated grazing would remove 1–9% of phytoplankton d⁻¹ (1983), while Sellner et al. measured clearance of 49% d⁻¹ for non-cyanobacterial algae (1993). In contrast to these relatively high clearance rates in the upper portion of estuaries, lower clearance rates in the more seaward
portion of estuaries (e.g., Lonsdale et al. 1996) due to lower resource availability and advection out of the estuary (Pace et al. 1992). Even when conservative (minimum) clearance estimates are applied to the Chowan River community, zooplankton appear to play a prominent role in cropping phytoplankton abundance in the Chowan River system.

Zooplankton abundance and clearance in the mainstem Chowan River were far lower during the early 1980s than during the late 2000s. Furthermore, while surveys of the downstream portion of Bennetts Creek in 1982 found virtually no zooplankton (Mozley 1984, Winslow et al. 1985), we found this site occasionally had the highest zooplankton abundances of all the sites we studied. Zooplankton abundances in the early 1980s yielded low clearance rates in the lower Chowan River site, with all but one of the estimates being less than 0.1 d\(^{-1}\). Even if the maximum estimates of individual clearance rates are used, zooplankton are expected to have had little effect on phytoplankton during the early 1980s. One potential explanation for the relatively low abundances of zooplankton in the early 1980s could be that the blue-green algal blooms prevalent during that time may have prohibited zooplankton grazing and growth through toxicity or mechanical means, but this is not supported by experimental data (Fulton and Paerl 1987) or by corresponding zooplankton and blue-green abundances in monitoring data of the Chowan River (Mozley 1984). Alternatively, zooplankton abundance may have been suppressed by planktivorous fish, particularly adult and juvenile river herring, which feed heavily on zooplankton (Brooks and Dodson 1965, Hutchinson 1971, Burbidge 1974, Vigerstad and Cobb 1978, Doermuth and Reed 1980, Guest and Drenner 1991, Post et al. 2008).

**Indirect effects of planktivorous fish on phytoplankton biomass**

The planktivorous fish community began to decline in the Chowan River in the early to mid-1980s, and relative abundance in the late 2000s was generally lower than in the historical data (Fig. 7). Of the three sites (upper, mid, and lower Chowan relative to the current study) and two gear types ( seine and trawl) summarized in our data, only beach seine data from the lower site do not suggest a long-term decline in planktivores. In contrast, river herring have clearly declined at all sites regardless of gear type, as expected from broader population trends of river herring in the Chowan River and Albemarle Sound (NCDMF 2007), and comprise a smaller fraction of the planktivorous community today than they did in the 1970s and 1980s. These adult and juvenile fish survey data were collected during the summer months of June through October and therefore span the period of the year when both zooplankton abundances and clearance rates are high and juvenile river herring are present. These changes in planktivore abundance (and presumed reduction in consumption of zooplankton) thus correspond with the period of the year when zooplankton exert the most impact on phytoplankton.

River herring can have a positive, indirect affect on phytoplankton, and this may help explain the reduction in phytoplankton biomass in the Chowan River. In lakes with landlocked populations of river herring phytoplankton biomass is higher than in lakes without resident populations of river herring due to this indirect, consumptive effect (Post et al. 2008). However, studies of lakes containing other species of planktivorous fish have not found as strong of an effect (Post and McQueen 1987), and this indirect consumptive effect does not occur during cyanobacterial blooms (Rondel et al. 2008). River herring are only one example of a secondary consumer that can initiate a trophic cascade in pelagic systems, and other consumers may dominate in lakes (Carpenter et al. 2010) and coastal oceans (Essington 2010, Estes et al. 2010).

A trophic cascade may have occurred in the Chowan River up until the mid 1980s, after which the decline in river herring allowed zooplankton to reach the relatively high abundances and clearance rates that we observed in the late 2000s. The time series data we have compiled on phytoplankton biomass, zooplankton grazing, and river herring abundance support this hypothesis (Fig. 7). The disparity in the time scales between data on fish, zooplankton, phytoplankton, and physical conditions, as well as gaps in data, do not permit a statistical test of this hypothesis using methods like path analysis or regression techniques. The circumstantial
evidence compiled here for a trophic cascade to have occurred in the Chowan River justifies future experimental research to evaluate the conditions (e.g., irradiance, temperature, water residence time, zooplankton and fish abundances) under which this process may occur in estuaries.

An additional process to examine in future experimental work is the indirect positive effect that nutrient excretion by anadromous fish can have on phytoplankton. Excretion and mortality can import significant quantities of nitrogen and phosphorus into freshwater ecosystems (Durbin et al. 1979, Garman 1992, Browder and Garman 1994). Fish-derived nutrients may not be important in stimulating phytoplankton growth in the Chowan River since phytoplankton growth is generally not nutrient-limited in this system (Stanley and Hobbie 1981), but future studies must incorporate this dimension in order to provide insight into estuaries with lower, growth-limiting levels of nutrients.

If a trophic cascade between fish, zooplankton, and phytoplankton occurs in estuaries, the tidal freshwater zone might be the location where this process is most acute for several reasons. First, residence time of water and associated phytoplankton and zooplankton communities can increase within the upper portion of estuaries, facilitating the accumulation of biomass within this region (Lucas et al. 2009). Second, smaller order tidal freshwater river channels are characterized by much greater water column irradiance than the non-tidal channels upstream, allowing for pulses of phytoplankton biomass to develop (Ensign et al. 2012). Third, this tidal freshwater portion of the estuary is the primary nursery habitat for juvenile anadromous fish, and therefore, predation on zooplankton may be particularly high during the same period of the year that phytoplankton growth is accelerated due to increased irradiance, temperature, and residence time.
Conclusions

Recent syntheses of decades of time series data are revealing unexpected patterns in ecosystem processes that indicate unforeseen responses to management actions. In some cases algal biomass appears to be, or more, sensitive to top-down pressure within the food web as algae are to resource availability (Heffernan et al. 2010, Perga et al. 2010). The importance of top-down effects on processes that have historically been considered symptoms of eutrophication has recently been examined in experimental research (Eriksson et al. 2009, Baden et al. 2010) and time series analysis (Baden et al. 2012). Our study took advantage of an ecosystem with the unique, long-term data on multiple trophic levels to explore a particular scenario of resource availability versus fish: the potential trophic cascade between anadromous fish and phytoplankton. Yet the environmental conditions of the estuary we reported on are similar to many estuaries across the eastern U.S. and Canada: historically high nutrient loading has been curtailed while anadromous fish populations have been lost. Estuarine modeling, data synthesis, and new experiments on trophic control are needed to evaluate how prevalent and intense the response of phytoplankton will be to anadromous fish restoration.

In summary, we concluded that the approximate 50% reduction of nitrogen concentration in the oligohaline Chowan River over a 30-year period was not the primary driver of change in phytoplankton growth. The observed decline in phytoplankton biomass during the 1980s may have been due to other factors, such as a shift in phytoplankton community, grazing by non-native Corbicula, and an increase in zooplankton grazing. Our comparison between predicted zooplankton grazing in the 1980s versus 2000s indicated that zooplankton are currently exerting much greater control on phytoplankton than occurred 30 years ago, corresponding with a decline in river herring and potentially the broader planktivorous fish community. The available time series data indicate that it is plausible that the shift in fish community has altered the Chowan River system into a top-down controlled environment for phytoplankton, and that future restoration of anadromous fish has the potential to positively influence phytoplankton.

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**SUPPLEMENTAL MATERIAL**

**APPENDIX**

Fig. A1. Mean rotifer abundance of samples collected at the surface and bottom of the water column at the Chowan River (A), Wiccacon River (B), and Bennetts Creek (C) between April 2008 and May 2010.
Table A1. Literature values of the minimum and maximum individual clearance rates of zooplankton species found in the Chowan River system in 2008–2010.

| Phylum or class | Order or genus | Minimum (μL·ind⁻¹·hr⁻¹) | Maximum (μL·ind⁻¹·hr⁻¹) | Reference |
|-----------------|---------------|--------------------------|--------------------------|-----------|
| Rotifera        | Ascomorpha†   | 3.180                    | 25.936                   | no study found |
| Rotifera        | Asplanchna    | 0.312                    | 0.635                    | Sellner et al. 1993 |
| Rotifera        | Brachionus     | 5.47                     | 27                       | Bogdan and Gilbert 1987, Rothhaupt 1990 |
| Rotifera        | Conochilus     | 1.4                      | 13                       | no study found |
| Rotifera        | Filinia†       | 3.108                    | 25.936                   | no study found |
| Rotifera        | Gastropus†     | 3.108                    | 25.936                   | no study found |
| Rotifera        | Keratella      | 6.916                    | 41.82                    | Lair and Ali 1990 |
| Rotifera        | Leptella†      | 3.108                    | 25.936                   | no study found |
| Rotifera        | Monostyla†     | 3.108                    | 25.936                   | no study found |
| Rotifera        | Nothelca†      | 3.108                    | 25.936                   | no study found |
| Rotifera        | Platias†       | 3.108                    | 25.936                   | no study found |
| Rotifera        | Polynemus†     | 3.108                    | 25.936                   | no study found |
| Rotifera        | Polycarthra    | 4.56                     | 47                       | Bogdan and Gilbert 1987, Sellner et al. 1993 |
| Rotifera        | Syncheata†     | 3.108                    | 25.936                   | no study found |
| Rotifera        | Trichocerca    | 0.098                    | 0.98                     | Sellner et al. 1993 |
| Rotifera        | Trochocerca†   | 3.108                    | 25.936                   | no study found |
| Crustacea       | Cyclopoida     | 9.288                    | 332.614                  | Adrian 1991, Fahnenstiel et al. 1991, Lair 1992, Persson 1985, Sellner et al. 1993 |
| Crustacea       | Calanoida      | 62.5                     | 790                      | Bogdan and Gilbert 1987, White and Roman 1992 |
| Crustacea       | Harpacticoida‡ | 35.894                   | 5461.307                 | no study found |
| Crustacea       | nauplii        | 154                      | 154                      | Bogdan and Gilbert 1987 |
| Crustacea       | copepodid      | 357                      | 357                      | Bogdan and Gilbert 1987 |
| Branchiopoda    | Alona          | 56.3                     | 56.3                     | Downing 1981 |
| Branchiopoda    | Alonella§      | 56.519                   | 379.281                  | no study found |
| Branchiopoda    | Alonopsis§     | 56.519                   | 379.281                  | no study found |
| Branchiopoda    | Bosmina        | 35.46                    | 415.75                   | Bogdan and Gilbert 1987, De Mott 1982, Haney 1973, Lair 1991, Persson 1985 |
| Branchiopoda    | Bosminopsis§   | 56.519                   | 379.281                  | no study found |
| Branchiopoda    | Camptocercus§  | 56.519                   | 379.281                  | no study found |
| Branchiopoda    | Ceriodaphnia   | 31                       | 541.25                   | Bogdan and Gilbert 1987, Haney 1973, Lair 1991, O’Brian and deNoyelles 1974 |
| Branchiopoda    | Chydrorida§    | 10.75                    | 267                      | Haney 1973, Lair 1991 |
| Branchiopoda    | Daphnia        | 68.943                   | 785.667                  | Lair 1991, Nauwerck 1963, Kasprzak et al. 1986 |
| Branchiopoda    | Diaphanosoma   | 66.7                     | 406                      | Haney 1973, Bogdan and Gilbert 1987 |
| Branchiopoda    | Holopedium     | 183                      | 183                      | Persson 1985 |
| Branchiopoda    | Leptodora§     | ...                      | ...                      | no study found |
| Branchiopoda    | Siida          | 0                        | 9929                     | Downing 1981 |

† An average of all rotifer species was used for minimum (3.108) and maximum (25.936).
‡ An average of cyclopid and calanoid was used for minimum (35.894) and maximum (561.307).
§ An average of all cladoceran genus was used for minimum (56.519) and maximum (379.281).
¶ No grazing was considered by Leptodora.
Fig. A2. Mean copepod abundance of samples collected at the surface and bottom of the water column on the Chowan River (A), Wiccacon River (B), and Bennetts Creek (C) between April 2008 and May 2010.

Fig. A3. Mean cladoceran abundance from samples collected at the surface and bottom of the water column in the Chowan River (A), Wiccacon River (B), and Bennetts Creek (C), April 2008 through May 2010.
Table A2. List of fish species considered zooplanktivorous during any life history phase based on information reported in Fishbase.org.

| Scientific name          | Common name                  |
|--------------------------|------------------------------|
| Alosa mediocris          | hickory shad                 |
| Notropis hudsonius       | spottail shiner              |
| Perci flavescens         | yellow perch                 |
| Hybognathus regius       | eastern silvery minnow       |
| Lepomis macrochirus      | bluegill                     |
| Alosa aestivalis         | blueback herring             |
| Alosa psuedoharengus     | alewife                      |
| Strongylura marina       | Atlantic needlefish          |
| Fundulus diaphanus       | banded killifish             |
| Morone americana         | white perch                  |
| Alosa sapidissina        | American shad                |
| Menidia beryllina        | inland silverside            |
| Lepomis gibbosus         | pumpkinseed sunfish          |
| Fundulus majalis         | striped killifish            |
| Notemigonius crysoleucus | golden shiner                |
| Mugil carema             | white mullet                 |
| Mugil cephalus           | striped mullet               |
| Anchoa mitchilli         | bay anchovy                  |
| Amietius natalis         | catfish, bullhead, yellow    |
| Dorosoma cepedianum      | gizzard shad                 |
| Cyprinus carpio          | common carp                  |
| Pomoxis nigromaculatus   | black crapple                |
| Brevoortia tyrannus      | Atlantic mendhaden           |
| Lepomis microlophus      | redear sunfish               |
| Bairdiella chrysoura     | silver perch                 |
| Notropis proce           | swallowtail shiner           |
| Gambusia holbrooki       | Eastern mosquitofish         |
| Micropogonias undulatus  | Atlantic croaker             |
| Lepomis cyanellus        | green sunfish                |
| Opisthomena oglinum      | Atlantic thread herring      |
| Aphredoderus sayanus     | pirate perch                 |
| Dorosoma petenense       | threadfin shad               |
| Membras maritima         | rough silverside             |
| Notropis petersoni       | coastal shiner               |