Factors affecting recruitment of key resident and anadromous fish species in the Santee-Cooper system

Final Report

Research supported by:
South Carolina Department of Natural Resources and
United States Fish and Wildlife Service Sport Fish Restoration Program

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Version: 20 June 2018

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ACKNOWLEDGEMENTS

This project was supported by the South Carolina Department of Natural Resources with funding from the United States Fish and Wildlife Service Sport Fish Restoration Program.

The framework for the project was developed by the Santee Cooper Comprehensive Study Group, re-convened by Ross Self, which included Scott Lamprecht, Bill Post, Jason Bettinger, among others, in addition to the authors of this report.

We gratefully acknowledge the advice and assistance of Jason Bettinger, Treye Byers, Charlie Poeta, Daniel Hood, and Evan Cartabiano. Summer interns Katherine Sandel and Blythe Davis assisted, respectively, in processing benthos and plankton samples. Larry McCord, John Morrison, and the staff and summer interns of the Environmental Resources program at Santee Cooper provided extensive logistic support for the benthos study, and John Morrison co-authored the published version of that study. Santee Cooper also provided access to extensive water quality data.

BET thanks her loyal husband and colleague Mark Brooks for support and advice. According to an old but relevant proverb, there is “None so bold as blynd Bayard.”

The cover illustration was prepared by Hugh Chrisp for the 1927-1940 New York Biological Survey (Kraft, Carlson, and Carlson, 2006).

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SUMMARY

- The general goal of this study was to characterize biological and physical processes in Lake Marion, with particular concern for processes affecting recruitment of key fish species, including striped bass, American shad, blueback herring, threadfin shad, and white perch. The report combines results from field data from this study and other sources to quantify components of the food web supporting the fish. Models are used to evaluate interactions among major components of the food web. The analyses focus on the upper main basin of Lake Marion, which functions as a nursery in spring for larvae of the key fish species. These larvae depend on zooplankton, which in turn depend on phytoplankton.
- Lake Marion is the largest lake in South Carolina. Habitats within the lake range from the shallow, heavily vegetated drowned floodplains of the Rimini Swamp and the upper backwaters to the deep, open water of the lower main basin. On average, the entire volume of Lake Marion is replenished about seven times annually. Hydrologic processes in Lake Marion show wide variation on daily, monthly, and annual time scales.
- In 1997-2014, turbidity and total phosphorus decreased between the influent waters and upper and lower regions (data from Santee Cooper and South Carolina Department of Health and Environmental Control). These downlake decreases are consistent with reservoir zonation models. In contrast, chlorophyll a, a measure of phytoplankton abundance, either increased (winter, spring, and fall) or did not change (summer) downlake. Strong inverse correlations between chlorophyll a and discharge into Lake Marion from the Santee River suggest the importance of hydrologic processes to algal dynamics in the upper main basin, particularly in spring. Comparisons of water quality between 1984-1995 and 1997-2014 showed striking declines (by more than half in all seasons) in chlorophyll a in the main basin.
- The benthos of Lake Marion was dominated by the clam *Corbicula* sp. and the snail *Viviparus subpurpureus*, which together made up nearly 90% of the biomass of benthic invertebrates. Benthic invertebrates were most abundant in the upper main basin. *Corbicula* is capable of consuming planktonic algae, particularly in shallow, well-mixed waters such as those of the upper main basin. *Corbicula* is thus positioned to influence planktonic resources down the lake by removing material imported from the river, controlling algal abundances in the upper region, and reducing exports to the middle and lower regions.
- We constructed a model to examine potential effects of advection and consumption on phytoplankton dynamics in the upper main basin. Simulations were run for 18 spring seasons; daily flushing rates for the simulations were computed from 1997-2014 hydrologic data. Four model scenarios used plausible ranges of influent algal concentrations and algal productivity. Among the four scenarios, the 18-year April-June means for imports, exports, production, and consumption (or settling) of algae were of similar magnitude (10-47 metric tons dry mass day^{-1}). Consumption consistent with requirements of the *Corbicula* population reduced algal production in the upper main basin by about half. Our results support earlier inferences (e.g., Tufford and McKellar, 1999) about the importance of hydrodynamics and riverine inputs to this system.
- Composition of the zooplankton in Lake Marion was typical for large impoundments of the region. Abundances of zooplankton in the upper main basin in spring of 2009 and 2012 were variable over time and among stations. Mean abundances were low, exceeding 100 animals

liter^{-1} only in June. A zooplankton dynamics model, which included advection, suggested that zooplankton productivity in spring would generally be insufficient to support plausible numbers of pelagic fish.

- Both threadfin shad and the Asiatic clam *Corbicula* sp. appear to occupy key positions in the food web of upper Lake Marion spring. Interactions among components of the food web are mediated by advective processes—driven by the vast quantity of water flowing through this system. Uncertainty about the spring abundances and diets of threadfin shad confounds the analysis of trophic processes. However, threadfin shad may contribute substantially to suppression of the zooplankton, the resource base for larval fish, in most years.

CHAPTER 1. Introduction

The Santee-Cooper Comprehensive Study Group was convened by the South Carolina Department of Resources (SCDNR) to provide an overview of current conditions in the Santee-Cooper system and to promote development of a scientific basis for management decisions about aquatic resources within the Santee-Cooper basin. The general goal was to characterize biological and physical processes in the system, with particular concern for processes affecting key fish species, including striped bass, American shad, blueback herring, threadfin shad, and white perch.

These key fish species have overlapping spawning seasons (April to June); they share nursery areas in Upper Lake Marion; and, in their larval stages, they feed on zooplankton as larvae. During the middle of the last decade, the population of striped bass dropped to lower than any reported during the preceding two decades (Lamprecht et al., 2013). The causes for the decline, and the implications for success of the Santee-Cooper anadromous fish passage and restoration efforts, were presently unknown. Striped bass have received more attention than the other key species in Lake Marion. However, because all of the key species share habitat and resources during early development, reduced recruitment of striped bass may indicate changing conditions for the other species.

Investigations of factors influencing successful striped bass recruitment were conducted in Santee-Cooper in the 1980s and early 1990s. Successful recruitment appeared to depend on the abundance of zooplankton, as well as on flow in the Congaree River, which transports eggs and larvae from spawning habitat in the Congaree River to nursery habitat in Lake Marion (Bulak et al., 1997; Chick and Van den Avyle, 1999a).

We hypothesized that spring zooplankton populations in the nursery areas of Upper Lake Marion are controlled by mortality due to predation, losses due to washout, and poor reproduction due to low phytoplankton populations. Feeding by larval fish or juvenile and adults of species such as threadfin shad suppress the zooplankton, resulting in competition among the fish for this resource (for example, the hypothesized interaction between anadromous American shad and salmon in the Columbia River; Fresh, 1996). Additionally, the benthos may affect the plankton in Lake Marion. *Corbicula* sp. the invasive Asiatic clam, appeared to be abundant in Lake Marion, although its abundance had not been quantified. *Corbicula* spp. have suppressed phytoplankton in other shallow systems (for example, Cohen et al., 1984; Lopez et al., 2006; Pigneur et al., 2014).

Our efforts to address these hypotheses included acquisition and analysis of hydrologic and water quality data from other agencies, field studies on the zooplankton, ichthyoplankton, and benthos, construction of a food web, and modeling to estimate strength of interactions among components of the food web.

Chapter 2 of this report describes hydrography and hydrology of the Lake Marion. The analyses focus on the period 1997-2014, but include comparisons with the period 1984-1996, when extensive studies were conducted. This chapter also presents the hydrologic model used to estimate flushing rates for the nursery area of upper Lake Marion. These flushing rates are typically high during the spring.

Chapter 3 summarizes water quality data, including chlorophyll a as a measure of phytoplankton abundances, from the United States Environmental Protection Agency and Santee

Cooper. As with the hydrologic data, the focus is on 1997-2014, but includes comparison with 1984-1995. These comparisons document substantial changes in chlorophyll a throughout the lake between the recent and earlier time periods.

Chapter 4 presents results of field studies of the benthos. Sampling was conducted in 2009 in upper Lake Marion and 2010 in upper, middle, and lower Lake Marion. The benthos in all regions is dominated by mollusks, principally the Asiatic clam, *Corbicula* sp.

Chapter 5 presents a model to evaluate the impact of advection and consumption on spring phytoplankton in the upper main basin of Lake Marion.

Chapter 6 presents results of field studies of the zooplankton. Sampling was conducted in April-June of 2009 and 2012 in upper Lake Marion and in April-October of 2014 in upper, middle, and lower Lake Marion. Chlorophyll a samples, collected with the zooplankton samples in 2009. The zooplankton abundances varied widely but were often low, relative to requirements of larval fish, but tended to be higher in toward the lower end of the lake.

Chapter 7 presents the food web and synthesis.

CHAPTER 2. Hydrography and Hydrology

Lake Marion is a drowned swamp at the lower end of one of the largest watersheds along the eastern seaboard of the United States. The form of the lake basin, as well as the quantity and quality of water moving through it, shape the destiny of the aquatic community. In this chapter, we provide an overview of hydrography and hydrology of Lake Marion. We analyze recent hydrologic data, mainly for the years 1997-2014, but also for 1983-1996 to aid interpreting prior studies. We also estimate flushing rates for the upper main basin. The flushing rates provide the basis for modeling advective processes in subsequent chapters.

This chapter depends heavily on hydrographic data and long-term hydrologic data from the United States Geological Survey National Water Information Service. Our analyses build on Tufford and McKellar's hydrologic model (Tufford, 1996; Tufford and McKellar, 1999). Their work, and ours, owes much to Patterson and Logan's maps (1988), Patterson and Harvey's dye studies of flow patterns (1995), and other studies during the 1980s and 1990s.

Hydrography

Lake Marion is situated in the Coastal Plain near the lower end of the watershed of Santee River (Figure 2.1). The Santee watershed covers about 40,000 km^2 in South Carolina and North Carolina, mostly within the Piedmont region (USGS, 2007). Its principal rivers are the Saluda and the Broad, which converge to form the Congaree in the Coastal Plain, and the Catawba, which becomes the Wateree in the Coastal Plain.

The lake and watershed are situated in a region of warm, moist temperate climate (South Carolina State Climatology Office, 2017). Precipitation averages 114-127 cm (45-50 in) annually over much of the watershed; air temperature, 15.6-18.5 ^{o}C (60-65 ^{o}F).

The watershed of Lake Marion (Fig. 2.1) covers about 38,000 km^2 of the Santee watershed. The Congaree River drains 58% of the Lake Marion watershed; the Wateree River, 38%. The two rivers join to form the Santee River just above Lake Marion. Lake Marion occupies 1% of its watershed, and the remaining 3% is drained by small creeks or by the lake itself.

The Santee River enters Lake Marion in the swamp region (Fig. 2.1), where it flows in a channel defined by natural levees through Rimini Swamp. It continues in this channel through the upper backwaters region, where the levees separate the river from Stump Hole Swamp to the south and Elliott's Flats to the north. The river submerges at the lower end of this region.

Upper Lake Marion, as designated for our analyses, extends from the submergence of the Santee River to the Interstate Highway 95 bridge. A levee supporting the bridge restricts water flow to the western side of the channel. Below the I-95 bridge, in its middle and lower regions, the lake becomes progressively wider and deeper. Maximum depth at full pool is 23.4 m. Upper and middle Lake Marion occupy the inundated former floodplain of the Santee River, and lower Lake Marion extends into tributary creek valleys (Patterson and Harvey, 1995).

Lake Marion, including the swamp and upper backwater regions, covers 351 km^2 (Table 2.1). The main basin portions, as shown in Figure 2.2, cover about half of this area. As mapped (Figure 2.2), swamp or marsh vegetation covers about 90% of the swamp region, about 45% of the upper backwaters region, about 30% of the upper lake region, and <1% of the middle and lower lake regions. Because the extent of swamp and marsh habitat varies over time, these estimates are inexact.

Mean depth of the lake, excluding the swamp region, is 5.1 m at full pool (Tufford, 1996) or 4.8 m at normal pool (our computations from Tufford's sectional bathymetry; normal pool set at 0.6 m below full pool). Similarly, for Tufford's Section 1 (our upper backwaters region), mean depth is 2.8 m at full pool or 2.3 m at normal pool. For Tufford's Section 4 (approximately, our lower lake region), mean depth was 6.1 m at full pool or 5.9 m at normal pool. At normal pool, about 80% of the lake's area has water depth exceeding 2 m.

Lake Marion has outlets to the Santee River and the Diversion Canal, which flows into Lake Moultrie. Discharge to the Santee River is controlled at Wilson Dam. Normally, discharge from the dam is regulated at the Santee Spillway Hydroelectric Station. During period of high flow, excess water can be released through tainter gates in the spillway section of the dam. Discharge through the Diversion Canal is unregulated. The canal crosses the natural boundary between watersheds of the Santee and Cooper rivers.

Hydrology

The Santee River channel carries main flow from the watershed into Lake Marion (Figure 2.2). Under both high and low flow conditions, some water is diverted from both the Santee and Wateree rivers into the Santee-Wateree Swamp (Patterson and Harvey, 1995). Further downstream at Rimini Trestle, about 10% of the flow in the Santee main channel is diverted through an artificial cut in the levee toward Elliott's Flats, and about 10% is diverted at Low Falls Landing toward Stump Hole Swamp (Patterson and Harvey, 1995).

Tufford and McKellar (1999) and others have estimated discharge from the Santee River into Lake Marion by the combined discharge of the Congaree River at Columbia and the Wateree River at Camden (Figure 2.1, USGS gages 02169500 and 02148000). The area above these two gages accounts for 87% of the watershed of Lake Marion. Both rivers develop broad floodplains downstream of these stations, precluding good estimates of discharge, and no major tributaries enter either river below these stations. Tufford and McKellar (p. 148) judged that net effects of gains and losses downstream of these gages, but above Lake Marion, were negligible.

In Tufford and McKellar's hydrologic model, these discharges into Lake Marion from the Santee River system accounted for 98% of the annual inflow. Small creeks around the lake accounted for the remainder (Tufford and McKellar, 1999; see Equation 7 and Tables 3 and 6; precipitation and evaporation terms were accounted as a net outflow).

Methods

Discharge and water level. We used long-term USGS hydrologic records for four stations: three at which discharge is monitored, and one at which water level is monitored (Figure 2.1). These data were downloaded from the National Water Information System (USGS, 2015; data sets derived from earlier downloads were reconciled to this version).

Records of daily mean discharge values extend back to October 1939 for the Congaree River at Columbia (USGS 02169500) and to October 1929 for the Wateree River at Camden (USGS 02148000). For the years 1983-2014, values were missing for 351 dates, mostly in 1983 (88 missing) and 1985 (200 missing). We estimated missing values for each river from values for the other, using lines fitted by piece-wise by eye to log-log plots of data for 1940-2009. Because minimum daily discharge values for the Wateree increased markedly after 1989, we used different lines for 1983–1989 and 1990–2014.

Records of daily mean discharge for the Santee River at Pineville extend back to May 1942. For the years 1983-2014, values were missing for 68 dates, most in 2006 and 2007. We did not estimate the missing values.

Records of daily mean water level for Lake Marion at Pineville extend back to October 1996. Earlier records exist, but are not marked as approved by USGS. For the years 1983-2014, values were missing for 67 dates, mostly in 2006 and 2007. We estimated the missing values by linear interpolation.

Basin volume. We estimated volume of the upper main bain from depths measured on ten evenly spaced, parallel transects across the lake in 2009 (sampled area = 28.6 km^2, as shown in Figure 2.2, mean depth=3.4 m, n=50 sample points). At full pool, V_{basin} = 103.54 10^6 m^3. We adjusted the volume according to the daily mean water level.

Volume estimates for other sections of the lake were derived from bathymetric analyses in Tufford (1996). Volume at 0.8 m below full pool was computed by treating Tufford's area estimates by 0- and 4 or 12-ft depth below full pool as conic sections and assuming linear variation in diameter with depth. Retention time was computed with the average combined discharge for 1997-2014.

Flushing rates and retention times. We computed daily flushing rate coefficients for the upper main basin f_{basin} from discharge into the basin by Santee River D_{river} and volume of the basin V_{basin}:

$$f_{basin} = D_{river} / V_{basin} \qquad \text{[Eq. 2.1]}$$

We adjusted V_{basin} according to the daily mean water level. Retention time is simply the inverse of the flushing rate.

We estimated D_{river} from the combined daily mean discharge of the Congaree River at Columbia and Wateree River near Camden. We assumed a 3-day travel time from these gages to the upper main basin of Lake Marion. From USGS flow data, Pickett (1992) computed 1.3-day average travel times in the Congaree River from Columbia to Fort Motte (USGS 02169740, see Figure 2.2) and from the Wateree River from Camden to Eastover (USGS 02148315 in Figure 2.1). From dye studies, Patterson and Harvey (1995) estimated that travel times from the Congaree River at Eastover to Browns Cut, just above the upper main basin, were 0.9 and 1.3 days under high and low flow conditions, respectively. Combined, these results yield an average travel time of 2.2-2.6 days, depending on flow conditions, from the Columbia and Camden gages to the upper main basin. For their hydrologic model, Tufford and McKellar (1999) set a 2-day travel time from the Columbia and Camden gages to Rimini Trestle, 7.3 km upstream of the upper main basin. They also incorporated time lags under high flow conditions to account for the diversions from the Wateree River through the Santee-Wateree Swamp.

Annual flushing rates and retention times for other sections of the lake were computed with the average combined discharge for 1997-2014 and volume estimated at normal pool.

Results

Discharge and water level. Daily discharge of the Santee River into Lake Marion, estimated as the combined discharge of the Congaree and Wateree rivers, varied by two orders of magnitude (Table 2.2). About 60% of the discharge comes from the Congaree River; about 40%, from the Wateree River. The regulated releases at Wilson Dam from Lake Marion to the Santee

River, gaged at Pineville, were typically near 10% of the discharge into Lake Marion. During periods of flooding, regulated releases were sometimes much higher.

Annual mean discharge of the Santee River above Lake Marion ranged from 14.2 10^6 m^3 day^{-1} (5,800 cfs) in 2008 to 55.2 10^6 m^3 day^{-1} (22,600 cfs) in 2003 (Figure 2.3). Although interannual ranges were similar, annual means for 1997-2014 were lower than for 1983-1996 (Wilcoxon rank-sum test, m = 14, n = 18, $P < 0.01$). Mean discharge for 1983-1996 was 37.0 10^6 m^3 day^{-1} (15,100 cfs) for 1997-2014, 27.1 10^6 m^3 day^{-1} (11,100 cfs).

Monthly mean discharge of the Santee River above Lake Marion varied by about an order of magnitude within months among years (Figure 2.4). Values differed among months (analysis of variance on log-tranformed data: $F(11, 204) = 6.60$, $P < 0.01$). The monthly means were typically highest in December to April and lowest in June to October. Pairwise comparisons (95% simultaneous confidence intervals by Tukey method) showed significant differences between all months from January to April and all months from August to October, as well as a few other pairs of months.

Mean water level for Lake Marion was 0.8 m below full pool (Table 2.2). Because this value was lower than most of the annual medians (Figure 2.5), we set normal pool at 0.6 m, the median of the annual median water levels. Water level fluctuated by 1.5 m or less in most years (Figure 2.5). The maximum range of fluctuation, as well as the minimum water level, occurred in 2007. In April-June, water levels were more stable, fluctuating by 0.7 m or less in any year.

Flushing rates and retention times. The average retention time for the entire lake, based on normal pool and average discharge for 1997-2014, was 55 days (Table 2.3). Retention times increased down the lake, ranging from 4 days in the upper backwaters to 27 days in the lower lake. These estimates assume homogeneous mixing through the entire section. Because much of the flow through the upper backwaters section is confined by levees to the main channel of the Santee, retention in the adjacent backwaters is underestimated.

For the upper main basin, excluding the backwaters, median daily flushing rates ranged from 0.15 day^{-1} (retention time of 6.6 days) in 2012 to 0.46 day^{-1} (retention time of 2.2 days) in 2003 (Figure 2.6). Daily variation within most of these years was wide. Median flushing rates for April-June, which are described in greater detail in subsequent chapters, ranged from 0.14/day (retention time of 7 days) in 2002 to 0.87/day (retention time of 1.1 days) in 2003.

Discussion

Habitat in Lake Marion ranges from the shallow, heavily vegetated drowned floodplains of the Rimini Swamp and the Backwaters to the deep, open water of the lower main basin. An enormous volume of water is delivered to the lake by the Santee watershed.

Movement of this water through the lake is largely unidirectional, as indicated by Patterson and Harvey’s dye studies of flow patterns (1995). This directionality of water movement, combined with increasing depth, contributes substantially to the downlake gradients in abundances of both pelagic and benthic organisms. These gradients are considered in subsequent chapters.

On average, the entire volume of Lake Marion is replenished about seven times annually. The influent water carries material, including nutrients, sediment, organisms, and detritus, into the lake. The effluent water removes material. Analyses in subsequent chapters suggest that riverine algal imports represent a substantial subsidy to food webs in the upper main basin of the lake.

Movement of water through the relatively small volume of the upper main basin is much faster. During spring of 2003, this part of the system was essentially riverine, according to Soballe and Kimmel's (1987) designation. Analyses in subsequent chapters will show that the rapid transit of water has important implications for dynamics of the algae and other pelagic components of the food web in this section of the lake.

Hydrologic processes in Lake Marion show wide variation on daily, monthly, and annual time scales. The wide hydrologic variation has consequences for the interpretation and application of both current and prior studies. To the extent that processes of interest depend on hydrologic conditions, results may not be directly comparable among years. Many earlier studies relevant to our current work were conducted during 1984-1995, when annual discharges were generally higher than during recent years.

Table 2.1. Areas (km^2) of Lake Marion. Features and regions, including main basin portions, are mapped in Figure 2.2. Computations were based on waterbodies delineated in the National Hydrography Dataset for the Edisto-Santee subregion (USGS, 2007).

Region	***Boundaries***	***Area of region (km^2)***	***Area of main basin portion (km^2)***
Swamp	Above Rimini Trestle; includes Rimini Swamp and Pack's Flats	33.1	-
Upper backwaters	Rimini Trestle to submergence of Santee River; includes Stump Hole Swamp and Elliott's Flats	34.8	-
Upper lake	Submergence of Santee River to I-95	48.7	32.5
Middle lake	I-95 to Tawcaw Creek	95.6	76.1
Lower lake	Tawcaw Creek to Wilson Dam	138.6	84.5
TOTAL		**350.8**	**193.0**

Table 2.2. Summaries of discharge (10^6 m^{-3} day^{-1}) and daily water level (m below full pool) at USGS gages, 1997-2014. Gage locations are shown in Figure 2.1. Discharge of the Santee River above Lake Marion was estimated as the combined discharge of the Wateree River near Camden and the Congaree River at Columbia.

		Discharge (10^6 m^{-3} day^{-1})			***Daily water level (m below full pool)***		
Gage	***Name***	***Mean***	***Median***	***Range***	***Mean***	***Median***	***Range***
02148000	Wateree River near Camden	11.1	7.0	4.2 – 129.2	-	-	-
02169500	Congaree River at Columbia	16.0	10.9	1.4 – 276.5	-	-	-
-	Santee River above Lake Marion (estimated)	27.1	18.1	3.9 – 404.4	-	-	-
02171500	Santee River near Pineville	3.4	1.6	0.7 – 208.9	-	-	-
02171000	Lake Marion near Pineville	-	-	-	0.8	0.7	0.0 – 3.1

Table 2.3. Volumes and retention times for Lake Marion, based on Tufford's area and volume estimates by section. Retention time was computed with the average combined discharge for 1997-2014 (27.1 10^6 m^3 day^{-1}). Correspondences between Tufford's sections and regions shown in Fig. 2.2 are inexact.

Section and corresponding region	***Area at full pool (km^2)***	***Volume at full pool (10^6 m^3)***	***Volume at normal pool (10^6 m^3)***	***Retention Time (days)***
Section 1 *Upper backwaters in Fig. 2.2*	43.8	122.3	96.4	4*
Section 2 *Upper lake + upper half of middle lake in Fig. 2.2*	71.2	313.9	271.9	10
Section 3 *Lower half of middle lake in Fig. 2.2*	81.5	432.8	386.0	14
Section 4 *Lower lake in Fig. 2.2*	134.1	815.8	738.1	27

*Because much of the flow through this section is confined by levees to the narrow channel of the Santee River, retention time for the adjacent backwaters is underestimated

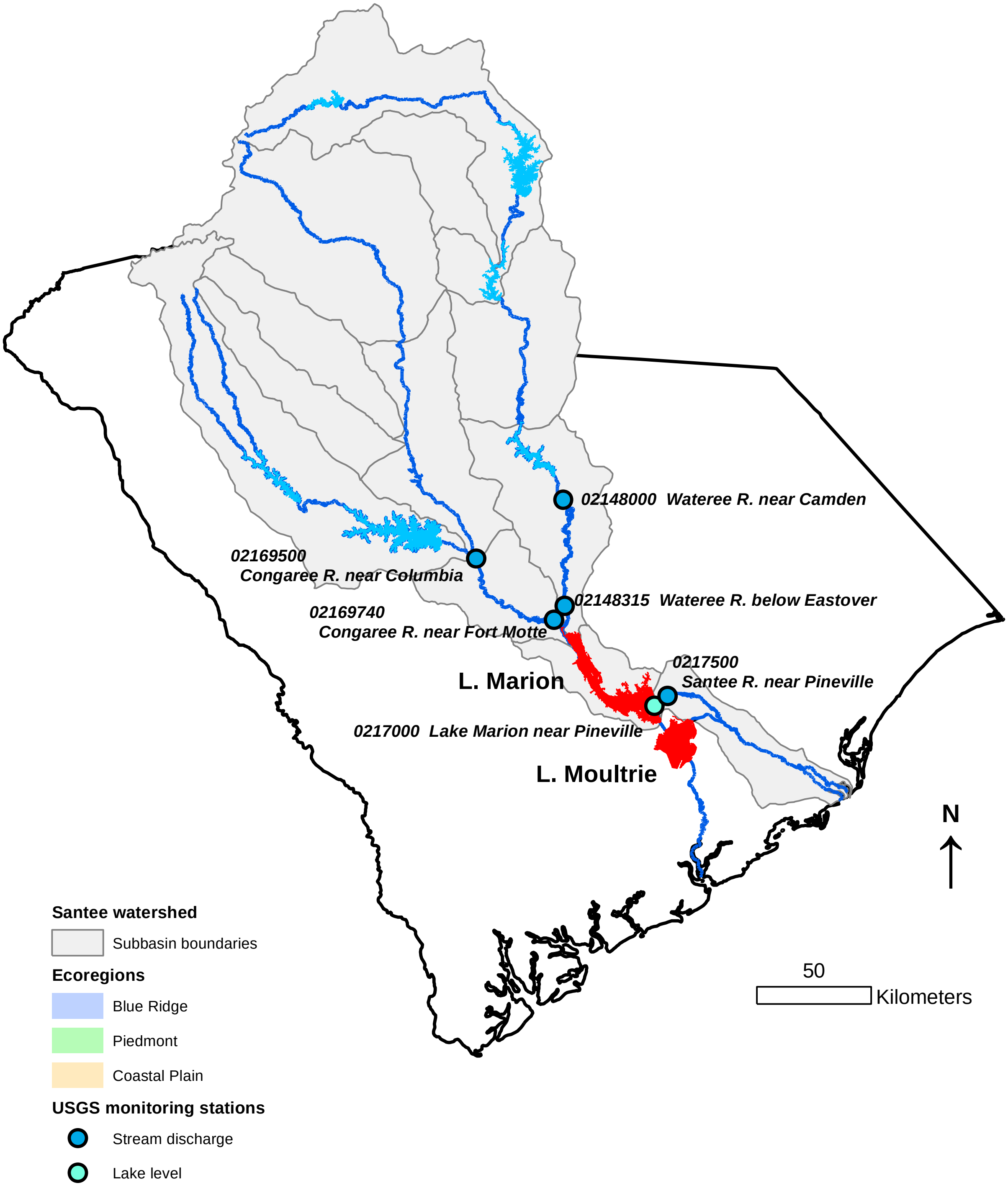

Figure 2.1. Map of the Santee watershed. The watershed boundaries illustrate the natural watershed of the Santee River, excluding the diversion of water from Lake Marion to Lake Moultrie, an impoundment on the Cooper River.

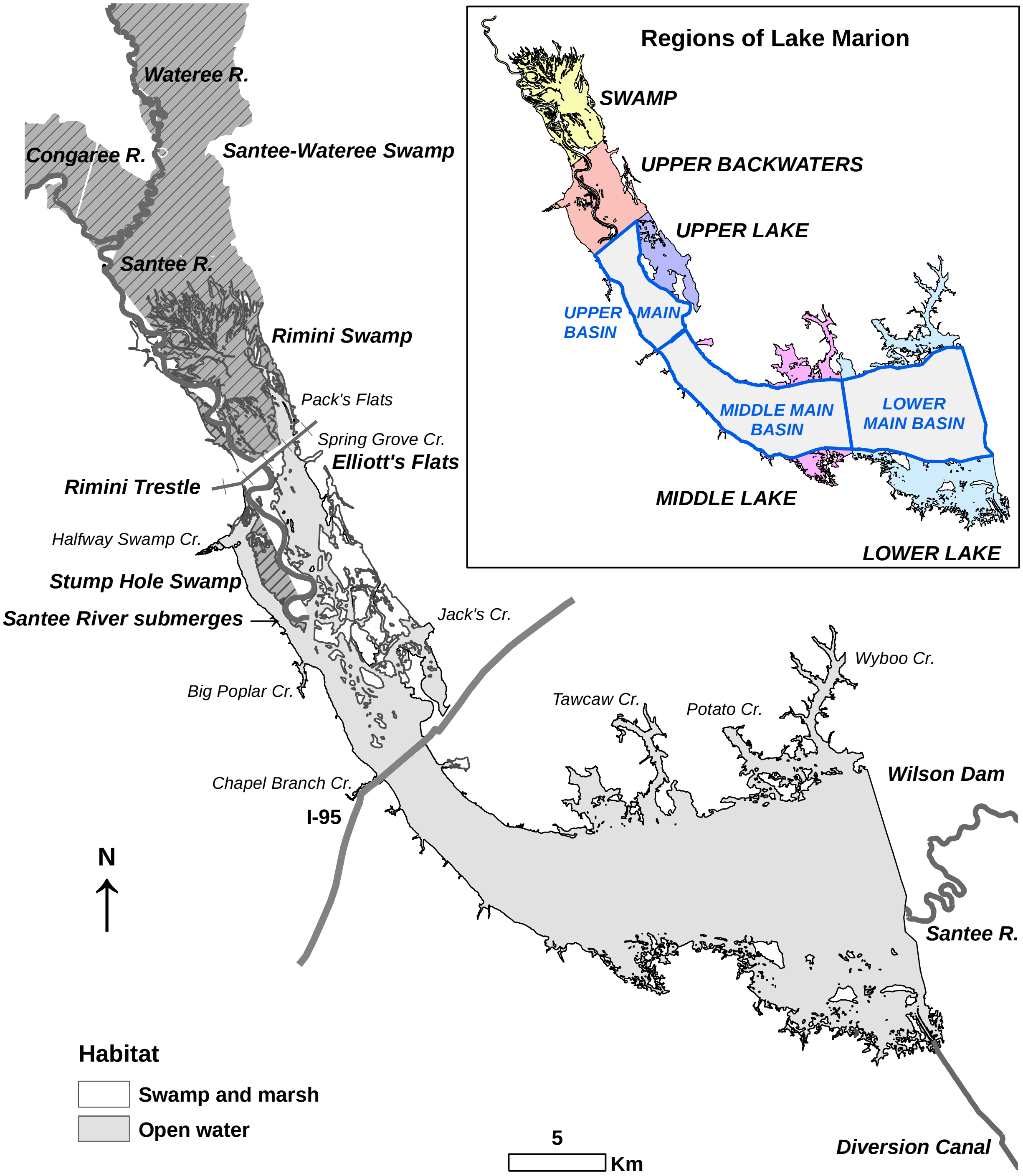

Figure 2.2. Map of Lake Marion. The inset shows regions and main basin portions of Lake Marion, as used in our analyses. The swamp, upper backwaters, and upper, middle, and lower lake regions are distinguished by shading color. The main basin sections within the lake regions are outlined in blue.

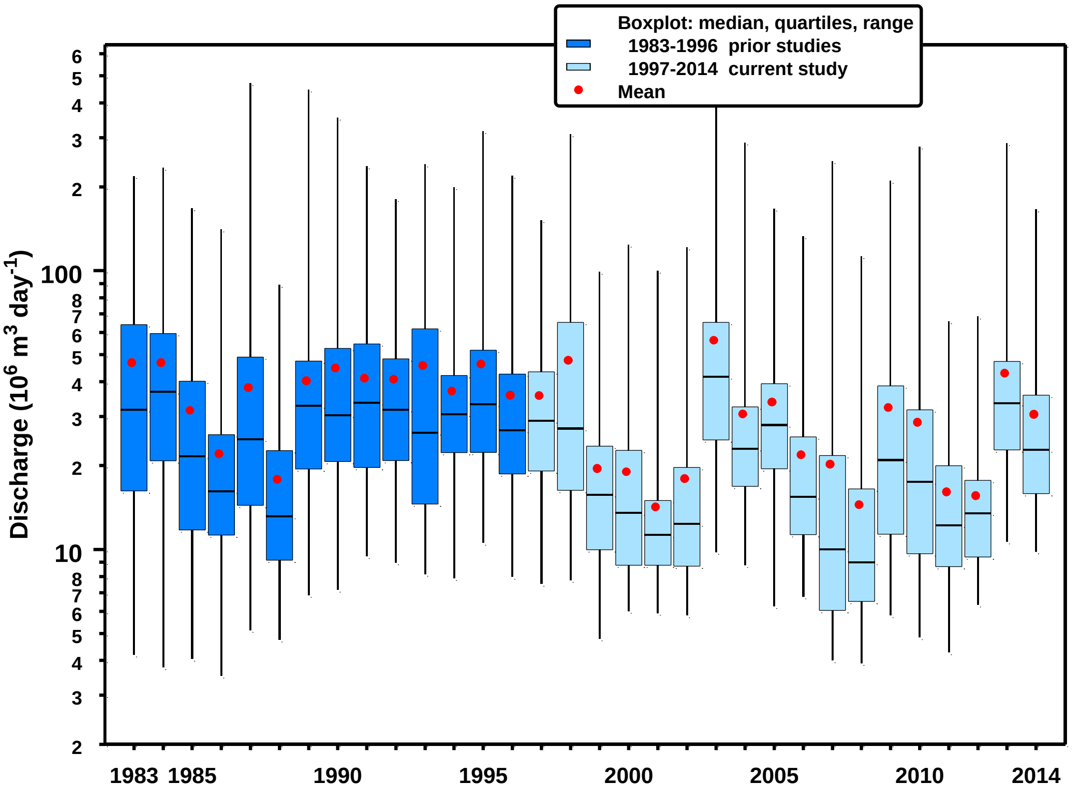

Figure 2.3. Discharge (10^6 m^3 day^{-1}) from the Santee River into Lake Marion by year, 1983-2014. Discharge from the Santee River was estimated from discharges of the Congaree River near Columbia (USGS 02169500) and the Wateree River at Camden (USGS 02164800), as described in Methods.

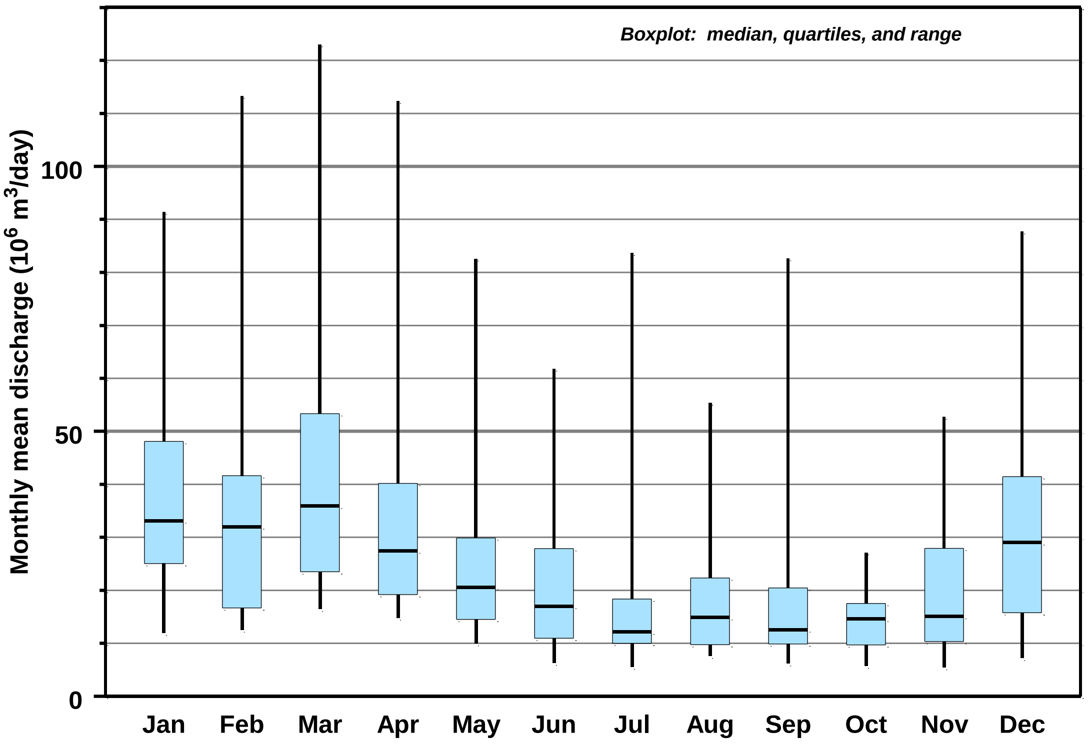

Figure 2.4. Discharge (10^6 m^3 day^{-1}) from the Santee River into Lake Marion by month, 1997-2014. Discharge from the Santee River was estimated from discharges of the Congaree River near Columbia (USGS 02169500) and the Wateree River at Camden (USGS 02164800), as described in Methods.

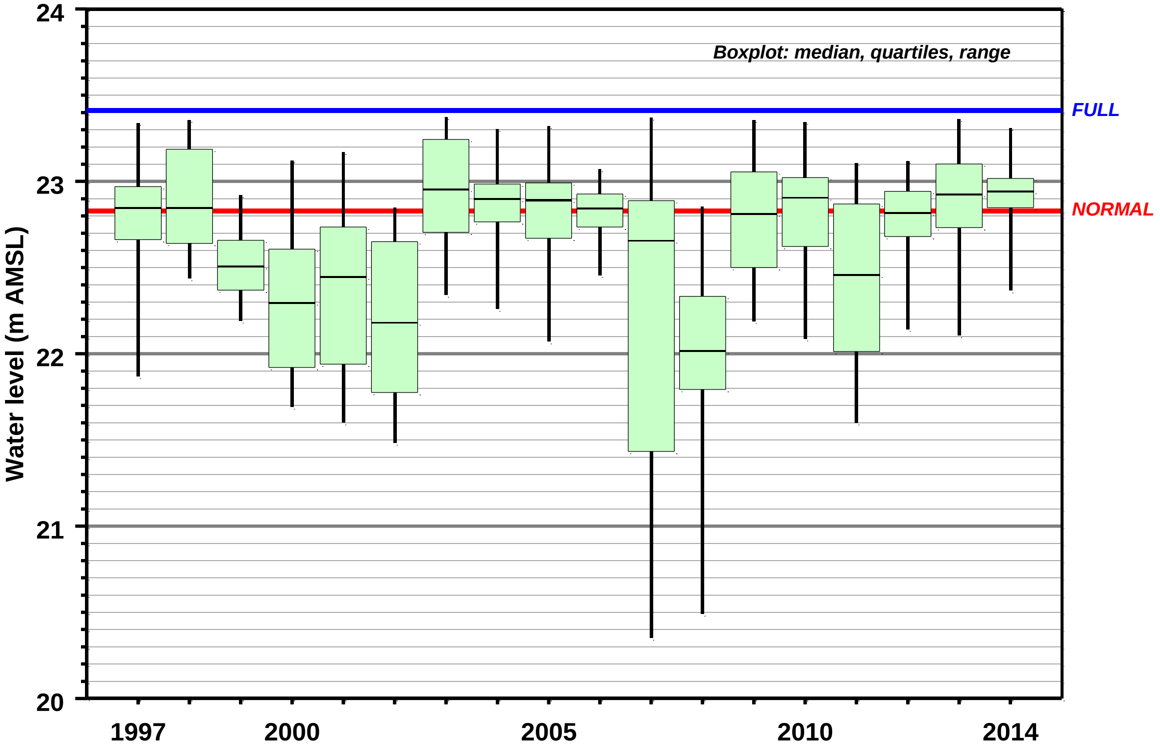

Figure 2.5. Water level (m above mean sea level) in Lake Marion by year, 1997-2014. Horizontal reference lines show full pool and normal pool.

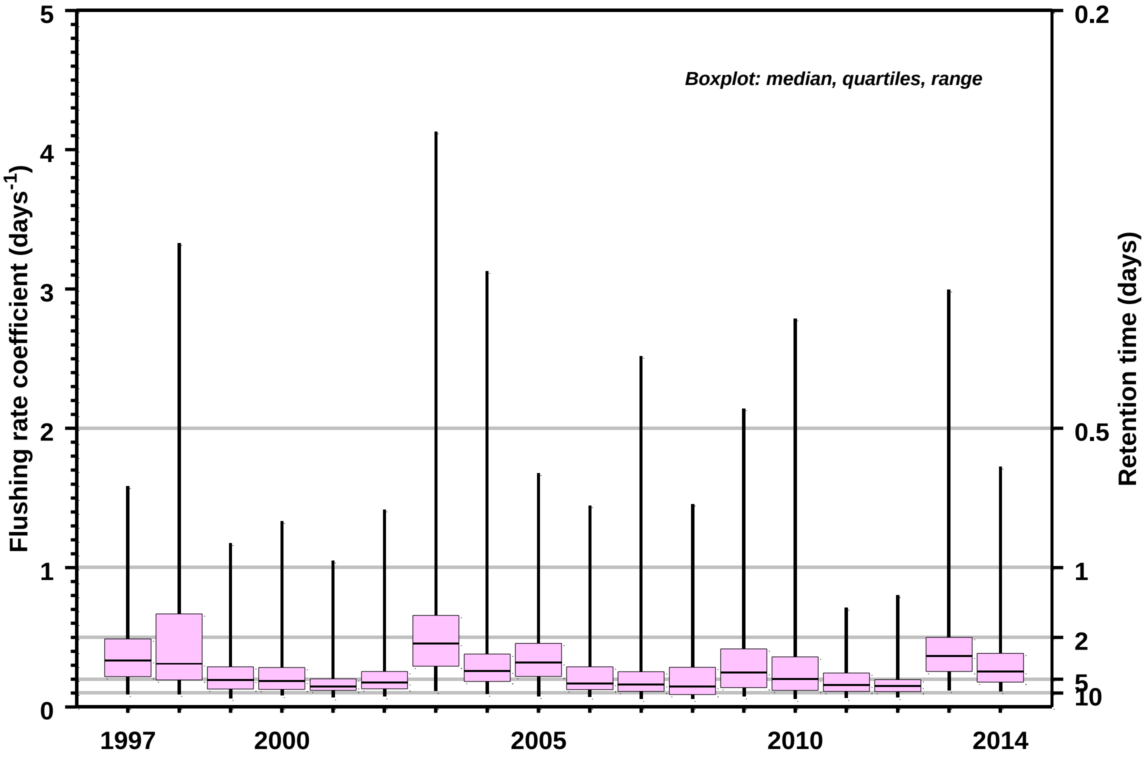

Figure 2.6. Flushing rate ($days^{-1}$) and retention time (days) for the upper main basin of Lake Marion by year, 1997-2014.

CHAPTER 3. Water Quality, Including Chlorophyll a

The parameters measured in water quality studies typically include water temperature, dissolved oxygen, pH, specific conductance, turbidity and other optical properties, dissolved and suspended materials, nutrients, and contaminants, as well as the plant pigment chlorophyll a. These measures include critical attributes of the physical and chemical environment for aquatic organisms. Most importantly, rates of biological processes are temperature-dependent. Respiration of most aquatic organisms requires dissolved oxygen. Many organisms have limited ranges of tolerance for pH. Primary production depends on availability of phosphorus and nitrogen, but may be inhibited by shading from turbidity. Chlorophyll a indicates the distribution and abundance of planktonic algae, which are a major component of aquatic food webs.

Water quality in long, narrow reservoirs, and natural water bodies with similar structure, typically varies along the length of the reservoir. According to the conceptual model described by Thornton (1990), these longitudinal gradients are governed primarily by changing current velocities as water moves through the reservoir. Turbidity decreases downlake as suspended material settles out at decreasing current velocities. Nutrients decrease downlake as they are lost to settling or uptake by phytoplankton. In the riverine zone, water depth is shallow, current velocity is high, and turbidity and nutrients are high. Phytoplankton biomass and production are low, due to light limitation resulting from turbidity. In the transition zone, current velocity slows with increasing depth and width of the basin. Phytoplankton production and biomass reach maxima in this zone. In the lacustrine zone, phytoplankton production becomes nutrient-limited, and both phytoplankton production and biomass diminish. The model predicts that sources of organic matter for consumers are primarily allochthonous in the riverine zone, mixed in the transition zone, and primarily autochthonous in the lacustrine zone. (Kimmel, Lind, and Paulson, 1990).

Extensive analyses of water quality data for Lake Marion in the 1980s and 1990s suggested general conformance to this model (Table 3.1). Turbidity and nutrients decreased downlake (Inabinet, 1985; Pickett and Harvey, 1988; Carswell, 1996). Where measured, chlorophyll a increased downlake from riverine stations. All of these studies recognized high temporal and spatial variability in the system. Tufford (1996) and Tufford and McKellar (1999) inferred that tributary discharge is a dominant forcing function in this system.

To document recent patterns of water quality, including chlorophyll a, we examined 1997-2014 data for stations in the tributary rivers, the upper backwaters, and the main basin of Lake Marion (Figure 3.1). For total phosphorus and chlorophyll a, we also compared results from 1984-1995 with the current period.

Methods

The hydrography and hydrology of Lake Marion are described in detail in Chapter 2. Figure 3.1 illustrates the main flow of water through the lake and locations of the 11 water quality sampling stations used in this study (Table 3.2). The five main basin stations lie along the submerged channel of the Santee River. Earlier data from most or all of the 11 stations of this study were analyzed by Inabinet (1985), Carswell (1996), and Tufford (1996). Eight of the stations fall within the regions sampled by Pickett and Harvey (1988).

Water quality data. Data for Lake Marion and the tributary rivers for 1983-2006 (or 2008 for field measurements) were obtained from the STORET database (US EPA, 2011). Data for subsequent years were obtained directly from Santee Cooper Analytical and Biological Services. Our record for the data available from STORET is complete. Due to late expansions in the scope of the analysis, we have not obtained all of the subsequent data for some stations and parameters.

Samples were collected at approximately monthly intervals. Temperature and dissolved oxygen were usually measured at multiple depths (usually top, middle, and bottom of the water column after 1998; closer intervals before). Nutrients and chlorophyll were measured only at the top of the water column (1 ft or 0.3 m). Analytic protocols met EPA standards. Chlorophyll a was corrected for phaeophytin. Chlorophyll a is routinely analyzed for the lake, but not the rivers. At our request, Santee Cooper analyzed chlorophyll a for the rivers in 2014 and 2015.

Data obtained from STORET or directly from Santee Cooper were combined into databases. Parameters included were: sample depth; field measures of water temperature, Secchi depth, specific conductance, pH, and dissolved oxygen; and laboratory measures of hardness, turbidity, water color, phosphorus (phosphate and total), nitrogen (nitrate, nitrite, ammonia, and total Kjeldahl nitrogen), solids (total suspended and total), and chlorophyll a. The data were screened for obviously erroneous outliers; only a few were encountered. If the data were available, we computed total nitrogen as the sum of reduced nitrogen (measured as total Kjeldahl nitrogen) and oxidized nitrogen (measured as nitrogen contained in nitrate and nitrite).

For the period 1997 to 2014, we summarized and analyzed data for water temperature, pH, specific conductance, dissolved oxygen, hardness (calcium and magnesium), turbidity, color, Secchi transparency, total phosphorus, total nitrogen (1997-2001 only), and chlorophyll a (1997-2014 for lake stations; 2014-2015 only for river stations). Gaps in the data records are noted as the data are used. For values below the minimum detection limit, we substituted the half the value of the detection limit. Except total phosphorus, the number of values below this limit was small. For total phosphorus, numbers of values below detection limits may compromise some of the statistical tests performed for the other parameters (see Helsel, 2006). We present the patterns, but omit some of the statistical tests.

For the period 1984 to 1995, we produced similar summaries for total phosphorus and chlorophyll a.

Most of the data manipulations and analyses were performed in S-Plus.

Results

Water temperature. Monthly median near-surface water temperatures in the main basin varied from 8 ^{o}C or 9 ^{o}C in January to 29 ^{o}C in July (Figure 3.2). The upper main basin, represented by SC-010, appeared to warm and cool slightly faster than the lower main basin, represented by SC-022. The means differed significantly only for the month of November ($F(1,23) = 1.31$, $P < 0.01$). For all other months, means did not differ ($P > 0.05$). Mean temperatures did not differ between either the upper backwaters (SC-039) or the Santee River (SC-004) and the upper main basin (SC-010) did not differ for any month ($P > 0.05$).

Thermal stratification was weak. The median difference between near surface and near bottom water temperatures was 0.5-0.8 ^{o}C for the five main basin stations during May-September (n=63-81observations per station) and 0.2-0.5 ^{o}C during October-April (n=79-100). Maximum differences ranged up to 6.1 ^{o}C in May-September and up to 4.3 ^{o}C in November-April.

Dissolved oxygen. The water column was typically well oxygenated (Figure 3.3). However, episodes of depletion (dissolved oxygen <4 mg/liter) occurred at depth during the warmer months at all stations. Most of these episodes occurred in June, July, or August. The monthly sampling interval, gaps in the records, and uncertainty about sampled depths relative to the bottom of the water column preclude reliable estimation of the frequency or duration of these episodes.

Water chemistry, optical properties, and nutrients. The waters of Lake Marion and its main tributary were circumneutral in pH (means of 7.0-7.6 among the 11 river and lake stations), low in specific conductance (82-122 µmho cm^{-2}), soft (18.3-26.5 mg $liter^{-1}$ Ca + Mg), moderately to highly turbid (6-20 NTU; Secchi transparency 0.8-1.3 m among the 7 lake stations), and moderately colored (35-50 PCU) (Appendix A).

Nutrient levels were moderate for both total phosphorus (medians of <0.02-0.8 mg $liter^{-1}$ among the 11 river and lake stations) and total nitrogen (0.49-0.77 mg $liter^{-1}$; 4 years only) (Appendix A).

pH, specific conductance, and hardness differed among the river stations; turbidity, and total nitrogen did not (Table 3.3, Figure 3.4). Broad overlap of interquartile ranges suggests that total phosphorus values did not differ. Values of specific conductance and hardness for the Santee River were intermediate between values for Congaree and Wateree rivers.

pH, hardness, turbidity, and total nitrogen, but not specific conductance, differed between the influent river station (SC-008) and some or all of the lake stations (Table 3.3, Figure 3.4). Total phosphorus values also appeared to differ, based on positions of the interquartile ranges. pH increased downlake from the influent river station among the main basin stations, while hardness, turbidity, total phosphorus, and total nitrogen decreased. Based on the numbers of differing pairs of stations, the gradients were strongest for pH and turbidity and weakest for total nitrogen. Only pH and specific conductance differed between the backwater stations; various parameters for the backwater stations differed from the influent and main basin stations.

For the three stations nearest to the upper end of the lake (SC-039 and SC-044 in the backwaters and SC-010 in the upper main basin), we tested for correlations with discharge from the Santee River into the lake. At the main basin station, the inverse correlations for pH and specific conductance and the direct correlation for turbidity were strong; and the correlations for hardness and total nitrogen were not significant (Table 3.4, Figure 3.5). The scatter plot suggests that the correlation would not be significant for total phosphorus. The pattern of strong and weak or not significant correlations was similar among the backwater station and main basins, except that the correlation for turbidity was not significant at SC-039.

Chlorophyll a. Because chlorophyll a appeared to vary widely among stations and among months (Figure 3.6), we separated by data by season (winter: December through February, spring: March through May; summer: June through August; fall: September through November) for analysis. Chlorophyll varied seasonally at all lake stations except SC-022 (Table 3.5). Seasonal means were lowest in winter, ranging from 1.5 µg $liter^{-1}$ at SC-010 to 7.2 µg $liter^{-1}$ at SC-022, and highest in summer, ranging from 8.1 µg $liter^{-1}$ at SC-022 to 22.2 µg $liter^{-1}$ at SC-044. Seasonal means among river stations were 3.8-4.7 µg $liter^{-1}$ in summer (2014-2015 only).

Chlorophyll a increased from the upper to the lower end of the main basin during fall, winter, and spring (Table 3.6, Figure 3.7). The increase was weak in spring: only one pair of stations differed. In summer, none of the main basin stations differed. In all seasons, the two backwater stations differed from each other. SC-039 did not differ from the upper main basin stations in any season; SC-044 differed from several of the main stations in each season.

For the three stations nearest to the upper end of the lake (SC-039 and SC-044 in the backwaters and SC-010 in the upper main basin), chlorophyll a was inversely correlated with discharge in spring and summer (Table 3.7, Figure 3.8). These correlations were stronger in spring. The correlations were not significant or weak (SC-044) in winter, and not significant for the backwaters but strong at SC-010 in fall.

Comparisons of total phosphorus and chlorophyll a between 1984-1995 and 1997-2014. Sufficient data were available to compare total phosphorus between the two periods for ten river and lake stations. Station SC-044 was omitted because it was sampled in only the latter half of the 1984-1995 period. Among the 10 river and lake stations, median total phosphorus ranged lower during the recent period (<0.02 mg liter^{-1} at SC-022 to 0.08 mg liter^{-1} at SC-002) than during the earlier period (medians of 0.3 at SC-022 to 0.8 mg liter^{-1} SC-002 and SC-004) (Figure 3.9, Appendices A and B). Comparisons of total phosphorus between 1984-1995 and 1997-2014 are limited by the high proportions of values below the detection limit in the 1997-2014 period. According to Wilcoxon rank sum tests, total phosphorus during the 1996-2014 period was lower at four of the ten stations: SC-001, SC-008, SC-010, and SC-022. Testing based on maximum likelihood techniques might be more appropriate (see Helsel, 2006).

Sufficient data were available to compare chlorophyll a between the two periods for six lake stations. Station SC-044 was omitted because it was sampled in only 3 or 4 years of the 1984-1995 period. Summer chlorophyll a during the 1996-2014 period was lower at all six stations, and winter chlorophyll a was lower at all but the lower main basin station (Figure 3.9). Differences in spring and fall patterns (not shown) were similar to those in summer. Seasonal means across the five main basin stations in 1997-2014 (Appendix A).were less than half of the corresponding values for 1984-1995 (Appendix B).

Discussion

The waters of Lake Marion provide a strongly seasonal thermal environment, ranging from hot in summer to cool but rarely cold in winter. Spatial variation was slight: a significant downlake thermal gradient in the main basin station occurred only in November, when the lowermost station was slightly warmer than the uppermost station.

Although thermal stratification was weak in the open waters of the main basin, episodes of oxygen depletion did occur. They did not extend into the near surface waters, and they were probably ephemeral. Such episodes are unlikely to have much direct impact on fish and other motile biota, but they may affect components of the benthos (Chapter 4).

Dense stands of aquatic macrophytes can restrict water circulation, promoting thermal stratification and oxygen depletion. Foltz and Kirk (1994) recorded severe hypoxia in shallow, vegetated areas of upper Lake Marion in 1991, when hydrilla was the dominant invasive. Similar effects undoubtedly occur now in shallow waters when stands of floating heart and other aquatic vegetation develop.

The 1997-2014 water quality data show downlake patterns in turbidity and total phosphorus that are consistent with Thornton's reservoir zonation model. The zonation model predicts a downlake decline in turbidity, or a downlake increase in Secchi transparency, due to the settling of suspended material as water velocity slows. The model also predicts a downlake decline in nutrients, due to both settling and uptake by plants. Both of these patterns were evident in the 1997-2014 data (Figure 3.4), as well as in previous studies (summarized in Table 3.1).

The zonation model predicts a chlorophyll minimum at the upper end of the transition zone, in consequence of dilution by influent waters, and maximum toward the lower end of the transition zone, in consequence of greater light availability with decreasing turbidity, followed by a decrease the lacustrine zone due to depletion of nutrients. Both Pickett and Harvey (1988) and Carswell (1996) identified this general pattern in Lake Marion. Their analyses combined data among seasons.

Our analyses show that the spatial pattern of chlorophyll a has a strong seasonal component in Lake Marion. In summer, chlorophyll a was relatively high (11 µg liter^{-1}) at the uppermost main basin stations, and the changes downlake were at best only marginally significant. The small sample of the influent river water suggests that chlorophyll a increased substantially after the water entered the lake. In winter, chlorophyll a was lowest at the uppermost main basin station (2 µg liter^{-1}), and downlake increases within the main basin were strong. The spring and fall patterns were transitional. The greatest seasonal change occurred in the upper main basin. Seasonal change was not significant at station SC-022 in the lower main basin. This general pattern held also in our analyses of the 1984-1996 data.

In the upper main basin and backwaters, the strong inverse correlations suggest the importance of discharge to algal dynamics, particularly in spring. We consider processes influencing algal abundances in the upper main basin during the April-June recruitment period for key fish species in Chapter 5.

Comparisons between the 1984-1995 and 1997-2014 periods indicate substantial change in processes influencing algal abundances. The striking declines (by more than half in all seasons) in chlorophyll a in the main basin were not commensurate with changes in total phosphorus concentrations in either the Congaree River (15% decrease in the median) or the Wateree River (no change in the median). (The decline in total phosphorus concentrations was associated in part with implementation of provisions of the Clean Water Act of 1972, including a state-wide restriction on phosphorus in detergents, beginning in 1992.)

However, because average inflow of water was substantially greater (by nearly 40%) during the earlier period, the phosphorus loads would likely have been similarly greater. The relations between nutrient loads and algal productivity are complex, and processes of settling and remobilization for particle-bound nutrients introduce time lags and other complications to the responses (e.g., Tufford, 1996). The extremely low nutrient concentrations at the lower end for the main basin during the recent period do suggest that nutrient removal, by physical, chemical, or biological processes, within the main basin may be more efficient during the recent period than during the earlier period.

Table 3.1. Water quality patterns reported in previous studies on Lake Marion. Water quality patterns are based on time period, sampling interval, and stations. Each of the studies included additional stations not considered here (Inabinet: 29 stations, including other stations in Lake Marion and Lake Moultrie; Pickett & Harvey: 12 stations, including Lake Moultrie; Carswell: 6 stations in Lake Moultrie; Tufford: 4 stations in small tributaries).

Study	***Water quality pattern in Lake Marion***
Inabinet (1985) 1984, monthly, 8 stations Rivers (4 stations) Main channel of lake (4 stations)	Spatial Strong downlake increases in Secchi transparency Downlake decreases in nutrients (total phosphorus, nitrate) No pattern in chlorophyll (lake stations only)
Pickett & Harvey (1988) March 1985-March 1986, bimonthly 78 stations, grouped by cluster analysis and identified as riverine, transitional, lacustrine, and backwater zones	Spatial Secchi transparency increased from riverine through transitional zones Nutrients decreased from riverine through transitional zones Chlorophyll a increased from river zone to a maximum near lower end of transitional zone, decreased in lacustrine zone
Carswell (1996) 1985-1995, monthly, 16 stations Upper region (above I-95, 6 stations) Middle region (upper two-thirds of region below I-95, 5 stations) Lower region (lower third of region below I-95, 5 stations)	Spatial Secchi transparency increased from upper to lower regions Total phosphorus decreased from upper to lower regions Chlorophyll a lowest in upper region, highest in middle region Seasonal Secchi transparency lowest in winter, highest in summer Chlorophyll a highest in summer, lowest in winter No seasonal variation in total phosphorus
Tufford (1996) 1985-1990, monthly,15 stations Rivers (3 stations) Up-stream lake (above I-95, 5 stations) Down-stream lake (below I-95, 7 stations)	Effects of discharge (results with $P<0.01$ only) Direct correlations with total phosphorus in rivers (1 station), up-stream lake region (2 stations), and down-stream lake region (3 stations) Inverse correlation with total nitrogen in rivers (1 station); direct correlation in down-stream lake region (1 station) Inverse correlations with chlorophyll a in up-stream lake region (2 stations)

Table 3.2. Water quality stations. Locations are shown in Figure 3.1. List is organized geographically.

Station ID	***Station name***	***Region***
SC-001	Congaree River at US 601 bridge	River
SC-002	Wateree River at Little River	River
SC-004	Upper Santee River 2 km upstream of mouth of Broadwater Creek	River
SC-008	Upper Santee River at Rimini railroad trestle	River
SC-039	Upper Lake Marion 2.0 km below Rimini (Seaboard Coastline) railroad trestle	Backwaters
SC-044	Upper Lake Marion 0.5 km northeast of Stump Hole public landing	Backwaters
SC-010	Upper Lake Marion at Channel Marker 150	Upper main basin
SC-015	Upper Lake Marion at I-95/ US 301 bridge	Upper main basin
SC-040	Mid Lake Marion at Channel Marker 79	Middle main basin
SC-016	Mid Lake Marion at Channel Marker 69	Middle main basin
SC-022	Lower Lake Marion at Old Santee River Channel Marker 44	Lower main basin

Table 3.3. Analysis of variance of pH, specific conductance, hardness, turbidity, and total nitrogen among stations by region, 1997-2014. All available data for 1997-2014 were used in the analyses (Appendix A: data from 10 or more years for most stations for all parameters except total nitrogen; data from 4 years for total nitrogen). Differences between pairs of stations were determined by the Tukey method using 95% simultaneous confidence intervals. Mean values of parameters are plotted by station in Figure 3.4.

Region	*ANOVA statistics*	*Differing pairs of stations*
pH		
Rivers	F(3, 641)=3.05, P=0.03	SC-002 & SC-008
Influent & lake	F(7, 1198) =31.0, P<0.001	SC-008 & SC-044, SC-010, …, SC-022
		SC-039 & SC-044, SC-015, …, SC-022
		SC-044 & SC-016, SC-022
		SC-010 & SC-016, SC-022
		SC-015 & SC-016, SC-022
		SC-040 & SC-016, SC-022
Specific conductance (log-transformed)		
Rivers	F(3, 565)=96.5, P<0.001	
		SC-001 & SC-002, SC-004, SC-008
		SC-002 & SC-004, SC-008
Influent & lake	F(7,1198) =4.90, P<0.001	
		SC-039 & SC-044, SC-015, …, SC-022
Hardness		
Rivers	F(3, 277)=23.1, P<0.001	SC-001 & SC-002, SC-004, SC-008
		SC-002 & SC-004, SC-008
Influent & lake	F(7,754) =4.90, P<0.001	SC-008 & SC-022
		SC-039 & SC-022
		SC-010 & SC-016, SC-022
Turbidity (log-transformed)		
Rivers	F(3, 343)=2.49, NS	-
Influent & lake	F(7,806) =37.7, P<0.001	SC-008 & SC-015, …, SC-022
		SC-039 & SC-040, …, SC-022
		SC-010 & SC-015, …, SC-022
		SC-015 & SC-016, SC-022
		SC-040 & SC-016, SC-022
Total nitrogen		
Rivers	F(3, 157)=0.40, NS	-
Influent & lake	F(7,301)=2.40, P=0.02	SC-008 & SC-022

Table 3.4. Correlations of pH, specific conductance, hardness, turbidity, and total nitrogen at stations in upper Lake Marion with discharge from the Santee River, 1997-2014. All available data for 1997-2014 were used in the analyses (Appendix A: data from 10 or more years for all parameters except total nitrogen; data from 4 years for total nitrogen). Discharge was estimated as the combined discharge of the Congaree River at Columbia and Wateree River with a 3-day lag (Chapter 2). Discharge was log-transformed. Data for upper main basin station SC-010 are shown in Figure 3.5.

Region	*Station*	*Correlation statistics and direction*		*n*
pH				
Backwaters	SC-039	r^2=0.27, P<0.001	NEGATIVE	119
	SC-044	r^2=0.25, P<0.001	NEGATIVE	108
Main basin	SC-010	r^2=0.30, P<0.001	NEGATIVE	165
Specific conductance (log-transformed)				
Backwaters	SC-039	r^2=0.23, P<0.001	NEGATIVE	113
	SC-044	r^2=0.60, P<0.001	NEGATIVE	109
Main basin	SC-010	r^2=0.60, P<0.001	NEGATIVE	167
Hardness				
Backwaters	SC-039	r^2=0.03, NS		93
	SC-044	r^2=0.08, P=0.008	NEGATIVE	90
Main basin	SC-010	r^2=0.00, NS		95
Turbidity (log-transformed)				
Backwaters	SC-039	r^2=0.02, NS		98
	SC-044	r^2=0.42, P<0.001	POSITIVE	96
Main basin	SC-010	r^2=0.27, P<0.001	POSITIVE	100
Total nitrogen				
Backwaters	SC-039	r^2=0.01, NS		29
	SC-044	r^2=0.09, NS		36
Main basin	SC-010	r^2=0.03, NS		42

Table 3.5. Analysis of variance of chlorophyll a among seasons by station, 1997-2014. All available data for 1997-2014 were used in the analyses (Appendix A: data from 13 or more years for each station in each season). Seasons were winter (December through February), spring (March through May), summer (June through August), and fall (September through November). Differences between pairs of stations were determined by the Tukey method using 95% simultaneous confidence intervals. Means are plotted by station and season in Figure 3.7.

Station	***ANOVA statistics***	***Differing seasons***
Backwaters		
SC-039	F(3, 129)=16.8, P<0.001	Winter & Spring, Summer, Fall Fall & Winter
SC-044	F(3, 131)=20.8, P<0.001	Winter & Spring, Summer, Fall
Upper main basin		
SC-010	F(3, 146)=32.2, P<0.001	Winter & Spring, Summer, Fall Spring & Summer Fall & Winter
SC-015	F(3, 163)=27.4, P<0.001	Winter & Spring, Summer, Fall Spring & Summer Fall & Winter
Middle main basin		
SC-040	F(3,134)=17.3, P<0.001	Winter & Spring, Summer, Fall Fall & Winter
SC-016	F(3,142)=15.0, P<0.001	Winter & Spring, Summer, Fall Spring & Summer
Lower main basin		
SC-022	F(3,147)=1.6, NS	-

Table 3.6. Analysis of variance of chlorophyll a among stations by season, 1997-2014. All available data for 1997-2014 were used in the analyses (Appendix A: data from 13 or more years for each station in each season). Seasons were winter (December through February), spring (March through May), summer (June through August), and fall (September through November). Differences between pairs of stations were determined by the Tukey method using 95% simultaneous confidence intervals (also, 90% intervals during summer). Means are plotted by station and season in Figure 3.7.

Region	***ANOVA statistics***	***Differing pairs of stations***
Chlorophyll a during winter (log-transformed)		
Backwaters and main basin	F(6, 232)=14.8, p<0.001	SC-039 & SC-044, SC-040, SC-016, SC-022 SC-044 & SC-010, SC-015, SC-022 SC-010 & SC-040, SC-016, SC-022 SC-015 & SC-016, SC-022 SC-016 & SC-022 SC-040 & SC-022
Chlorophyll a during spring (log-transformed)		
Backwaters and main basin	F(6, 272)=7.4, p<0.001	SC-039 & SC-044 SC-044 & SC-015, SC-040, SC-016 SC-010 & SC-022
Chlorophyll a during summer (log-transformed)		
Backwaters and main basin	F(6, 283)=5.1, p<0.001	SC-039 & SC-044, SC016* SC-044 & SC-010, SC-015, SC-022 SC-016 & SC-022*
Chlorophyll a during fall (log-transformed)		
Backwaters and main basin	F(6, 212)=11.0, p<0.001	SC-039 & SC-044, SC-016, SC-022 SC-044 & SC-010, SC-015 SC-010 & SC-015, SC-040, SC-016, SC-022 SC-015 & SC-016, SC-022

*Significant using 90% simultaneous confidence intervals

Table 3.7. Correlations of chlorophyll a at stations in upper Lake Marion with discharge from the Santee River by season, 1997-2014. All available data for 1997-2014 were used in the analyses (Appendix A: data from 16 or more years for each station in each season). Seasons were winter (December through February), spring (March through May), summer (June through August), and fall (September through November). Discharge from the Santee River into Lake Marion was estimated as the combined discharge of the Congaree River at Columbia and Wateree River with a 3-day lag (Chapter 2). Discharge was log-transformed. Data for upper main basin station SC-010 are shown in Figure 3.8.

Region	*Station*	*Correlation statistics and direction*	*n*
Chlorophyll a during winter (log-transformed)			
Backwaters	SC-039	r^2=0.00, NS	32
	SC-044	r^2=0.13, p=0.03 NEGATIVE	36
Main basin	SC-010	r^2=0.00, NS	35
Chlorophyll a during spring (log-transformed)			
Backwaters	SC-039	r^2=0.28, p<0.001 NEGATIVE	38
	SC-044	r^2=0.40, p<0.001 NEGATIVE	38
Main basin	SC-010	r^2=0.39, p<0.001 NEGATIVE	41
Chlorophyll a during summer (log-transformed)			
Backwaters	SC-039	r^2=0.07, p=0.03 NEGATIVE	38
	SC-044	r^2=0.21, p<0.001 NEGATIVE	36
Main basin	SC-010	r^2=0.09, p=0.01 NEGATIVE	44
Chlorophyll a during fall (log-transformed)			
Backwaters	SC-039	r^2=0.08, NS	25
	SC-044	r^2=0.13, NS	25
Main basin	SC-010	r^2=0.29, p=0.002 NEGATIVE	30

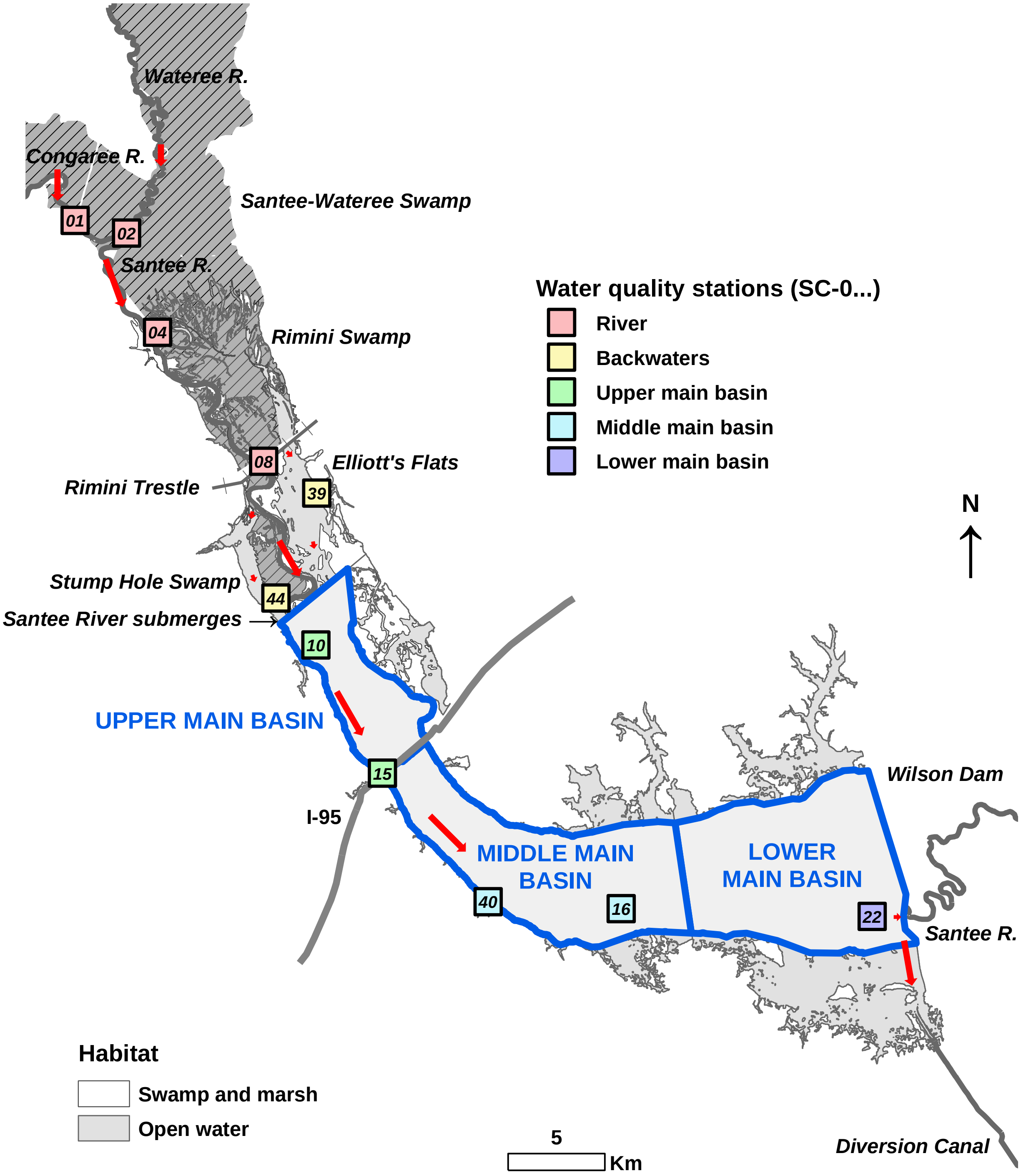

Figure 3.1. Water quality stations in and above Lake Marion. The stations are described in Table 3.2. Stations are labelled on the map by the last two digits of the identification code. Red arrows show main flow paths of water; length of arrow indicates magnitude of discharge (see Chapter 2).

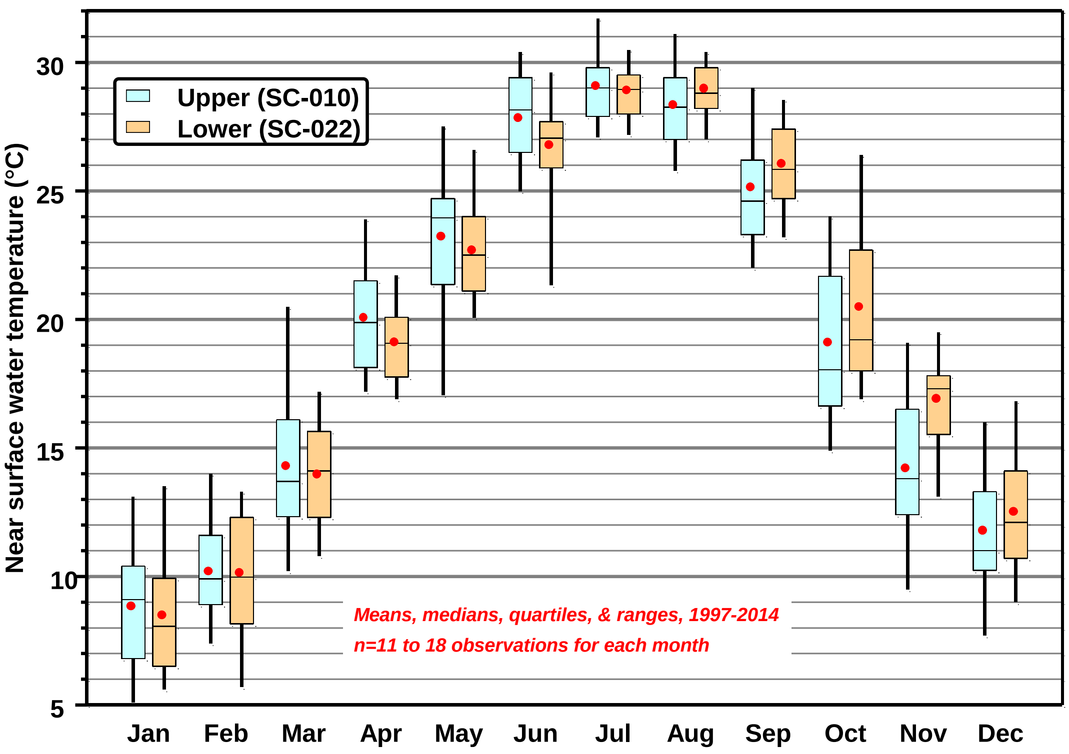

Figure 3.2. Surface temperature by month at upper main basin station SC-010 and lower main basin station SC-022, 1997-2014.

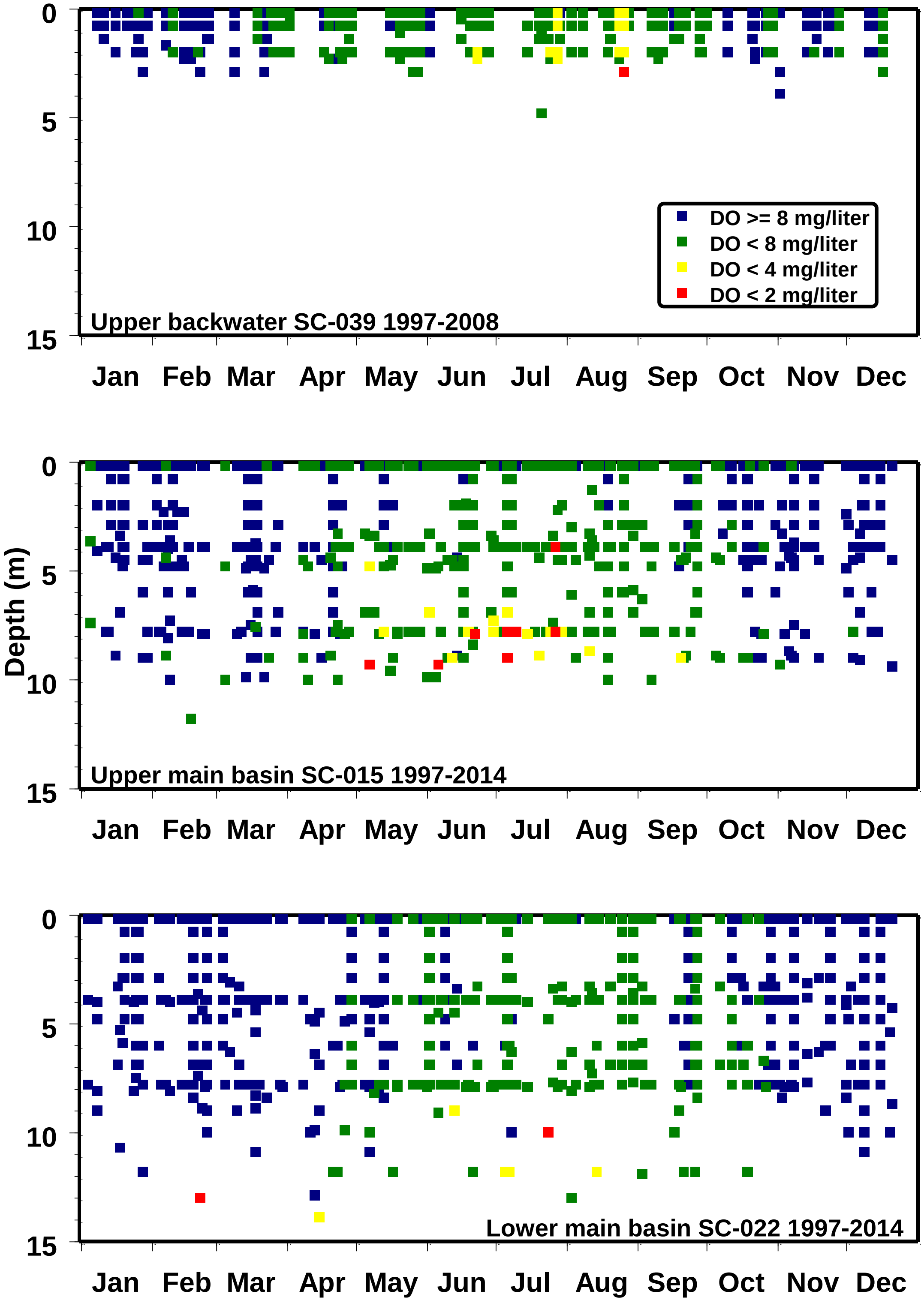

Figure 3.3. Dissolved oxygen by month and depth at stations in the upper backwaters, upper main basin, and lower main basin, 1997-2014.

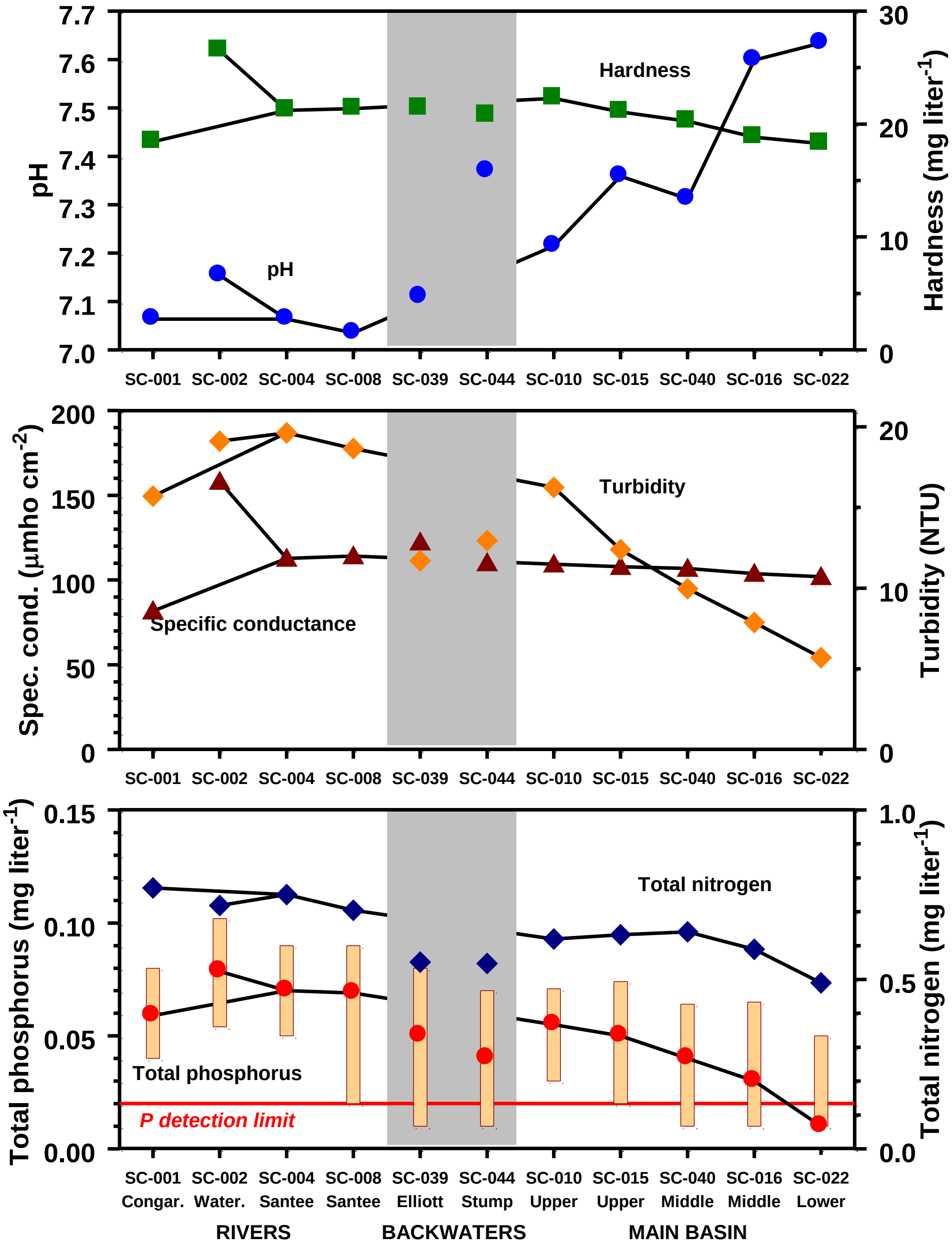

Figure 3.4. Variation in water quality among stations, 1997-2014. Mean values are shown for pH, hardness, specific conductance, turbidity, and total nitrogen; medians and quartiles are shown for total phosphorus. Note the minimum detection limit for total phosphorus. Standard summary statistics are reported in Appendix A; analyses of variance, in Table 3.3.

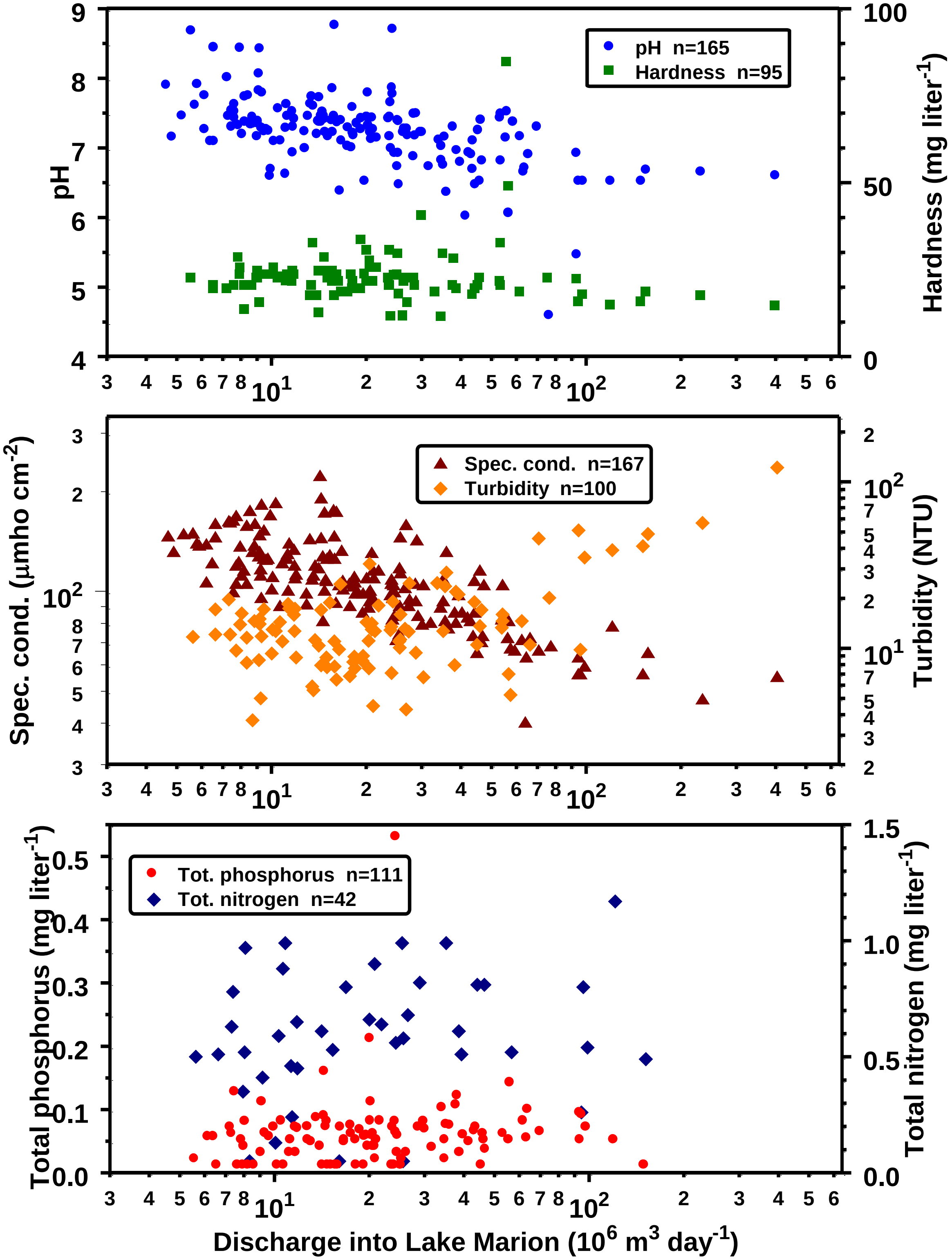

Figure 3.5. Plots of water quality at station SC-010 against estimated discharge from the Santee River. Correlations are reported in Table 3.4.

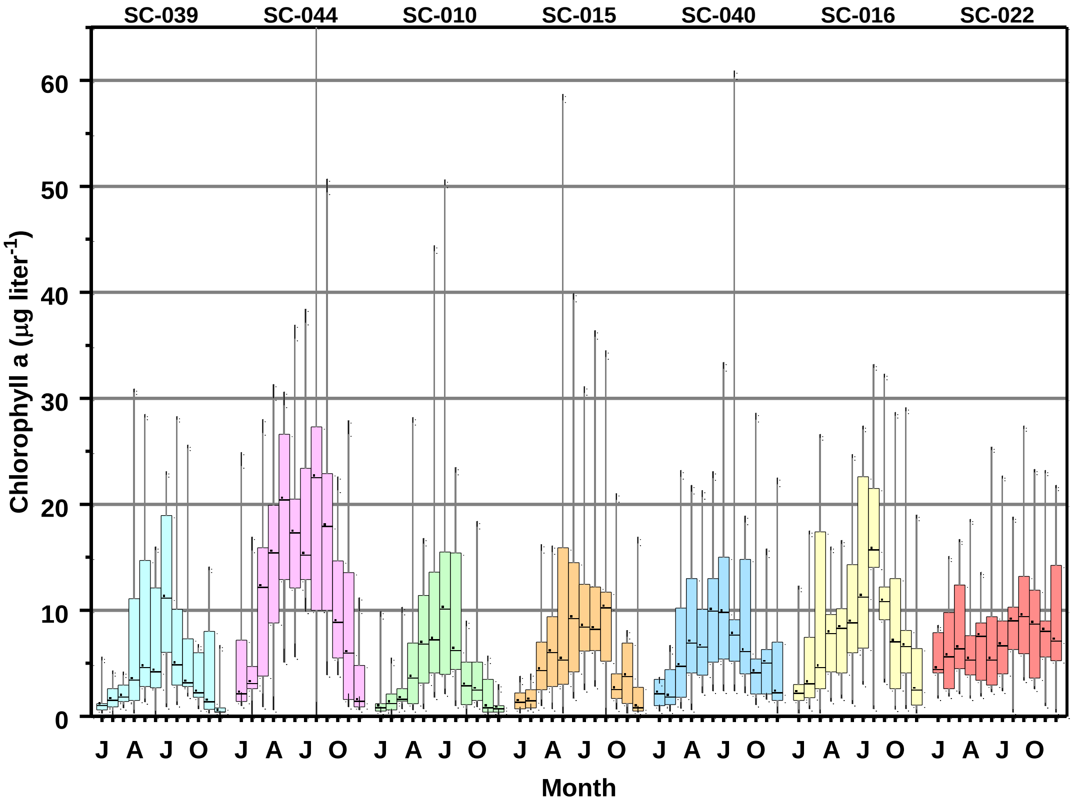

Figure 3.6. Boxplots of chlorophyll a by station and month, 1997-2014.

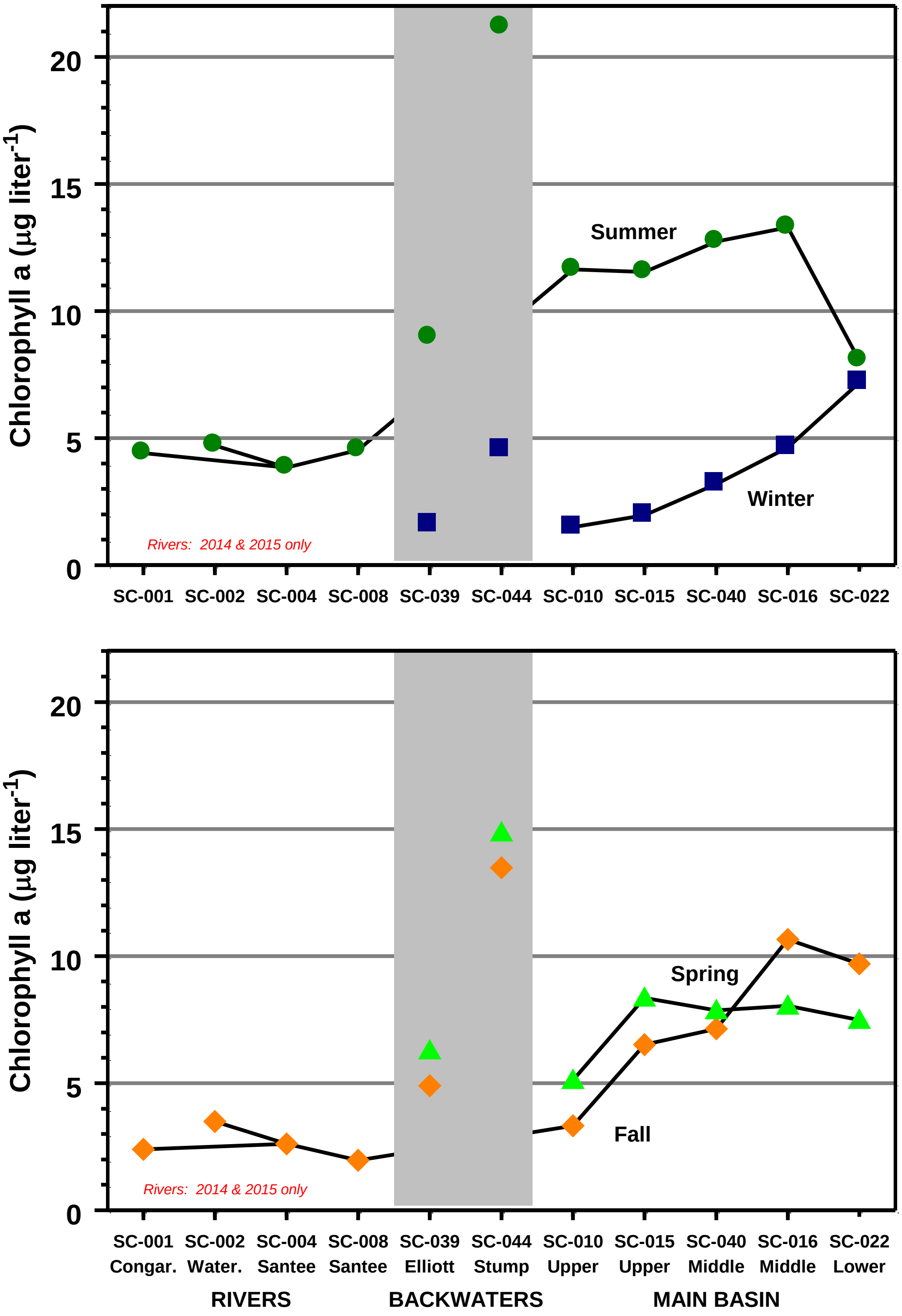

Figure 3.7. Variation in chlorophyll a among stations by season, 1997-2014. Standard summary statistics are reported in Appendix A; analyses of variance, in Table 3.5.

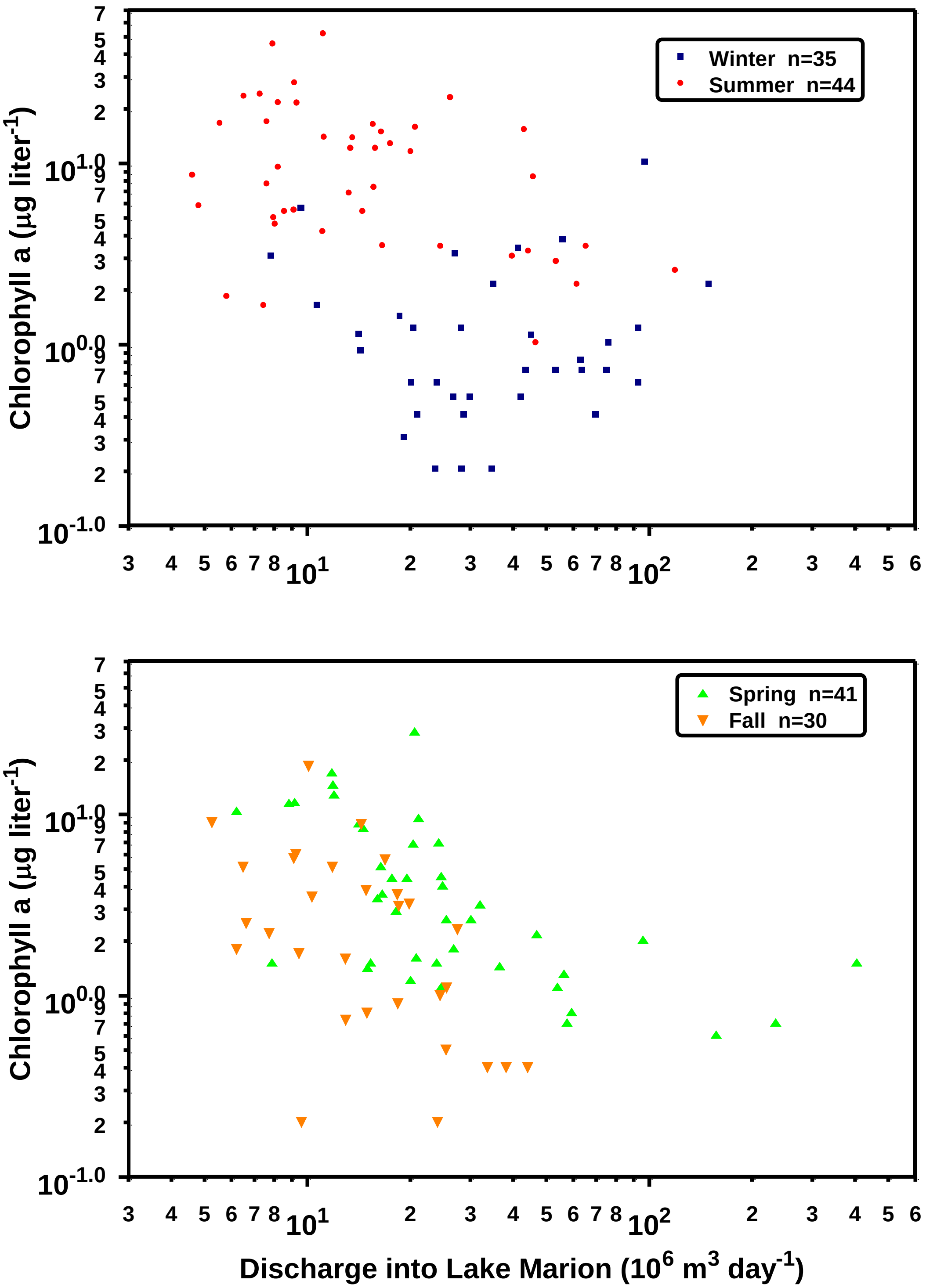

Figure 3.8. Plots of chlorophyll a at station SC-010 by season against discharge from the Santee River, 1997-2014. Correlations are reported in Table 3.6.

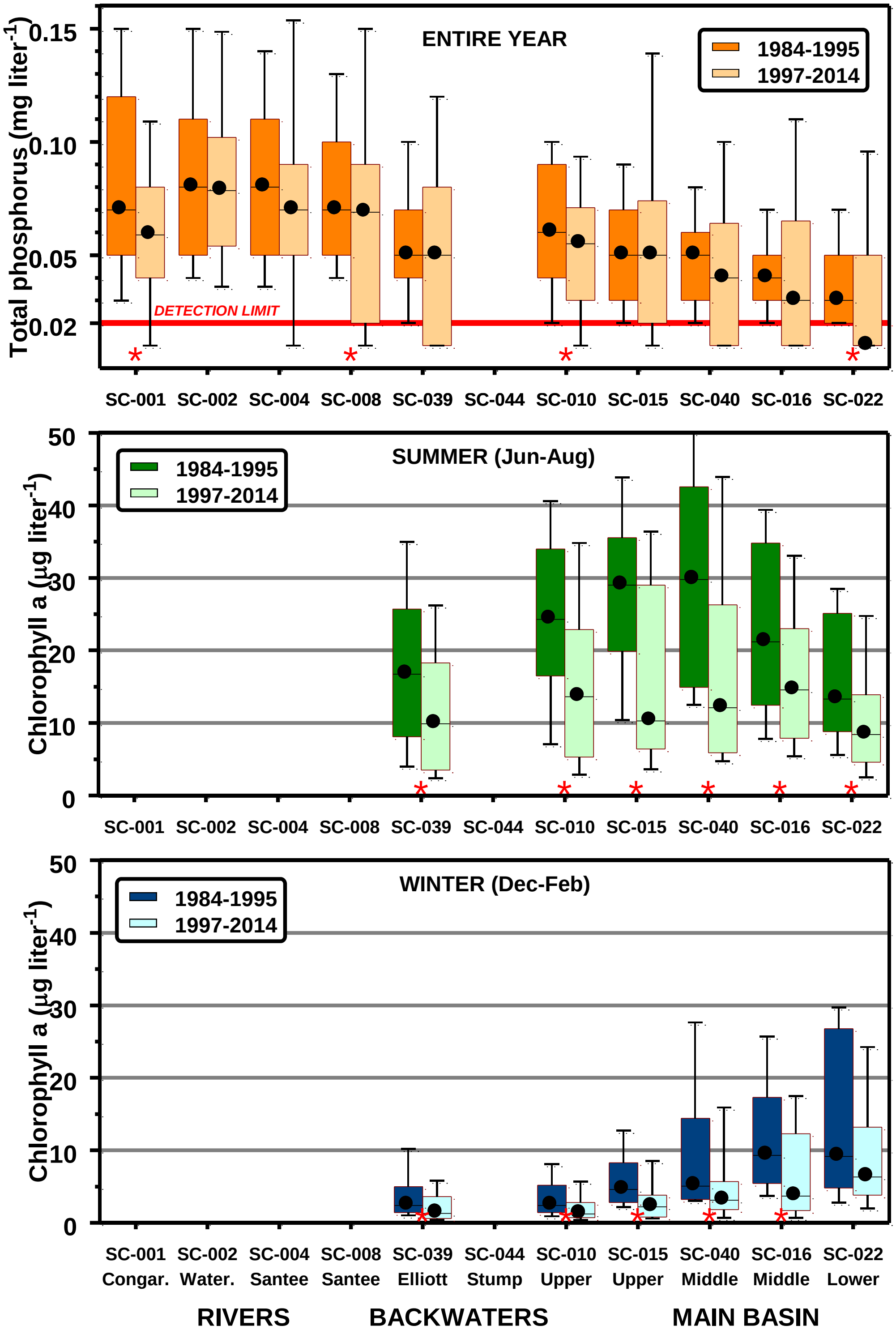

Figure 3.9. Comparisons of total phosphorus (entire year) and chlorophyll a (summer, winter) by station between 1984-1995 and 1997-2014. Medians, quartiles, and ranges are shown for each period. Standard summary statistics are reported in Appendices A and B. Asterisks mark significant differences between periods (Wilcoxon signed rank test: $P < 0.05$).

CHAPTER 4. The Benthos

The benthos plays central roles in the food webs of most lacustrine systems (Vadeboncoeur et al., 2002). Among lakes of northern temperate regions of North America, about half of the production of the main fish species is supported directly or indirectly by the benthos (Vander Zanden and Vadeboncoeur, 2002). The relations among benthic and pelagic consumers are complex: they may depend on separate resources, or they may compete. Large populations of filter-feeding benthic mollusks are capable of removing substantial proportions of planktonic primary production (e.g., Madenjian, 1995) and altering the availability of benthic and pelagic resources to the fish community (e.g., Johannsson et al., 2000). The potential depletion of resources for pelagic species has fueled the concern for impact on fisheries by invasives such as the Asiatic clam *Corbicula fluminea* (e.g., Lopez et al., 2006; review by Sousa et al., 2008) and the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis* (e.g., Schneider, 1992; Madenjian, 1995; Zhang et al., 2011). In practice these effects have proven difficult to demonstrate unambiguously, due to the complexity and temporal variability of the invaded systems, as well as limitations of the data, but the effects appear strong in some systems, such as the Hudson River estuary, invaded by *D. polymorpha* (Strayer et al., 1994).

Prior information about the benthos of Lake Marion is sparse. *C. fluminea* was first reported from the Santee Cooper system, which includes Lake Marion, in 1976 (Fuller, 1978). Alderman (2005) documented 17 species of unionid mussels, including five species listed as imperiled or critically imperiled; occurrences of *C. fluminea* and the Chinese mystery snail *Cipangopaludina* (*Bellamya*) *chinensis malleata* were also noted. The olive mystery snail *Viviparus subpurpureus*, a native transplant from Gulf Coast drainages (Benson, 2014), became abundant in Lake Marion sometime before 2003 (Dillon and Stewart, 2013). The banded mystery snail *Viviparus georgianus*, probably another native transplant, has also been reported (see Fuller, 1978; Kipp et al., 2015). Conspicuous numbers of the burrowing mayfly *Hexagenia limbata* emerge during spring and summer (authors' observations).

Until recently, *C. fluminea* in North America has been treated as a single species with distinct morphotypes: the A form, which has white nacre, and the B form, which has purple nacre (Cummings and Graf, 2010). The A form is widely distributed; the B form is limited to southwestern states. Mitochondrial genetic markers identify the A form with Asian populations of *C. leana*; the B form, with Asian *C. fluminea* (Siripattrawan et al., 2000). Both morphology (white nacre) and geography suggest that the Lake Marion population belongs to *C. leana*. Lacking a genetic evaluation, we refer to it as *Corbicula* sp. In references to published literature, we retain the authors' designations.

The goal of this study was to estimate composition, abundance, and biomass of the benthic invertebrates in Lake Marion to provide a basis for considering benthic contributions to the food web. We sampled the benthos in spring and early summer of 2009 and 2010. Using published information from other systems, we classified the benthic invertebrates by functional feeding group and resource base. We discuss possible direct and indirect effects of the benthos on the lake's food web and fisheries. An earlier version of this chapter was published by Taylor, Bulak, and Morrison (2016).

Methods

The benthos was sampled at stations on transects across the main basin of Lake Marion (Figure 4.1). Five stations were evenly spaced across each transect. The upper main basin was sampled on 24 June and 1 July 2009 (50 samples on 10 transects) and 22 April 2010 (25 samples on 5 transects); the middle main basin, on 23 June 2010 (25 samples on 5 transects); the lower main basin, on 24 and 30 June 2010 (15 samples on 3 transects). Stations were located with a hand-held GPS unit. Water depth was determined using Sonar or a sounding line.

Two samples were taken at each station with a Petite Ponar Bottom Grab sampler (152 mm by 152 mm). One sample was placed on a 0.5-mm stainless steel screen and gently rinsed with water pumped from the lake. Benthic organisms and other material retained on the screen were preserved in 70% alcohol. Sediment was collected from the other sample for analysis of texture and organic carbon content.

Sediment particles <500 µm were analyzed on a Cilas 930 Laser Particle Size Analyzer; samples were sieved to remove particles >500 µm before processing. Particles >500 µm were analyzed by screening dry sediment with a 500-µm sieve, then weighing both fractions. Two replicates were run for each of the textural analyses. Particles were classified as clay (<4 µm; 8 phi), silt (4-62 µm; 4 phi), very fine sand (62-125 µm; 3 phi), fine sand (125-250 µm; 2 phi), medium sand (250-500 µm; 1 phi), and coarse sand (>500 µm; 0 phi). Grain size statistics were computed according to Folk (1974). Samples for organic carbon content were dried and ground with a mortar and pestle before analysis with a LECO 628 Carbon/Hydrogen/Nitrogen Determinator.

In the laboratory, each benthic sample was rinsed on a 0.5-mm Nitex sieve to remove sediment and preservative, then placed in a metal tray for sorting. Volumes of living aquatic vegetation and woody debris were estimated. All visible invertebrates were removed. Most were grouped into 5-mm size classes for counting. Prior simulations with plausible length distributions indicated that this grouping would have little impact on the accuracy of the biomass estimates (<5% difference from estimates based on 1-mm size classes). We identified common benthic invertebrates, except dipterans, to genus or species, rarer taxa to family or higher level using standard keys and additional reference materials.

Dry biomasses, exclusive of shell for mollusks, were estimated using regressions compiled by Benke et al. (1999) for *C. fluminea* (Lauritsen and Mozley's summer equation for a population in North Carolina), unionids (Balfour and Smock's equation for *Elliptio complanata* in Virginia and Cameron et al.'s equation for *Lampsilis ochracea* in New Brunswick), and *H. limbata* (Smock's equation for *H. munda* in North Carolina). The equation for *C. fluminea* was also used for the sphaeriids, which are similar in form to small *Corbicula*. Dry biomass for *V. subpurpureus* was estimated from a function fitted to data in Richardson and Brown (1989):

$$B = \exp(2.925 * \ln(L) - 11.0152) , \qquad \text{[Eq. 4.1]}$$

where B is dry biomass in grams and L is shell length in mm. Values of 0.1 mg and 0.04 mg were used for larvae of the phantom midge *Chaoborus punctipennis* and for larvae of midges in the family Chironomidae, respectively (Taylor, extensive unpublished data for samples from an impoundment on the Savannah River Site, South Carolina). A biomass of 2 mg, computed from equations in Benke et al. (1999), was used for amphipods.

Confidence intervals for abundances were generated by bootstrapping in S-Plus (TIBCO Software, Inc., Palo Alto, CA). Relations between abundances of the benthic organisms and substrate attributes were explored with regression tree models in S-Plus. Abundances were square-root transformed to normalize variance. In tree construction, observations were split to minimize the sum of deviances across groups. Deviance for each group was computed as the sum of squared deviations from the group mean. Minimum node size was set at 10; the minimum number of observations for a split, at 5. Trees were pruned to remove branches with little effect on total deviance.

To evaluate the resource base for the benthos, we used functional feeding group designations compiled by Cummins and Merritt (1984; insects only) and Barbour et al. (1999), supplemented with other literature.

Results

Environmental variables

Median sample depths were 3.4 m (1.2-5.1 m) in the upper main basin (2009 samples), 5.5 m (1.2-8.5 m) in middle main basin, and 7.8 m (1.2-12.8 m) in the lower main basin. Average daily lake surface elevation varied by 0.24 m among sampled dates.

Woody debris, leaf litter, and empty mollusk shells occurred in most of the samples. Algal mat was present in about 10% of the samples; macrophytes were sparse.

Sediment texture ranged from fine sand to clay, becoming finer with increasing depth (Figure 4.2A). Total organic carbon ranged <0.1% to 6% of sediment dry weight, becoming greater with increasing depth (Figure 4.2B). Log-transformed total organic carbon was inversely correlated with mean grain size of the sediment ($r^2 = 0.57$, $P < 0.0001$, $n = 89$).

Benthos

Mollusks, mainly *Corbicula* sp. and *Viviparus subpurpureus*, were most abundant numerically in the benthic samples. Insects, mainly nymphs of *Hexagenia limbata* and larvae of Chironomidae and *Chaoborus punctipennis*, were common (Table 4.1, Figure 4.3). Amphipods were the most abundant taxon among the crustaceans. Oligochaetes and leeches were present in low numbers.

In the summer samples, abundances of *Corbicula* sp., *V. subpurpureus*, and *H. limbata* decreased from the upper to the lower main basin. *H. limbata* was entirely absent from the lower main basin. Abundances of both *C. punctipennis* and Chironomidae were similar among these regions.

In the upper main basin, size structure of the *Corbicula* sp. population was weakly bimodal in both summer 2009 and spring 2010 (Figure 4.4, upper panel). The first modes fell at 10-15 mm in 2009 and 15-20 mm in 2010, but broadly overlapping 95% confidence interval estimates suggest that the difference was not significant. The second, smaller mode fell at 25-30 mm in both years. The *V. subpurpureus* population was strongly unimodal in both years with the modal class near the upper end of the size distribution (Figure 4.4, middle panel). The *H. limbata* population included much higher numbers in the smallest size classes (5-10 and 10-15 mm) in the spring samples than in the summer samples; it was dominated by larger size classes (15-20 and 20-25 mm) in the summer samples (Figure 4.4, lower panel).

Analyses of summer data (2009 and 2010 combined) identified water depth as the most important factor influencing numerical abundance of the benthic invertebrates (Table 4.2). Further splits due to water depth, sediment texture, and total organic carbon were weak or trivial, separating narrow portions of the distributions. *Corbicula* sp., *V. subpurpureus*, and *H. limbata* were less abundant in samples from deep water (>5 m or more, depending on species). *V. subpurpureus, H. limbata*, and *C. punctipennis* were sparse or absent in samples from shallow water (<2 m).

Chironomidae were abundant (>1000 animals m^{-2}) in only two samples, both from shallow water in the upper main basin; abundances elsewhere were typically 100-300 animals m^{-2}.

Dry biomass, exclusive of shell, was overwhelmingly dominated by the mollusks, with *Corbicula* sp. contributing 60-80% of the totals by region (Table 4.3). Unionids contributed about 10% of the totals for the upper and middle main basins; these estimates are based on a small number of large individuals. Among insects, *H. limbata* contributed less than 10% of the total biomass in the upper and middle main basins. Despite the numerical abundances of *C. punctipennis* and Chironomidae, their biomasses were <1% of the totals. Estimated total benthic biomass was 6,400 metric tons (40% in the upper main basin, 45% in the middle main basin, and 15% in the lower main basin). The average was 32 g dry mass m^{-2}.

Benthic biomass was greatest at water depths of 3-4 m (Figure 4.5). Biomass of *Corbicula* sp. was greatest at 3-5 m; biomass of *V. subpurpureus*, at 2-4 m; biomass of *H. limbata*, at 3-5 m. Within the 2-6 m depth range, where all of these taxa occurred, biomasses of *Corbicula* sp. and *H. limbata* were positively correlated (r^2=0.15, N=61, p=0.002). Correlations for the other two pairs of species were not significant (p>0.05).

By functional feeding group, 73% of the average benthic biomass was composed of collector filterers; 5%, of collector gatherers (Table 4.4). Nearly all of the remainder (22%) was composed of *V. subpurpureus,* whose feeding habits have received little attention. Its classification as a scraper by Barbour et al. (1999) conflicts with the observations of Brown et al. (1989), which suggest that it functions as a collector filterer. In either case, most of the benthic biomass is supported by algae or fine particulate material. Biomass of the only abundant predator, the planktivore *C. punctipennis*, was very low (0.01-0.1%) in all three regions of the main basin. Differences in composition by functional group among these regions were slight.

Discussion

The benthos of Lake Marion was dominated by the clam *Corbicula* sp. and the snail *Viviparus subpurpureus*, which made up nearly 90% of the biomass of benthic invertebrates. Unionid clams and the mayfly *Hexagenia limbata* made up most of the remainder. All of these species are large: up to 30-40 mm, more for the unionids, as adults or mature nymphs. Trophically, these taxa function as collectors, filtering or gathering algae and fine particulate detrital material.

Corbicula sp. and *H. limbata*, but not *V. subpurpureus*, are commonly observed in other large southeastern impoundments. Both the clam and the mayfly can be important components of the benthos, but few data are available for comparison. In Lake Nocogdoches, Texas, Karatayev et al. (2003) reported that *C. fluminea* made up 97% of the wet biomass (including shell) of benthic invertebrates in the open water region of the impoundment. Abundances of *C. fluminea* averaged 16 animals m^{-2}, an order of magnitude less than in Lake Marion. In contrast, in Lake Dardanelle, Arkansas, *Hexagenia* dominated the benthic invertebrate biomass (Rickett and Watson, 1994; our assessment of relative biomass from reported abundances). In spring and summer over a 24-year period, abundances of *Hexagenia* were typically 50-100 animals m^{-2}, similar in magnitude to Lake Marion. *Corbicula* sp. appeared half-way through the study, but never became abundant and had no obvious effect on *Hexagenia* or other taxa. The average biomass of the benthos in Lake Marion appears to be high: one to two orders of magnitude greater than values summarized by Ploskey and Jenkins (1982; 0.1-2.2 g dry mass m^{-2}) for 12 impoundments in Europe and North America.

In Lake Marion, the benthic invertebrates, with the exception of dipterans, were most abundant at intermediate (2-4 m) water depths. Fluctuating water levels (typically >1 m annually in Lake Marion) and wave action may limit abundances in shallower water (e.g., White and White, 1977; effects of water level fluctuation are reviewed by Soballe et al., 1992). Although Lake Marion does not stratify consistently in summer, episodes of hypoxia may affect the benthos in deeper water. *Corbicula* sp. cannot survive prolonged hypoxia, particularly at warm water temperatures (Johnson and McMahon, 1998). *Hexagenia* spp. are also strongly affected by hypoxia (Schloesser et al., 2000).

The decrease in biomass of benthic invertebrates from the upper to the lower main basin was associated with the increase in water depth. Statistically, we could not separate effects of substrate from effects of depth on distributions of the benthos. Sediments were fine-grained throughout the lake, although mean grain size decreased and organic carbon content increased with depth. *H. limbata* occurred only at water depths of 2-6 m in the upper and middle regions. Its apparent absence in the lower region may simply reflect a lack of samples from this depth range: all of the samples were collected from shallower or deeper water.

Except for the absence of the phantom midge *C. punctipennis* in spring, composition and abundance of the benthos in the upper region differed little between spring and summer. The absence of *C. punctipennis* probably reflects emergence of an overwintering generation (e.g., Saunders, 1997); the early instars are typically planktonic. For *H. limbata*, the larger size in the summer samples suggests growth during late spring before emergence in late spring and early summer. The paucity of small size classes suggests that substantial recruitment to benthic habitats had not occurred prior to our sampling in spring for *Corbicula* sp. or in spring and summer for *V. subpurpureus*. Typically, *C. fluminea* reproduces in warm months (e.g., Cataldo and Boltovskoy, 1999), and planktonic larvae have been observed in the Santee River above Lake Marion in April-May (Chick and Van Den Avyle, 1999a). Less is known about seasonality of reproduction of *V. subpurpureus*: Brown et al. (1989) observed release of young embryos between January and April in a Louisiana bayou.

Functional feeding groups indicate that algae and fine detrital material are the main trophic resources for the benthic invertebrates. Lake nutrient concentrations are sufficient to support moderate to high planktonic algal productivity. Nothing is known about abundance or productivity of benthic algae in Lake Marion, although light attenuation due to low transparency of the water must limit productivity at depth (Vadeboncoeur et al., 2014). Influent total organic carbon concentrations from the Santee River are typically low (5 mg l^{-1}; Bates and Marcus, 1990), but, episodically, higher loads of organic carbon flush into the lake from the extensive wetlands upstream.

Among the benthic invertebrates in Lake Marion, *Corbicula* sp. probably has the greatest dependence on pelagic resources, although it can also consume benthic material through pedal feeding (Vaughn and Hakenkamp, 2001). Little is known about the relative importance of pedal and filter feeding modes; an experiment with *C. fluminea* from a stream population showed increased pedal feeding in the absence of seston (Hakenkamp and Palmer, 1999). Estimated filtration rates for *Corbicula* are typically high (on the order of 0.1-1 l animal^{-1} hr^{-1}), but vary widely with environmental conditions and experimental protocols (e.g., Lauritsen, 1986; Hwang et al., 2004).

As a filter feeder, *Corbicula* sp. can augment the resource base for other benthic consumers by diverting material from pelagic to benthic habitat. This enrichment occurs through production of pseudofeces, which contain undigested material (Way et al., 1990; Hakenkamp and Palmer, 1999), as well as excretion of nutrients (Lauritsen and Mozely, 1989). Schloesser et al. (2000) hypothesized that diversion of pelagic material to benthic habitat by the mussel *Dreissena polymorpha* contributed to the return of *Hexagenia* spp. to the western basin of Lake Erie. The positive correlation between abundances of *Corbicula* sp. and *H. limbata* in the upper and middle regions of Lake Marion may reflect a similar facilitation.

Corbicula sp. and other mollusks also add physical structure to the benthos. Shell of *C. fluminea* provides habitat for other benthic invertebrates (Werner and Rothhaupt, 2007, 2008), although this effect is probably not important for burrowing species such as *H. limbata*.

The availability of pelagic resources, mainly phytoplankton, to benthic consumers depends in part on the hydrodynamics of mixing. For *D. polymorpha* in Lake Erie, Zhang et al. (2011) concluded that weak mixing reduced replenishment of the phytoplankton to the 1-m boundary layer grazed by the mussels. In contrast, because its shallow depth and weak thermal stratification, we surmise that much of the upper region of Lake Marion is well-mixed. We speculate that pelagic resources may be less available to benthic consumers at the greater depths of the middle and lower regions due to less efficient mixing of the water column.

While supporting some components of fish production, the benthos, particularly *Corbicula* sp., may compete with others through the consumption of planktonic algae, the main trophic resource for zooplankton. In Lake Marion, larval stages of important species of pelagic fish, including *Dorosoma petenense*, *Alosa sapidissima*, and *Morone saxatilis*, depend on zooplankton. In upper Lake Marion, Chick and Van Den Avyle (1999a) judged that April-May zooplankton abundances were inadequate (<100 animals l^{-1}, including rotifers and copepod nauplii) to support successful foraging of *M. saxatilis* larvae in one of three years in their study. Abundances were similarly low in one of three years in an earlier study (Bulak et al., 1997). Data on cladoceran fecundity suggest that episodes of food limitation influence zooplankton dynamics in spring in the upper main basin (see Chapter 6).

Consumption by *Corbicula* sp. has been associated with depletion of pelagic resources in other systems. Its impact depends generally on advection and phytoplankton productivity, as well as consumption (e.g., Strayer, 1999). Cohen et al. (1984) concluded that high populations (near 1500 animals m^{-2}) of *C. fluminea* in some years caused a sag in phytoplankton abundances in a reach of the Potomac River; the inference was supported by experimentally measured filtering rates and estimated water residence times. Using a detailed simulation model, Pigneur et al. (2014) estimated that abundant *Corbicula* spp. (up to 900 animals m^{-2}) could account for substantial reductions in phytoplankton biomass (70%) and productivity (61%) in reaches of the

Meuse River. From estimates of phytoplankton production and consumption by zooplankton and *C. fluminea* among patches of habitat in the Sacramento-San Joaquin Delta, Lopez et al. (2006) concluded that patches were sources or sinks for phytoplankton production, depending on whether the clams were sparse or abundant.

In Lake Marion, the impact of *Corbicula* sp. on pelagic resources would be greatest in the shallow upper region, where its abundance is highest. Abundances of phytoplankton and, indirectly, zooplankton in Lake Marion are also affected by factors other than consumption by *Corbicula* sp. Advective transport appears to influence dynamics of both phytoplankton and zooplankton in the upper region of Lake Marion (see Chapters 5 and 7), and fish predation is probably important for zooplankton throughout the lake. Given the wide variation in inflow to Lake Marion, these influences will vary among seasons and years.

Shallow depth, limited episodes of hypoxia, and modest fluctuations in water level may all promote the importance of the benthos in Lake Marion. For a number of other southeastern reservoirs, widely fluctuating water levels and hypolimnetic oxygen depletion seem to limit abundances of the benthos and, consequently, their contributions to the food webs (Isom 1971, Soballe et al. 1992). Mean annual fluctuation in water level was 4.6 m among 51 southeastern reservoirs managed by the US Army Corp of Engineers (Soballe et al. 1992). In Lake Marion, water level fluctuated by 1.5 m or less in most of the 18 years from 1997 to 2014.

Benthic invertebrates are most abundant in the upper main basin of Lake Marion, which receives much of its water directly from the Santee River. Although this region is relatively small, the benthic filter feeder *Corbicula* sp. is positioned to influence planktonic resources down the lake by removing material imported from the river, limiting algal productivity in the upper region, and reducing exports to the middle and lower regions. Excess consumption by *Corbicula* sp. may subsidize other benthic consumers, including insects, partially offsetting adverse effects on planktonic resources for fish.

Table 4.1. Abundances of benthic invertebrates in the main basin of Lake Marion. Size ranges are given for common or very large taxa. Confidence intervals (CI) were estimated by bootstrap with 1000 replications.

			Upper Summer 2009 (animals m^{-2})		***Middle Summer 2010 (animals m^{-2})***		***Lower Summer 2010 (animals m^{-2})***	
	Taxon	***95% CI***	***Mean***	***95% CI***	***Mean***	***95% CI***	***Mean***	***95% CI***
	Bivalves							
Sphaeriidae[a] (2-15 mm)	88	(21, 191)	121	(46, 216)	14	(0, 35)	87	(17, 193)
Corbiculidae: *Corbicula* sp. (2-40 mm)	360	(260, 461)	424	(345, 510)	232	(139, 336)	133	(40, 242)
Unionidae: *Elliptio*[b] (5-110 mm)	10	(3, 17)	9	(4, 14)	2	(0, 5)	0	
Lampsilis	2	(0, 5)	2	(0, 4)	0		0	
Total	461	(352, 584)	555	(462, 661)	248	(145, 357)	219	(87, 398)
Gastropods								
Physidae	2	(0, 5)	3	(0, 6)	0		12	(0, 35)
Planorbidae	0		1	(0, 3)	0		0	
Viviparidae: *Viviparus subpurpureus* (2-30 mm)	341	(248, 426)	320	(254, 399)	241	(166, 327)	81	(35, 139)
Valvatidae: *Valvata bicarinata*	2	(0, 5)	5	(0, 16)	0		0	
Total	345	(248, 443)	329	(260, 416)	241	(166, 331)	92	(40, 150)
Insects								
Ephemeroptera: *Hexagenia limbata* (5-30 mm)	258	(177, 338)	159	(125, 194)	130	(48, 239)	0	
Caenis	2	(0, 5)	7	(0, 20)	0		0	
Odonata: Gomphidae	5	(0, 16)	4	(0, 10)	0		0	
Trichoptera	10	(2, 23)	3	(0, 5)	0		9	(0, 26)
Coleoptera	3	(0, 14)	2	(0, 4)	0		0	
Diptera: *Chaoborus punctipennis* (<10 mm)	0		123	(78, 172)	213	(119, 340)	124	(38, 231)
Chironomidae[c] (<10 mm)	289	(211, 374)	279	(163, 430)	177	(139, 215)	202	(141, 271)
Total	568	(471, 677)	576	(452, 748)	520	(362, 684)	335	(248, 436)
Crustaceans								
Copepoda	0		1	(0, 3)	0		0	
Amphipoda	16	(0, 45)	10	(4, 19)	2	(0, 5)	69	(0, 202)
Isopoda	0		1	(0, 3)	0		0	
Ostracoda	0		0		0		3	(0, 9)
Total	16	(0, 45)	12	(5, 21)	2	(0, 5)	72	(0, 214)

[a] Includes sphaeriids *Eupera cubensis*, *Pisidium* sp., *Sphaerium/Musculium* sp., *Corbicula* sp. <5mm (2009 only)

[b] Includes forms resembling *E. producta*, *E. fisheriana*, and *E. folliculata/angustata*

[c] May include small numbers of midges from other families

Table 4.2. Environmental attributes associated with variations in numerical abundance of benthic invertebrates, as explained by regression trees. The number of terminal nodes and the reduction in deviance as a percentage of deviance for the entire dataset are given for each pruned tree. All retained splits were based on water depth (Depth).

					Population (animals m^{-2})	
Tree	***1st split***	***2nd split***	***3rd split***	***n***	***Mean***	***Range***
Corbicula sp.: 2 terminal nodes; 36% reduction in deviance						
	Depth <6 m			70	395	(0, 1,212)
	Depth >6 m			18	34	(0, 173)
Viviparus subpurpureus: 4 terminal nodes, 31% reduction in deviance						
	Depth <7.7 m	Depth <3.45 m	Depth <2.1 m	9	178	(0, 606)
			Depth >2.1 m	24	444	(87, 1,602)
		Depth >3.45 m		46	215	(0, 953)
	Depth >7.7 m			9	53	(0, 216)
Hexagenia limbata: 3 terminal nodes, 36% reduction in deviance						
	Depth <6.4 m	Depth <2.1 m		9	0	(0, 0)
		Depth >2.1 m		65	167	(0, 996)
	Depth >6.4 m			14	3	(0, 43)
Chaoborus punctipennis: 2 terminal nodes, 17% reduction in deviance						
	Depth <2.7 m			17	13	(0, 87)
	Depth >2.7 m			71	183	(0, 1,039)
Chironomidae: 2 terminal nodes, 26% reduction in deviance						
	Depth <1.55 m			5	1,195	(130, 3,464)
	Depth >1.55 m			83	3	(0, 606)

Table 4.3. Dry biomasses, exclusive of shell, of benthic invertebrates in the main basin of Lake Marion. Biomasses for the three regions were weighted by relative area to compute the average. Taxa listed in Table 1 but omitted here were negligible due to small size or low population.

	Upper Spring 2010		***Upper Summer 2009***		***Middle Summer 2010***		***Lower Summer 2010***		***Average Summer***	
Taxon	***(g m^{-2})***	***%***	***(g m^{-2})***	***%***	***(g m^{-2})***	***%***	***(g m^{-2})***	***%***	***(g m^{-2})***	***%***
Sphaeriidae	0.34	0	0.18	0	0.01	0	0.07	1	0.07	0
Corbicula sp.	49.96	62	48.11	59	24.96	68	9.39	77	21.43	66
Unionidae	6.30	8	9.89	12	2.12	6	0.00	0	2.33	7
Viviparus subpurpureus	17.33	22	17.66	22	8.01	22	2.58	21	7.02	22
Hexagenia limbata	6.41	8	5.87	7	1.73	5	0.00	0	1.57	5
Chaoborus punctipennis	0.00	0	0.01	0	0.02	0	0.01	0	0.02	0
Chironomidae	0.01	0	0.01	0	0.01	0	0.01	0	0.01	0
Amphipoda	0.03	0	0.02	0	0.00	0	0.14	1	0.07	0
Total	80.39	100	81.77	100	36.86	100	12.20	100	32.50	100

Table 4.4. Percentages of benthic invertebrate biomass by functional feeding group in the main basin of Lake Marion in summer. Only taxa making up >1% of biomass in any region are shown; percentages are taken from Table 4.3.

Functional feeding group	***Taxa***	***Primary food***	***Upper (%)***	***Middle (%)***	***Lower (%)***	***Average (%)***
Collector filterer[a]	*Corbicula* sp., Unionidae	Planktonic and benthic algae, fine particulate detritus[d]	71	73	77	73
Collector filterer[b]	*Viviparus subpurpureus*	Benthic deposits; benthic algae and detritus[b]	22	22	21	22
Collector gatherer[a,c]	*Hexagenia limbata*	Benthic algae, fine particulate detritus[e]	7	5	0	5
Total			100	100	98	100

[a] Barbour et al. (1999)
[b] Brown et al. (1989)
[c] Cummins & Merritt (1984)
[d] Vaughn & Hakenkamp (2001), Cummings & Graf (2010)
[e] Zimmerman & Wissing (1980)

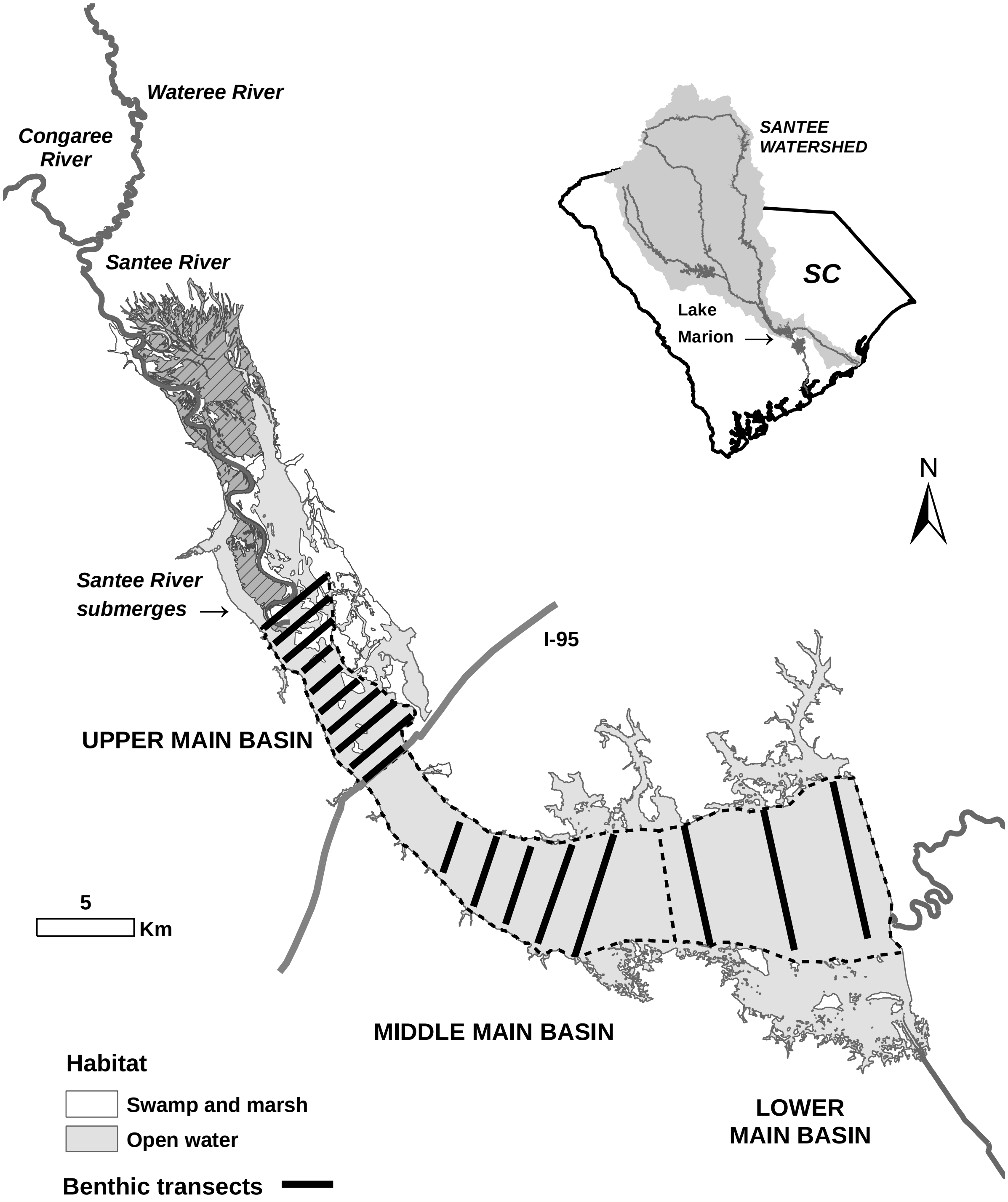

Figure 4.1. Lake Marion, including locations of benthic samples. The map, including habitat delineation, was derived from the National Hydrography dataset 0305 (USGS, 2007). Our approximate delineation of the main basin regions (dashed lines) is based on field sampling and other observations.

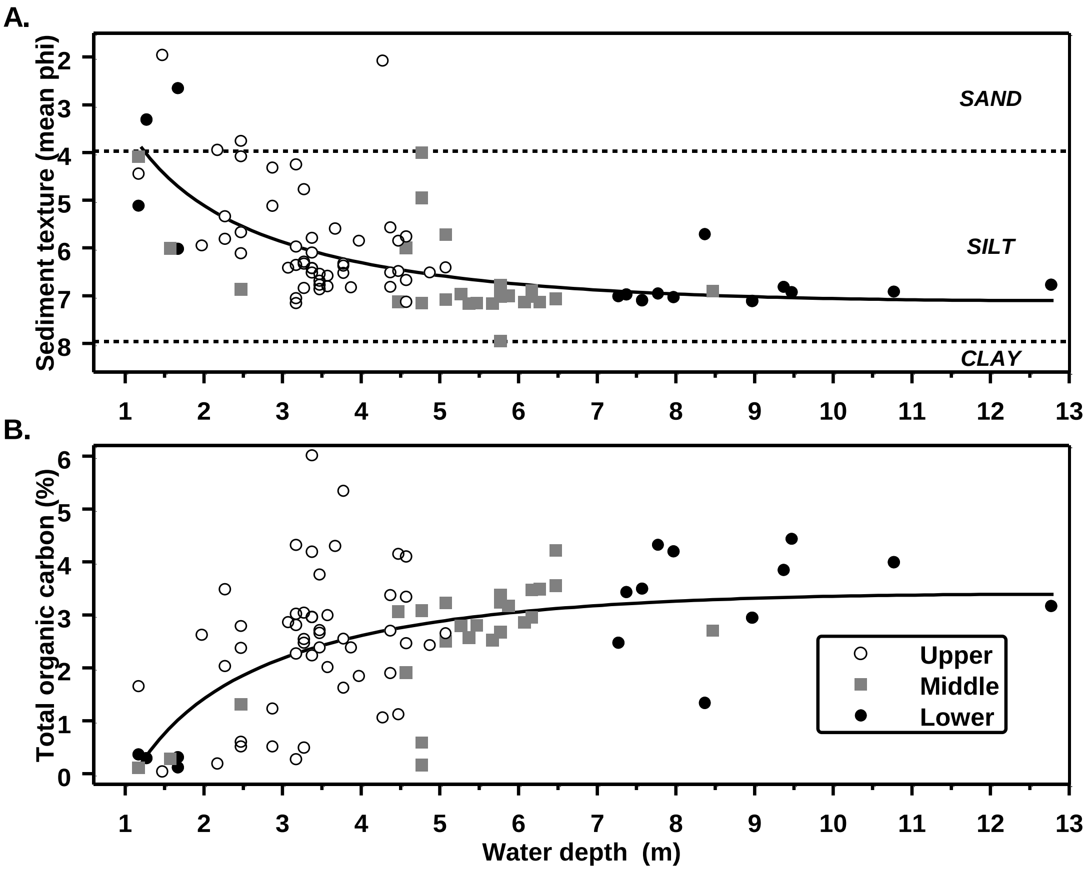

Figure 4.2. Sand and total organic carbon content of sediments from the main basin of Lake Marion as a function of water depth. Fitted curves are 2nd-degree polynomial functions of log-transformed depths.

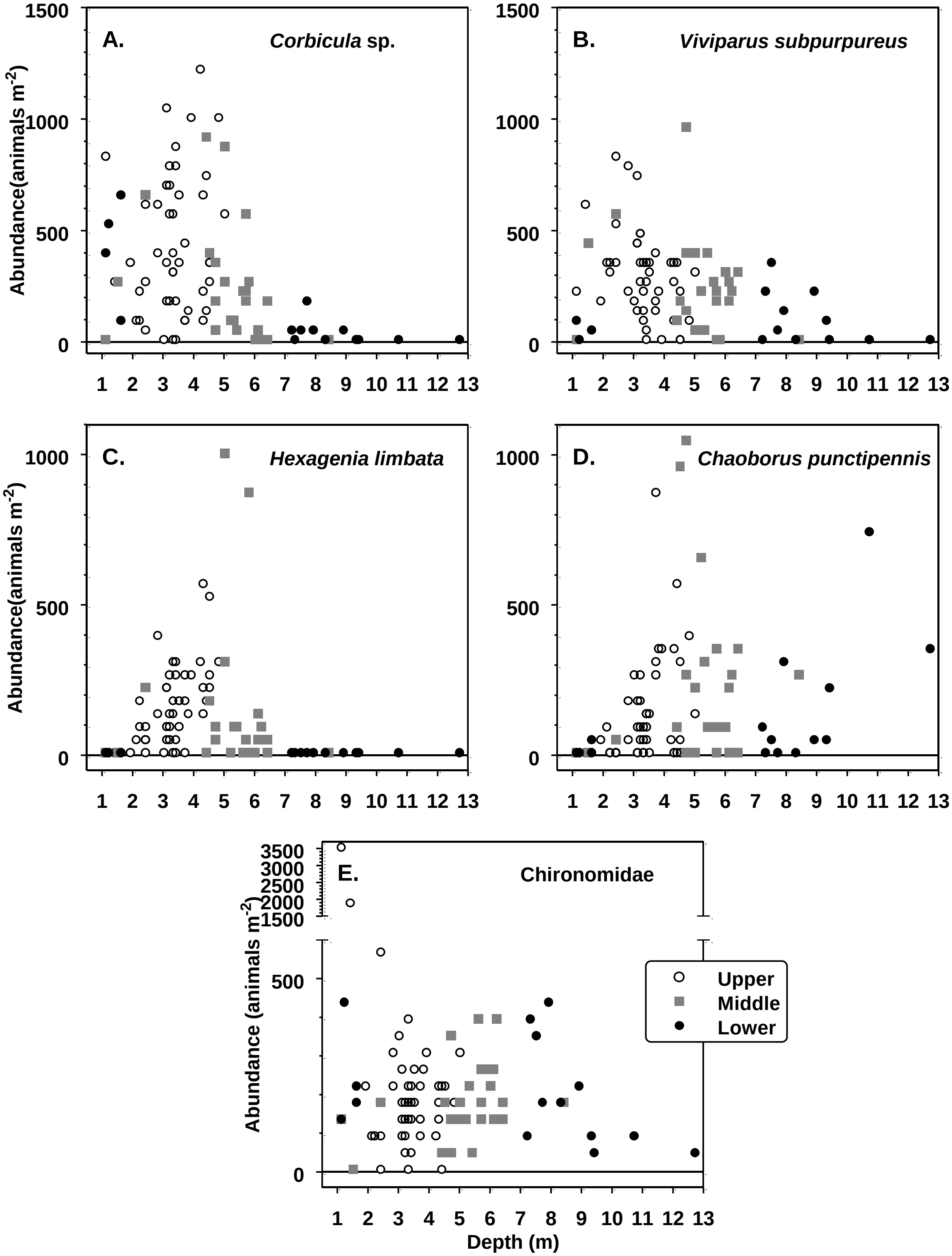

Figure 4.3. Abundances of five benthic taxa in the main basin of Lake Marion by depth in summer (2009 and 2010 combined) as a function of water depth.

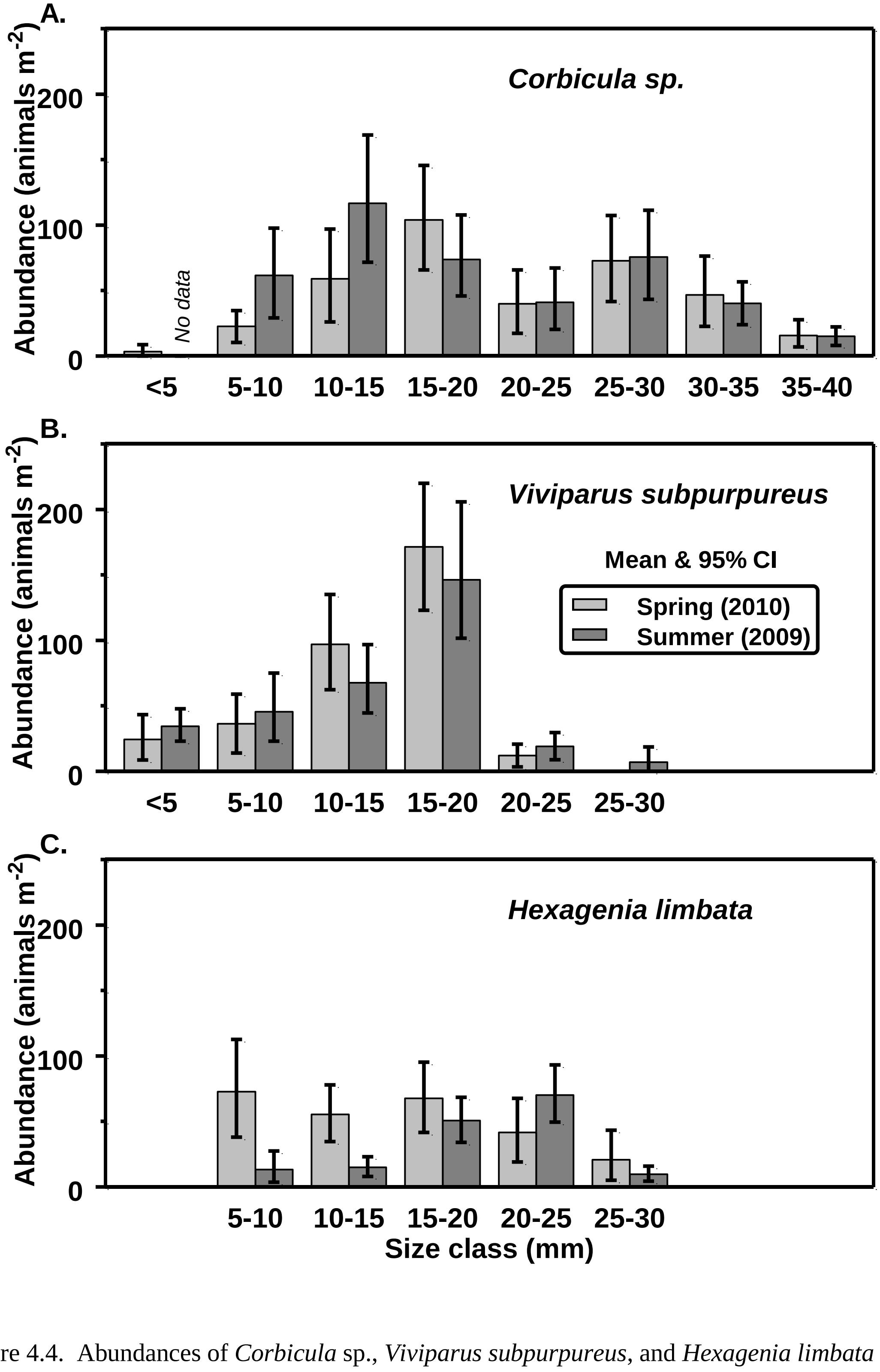

Figure 4.4. Abundances of *Corbicula* sp., *Viviparus subpurpureus*, and *Hexagenia limbata* by size class in the upper main basin of Lake Marion in spring (2010) and summer (2009). Confidence intervals were generated by bootstrapping.

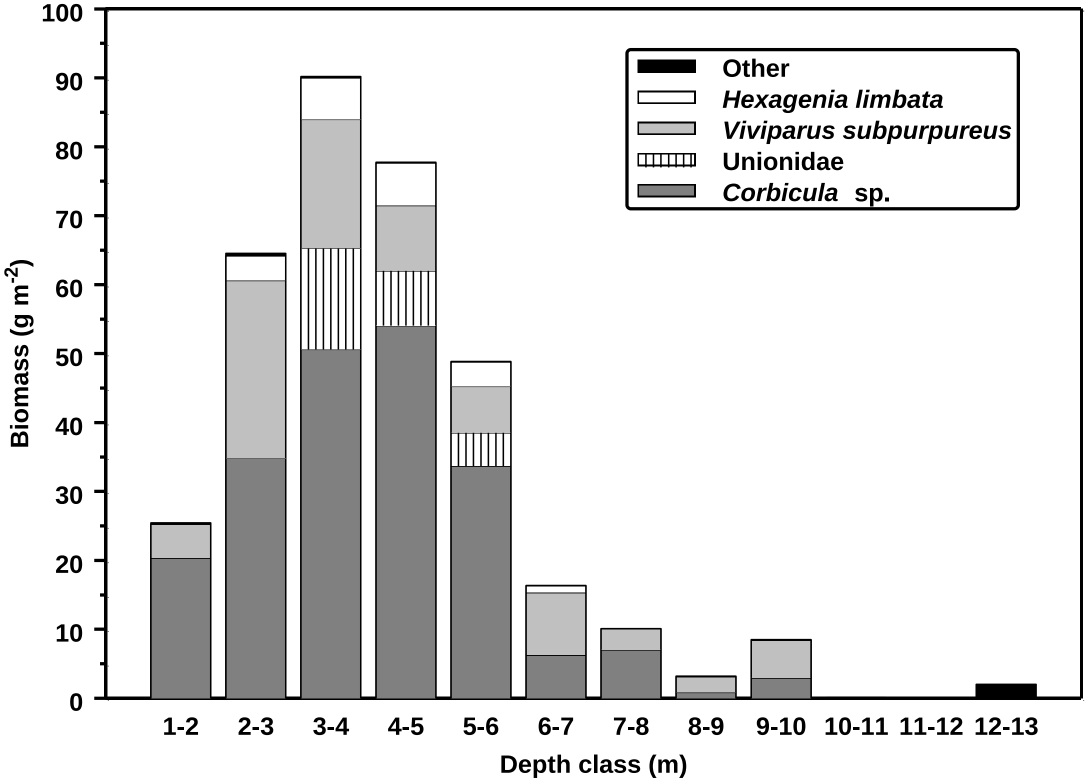

Figure 4.5. Benthic invertebrate biomass in Lake Marion as a function of water depth. Category "Other" includes *Chaoborus punctipennis*, Chironomidae, and crustaceans.

CHAPTER 5. Phytoplankton Dynamics in Upper Lake Marion

Although the upper main basin of Lake Marion is well-supplied with nutrients, phytoplankton populations vary widely (Chapter 4). The consequences of this variation are potentially important to the fisheries in the months of April to June when larvae of pelagic fish, including American shad, striped bass, and threadfin, shad depend on planktonic resources. In upper Lake Marion, Chick and Van Den Avyle (1999a) judged that April-May zooplankton abundances were inadequate to support successful foraging of striped bass larvae in one of three years in their study; zooplankton abundances were generally <100 animals liter^{-1} in one of three years in an earlier study (Bulak et al., 1997). In our more recent studies, April-May zooplankton abundances were temporally variable, but often low, and abundances of zooplankton were strongly correlated with chlorophyll a (Chapter 6).

We constructed a simulation model to provide a framework for examining how advection and consumption, by the Asiatic clam *Corbicula* sp. or other consumers, may affect spring phytoplankton dynamics in this system. Among potential consumers of phytoplankton in the upper main basin, *Corbicula* sp. appears to be the most important. Its biomass exceeds biomass of the zooplankton by about three orders of magnitude and that of threadfin shad by one or two orders of magnitude (Chapter 7; comparisons of dry biomass, exclusive of shell). Our approach to the model was guided, and constrained, by the information available. Our goal was to evaluate whether these processes had strong or consistent effects in the models. The model allows us to see how the principal variables interact. From these results, we can make inferences about processes limiting phytoplankton abundances and influencing dynamics of populations dependent on planktonic components of the food web.

Methods

Hydrology of the upper main basin (Figure 5.1), including estimates of discharge from the Santee River, volume of the upper main basin, and the flushing rate, is described in Chapter 2. Water quality data, including chlorophyll a as a measure of phytoplankton abundance, are presented in Chapter 3. Because of the sparsity of recent chlorophyll a data for the rivers, we also consider results from an earlier study (Lacy, 1992), in which chlorophyll a was sampled at weekly intervals at stations on the Congaree and Wateree rivers in 1989-1990.

General model for phytoplankton dynamics. We describe dynamics of the planktonic algae as the sum of gains due to production and import and losses due to export and consumption by *Corbicula* (or other agents or processes of removal). The growth rate of the population in the basin is

$$\mathrm{d}A/\mathrm{d}t = p_{alg}\,A + f_{basin}\,A_{river} - f_{basin}\,A - C \qquad \text{[Eq. 5.1]}$$

where A and A_{river} are algal abundances in the basin and the influent waters, respectively, p_{alg} is the algal production rate (algal productivity), f_{basin} is the flushing rate (Eq. 2.1), C is the consumption rate, and t is time. In the analyses that follow, algal abundances are variously given as concentrations of dry biomass or chlorophyll a per unit volume of water.

Simulations. The simulations were programmed in S-Plus (Tibco Software Inc., Palo Alto, CA). For the simulations, we divided the upper main basin into three linearly connected subbasins of equal volume. Algal populations in each subbasin were described by Eq. 1, expressed as a difference equation. The time step for the simulations was 0.1 day. The influent algal abundance for the subbasin 1, the first in the series, was A_{river}. The influent algal abundances for subbasins 2 and 3 were, respectively, the effluent algal abundances from subbasins 1 and 2. The effluent algal abundance for each subbasin was assumed to be same as the abundance within the subbasin. Basin volume was held constant at 97.2 10^6 m^3 (area = 26.8 km^2, mean depth = 3.4 m). The flushing rate coefficient for each subbasin, $f_{subbasin} = 3 \cdot f_{basin}$ was varied on a daily basis according to the 18-year record.

Initial algal abundances in all subbasins were set to the influent abundance from the river, including contributions from the upper backwaters. Simulations were initiated 10 days prior to the start of the period of interest (April-June).

We compared simulated algal abundances in subbasins 1 and 3 with observed abundances, measured as chlorophyll a, on corresponding dates at stations SC-010 (n=42) and SC-015 (n=47). “Best-fit” consumption was the value that minimized the median difference. We minimized the median, rather than the mean, to reduce the influence of a few extremely high field observations. We based the choice on the fit at SC-015, because we judged that the outcome there better integrated the influence of processes within the basin. We report the fits to both sets of field data.

Algal productivity. We set algal productivity p_{alg} = 0.3 day^{-1} or 0.5 day^{-1} to represent a plausible range of algal productivity. The lower value is based on modeled algal productivity in an upper reach of Lake Greenwood, South Carolina. Algal productivity averaged around 0.3 day^{-1} for spring months when water quality, including total suspended solids, was similar that in the main basin of upper Lake Marion. We computed these averages using the CE-QUAL-W2i model described by McKellar et al. (2008) and Taylor et al. (2013). The upper value is based on rates for planktonic algae in laboratory culture (Lürling et al., 2013).

To model density and temperature dependencies of algal growth, we used the logistic density dependency factor *pMod1* and the temperature dependency factor *pMod2*, a simplified form of the algal temperature rate multiplier described by Cole and Wells (2008). With these factors, algal productivity, computed at each time step for each subbasin, becomes:

$$p(A,T) = p_{alg}\, pMod1(A)\, pMod2(T) \qquad \text{[Eq. 5.2]}$$

where $pMod1(A) = 1$ for $A \le A_{min}$

$pMod1(A) = (A_{max} - A)/(A_{max} - A_{min})$ for $A > A_{min}$

and $pMod2(T) = K_1 + (K_2 - K_1) / (T_2 - T_1) * \mathrm{T}$ for $T > T_1$ and $T < T_2$

$pMod2(T) = K_1$ for $T \ge T_2$;

where A is algal abundance in µg chlorophyll a $liter^{-1}$ and T is water temperature in °C. For algal density dependence, we set A_{min} = 10 µg $liter^{-1}$ and A_{max} = 30 µg $liter^{-1}$ to curtail growth beyond the ranges of values typical for Lake Marion. For the algal temperature dependence, we set K_1 = 0.2, K_2 = 1, T_1=10 °C, and T_2 =18 °C, according to parameters for green algae in the Lake Greenwood model (McKellar et al., 2008).

Water temperature was modeled with a function fitted to water temperatures at 0.3 m depth (25-year record of approximately monthly observations at SC-010 and SC-015).

$$T = a \sin(2 \pi (Jday - b) / c)) + d, \qquad \text{[Eq. 5.3]}$$

where *Jday* is Julian day and the parameters are a = 11 °C, b = 108.75 days, c = 365 days, and d = 19 °C. Water temperature was held constant during each day.

Consumption of algae. To report the consumption rate as a percentage of *Corbicula* biomass, we used the spring 2010 estimate of 50 g m^{-2} for biomass of *Corbicula* sp. (Chapter 3). We assumed that the ratio of algal chlorophyll a to algal dry biomass was 0.0072 (Bicknell et al., 2001; the variability in this factor is large).

To evaluate plausibility of the modeled "best fit" algal consumption rates for *Corbicula* sp., we compared them with estimates derived from a bioenergetics model for *Dreissena polymorpha* (Schneider, 1992). *Dreissena* is a small, productive, invasive filter-feeding bivalve. Its size range overlaps that of *Corbicula*. We used Schneider's (1992) model from Fish Bioenergetics 3.0 (University of Wisconsin, Madison, WI), incorporating modifications made by Madenjian (1995). The model was implemented in S-Plus. In the bioenergetics model, consumption is computed as grams wet mass of phytoplankton per gram wet mass of mussel. For mussels, we assumed that dry mass was 15% of wet mass (Schneider, 1992). For phytoplankton, we assumed that dry mass was 25% of wet mass (Madenjian, 1995; published estimates range as low as 10%).

We also compared the modeled "best fit" algal consumption rates with consumption rates derived from published filtering rates for *Corbicula*. The filtering rates, expressed as the rate of clearance of phytoplankton from the water column, vary widely (e.g., Lauritsen, 1986; Cahoon and Owen, 1996). We used Lauritsen's rates, which were based on extensive experimental measurements on populations from the coastal plain of North Carolina. Environmental conditions were similar to those in Lake Marion, including spring and summer chlorophyll concentrations of <5 and 10-14 µg/L, respectively, and water temperatures of 8, 20, and 31 °C. At spring phytoplankton concentrations and 20 °C,

$$\mathrm{FR} = 3.534\ \mathrm{SL}^{1.723}, \qquad \text{[Eq. 5.4]}$$

where FR is filtering rate in ml hr^{-1} $animal^{-1}$ and SL is shell length in mm. Summer rates were about one-third as high as spring rates.

Results

Hydrology and water temperature. Over the 18-year record (1997-2014), the mean flushing rate for the upper main basin was 0.40 day^{-1} in April (range 0.16-1.13 day^{-1}), declining to 0.23 day^{-1} (range 0.08-0.65 day^{-1}) in June. The mean flushing rate for April-June was 0.31 day^{-1} (range 0.14 day^{-1} in 2002 to 0.87 day^{-1} in 2003) (Chapter 2).

At the main basin stations in April, May, and June, mean near surface water temperatures increased from 19.8 °C in April to 27.6 °C in June (Chapter 3)

April-June algal abundances in the main basin, backwaters, and rivers. Mean chlorophyll concentrations at the two upper main basin stations were 6.3-13.4 µg $liter^{-1}$ in April-June of 1997-2014 (Table 5.1). Values varied by more than an order of magnitude in all three months at both stations. Mean chlorophyll concentrations at backwater station SC-039 (6.9-9.1 µg/liter) were lower than at backwater station SC-044 (15.0-18.6 µg/liter). Mean chlorophyll concentrations in Lacy's 1989-1990 study of the rivers were 3.6-7.4 µg/liter. The values from June 2014 river stations fell mainly within this range.

In a step-wise multiple regression of chlorophyll a (log-transformed) at SC-010 on water temperature, Secchi depth, total phosphorus, and discharge from the Santee River, only water temperature and discharge were significant. These effects were strong (F(2,22)=20.81, $P < 0.001$, $r^2 = 0.61$). At SC-015, only water temperature and Secchi depth were included, and the effects were weaker (F(2,25) = 3.7, P = 0.04, $r^2 = 0.23$). Sample sizes for these analyses are substantially smaller than the number of chlorophyll a observations because corresponding values for other variables on some dates.

Zero growth isolines for the general phytoplankton dynamics model. According to the model, algal abundance in the basin will increase when either 1) algal abundance in the basin is high, relative to algal abundance in the river and the flushing rate is low, relative to algal productivity or 2) algal abundance is low, relative to algal abundance in the river, and the flushing rate is high, relative to algal productivity (Figure 5.2). The zero growth isolines define the extent of these regions. In case 1), algal growth is unlimited, according to the model. Practically, it would be limited by factors such as nutrients, light, or other consumers. In case 2), the algal concentration in the lake decreases until it reaches the zero growth isoline, which lies somewhat above the algal abundance in the river (shown by the horizontal reference line).

The consumption rate modifies the positions of the zero growth isolines. If $C/p_{alg} < A_{river}$ (as in Figure 5.1), the isolines lie in the upper right and lower left quadrants defined by the reference lines, and the intersection of the reference lines falls within the zone of algal increase. If $C/p_{alg} > A_{river}$, the isolines lie in the lower right and upper left quadrants defined by the reference lines, and the intersection of the reference lines falls within the zone of algal decrease.

Influent algal abundances for the simulations. In the simulations, the algal abundances in the influent water were set at 3 or 6 µg chlorophyll a liter^{-1}. These concentrations were set to account for water entering from directly from the Santee River (~80%; see Chapter 2) and for water entering after passage through the backwater channels (~10% each for Elliott's Flats and Stump Hole Swamp). The high value could be construed as 4 µg liter^{-1} from the river directly and an average of 14 µg liter^{-1} from the two backwaters. These values are not inconsistent with field results in Table 5.1 or with the mean summer values for SC-008 (Appendix B). The low value is simply half of the high value.

Simulation results. Values of the consumption rate that minimized the median deviation between simulated and observed algal abundances at SC-015 ranged from 0.7 % day^{-1} to 2.6% day (Table 5.2). Consumption rates producing the best fit at subbasin 3 did not give the best fit at subbasin 1: the algal abundances in subbasin 1 were underestimated for simulations with $p_{alg} = 0.3$ day^{-1} and $A_{river} = 3$ µg/L and overestimated for simulations with $p_{alg} = 0.3$ or 0.6 day^{-1} and $A_{river} = 6$ µg/L. However, overall, the "best fit" simulations gave results generally near the medians and means of the field data (Table 5.3). The range of variation in algal abundance in the simulations increased with algal productivity.

The simulation results were sensitive to consumption. In all four scenarios, mean algal abundances within the basin increased by a factor near two when the consumption rate was set to zero (Table 5.4).

The simulation results were also sensitive to influent algal abundances. Setting the influent algal abundance to zero produced extremely low algal abundances in the basin, even when the consumption rate was set to zero. For these simulations, initial algal abundances were 4 µg chlorophyll a liter^{-1} throughout the basin. Eighteen year means were <0.01 µg chlorophyll a liter^{-1} at $p_{alg} = 0.3$ day^{-1} and 0.05 µg liter^{-1} at $p_{alg} = 0.5$ day^{-1}. At the higher level of algal productivity, seasonal means exceeded 1 µg liter^{-1} in the two years with the lowest mean flushing rates. At the lower level of algal productivity, the seasonal means did not exceed 1 µg liter^{-1} in any year.

The simulations showed rapid responses to temporal variation in the flushing rate (Figure 5.3). Periods of elevated flushing rates pushed the algal abundances in the basin sharply down toward influent algal abundances. Algal abundances in the basin rose above this base only during periods of diminished flushing rates. Again, the scenarios with higher productivity exhibited greater ranges of algal abundances.

Among years, April-June median and mean algal abundances in the basin generally decreased as the mean flushing rate increased (Figure 5.4). Among all 18 years, the correlations between mean algal abundance and mean flushing rate (log-transformed) were strong (r^2 = 0.53 to 0.87 among scenarios). Among the 11 years of low discharge, however, the correlations were weaker or insignificant (r^2 = 0.03 to 0.47 among scenarios). Variation among years was wider in the scenarios with higher productivity. In all scenarios, the algal abundances in the basin ranged closer to the algal abundances in the river as the mean flushing rate increased.

Averaged among years, combined algal inputs averaged 32-72 metric tons of dry biomass per day (Table 5.5). Algal production exceeded algal imports in all cases, but the imported algae made a substantial contributions (25-48% on average). Consumption removed 10-35 metric tons per day (32-51% of the combined algal input), leaving 21-35 metric tons per day for export to the lower portion of the lake.

In all four scenarios, seasonal average algal imports and exports were greatest in 2003, when the average flushing rate was greatest. Seasonal average algal production was least in 2003 for all but the scenario with higher algal productivity and influent algal concentrations, for which minimum algal production occurred in 2006, a year in which the flushing rate coefficient was very low (f_{basin} = 0.15 day^{-1}). Patterns of low discharge resulted in extreme depletion of the algal populations by consumption in the lower two subbasins in this year.

In all four scenarios, seasonal average imports were least in 2002, which the flushing rate was lowest. In three of the scenarios, exports were lowest in 2002 or 2006, when average discharge was also very low. However, the lowest export for the scenario with lower algal productivity and influent algal abundances occurred in 2006, year in which average discharge was 0.27 day-1. Again, pattern was important. Seasonal algal production was greatest years of moderate flushing rates (2001: f_{basin} = 0.18 day^{-1}; 2011: f_{basin} = 0.21 day^{-1}).

From the bioenergetic model for *Dreissena*, consumption requirements, expressed in terms of dry biomass of phytoplankton per unit dry biomass of *Dreissena*, ranged from 0.6% day^{-1} at maintenance to 4.9% day^{-1} at maximum. The fitted rates of consumption in the four scenarios (0.7%-2.6% day^{-1}) lie within this range.

For Upper Lake Marion the estimated filtering rate for the 2009 *Corbicula* population per m^2 of substrate was 6.4 m^3 day^{-1}, according to Eq. 5.4. Applied to simulated mean algal abundances for the scenarios with the “best fit” consumption rates (Table 5.4), this filtering rate yielded consumption rates ranging from 10% day^{-1} at an algal abundance of 5.5 µg chlorophyll a liter^{-1} (Scenario 1) to 17% day^{-1} at 9.5 µg liter^{-1} (Scenario 4). These rates were more than double the maximum from the bioenergetics model.

Discussion

The strength of the model lies in the long records of hydrologic data (Chapter 2) and water quality data (Chapter 3). The hydrologic data provide the basis for a model that describes a wide range of hydrologic conditions, including seasons with very low and very high discharge. The chlorophyll data enabled us to fit the algal dynamics over this wide range of conditions. Limitations lie in the paucity of information about details of hydrodynamics, such as discharge through the backwaters, algal productivity, consumption by *Corbicula*, and algal concentrations of the influent water.

For the transitional zone represented by the main basin of upper Lake Marion, the simulations suggest that 1) variation in April-June planktonic algal abundance is driven in part by variation in discharge from the Santee River; 2) consumption by *Corbicula* is capable of limiting the abundance of planktonic algae; and 3) imported algae make a critical contribution to planktonic algal dynamics.

The similarity of results across the scenarios suggests that patterns generated by the model are robust. The magnitude of consumption required to fit the model to the field data is substantial. It is not inconsistent with an approximation of the bioenergetic requirements of *Dreissena*, and it is notably lower than the consumption rates derived from Lauritsen's (1986) experimentally measured filtering rates for *Corbicula*. These results do not confirm that *Corbicula* is the consumer! Other processes, including settling of the influent chlorophyll a (e. g., Søballe and Bachmann, 1984), and activities of other consumers, might cause or contribute to the losses.

Across all years in this simple system, the correlation with mean flushing rate explained a relatively high proportion (half or more, depending on the scenario) of the variation in mean algal abundance in April-June. For all scenarios, mean algal concentrations were generally near influent algal concentrations when discharge was high ($f_{basin} > 0.45$ day^{-1}; 3 of 18 years) or moderate ($0.25 < f_{basin} < 0.45$ day^{-1}; 5 of 18 years). Thus, for a population thriving only when algal concentrations usually exceeded this level, poor success would be predicted in 8 of 18 years. However, years of low discharge, episodes of high discharge caused sharp declines in algal concentrations in the simulations. For a population sensitive to conditions during a specific window of time, failure might ensue despite the favorable seasonal mean. Conversely, windows of more favorable conditions sometimes occurred in the years of moderate discharge. In all four scenarios, the highest mean algal abundances occurred in years when the mean flushing rate was less than 0.25 day^{-1} (mean discharge < 21 10^6 m^3 day^{-1} or 8,700 cfs).

Imported algae is a poorly characterized resource for this system. One of the strongest, most striking results of the simulations is magnitude and importance of imported algae to the system. The arithmetic (discharge volume multiplied by algal concentration per unit volume) indicates that large quantities of algae are transported into the upper main basin. The influent algal abundances (3 and 6 µg chlorophyll a liter^{-1}) in the simulations are not inconsistent with values from other systems. For example, Lauritsen (1986) reported values of <5 µg chlorophyll a liter^{-1} in spring and 10-14 µg liter^{-1} in summer for the Chowan River in North Carolina; Cohen et al. (1984) reported 20-40 µg chlorophyll a liter^{-1} in summer in the Potomac River near Washington, D.C; and Søballe and Bachmann (1984) reported values exceeding 400 µg chlorophyll a liter^{-1} in summer for the nutrient-enriched, sediment-laden Des Moines River in Iowa. Pigneur et al. (2014) reported values during the growing season of 17.5-164.2 µg chlorophyll a liter^{-1} and 0.5-4.34 µg liter^{-1} before and after invasion of the Meuse River in Belgium by *Corbicula* spp.

Our results support Tufford and McKellar's (1999) inferences about the importance of hydrodynamics and riverine inputs to this system. Among the four scenarios, the 18-year April-June means for imports, exports, production, and consumption (or settling) of algae were of similar magnitude (10-47 metric tons dry mass day^{-1}). Although consumption (or settling) of imported algae appears to limit planktonic algal production in the model, this process of removal may enhance productivity of the upper main basin through benthic pathways with material that would otherwise have been transported downlake.

Table 5.1. Summary of chlorophyll a concentrations (µg liter^{-1}) by month for upper Lake Marion and tributary rivers. Main basin and backwater stations were sampled monthly; n represents number of years for which data were available. Sources of the STORET and Santee Cooper data are described in Chapter 3. River stations were sampled weekly in spring 1989-1990 (data from Lacy, 1992). The river stations were sampled only once in spring 2014. To estimate the mean for the Santee River, the concentrations in the Congaree and Wateree rivers were weighted by the average discharge for each river (see Chapter 2).

Station	***April Mean (range) (µg liter^{-1})***	***N***	***May Mean (range) (µg liter^{-1})***	***n***	***June Mean (range) (µg liter^{-1})***	***n***
Upper main basin, 1997-2014 (STORET and Santee Cooper)						
SC-010 State Park	6.3 (0.6 - 28.2)	11	6.9 (0.7 - 16.8)	15	11.7 (1.8 - 44.4)	16
SC-015 I-95	6.5 (0.7 - 16.1)	15	13.4 (0.3 - 58.7)	15	12.6 (1.7 - 39.9)	17
Upper backwaters, 1997-2014 (STORET and Santee Cooper)						
SC-039 Elliott's Flats	7.8 (0.3 - 30.9)	13	9.1 (1.4 - 28.5)	12	6.9 (0.2 - 16)	14
SC-044 Stump Hole Sw.	15.0 (0.6 - 31.3)	14	18.6 (5.1 - 30.6)	11	17.5 (5.6 - 36.9)	14
Mean	11.4		13.5		12.7	
Rivers, 1989-1990 (Lacy, 1992)						
SC-001 Congaree	3.9 (2.6 - 5.8)	8	3.6 (2.2 - 5.5)	10	7.5 (4.2 - 13.6)	8
(no number) Wateree	6.0 (3.8 - 7.1)	7	4.2 (2.7 - 7.5)	10	4.2 (2.9 - 5.2)	8
Santee River (discharge-weighted mean)	4.7		3.8		6.2	

Table 5.2. Simulation scenarios with "best fit" consumption rates.

Scenario	***Algal productivity*** **p_{alg}** ***(day^{-1})***	***Influent algal abundance*** **A_{river}** ***(chlorophyll a, µg liter^{-1})***	***"Best fit" consumption*** **C** ***(%*** **Corbicula** ***biomass day^{-1})***
1	0.3	3	0.7
2	0.3	6	1.6
3	0.5	3	1.2
4	0.5	6	2.6

Table 5.3. Summaries for simulated and observed algal abundances in spring (April-June, 1997-2014). All available field data were included. Scenarios are described in Table 5.2.

	Algal abundance (chlorophyll a, µg liter^{-1})					
	Min	***Q1***	***Med.***	***Mean***	***Q3***	***Max***
Subbasin 1						
Scenario 1 with "best fit" consumption	2.4	3.1	3.3	3.8	3.9	14.7
Scenario 2 with "best fit" consumption	4.2	6.0	6.2	6.4	6.6	13.2
Scenario 3 with "best fit" consumption	1.4	3.1	3.7	6.3	7.4	20.2
Scenario 4 with "best fit" consumption	0.8	6.0	6.7	8.0	9.7	18.1
Station SC-010 (n=42)	0.6	3.2	5.4	8.7	11.5	44.4
Subbasin 3						
Scenario 1 with "best fit" consumption	0.3	3.2	4.5	7.3	9.4	26.0
Scenario 2 with "best fit" consumption	0.0	5.7	6.8	8.1	9.7	22.7
Scenario 3 with "best fit" consumption	0.0	3.2	7.8	11.7	21.8	27.6
Scenario 4 with "best fit" consumption	0.0	3.9	9.1	10.9	18.3	25.0
Station SC-015 (n = 47)	0.3	3.1	7.4	10.9	12.1	58.7

Table 5.4. Simulated mean algal abundances in scenarios with "best fit" or no consumption by *Corbicula* in spring (April-June, 1997-2014). Scenarios are described and "best fit" consumption rates are given in Table 5.2.

	Mean algal abundance in basin (chlorophyll a, µg liter^{-1})	
Scenario	***"Best fit" consumption***	***No consumption***
1	5.5	10.3
2	7.2	14.7
3	9.1	15.3
4	9.5	18.7

Table 5.5. Simulated imports, production, exports, and consumption of algae in spring (April-June, 1997-2014). Scenarios are described and "best fit" consumption rates are given in Table 5.2. Small discrepancies between totals for gains and losses are due to net changes in the populations over the simulation period.

	Gains (metric tons day^{-1}, % of gains)			***Losses (metric tons day^{-1}, % of gains)***		
Scenario	***Import***	***Prod.***	***Gains***	***Export***	***Cons.***	***Losses***
Scenario 1 with "best fit" consumption	12 (40%)	19 (60%)	31	20 (65%)	10 (32%)	30
Scenario 2 with "best fit" consumption	25 (48%)	27 (52%)	52	28 (54%)	23 (44%)	51
Scenario 3 with "best fit" consumption	12 (25%)	37 (75%)	50	31 (62%)	17 (34%)	48
Scenario 4 with "best fit" consumption	25 (35%)	47 (65%)	72	35 (48%)	35 (49%)	70

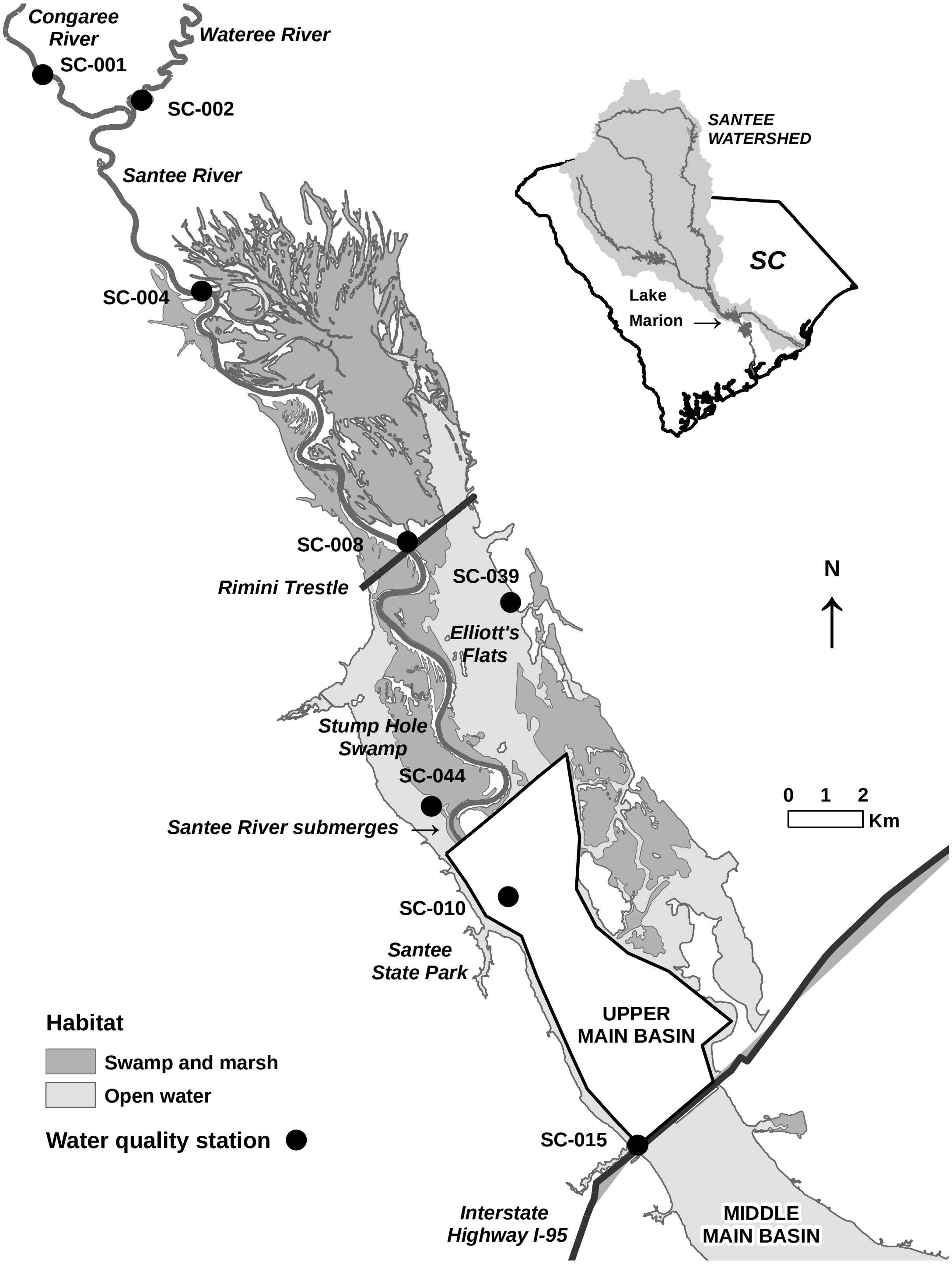

Figure 5.1. Upper region of Lake Marion. The map was derived from the National Hydrography Dataset for the Edisto-Santee Subregion (USGS, 2007). Cross-hatched area shows area of upper main basin, as modeled. Circles show water quality stations used in the analyses.

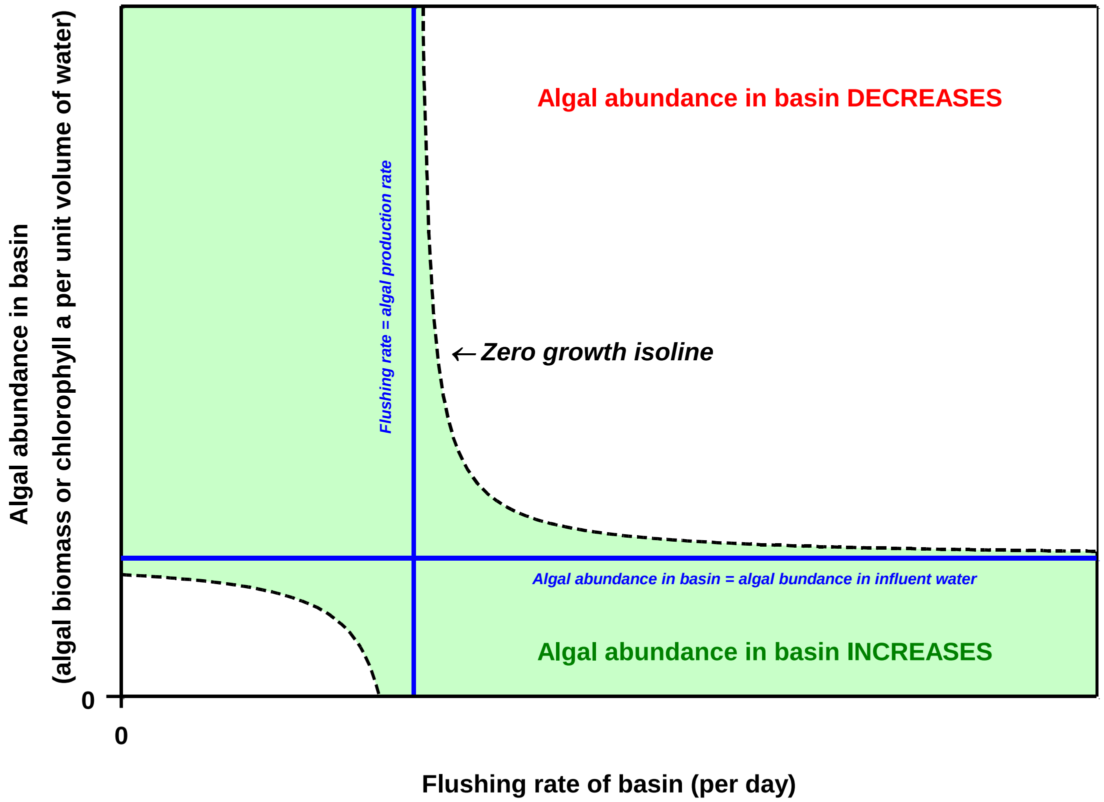

Figure 5.2. Zero growth isolines for general phytoplankton dynamics model. According to the model (Eq. 5.1), algal abundance in the basin is a function of the flushing rate, the algal production rate, the algal abundance in influent water from the river, and the consumption rate. Along the zero growth isolines (dashed lines), algal abundance does not change over time (Eq. 5.1: conditions where d*A*/d*t*=0). Within the shaded region bounded by the isolines, algal abundance increases; outside the shaded region, it decreases.

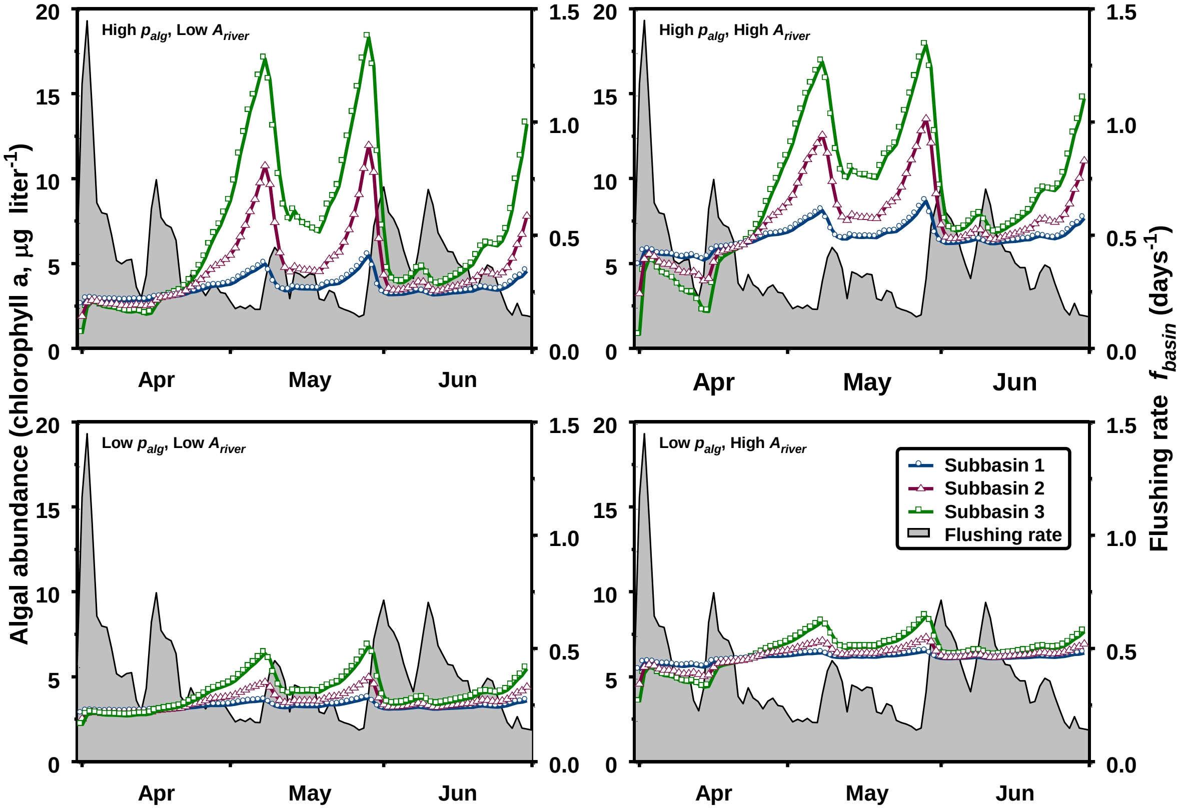

Figure 5.3. Simulated algal abundances and flushing rates in April-June 2009. The mean flushing rate was moderate (f_{basin} = 0.38 day^{-1}). Scenarios are described in Table 5.2.

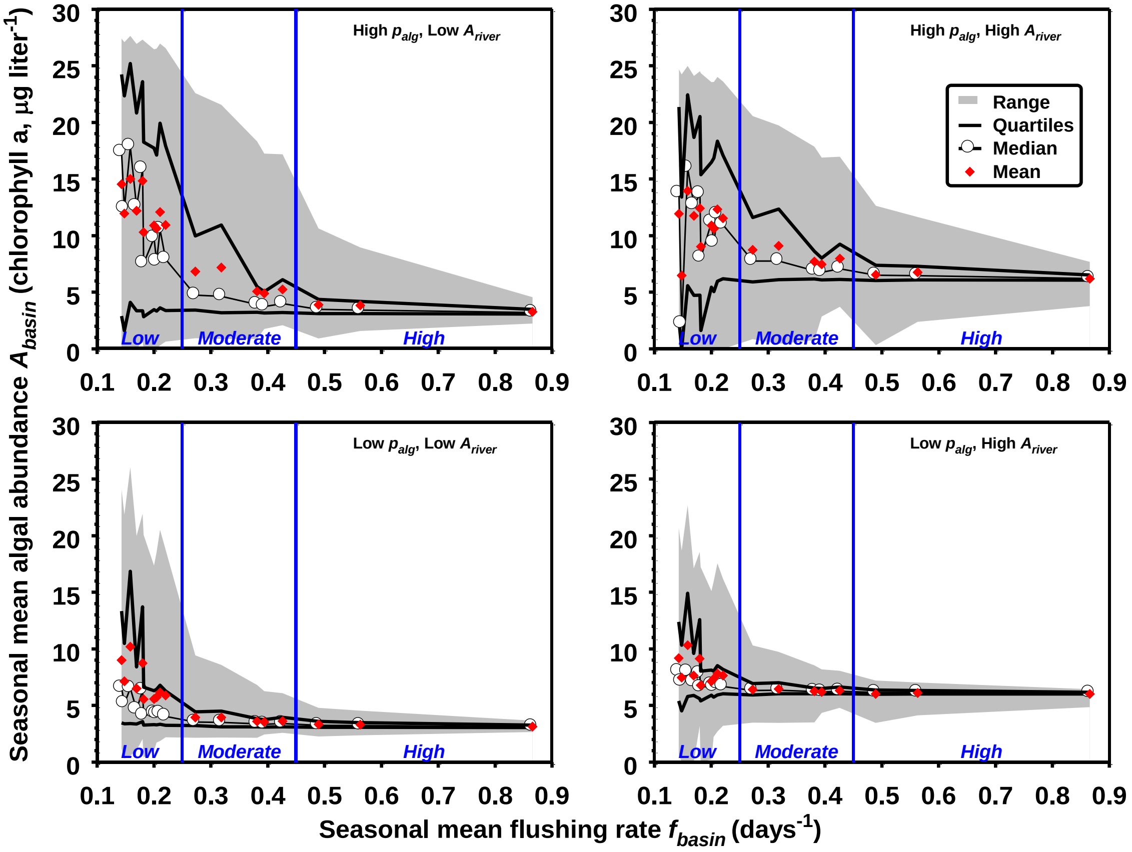

Figure 5.4. Simulated spring (April-June) algal abundances, plotted as a function of spring mean flushing rates, for 1997-2014. Means, medians, quartiles, and ranges for algal abundances are shown. Scenarios are described in Table 5.2; simulations were run with "best fit" consumption rates. Reference lines separating the ranges of low, moderate, and high mean flushing rates were drawn at 0.25 and 0.45 days^{-1}. These flushing rates correspond approximately to mean discharges of 21 and 40 10^6 m^3 day^{-1} or 8,700 and 17,000 cfs. The highest seasonal mean flushing rate, 0.87 days^{-1}, corresponds to a mean discharge of 80 10^6 m^3 day^{-1} or 33,000 cfs.

CHAPTER 6. The Zooplankton

Zooplankton usually play a substantial role in the food webs of lakes. A zooplankton assemblage is typically comprised of mainly of rotifers, cladocerans, and copepods. Most are very small in size; most can reproduce rapidly under favorable conditions. They variously consume phytoplankton, bacteria, and other fine particulate matter, as well as other zooplankton. They are consumed by a host of other predators, including fish. They function mainly as primary consumers, linking the phytoplankton to fish and other consumers at higher trophic levels.

In southeastern impoundments, zooplankton constitute a vital trophic resource for pelagic larval stages of fish, including striped bass, threadfin shad, and other clupeids. The zooplankton can also serve as an important resource for juvenile and adult clupeids, including threadfin shad.

Previous studies at Lake Marion have considered the importance of zooplankton to survival and growth of larval striped bass. Bulak et al. (1997) observed higher recruitment to the juvenile stage when mean spring zooplankton abundances in the upper main basin were near 100 animals liter^{-1} (two years) than when abundances were near 20 liter^{-1} (one year). Chick and Van Den Avyle (1999b) observed substantially higher growth and survival in experimental studies at high abundances of zooplankton (354 and 740 animals liter^{-1}) than at low abundances (7 animals liter^{-1}). Studies on responses of larvae of other key species to zooplankton have not been made at Lake Marion. However, at Lake Thurmond on the Savannah River, Betsill and Van Den Avyle (1997) found that zooplankton abundance had a significant influence on growth of larval threadfin shad up to 3 weeks in age. Growth increased with zooplankton abundance up to thresholds near 200-300 animals liter^{-1}, depending on larval age.

The main goal of this component of the study was to estimate the abundance of zooplankton resources for pelagic fish larvae during the spring season. We assessed composition and abundance of the zooplankton in the upper main basin in April-June of 2009 and 2012. Further sampling in 2014 extended the spatial scope of the study to the middle and lower main basins and the temporal scope to October.

Additional goals were to evaluate factors influencing the abundances of zooplankton and to estimate the contribution of the zooplankton to general food web. As for the phytoplankton (Chapter 5), we model zooplankton dynamics as the sum of gains due to production and import and losses due to export and consumption. In this chapter, we examine correlations in spring 2009 between abundances of zooplankton and phytoplankton, measured as chlorophyll a. We estimate birth rates for two important zooplankton taxa from field data on egg ratios and water temperature. We also consider the impact of losses due to advection and to predation by larval fish and by pelagic juvenile and adult fish.

Methods

Field sampling. Zooplankton were sampled in Lake Marion in April-June 2009, April-June 2012, and April-October 2014. The 2009 samples were collected in the upper main basin; the 2012 samples, in the upper main basin, the upper backwaters, and Santee River; the 2014 samples, in the upper, middle, and lower main basin (Figure 6.1, Table 6.1). Chlorophyll a was sampled in conjunction with the 2009 zooplankton samples (see Appendix B).

At each station, 2.2-liter Van Dorn bottle samples were collected at 1-m depth intervals from 0 to 4 m. For each station, the samples from all depths were combined, filtered onto an 80-

micron mesh sieve, and preserved with sugar and 4% formalin. In 2009, 0.5-liter subsample of the pooled sample was removed before filtering for analysis of chlorophyll a. To provide a better sample of larger taxa, we collected a vertical tow (0-4 m, depth permitting) at each station in 2012 and 2014 using a net with 25-cm aperture and 80-micron mesh. Secchi transparency and water depth were recorded at each station, and water temperature was measured at 1- to 5-m intervals to the bottom of the lake with a YSI Model 58 meter.

Zooplankton were identified using standard keys. We caution that the taxonomy of many southeastern zooplankton taxa has not been well-studied.

Zooplankton samples were stained with Eosin B and rinsed on a 53-µm mesh screen before counting. Animals were identified to genus or species if mature adults were present. Eggs were tallied for cladocerans and for a few rotifer species that carry eggs attached externally.

Instantaneous birth rates in days^{-1} were estimated for the several rotifer and cladoceran taxa using the Paloheimo's equation (Paloheimo, 1974):

$$b = \{\ln (E/N + 1)\}/D \qquad \text{[Eq. 6.1]}$$

where E is the number of eggs, N is the number of animals, and D is the duration of egg development in days. D was estimated as a function of water temperature using equations from Bottrell et al. (1976, Table XV) for Rotifera (*Keratella*, *Brachionus*, *Ploesoma*) and All Cladocera (*Bosmina*, *Bosminopsis*, *Diaphanosoma*). A count of around a hundred animals, depending on fecundity and proportion of ovigerous females, is needed put reasonable constraints on the variance of the birth rate estimate (see Taylor, 1988). This minimum was not achieved in most of the 2009 and 2012 bottle samples. For these samples, we computed birth rates for samples where counts were as low as 21 animals. For 2012, we also computed birth rates for cladocerans from vertical net haul samples, which yielded larger counts.

For larval fish, we examined a plausible range for consumption rates using Stewart and Binkowski's (1986) model for young-of-year alewife and Johnson's (1995) model for striped bass (*Morone* spp.) larvae. For fish of 0.5-1 g wet mass at spring temperatures (20-25 ^{o}C), modeled *maximum* consumption rates were 0.8-1 g prey wet mass g^{-1} fish wet mass d^{-1} for alewife. For a simulated population of young-of-year alewife in Lake Michigan, Stewart and Binkowski estimated that actual consumption was about half of this maximum, or 0.4-0.5 g prey wet mass g^{-1} fish wet mass d^{-1}. Modeled *maximum* consumption rates were 0.6-0.8 g prey wet mass g^{-1} fish wet mass d^{-1} for striped bass larvae. Given the low abundances of zooplankton in the upper main basin of Lake Marion, we applied a consumption rate of 0.5 g prey wet mass g^{-1} fish wet mass d^{-1} to estimate loss rates to the zooplankton population. We assumed that dry mass was 10% of wet mass for the zooplankton. Estimates of larval fish biomass were based on samples from the upper main basin collected in spring 2009 (Appendix F).

The impacts of advection and consumption by fish on zooplankton were estimated using a model similar that used in Chapter 5 for the impacts of advection and consumption by *Corbicula* on phytoplankton. Growth of the zooplankton population Z in the basin over time t is

$$dZ/dt = b\,Z + f_{basin}\,Z_{river} - f_{basin}\,Z - F \qquad \text{[Eq. 6.2]}$$

where Z and Z_{river} are zooplankton abundances in the basin and the influent waters, respectively, b is the birth rate coefficient, and F is consumption by fish.

Rather than constructing a simulation model based on this equation, we simply examined the growth rates to assess the conditions under which the zooplankton populations might be sustained under the combined effects of advection and predation.

Because estimates of pelagic fish populations for Lake Marion in spring were not available, we relied on summer and fall hydroacoustic survey data for lakes Marion and Moultrie (Bulak, 2016), adjusting abundances for a plausible seasonal fluctuation. Censused fish were 2-20 cm TL (0.1-65 g wet mass). The mean fish biomass was 87 kg wet mass ha^{-1} in summer and fall 2012-2014. We assumed that biomass of the population declined by 50% from fall to spring (due to mortality of the fish), resulting in a mean fish biomass of 43.5 kg wet mass ha^{-1} in spring.

We examined a range for consumption rates using Stewart and Binkowski's model for young-of-year alewife. For fish of 1-5 grams wet mass at spring temperatures (20-25 ^{o}C), estimated maximum consumption rates were 0.5-0.8 g prey wet mass g^{-1} fish wet mass d^{-1}. Stewart and Binkowski estimated that Lake Michigan alewife consumed 0.3 g prey wet mass g^{-1} fish wet mass d^{-1} during their season of greatest growth. We applied the latter rate. We assumed that consumption of zooplankton by fish was nonselective and that the proportion of rotifer or cladoceran biomasss in the diet was the same as its proportion in the lake. Data for summer and fall diets of threadfin shad in lakes Marion and Moultrie (Appendix H) suggest that larger fish feed more heavily on copepods and cladocerans than on rotifers or naupii, but we lack corresponding information on prey availability. Based on 2012 field results for the rivers (presented below), we also assumed that the influent zooplankton biomass was negligible.

Results

Common rotifers included the genera *Brachionus*, *Keratella*, *Polyarthra*, *Synchaeta*, and *Conochilus* (Table 6.1) Common cladocerans included *Bosmina longirostris*, *Bosminopsis dietersi*, *Moinodaphnia maclayei*, other small-bodied taxa, and the sidid *Diaphanosoma*. A few larger cladocerans were occasionally present: *Daphnia lumholtzi*, which is equipped with long spines; *Holopedium*, which is enclosed in a gelatinous material, and *Leptodora*, which is nearly transparent. Copepods included the calanoids *Eurytemora affinis*, *Epischura fluviatilis*, *Osphranticum labronectum*, and *Diaptomus* spp., as well as cyclopoids.

The microzooplankton, rotifers and naupliar stages of copepods, were typically 0.2 mm or less in length. Cladocerans and copepodid stages of copepods were typically 0.2-1 mm in length.

Abundances of zooplankton in Upper Lake Marion, 2009 and 2012. Zooplankton abundances varied widely across dates and among stations in the upper main basin (Figure 6.2). Mean abundances of zooplankton in the upper main basin increased from 10-20 animals liter^{-1} in April to 100-200 animals liter^{-1} in June. Variation among stations ranged up to more than an order of magnitude. Composition was dominated by rotifers and nauplii; they constituted 80% or more of the totals on most dates (Figure 6.3).

The increases in total abundances from April to late May or early June in both years were due almost entirely to increases in rotifers. The increases during June 2012 included substantial contributions from cladocerans (40%), rotifers (30%), and nauplii (20%). The larger zooplankton (copepodids, cladocerans, and other) exceeded mean abundances of 10 animals liter^{-1} only in June 2010.

Although the variation in zooplankton abundances among stations in the upper main basin was high, the spatial pattern of variation was weak (Figure 6.4). Deviations from the mean on each date did not differ among stations (analysis of variance: F(5,60) = 2.25, P = 0.06).

Abundances at one of the backwater stations and both of the Santee River stations differed from abundances in the main basin in 2012. Abundances at Stump Hole Swamp backwater station (April-June) were consistently an order of magnitude above the means for the main basin, while abundances at Pack's Flats backwater station (May-June only) were near or below the means for the main basin (Figure 6.5). In contrast, abundances at the Santee River stations were substantially below the means for the upper main basin.

Zooplankton biomass in the upper main basin increased from April to June in both 2009 and 2012 (Table 6.4; because only one station was sampled in the upper main basin in 2014, we omitted it from this comparison). The highest estimates occurred in June. Averaged across dates, percentage composition of biomass was divided more or less evenly among rotifers, nauplii, copepodids, and cladocerans. Among dates, biomasses of rotifers (2-73%) varied more than those of the other groups.

Zooplankton in the main basin of Lake Marion, 2014. Zooplankton abundances varied widely across dates and among stations in the main basin (Figure 6.6, Table 6.5). Mean abundances of zooplankton increased from <100 animals liter^{-1} in April to >200 animals liter^{-1} in late May, but decreased to <100 animals liter^{-1} in subsequent months. Variation among stations by date ranged up to two orders of magnitude. Composition was dominated by rotifers and nauplii; they constituted 80% or more of the totals on most dates (Figure 6.7).

In 2014, zooplankton abundances increased downlake (Figure 6.8). Deviations from the mean on each date differed among stations (analysis of variance: F(3,20) = 4.76, P = 0.01). Pair-wise comparisons showed that M044 in the lower main basin differed from both M079 in the middle main basin and M150 in the upper main basin; other pairs of stations did not differ.

Correlations between zooplankton and chlorophyll a, 2009. Among stations, concentrations of chlorophyll a varied by nearly two orders of magnitude in April-June 2009 (Appendix C). Abundances of rotifers, copepodids, and cladocerans were positively correlated with chlorophyll a (Figure 6.9). The correlations were strong for rotifers ($r^2 = 0.79$, $P = 0$, $n = 28$), moderate for copepodids ($r^2 = 0.42$, <0.001, $n=25$) and cladocerans ($r^2 = 0.29$, $P = 0.004$, $n = 26$), and not significant for nauplii ($r^2 = 0.14$, $p >0.05$, $n=28$). The fitted estimates of abundance for rotifers increased by two orders of magnitude over the range of observed chlorophyll a concentrations; for copepodids and cladocerans, by an order of magnitude or less.

Birth rates, 2009 and 2012. Because birth rate calculations require counts of both animals and eggs, we were able to make plausible estimates only for cladocerans and some of the rotifers. All of the common cladoceran species carry eggs and developing embryos in brood chambers, where they are readily observed. Several of the common rotifer taxa carry eggs attached externally. Among the copepods, some of the calanoid and all of the cyclopoid species carry their developing eggs in sacs, but adult females with egg sacs were very sparse in our samples. Further, one of the most common calanoids, *Epischura fluviatilis*, does not carry its eggs.

Mean birth rates of rotifers ranged generally between 0.2 and 0.5 day^{-1} (Table 6.6). The highest values occurred in early June 2009 (*Brachionus* sp., 0.49 day^{-1}; *B. angularis,* 0.41 day^{-1}) and late May 2012 (*Brachionus* sp., 0.47 day^{-1}). Mean birth rates of cladocerans ranged generally between 0.1 and 0.5 day^{-1} (Table 6.6). The highest values occurred in mid-June 2012 (*Bosmina*, 0.44 day^{-1}; *Bosminopsis*, 0.47 day^{-1}).

Among samples, the range of birth rates estimates was fairly wide, a phenomenon that could be a consequence of the relatively small numbers of animals counted. However, a similarly wide range occurred among estimates from the vertical hauls in 2012, suggesting a spatial component to the variation. For example, the mean birth rates of *Bosmina* from the net samples at the six main basin stations on 27 April 2012 was 0.13 day^{-1} (range 0.07-0.18 day^{-1}); in these samples, all but one of the counts exceeded 100 animals.

Predation on zooplankton by fish. For larval fish, the consumption rate of 0.5 g prey wet mass g^{-1} fish wet mass day^{-1}, applied to the maximum biomass of larval fish at 0.016 g wet mass m^{-3} (Appendix F) yielded a consumption rate of 0.008 g wet mass m^{-3} day^{-1} or 0.8 µg dry mass liter^{-1} day^{-1}. Because this rate is small in relation to the corresponding biomass of zooplankton (Table 6.6), we did not pursue refinements.

To illustrate the potential effects of advection and predation by pelagic juvenile and adult fish, we constructed a diagram illustrating zero growth isolines for rotifer and cladoceran populations as a functions of the flushing rate coefficient and population abundance, expressed as animals liter^{-1} (Figure 6.10). Birth rate coefficients were set at 0.4 day^{-1} for rotifers and 0.3 day^{-1} for cladocerans, based on estimates in Table 6.6. The zero growth isolines are shown for feeding rates estimated for a fish population of 43.5 kg wet mass ha^{-1} (half of the 3-year mean for summer and fall populations in lakes Marion and Moultrie; Bulak, 2016) under the assumption that the entire bioenergetic requirement of population was met by consumption of zooplankton, We further assumed that rotifers and cladocerans contributed 20% and 25%, respectively, of the bioenergetic requirement. (As reported above, averaged across dates, percentage composition of biomass was divided more or less evenly among rotifers, nauplii, copepodids, and cladocerans.) The model predicts decreases for the rotifer populations on all sampled dates; for the cladoceran populations, on all but one date. With the fish feeding rate on zooplankton reduced to the equivalent of 15% of the bioenergetic requirement, the model predicts increases for the rotifer population on six dates; for the cladoceran population, on only two dates.

Discussion

Composition of the zooplankton in Lake Marion was typical for large impoundments of the region (e.g. Mallin, 1986; Taylor et al., 1993; DeBiase and Taylor, 2005). The dominance by small-bodied species is generally attributed to selective pressures imposed by fish predation; Wetzel (2001), among others, provides a good overview of this topic.

The assemblages include species of special biogeographic interest. The large, spiny cladoceran *Daphnia lumholtzi*, native to Africa, Asia, and Australia, is present but not so abundant as to suggest that it may be disruptive. The brackish water copepod *Eurytemora affinis* has repeatedly invaded freshwaters throughout its range (Lee, 1999). It has been present in Lake Marion at least since the 1980s (Lacy, 1992). Construction of large impoundments may have facilitated expansion of the freshwater copepod *Epischura fluviatilis*, which was poorly known and probably rare in the region before the 1990s (DeBiase and Taylor, 1993).

Based on Bulak et al. (1997), we use a zooplankton abundance of 100 animals liter^{-1} as a threshold for defining a good resource base for larval fish. For many reasons, this is an inexact value, but it provides with a nicely rounded basis for considering range of variation in this system.

For the six stations sampled in 2009 and 2012, mean abundances of zooplankton in the upper main basin of Lake Marion exceeded 100 animals liter^{-1} only in June. However, spatial variability was high (but not consistent), and this threshold was reached at a few stations in May of both years.

The abundances of zooplankton in April and May fell within ranges reported in previous studies in upper Lake Marion (Table 6.5). However, in both 1988-1990 (Bulak et al., 1997) and 1993-1995 (Chick and Van Den Avyle, 1999a), two of the three study years yielded average abundances exceeding 100 animals liter^{-1}. By this measure, the main basin of upper Lake Marion did not provide good resources for larval fish in any of the three years of our study, although abundances were not so low as in either 1989 or 1993. (We note that limited data in 2014 do not give a strong basis for evaluating the resource base in that year.)

Comparable data for other impoundments in the region are sparse. Mean April-May microzooplankton abundances exceeding 100 animals liter^{-1} have been reported at Lake Thurmond (Betsill and Van Den Avyle, 1997; weekly samples at four stations) and Lake Murray (DeBiase, unpublished report; bi-weekly samples at nine stations).

For larval fish transported into the system from the Santee River, our results affirm a substantial increase in zooplankton abundances between the Santee River and the upper main basin (Figure 6.5). Zooplankton abundances at both river stations were sparse. A similar pattern was reported by Chick and Van Den Avyle (1999a). Our results also indicate that some parts of the upper backwaters may offer favorable forage: zooplankton abundances at one of the backwater stations consistently exceeded the 100 animals liter^{-1} threshold. In contrast to expectations based on the Thornton’s reservoir zonation model (see Chapter 3), zooplankton abundances were also higher in the lower main basin.

In the upper main basin, birth rates for cladocerans and rotifers, which generally fall well below demographic maxima based on life table studies (e.g., Bottrell et al. 1976), suggest some level of resource limitation may influence zooplankton dynamics. The correlations between abundances of zooplankton and phytoplankton also suggest an influence of food resources, particularly for the rotifers.

The zooplankton dynamics model demonstrates that advection, combined with plausible levels of predation by pelagic fish, could have great impact on the spring populations of zooplankton in upper Lake Marion. The intent of this analysis was simply to estimate the potential magnitude of these effects: our parameter estimates are reasonable or plausible, but not precise! The effects of advection become dominant when flushing rate coefficients approach or exceed the birth rate coefficients. We suspect zooplankton imported from the backwaters, although not included in the model, could be important to maintaining the zooplankton populations in the main basin. These effects would be analogous to the effects of influent algal concentrations in the phytoplankton dynamics model (Chapter 5).

The model strongly suggests that the zooplankton populations in the upper main basin cannot sustain the abundance of pelagic fish that we modeled. The fish population estimates may be too large, or the fish may depend on other resources, either consistently or opportunistically.

The greater zooplankton abundances in the lower main basin, relative to the upper and middle regions of Lake Marion, may reflect the differences in the impact of advective processes. The flushing rate in the lower main basin is lower, and the influent zooplankton populations (from the upper and middle main basins) are larger. The greater abundances in the lower main basin may also reflect the better resource base (see Chapter 4) or some aspect of the distribution of planktivorous fish.

Table 6.1. Zooplankton samples in Lake Marion. Stations are named by Santee Cooper channel marker number (M…; South Carolina Wildlife and Marine Resources Department et al., 1973), Santee Cooper water quality station number (SC-…), or verbal description. All stations are shown in Figure 6.1. A few stations were not sampled on all dates.

Region	***2009 Apr-Jun 5 dates***	***2012 Apr-Jun 6 dates***	***2014 Apr-Oct 8 dates***
Santee River	-	Santee River 2 SC-008 Santee River 1 near M176	-
Upper backwaters	-	Pack's Flats at Rimini Trestle Stump Hole Swamp SC-044	-
Upper main basin	M149 M142 M137 M132 M123 M111	M149 M142 M137 M132 M123 M111	M150 (SC-010)
Middle main basin	-	-	M79 (SC-044) M69 (SC-016)
Lower main basin	-	-	M44 (SC-022)

Table 6.2. Taxa identified from Lake Marion zooplankton samples, 2009, 2012, and 2014. Other notable taxa included flatworms, oligochaete worms, water mites, and ostracods.

Higher taxon	***Family***	***Taxon***
Rotifera	Asplanchnidae	*Asplanchna*
	Brachionidae	*Brachionus* (incl. *B. angularis*)
		Colurella
		Diplois
		Euchlanis
		Keratella
		Mytilina
		Trichotria
	Conochilidae	*Conochilus*
	Gastropidae	*Gastropus*
	Hexarthridae	*Hexarthra*
	Lecanidae	*Monostyla*
	Synchaetidae	*Ploesoma*
		Polyarthra
		Synchaeta
	Testudinellidae	*Filinia*
		Pompholyx
		Testudinella
	Trichocercidae	*Trichocerca* (2 or more species)
Branchiopoda: Cladocera	Bosminidae	*Bosmina longirostris*
		Bosminopsis dietersi
	Chydoridae	*Alona*
		Chydorus
	Daphnidae	*Ceriodaphnia lacustris*
		Ceriodaphnia laticaudata
		Daphnia lumholtzi
		Daphnia parvula
		Scapholeberis
		Simocephalus vetulus
	Holopedidae	*Holopedium*
	Ilyocryptidae	*Ilyocryptus*
	Leptodoridae	*Leptodora kindtii*
	Moinidae	*Moinodaphnia maclaeyii*
	Sididae	*Diaphanosoma*
		Sida
Copepoda: Calanoida	Diaptomidae	*Skistodiaptomus mississippiensis*
		Skistodiaptomus pallidus
	Temoridae	*Eurytemora affinis*
		Epischura fluviatilis

(continued on following page)

Table 6.2. Taxa identified from Lake Marion zooplankton samples, 2009, 2012, and 2014. (continued)

Higher taxon	***Family***	***Taxon***
Copepoda: Cyclopoida	**Cyclopidae**	*Acanthocyclops robustus/vernalis*
		Macrocyclops
		Mesocyclops edax
		Microcyclops
		Tropocyclops prasinus mexicanus
Copepoda: Poecilostomatoida	Ergasilidae	*Ergasilus*
Insecta: Diptera	Chironomidae	
	Chaoboridae	*Chaoborus punctipennis*
Mollusca: Bivalvia	Corbiculidae	*Corbicula* sp. (larvae)

Table 6.3. Abundances of zooplankton in the upper main basin of Lake Marion in 2009 and 2012. Six stations were sampled on each date.

	Mean and range (animals liter^{-1})											
Date	***Rotifers***		***Nauplii***		***Copepodids***		***Cladocerans***		***Other***		***Total***	
10-Apr-09	3.8	(1, 14.9)	3.0	(0.7, 9.5)	0.5	(0, 2.6)	0.6	(0, 2.8)	0.2	(0, 0.4)	8.1	(2.4, 30.2)
23-Apr-09	23.2	(2.4, 73.3)	5.5	(3.5, 45.2)	0.4	(0, 1.7)	0.6	(0, 1.3)	0.2	(0, 0.5)	29.9	(5, 77.1)
07-May-09	30.6	(10.5, 58.9)	11.2	(1.3, 11.4)	1.4	(0.2, 3.9)	2.6	(1.2, 4.6)	0.1	(0, 0.2)	45.8	(20.9, 65.5)
21-May-09	67.5	(5.9, 151.6)	10.3	(1.1, 20.3)	1.1	(0.3, 3.2)	1.7	(0.8, 4.6)	0.2	(0, 0.5)	80.9	(8.5, 204.6)
04-Jun-09	167.2	(11.8, 497.1)	4.5	(5.8, 24.9)	1.1	(0.4, 2.2)	1.2	(0.3, 2.8)	0.1	(0, 0.2)	174.0	(14.8, 511.3)
13-Apr-12	3.0	(0.5, 9.6)	10.0	(3.3, 13.6)	3.0	(1, 8.1)	4.1	(1.1, 10)	0.2	(0.1, 0.4)	20.2	(12.7, 35.2)
27-Apr-12	6.9	(1.9, 25.2)	11.2	(1.8, 29.8)	1.6	(0.9, 2.6)	3.1	(1.8, 5.5)	0.2	(0, 0.5)	22.9	(8, 39.7)
16-May-12	52.2	(7.4, 149.5)	8.3	(3.3, 35)	3.2	(1.1, 7.4)	3.3	(2.2, 6.1)	0.3	(0.1, 0.7)	67.2	(24.1, 167.5)
31-May-12	62.2	(12.3, 183.3)	10.8	(2.5, 66.4)	1.8	(0.8, 2.9)	3.6	(0.9, 13.3)	0.5	(0, 1.2)	79.0	(20.4, 195.9)
14-Jun-12	65.4	(18.9, 128.5)	14.0	(8.1, 0)	2.4	(0.6, 7.6)	8.8	(3.9, 18.8)	0.6	(0, 1.4)	91.1	(38.8, 184.9)
28 Jun-12	89.6	(20.4, 255.3)	29.7	(0, 0)	8.5	(2.7, 15.6)	42.1	(20.4, 84.1)	0.6	(0.2, 1.4)	170.4	(67.4, 360.1)

Table 6.4. Biomasses of zooplankton in the upper main basin of Lake Marion in 2009 and 2012. Six stations were sampled on each date. For these estimates, biomass for typical animals in each group (0.2 µg for rotifers, 1 µg for nauplii, 5 µg for copepodids, and 2 µg for cladocerans) was based on length-weight relations compiled by Bottrell et al. (1976).

	Mean and range (micrograms dry mass liter^{-1})									
Date	***Rotifers***		***Nauplii***		***Copepodids***		***Cladocerans***		***Total***	
10-Apr-09	0.8	(0.2, 3)	3.0	(0.7, 9.5)	2.7	(0, 13)	1.3	(0, 5.6)	7.7	(1.5, 31.1)
23-Apr-09	4.6	(0.5, 14.7)	5.5	(2, 20.1)	1.8	(0, 8.5)	1.2	(0, 2.6)	13.2	(3.2, 39.2)
07-May-09	6.1	(2.1, 11.8)	11.2	(3.5, 25.8)	7.0	(1, 19.5)	5.1	(2.4, 9.2)	29.4	(16.8, 51.9)
21-May-09	13.5	(1.2, 30.3)	10.3	(1.3, 45.2)	5.5	(1.5, 16)	3.3	(1.6, 9.2)	32.7	(6.1, 100.7)
04-Jun-09	33.4	(2.4, 99.4)	4.5	(1.1, 11.4)	5.3	(2, 11)	2.5	(0.6, 5.6)	45.6	(7.7, 123)
13-Apr-12	0.6	(0.1, 1.9)	10.0	(5.8, 20.3)	14.8	(5.1, 40.5)	8.3	(2.2, 20)	33.6	(17.9, 71.7)
27-Apr-12	1.4	(0.4, 5)	11.2	(3.3, 24.9)	7.8	(4.5, 13.2)	6.3	(3.6, 11.1)	26.7	(11.9, 50.2)
16-May-12	10.4	(1.5, 29.9)	8.3	(1.8, 13.6)	15.9	(5.3, 36.8)	6.5	(4.4, 12.2)	41.1	(15.7, 61.8)
31-May-12	12.4	(2.5, 36.7)	10.8	(3.3, 29.8)	9.2	(4.1, 14.6)	7.3	(1.8, 26.5)	39.7	(13.8, 82.2)
14-Jun-12	13.1	(3.8, 25.7)	14.0	(2.5, 35)	11.9	(2.8, 38.2)	17.5	(7.8, 37.6)	56.5	(33.3, 123.8)
28 Jun-12	17.9	(4.1, 51.1)	29.7	(8.1, 66.4)	42.5	(13.7, 77.8)	84.1	(40.9, 168.2)	174.2	(89.7, 263.9)

Table 6.5. Abundances of zooplankton in the upper, middle, and lower main basins of Lake Marion in 2014. Four stations were sampled on each of the dates included in the table.

	Mean and range (animals liter^{-1})											
Date	***Rotifers***		***Nauplii***		***Copepodids***		***Cladocerans***		***Other***		***Total***	
29-Apr-14	67.7	(0.1, 259.1)	4.1	(0.2, 10.4)	1.3	(0, 3.9)	6.3	(1.3, 15.7)	0.0	(0, 0.1)	79.5	(1.5, 289.1)
30-May-14	214.1	(56.1, 472.7)	11.3	(0.2, 36.6)	1.1	(0.1, 3.4)	9.3	(1.3, 24.9)	0.1	(0, 0.2)	236.0	(59.3, 537.5)
16-Jun-14	63.6	(48, 82.8)	9.0	(1, 16.7)	0.2	(0, 0.4)	4.4	(0.8, 14.6)	0.2	(0, 0.4)	77.3	(53.1, 114.7)
08-Jul-14	22.9	(4.1, 40.1)	11.9	(1, 37.1)	0.3	(0, 0.8)	2.6	(0.2, 6.9)	0.1	(0, 0.4)	37.9	(6.9, 59.6)
30-Jul-14	42.8	(32.2, 52.5)	7.3	(2.7, 11)	0.2	(0, 0.4)	4.3	(1.2, 8.8)	0.4	(0.2, 0.6)	54.9	(39.9, 65)
29-Oct-14	23.0	(5.6, 47.6)	15.2	(3.3, 30.2)	1.2	(0.3, 2.3)	0.8	(0.1, 2.1)	0.2	(0, 0.3)	40.3	(11.1, 63.3)

Table 6.6. Birth rates of rotifers and cladocerans in the upper main basin of Lake Marion in 2009 and 2012. The number of samples for which birth rates were estimated is given by n. More than 20 animals were counted in each sample for which a birth rate was estimated. Mean counts in 2009 were 40 rotifers and 37 cladocerans; mean counts in 2012 were 67 rotifers and 52 cladocerans.

	Rotifers				***Cladocerans***			
			b (days^{-1})				***b (days^{-1})***	
Date	***Species***	***n***	***Mean***	***Range***	***Species***	***N***	***Mean***	***Range***
10-Apr-09					*Bosmina*	1	0.06	
23-Apr-09	*Keratella*	2	0.26	(0.25, 0.26)				
07-May-09	*Keratella*	2	0.28	(0.09, 0.46)	*Bosmina*	3	0.22	(0.07, 0.31)
21-May-09	*Keratella*	1	0.21		*Bosmina*	1	0.12	
04-Jun-09	*Brachionus* sp.	3	0.49	(0.41, 0.53)				
	B. angularis	1	0.41					
13-Apr-12					*Bosmina*	4	0.13	(0.07, 0.16)
27-Apr-12					*Bosmina*	6	0.16	(0.09, 0.23)
16-May-12	*Brachionus* sp.	2	0.25	(0.09, 0.41)	*Bosmina*	5	0.15	(0.09, 0.19)
	Keratella	3	0.24	(0.12, 0.35)				
	Ploeosoma	1	0.15					
31-May-12	*Brachionus* sp.	3	0.47	(0.35, 0.55)	*Bosmina*	1	0.12	
14-Jun-12	*Brachionus* sp.	2	0.21	(0.13, 0.28)	*Bosmina*	2	0.44	(0.35, 0.52)
					Bosminopsis	3	0.47	(0.19, 0.72)
28-Jun-12	*Brachionus* sp.	2	0.15	(0.15, 0.16)	*Bosmina*	5	0.14	(0.10. 0.19)
					Bosminopsis	5	0.13	(0.05, 0.21)
					Diaphanosoma	4	0.07	(0.04, 0.11)

Table 6.7. Comparison of zooplankton abundances in the upper main basin of Lake Marion in April-May among studies. Microzooplankton includes rotifers and nauplii in all four studies. Macrozooplankton includes only cladocerans and copepodid stages of copepods in Bulak et al. (1997). Median is reported for Chick and Van Den Avyle (1999a). Microzooplankton includes rotifers and nauplii. Macrozooplankton includes cladocerans, copepodid stages of copepods, and other taxa for all studies except Bulak et al. (1997), which did not include other taxa. Stations differed among studies, but all were located within or near the upper main basin, as described in this study. All studies used nets or sieves with 80-µm mesh.

	Mean or median and range (animals liter^{-1})				
Year	***Microzooplankton***		***Macrozooplankton***		***Source***
1988	116	-	3.5	-	Bulak et al. (1997; Fig. 6) Means for 3 stations, weekly samples; vertical net haul
1989	12	-	1.5	-	
1990	182	-	1.7	-	
1993	6	(2, 15)	0.9	(0.5, 2.6)	Chick and Van Den Avyle (1999a; Fig. 2) Medians for 1 station, weekly duplicate samples; vertical net haul
1994	260	(8, 530)	2.0	(1, 6.0)	
1995	460	(5, 900)	1.0	(0.3, 2.0)	
1996	53	(5, 315)	9.8	(1.1, 54.4)	Bulak (1999) Means for 1-3 stations, weekly triplicate samples; Van Dorn sampler
2009	39	(7, 77)	2.4	(1.2, 4.0)	This study (Table 6.3) Means for 6 stations, bi-weekly samples; Van Dorn sampler
2012	41	(13, 73)	6.2	(4.8, 7.3)	
2014	85	(0.3, 169)	2.7	(1.3, 4.1)	This study (Table 6.6) Values for 1 station, monthly samples; Van Dorn sampler

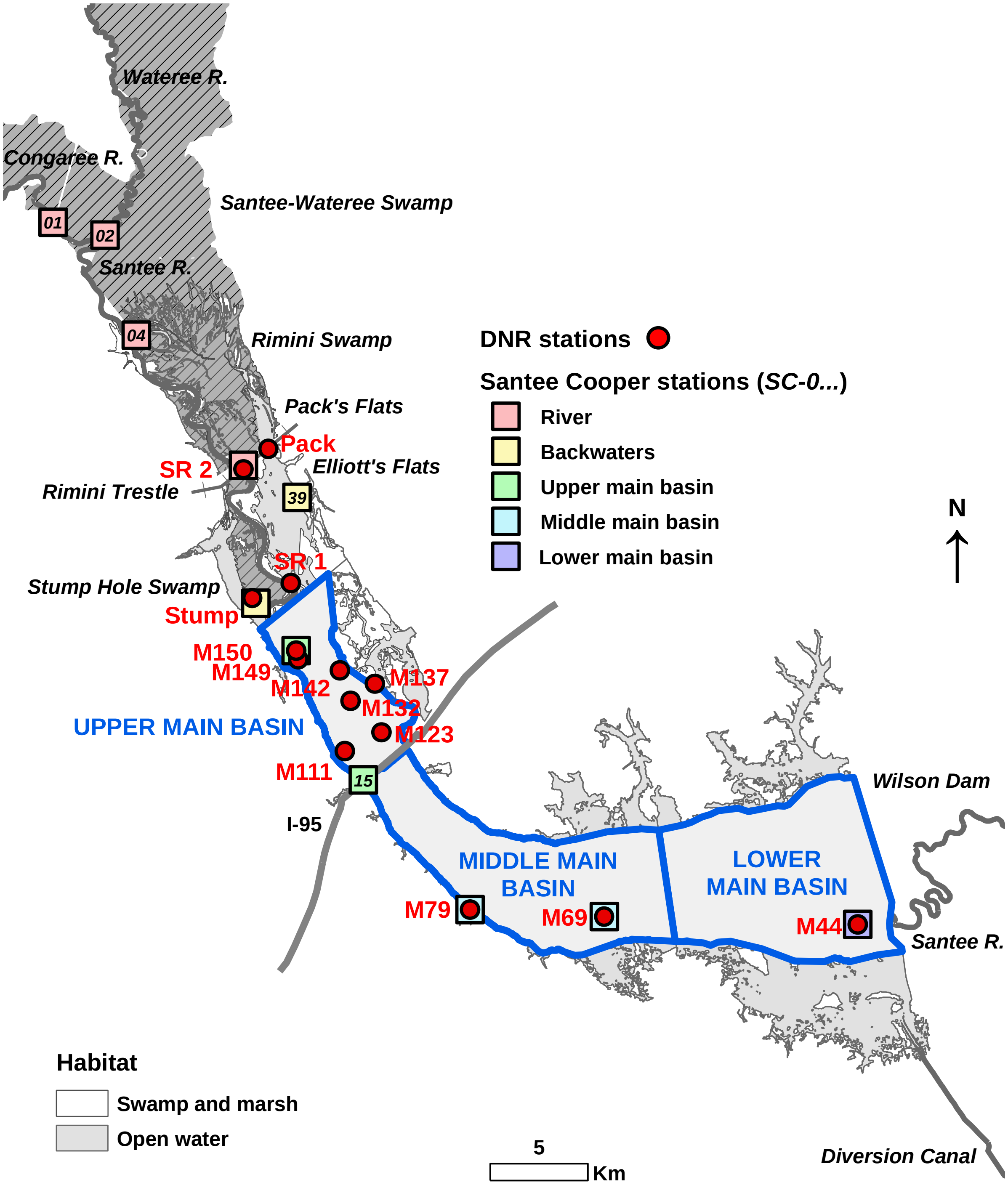

Figure 6.1. Zooplankton sampling stations in Lake Marion. Water quality stations are included for reference.

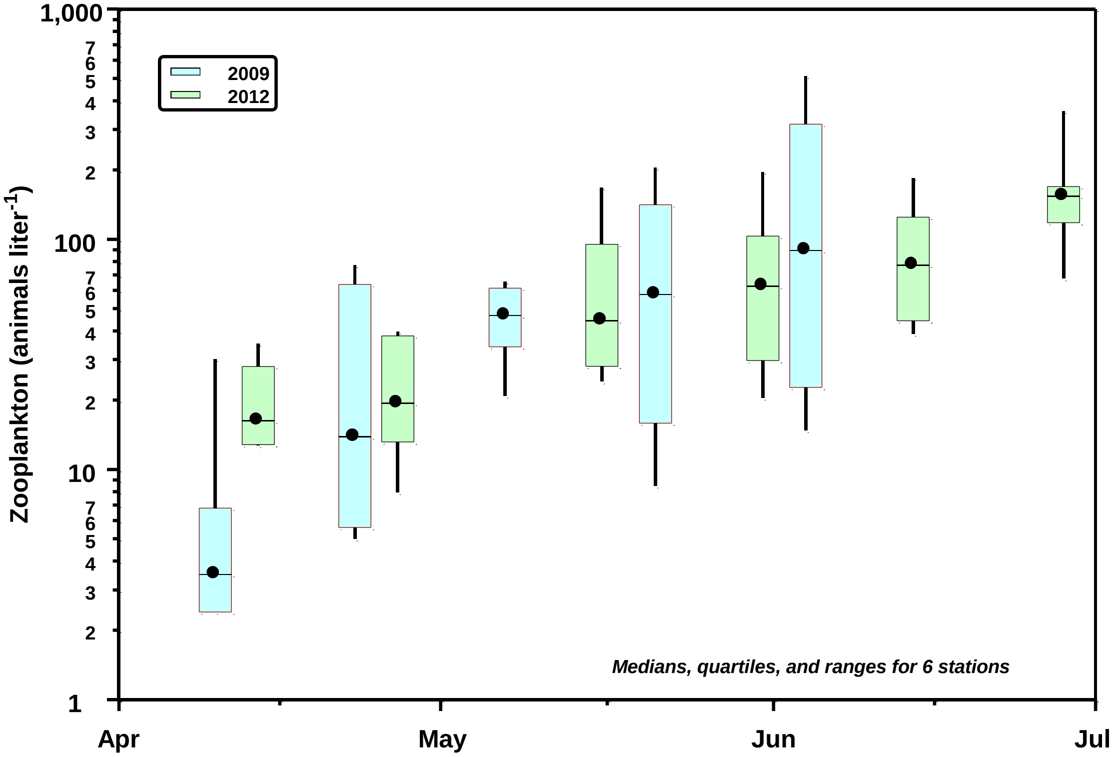

Figure 6.2. Zooplankton abundances in the upper main basin of Lake Marion in April-June of 2009 and 2012. Data are given in Appendices D and E.

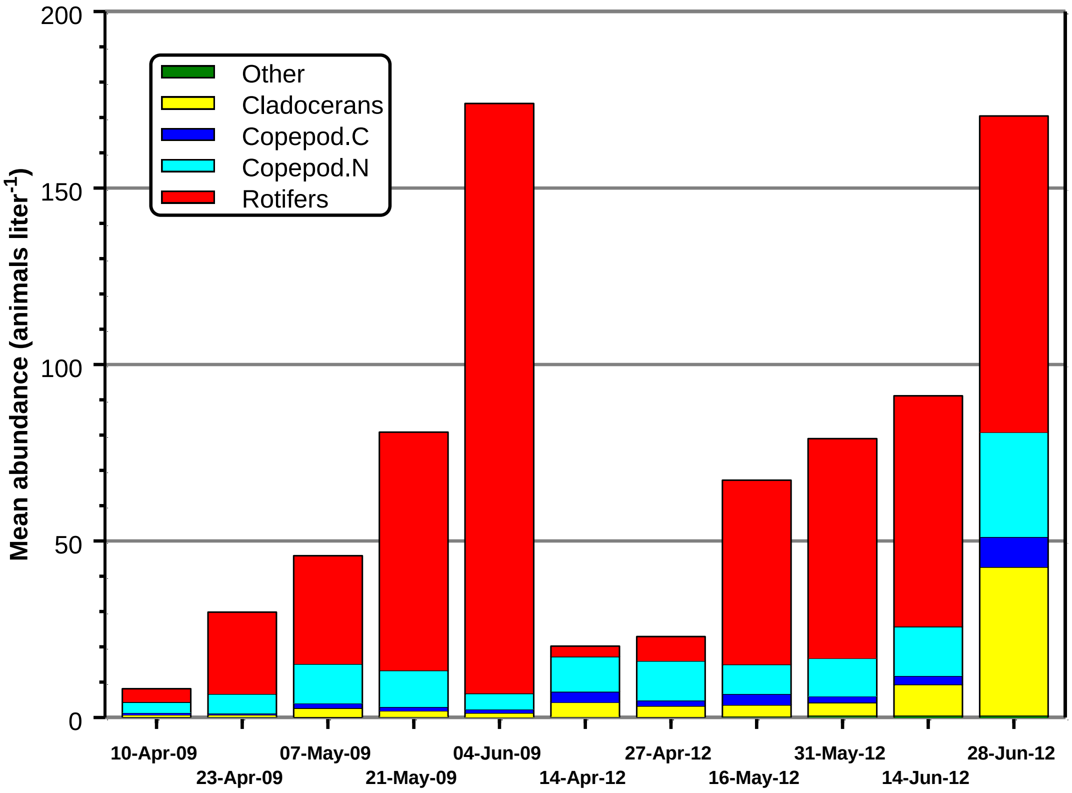

Figure 6.3. Mean zooplankton abundances in the upper main basin of Lake Marion by date and group in April-June of 2009 and 2012. Data are given in Table 6.2.

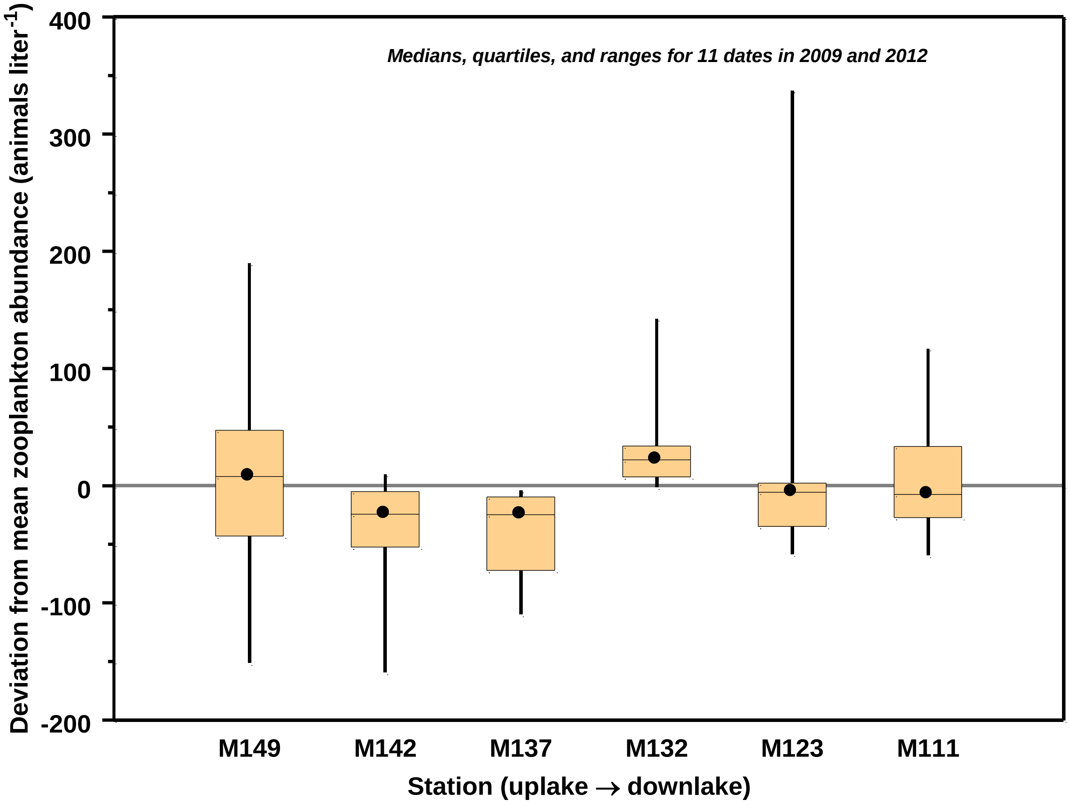

Figure 6.4. Spatial pattern in total zooplankton abundances in the upper main basin of Lake Marion in April-June of 2009 and 2012. Deviations by station were computed from the mean for each date.

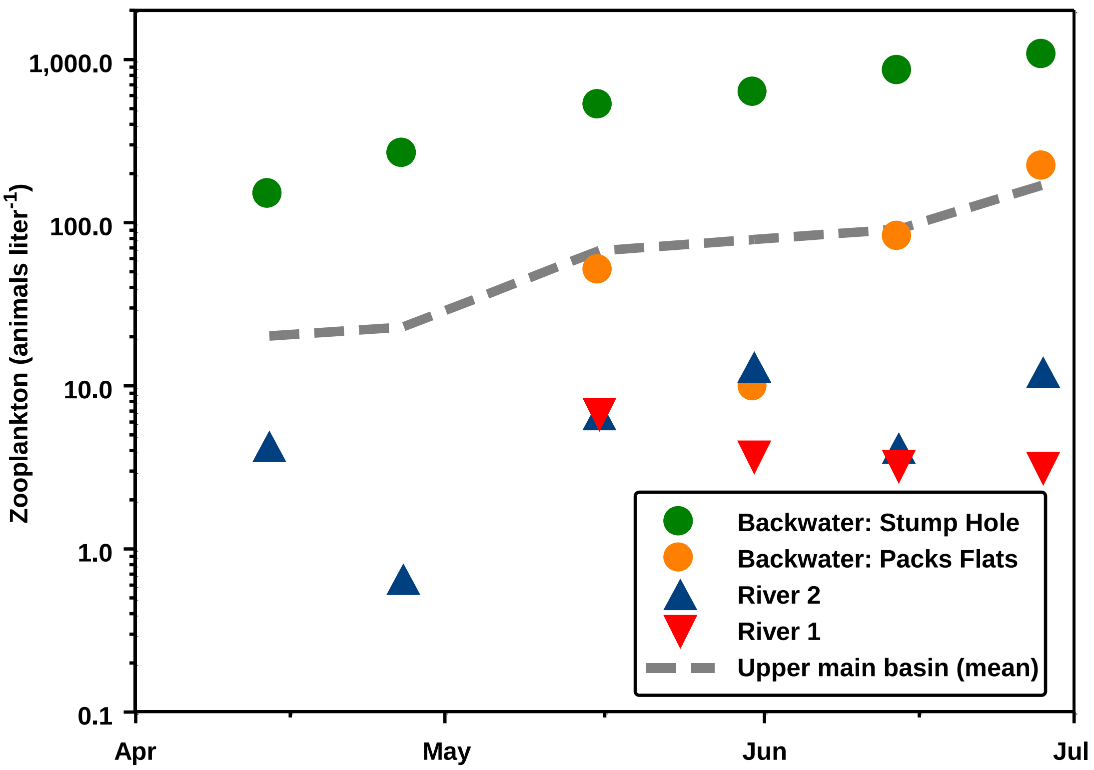

Figure 6.5. Zooplankton abundances in the upper backwaters and Santee River stations of Lake Marion in 2012. Data are given in Appendix E.

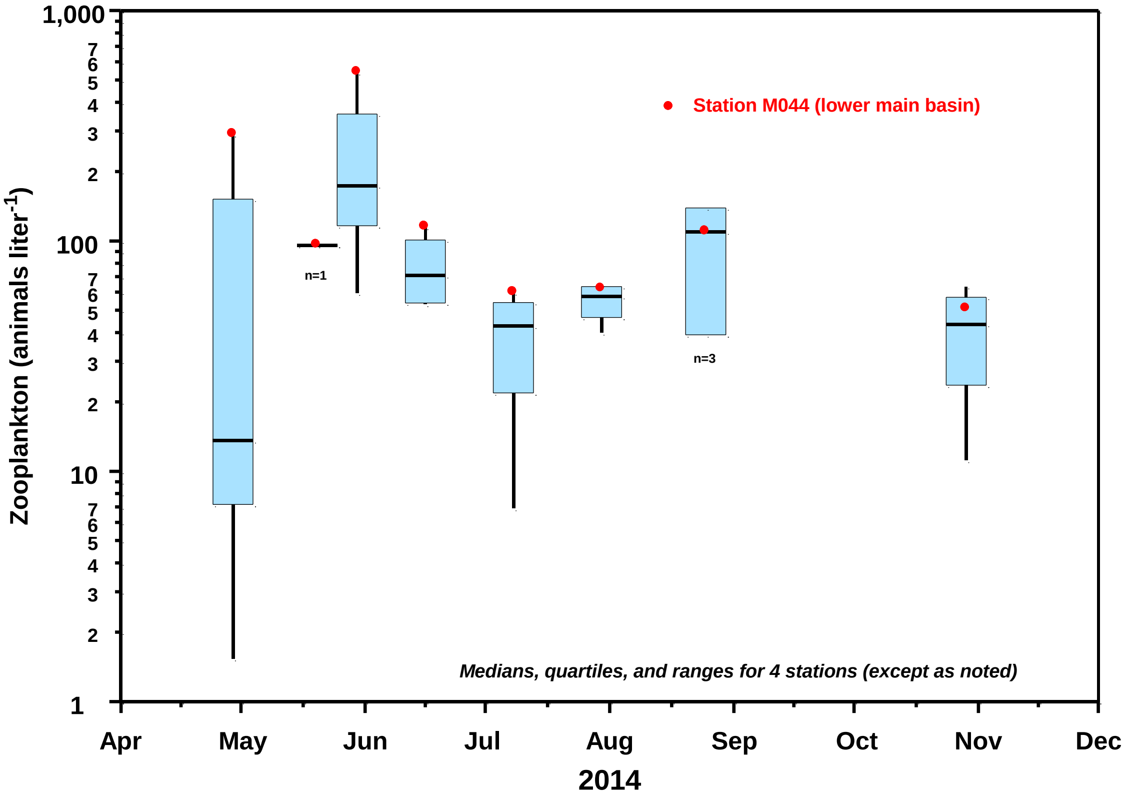

Figure 6.6. Zooplankton abundances in the main basin of Lake Marion in April-October of 2014. Data are given in Appendix F.

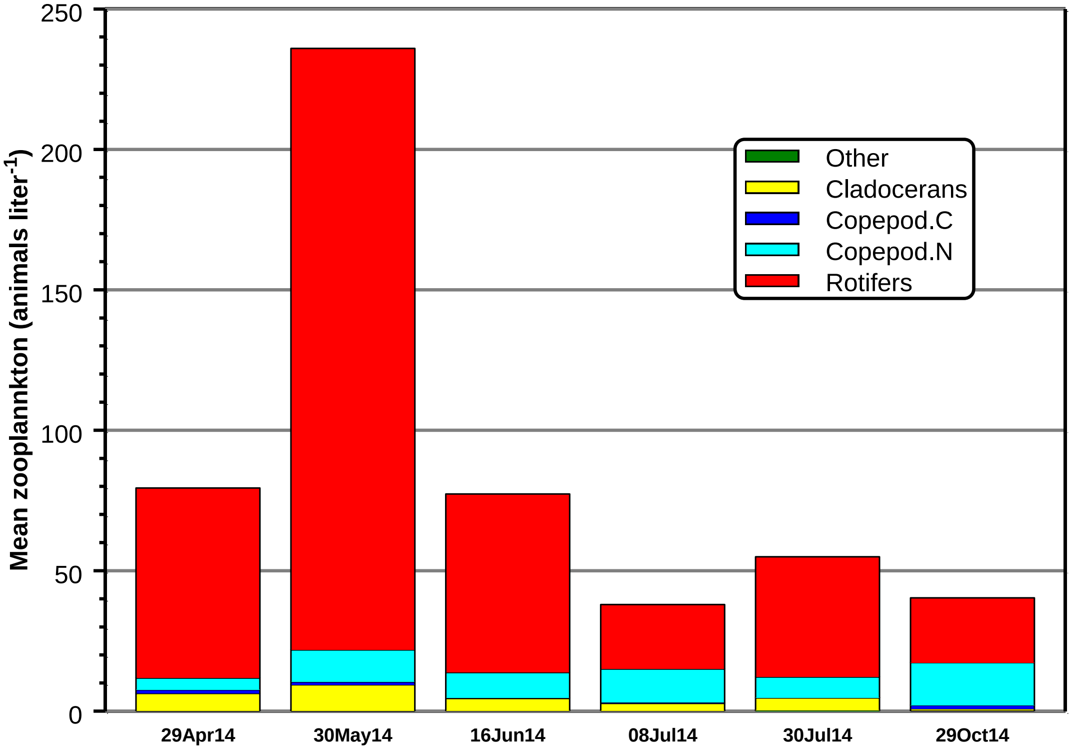

Figure 6.7. Mean zooplankton abundances in the main basin of Lake Marion by date and group in April-October of 2014. Data are given in Table 6.5.

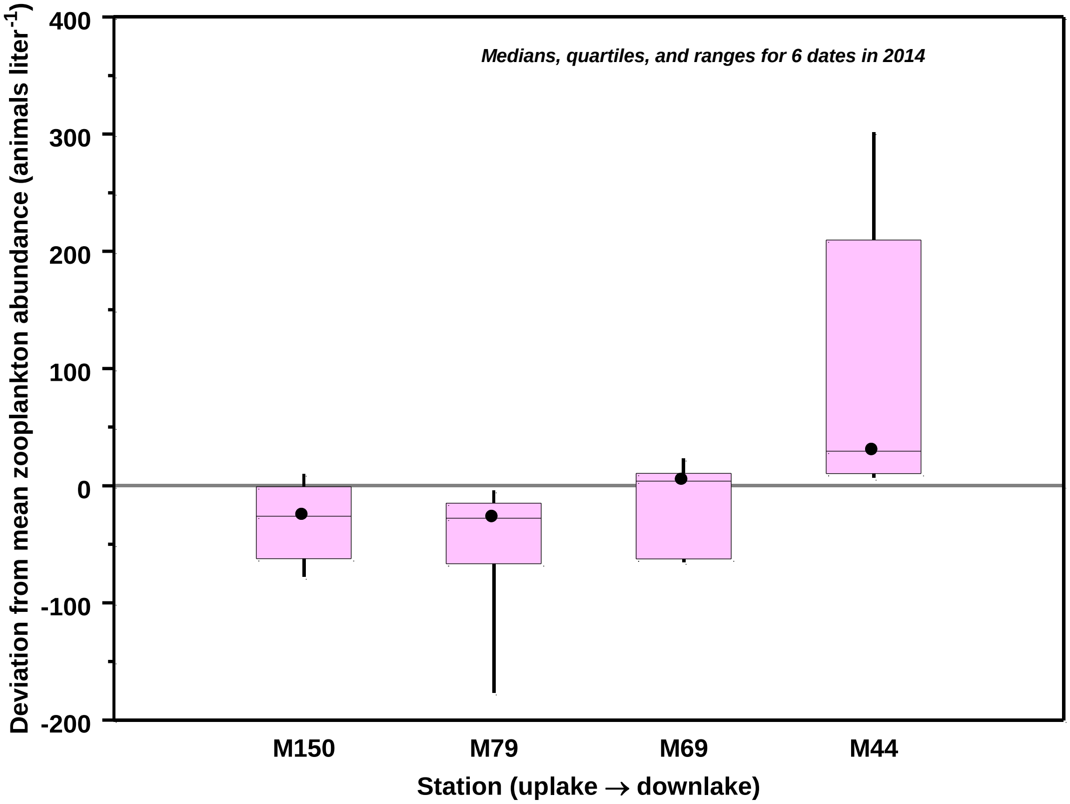

Figure 6.8. Spatial pattern in total zooplankton abundances in the main basin of Lake Marion in April-October of 2014. Deviations by station were computed from the mean for each date.

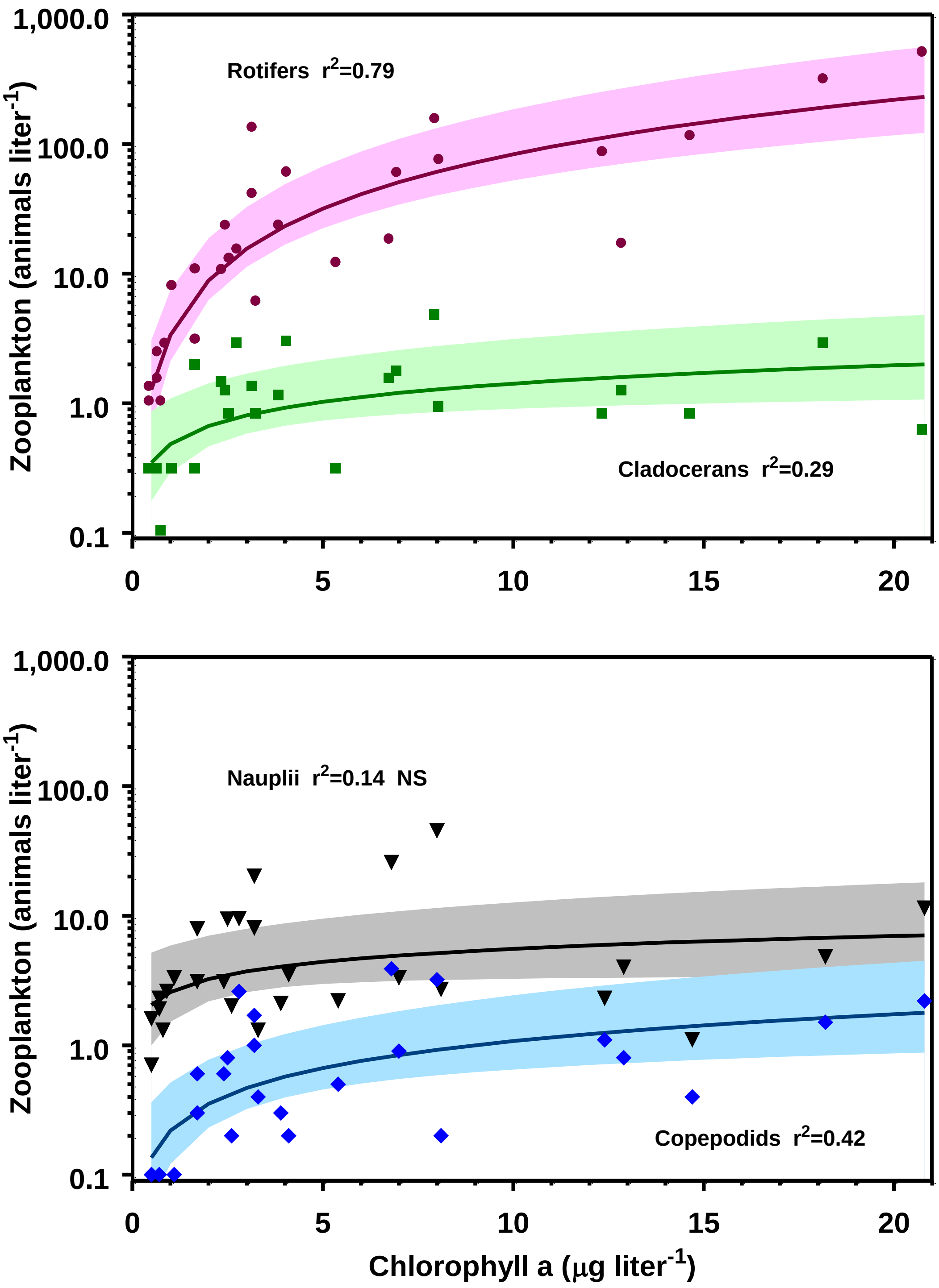

Figure 6.9. Zooplankton abundance by group as a function of chlorophyll a in the upper main basin of Lake Marion in April-June of 2009. Fitted regressions are shown as lines; 95% confidence intervals, as shaded areas.

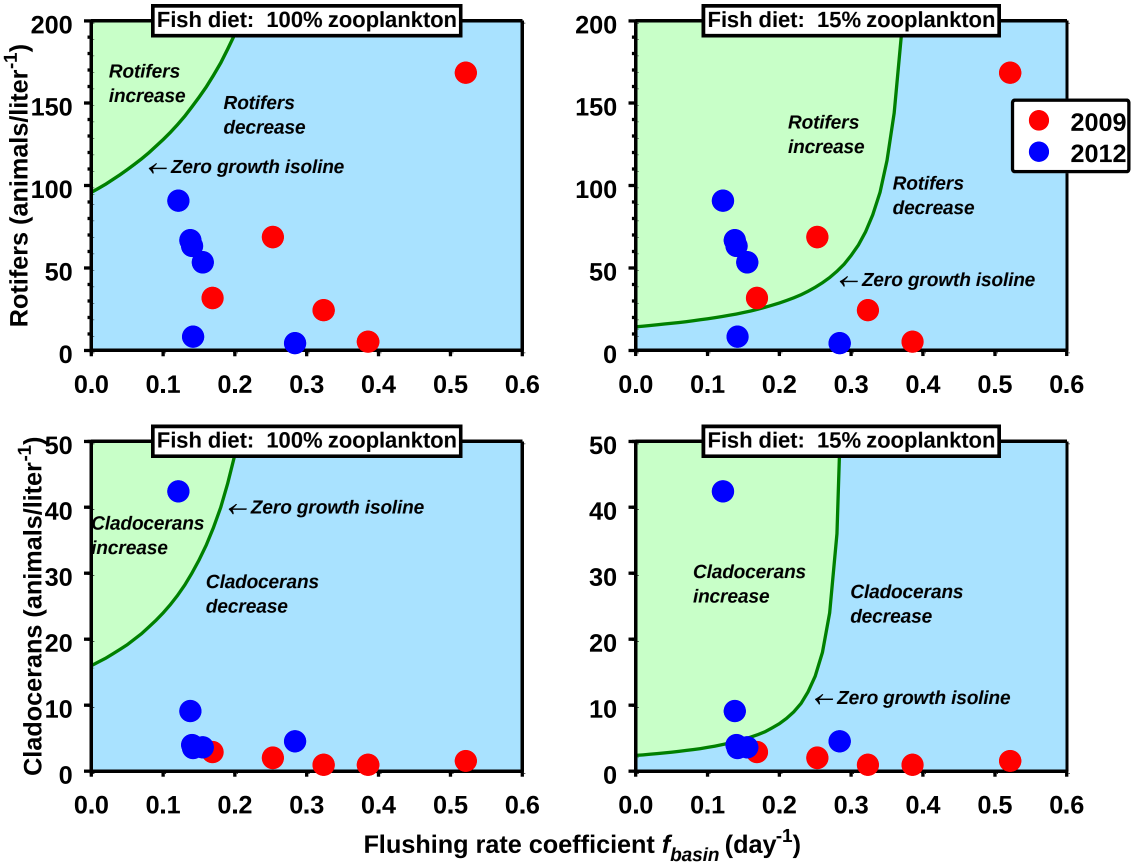

Figure 6.10. Modeled zero growth isolines for a rotifer population with birth rate b = 0.4 day^{-1} and a cladoceran population with birth rate b = 0.3 day^{-1} as functions of the flushing rate and population abundance. For combinations of population size and flushing rate that lie above the zero growth isoline, the modeled populations increase; below it, they decrease. Results for two levels of fish predation, based on the percentage of zooplankton in diets of the fish, are illustrated; see text for details. Filled circles show mean rotifer and cladoceran populations in the upper main basin, plotted against estimated flushing rate of the upper main basin, for all sampled dates in 2009 and 2012.

CHAPTER 7. The Food Web

The preceding chapters describe components of the biota in Lake Marion, as well as some of the processes and conditions likely to influence composition and dynamics. Here, we combine these results, supplemented with results from other recent studies, to sketch a picture of the food web in Lake Marion and to consider its influences on the fishery.

The benthos forms the largest component of the biomass in the spring food web in the upper main basin of Lake Marion (Tables 7.1 and 7.2, Figure 7.1). Although this region is relatively small, representing about 10% of the total area of the lake (Chapter 2), the Asiatic clam *Corbicula* sp., a benthic species, is positioned to influence planktonic resources throughout the main basin by removing material imported from the river, limiting algal productivity in the upper region, and reducing exports to the middle and lower regions (Chapter 5). Excess consumption by *Corbicula* sp. may subsidize other benthic consumers, including insects, partially offsetting adverse effects on planktonic resources for fish (Chapter 4).

While supporting some components of fish production, the benthos, particularly *Corbicula* sp., may compete with others through the consumption of planktonic algae, the main trophic resource for zooplankton. Consumption by *Corbicula* has been associated with depletion of pelagic resources in other systems (Chapter 4), and it appears to have similar effects in the upper main basin (Chapter 5).

In other large southeastern impoundments, the importance of the benthos in food webs may generally be small (Chapter 4). For a number of these reservoirs, widely fluctuating water levels and hypolimnetic oxygen depletion seem to limit abundances of the benthos and, consequently, their contributions to the food webs. In contrast, shallow depth, limited episodes of hypoxia, and modest fluctuations in water level may all promote development of the benthos in Lake Marion.

Phytoplankton abundances are often relatively low in the upper main basin (Chapter 3). Simulations results suggest that the clam population suppresses phytoplankton abundances and diverts a substantial proportion of phytoplankton production from pelagic to benthic habitat (Chapter 5). One robust and surprising result was the importance of imported phytoplankton to the upper main basin.

Zooplankton populations are also often relatively low in the upper main basin (Chapter 6). Phytoplankton abundances appear to limit birth rates for several of the important rotifer and cladoceran species. The largest uncertainty in the model for zooplankton dynamics remains the magnitude of predation by pelagic adult and young-of-year fish. Given the relatively high spring flushing rates of the upper basin, results from the model suggest that zooplankton populations could not sustain consumption by even a modest population of fish in most years (Chapter 6). However, estimates of the magnitude of predation on zooplankton in upper Lake Marion are limited by information about both abundances and feeding habits of the pelagic fish.

Pelagic fish populations in Lake Marion fluctuate widely (e.g., Bulak, 2016). Overwintering populations of threadfin shad can be decimated by cold temperatures in certain years. Fluctuations in abundances of juvenile and adult planktivorous fish could affect their impact on pelagic resources for larval fish in spring.

Among the pelagic fish, threadfin shad *Dorosoma petenense* constitutes the largest component of the biomass (Table 7.2). However, its trophic position is uncertain. Diets of threadfin shad include zooplankton, detritus, and phytoplankton (Baker and Schmitz, 1971;

Hendricks and Noble, 1979; Jackson et al. 1990; Davis and Foltz, 1991). It often feeds mainly as a detritivore (e.g., Hendricks and Noble, 1979). In Lake Jordan, North Carolina, Jackson et al. (1990) characterized both threadfin and gizzard shad were detritivores, except during “a brief period early in the growing season coincidental with peak zooplankton densities.” Zooplankton made up only 15% of the diets of threadfin shad collected from pelagic habitats of lakes Marion and Moultrie in late spring and summer (Appendix H). We speculate that threadfin shad are supported mainly by algal and detrital material in Lake Marion, but take advantage of temporal or spatial fluctuations in zooplankton populations.

Advective transport appears to have a strong influence on dynamics of both phytoplankton and zooplankton in the upper main basin of Lake Marion (Chapters 5 and 6). Given the wide variation in discharge from the Santee River to Lake Marion, these influences will vary among seasons and across years. Advective transport is also influential in the dynamics of fish species such as striped bass, whose eggs and larvae are transported into Lake Marion from spawning sites upriver (Bulak et al., 1997).

The fish larvae are small in biomass, but the successful recruitment is essential to maintenance of their species. In Lake Marion, larval stages of important species of pelagic fish, including threadfin shad, American shad *Alosa sapidissima*, and striped bass *Morone saxatilis*, depend on zooplankton. This resource is probably often limiting to the larval fish, although it seems unlikely that their feeding has much impact on it (Chapter 6). To the extent that predation by juvenile and adult pelagic fish (mainly threadfin shad; based on their biomass, the impact of American shad is probably negligible) suppresses the zooplankton abundances, the larval fish compete with the juveniles and adults.

Both threadfin shad and the Asiatic clam *Corbicula* sp. appear to occupy key positions in the food web of upper Lake Marion (and beyond). Interactions among components of the food web are mediated by advective processes—driven by the vast quantity of water flowing through this system.

Table 7.1. Components of the food web in the upper main basin of Lake Marion in spring. Except for forage fish and striped bass, the estimates are based on this study. Biomass computations included all numerically important components of the plankton and benthos. For post-larval fish, a dry biomass of 1 g m^{-2} is roughly equivalent to a wet biomass of 50 kg ha^{-1}.

Habitat, higher taxa, and functional or taxonomic descriptions of food web components		***Dry biomass ($g\ m^{-2}$)***
Plankton and nekton	**Component**	**3.4**
Algae	Phytoplankton[a]	2.2
Crustacea, Rotifera	Zooplankton[b]	0.11
Fish	Ichthyoplankton[c]	0.011
Fish	Forage fish (<20 cm TL)[d] 90% *Dorosoma petenense*[e] 4% *Alosa sapidissima*	1.0
Fish	Striped bass (all ages)[f]	0.08
Benthos	**Component**[g]	**75**
Molluscs (Bivalvia)	*Corbicula fluminea*	48
Molluscs (Bivalvia)	Sphaeriidae	0.18
Molluscs (Bivalvia)	Unionidae	6.0
Molluscs (Gastropoda)	*Viviparus subpurpureus*	18
Insects (Ephemeroptera)	*Hexagenia limbata*	2.8
Insects (Diptera)	*Chaoborus punctipennis*	0.012
Insects (Diptera)	Chironomidae	0.028

[a] Chlorophyll data: Appendix C; conversion to biomass: Chapter 5

[b] Chapter 6

[c] Appendix G

[d] Estimated as 50% of 3-year mean for summer and fall in Bulak (2016)

[e] Percentages of clupeid biomass based on combined data for September-December gill net samples in lakes Marion and Moultrie; clupeids constituted 98% of total number of fish caught (Bulak, 2014)

[f] Data and functions in Bulak et al. (1995)

[g] Chapter 4

Table 7.2. Main interactions among components of food web in upper Lake Marion in spring.

Component	***Interactions***
Phytoplankton	Consumption by zooplankton is negligible Modeled consumption by *Corbicula*, if feeding mainly on phytoplankton, is substantial Import from river and upper backwaters is be substantial Phytoplankton dynamics is responsive to discharge from the river
Benthos	Feeding by *Corbicula* potentially transfers large quantity of material from pelagic to benthic habitat Excess consumption by *Corbicula* may supplement diets of other benthic consumers, including *Hexagenia*
Zooplankton	Import from the river is negligible, but import from backwaters may be important Zooplankton dynamics is responsive to discharge from the river Abundances of rotifers, cladocerans, and copepodids are correlated with abundances of phytoplankton; variations in birth rates of rotifers and cladocerans suggest limitations by phytoplankton abundance Predation by planktivorous larval fish, such as threadfin shad, is negligible Populations planktivorous young-of-year and pelagic fish could deplete zooplankton
Planktivorous larval fish	Abundance of zooplankton is often low, relative to densities reported to sustain maximum growth and survival
Pelagic YOY and adult fish	Spring zooplankton populations are on average generally insufficient to support even low populations of planktivorous fish; threadfin shad may feed mainly on algae and detritus

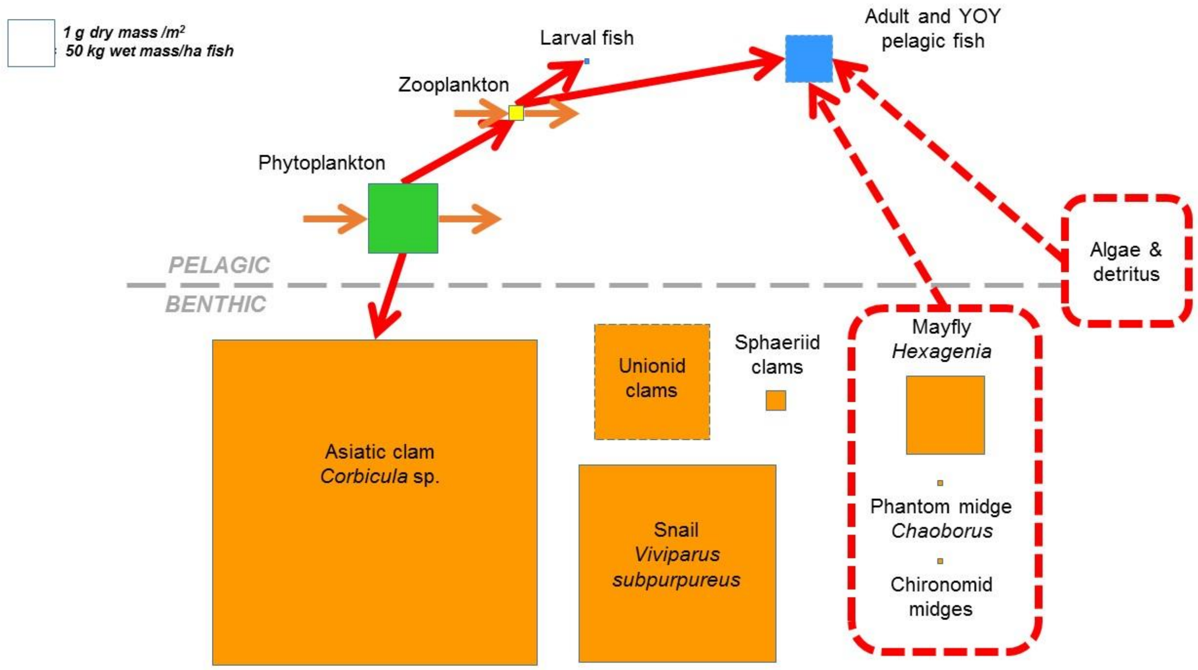

Figure 7.1. Spring food web for the upper main basin of Lake Marion. The boxes are proportional in size to dry biomass (exclusive of shell for mollusks) (Table 7.1). We have no biomass estimate for “Algae & detritus” (see text). The red arrows represent trophic transfers; the blue, advective transfers. The solid arrows indicate rates that we have estimated or modelled. The dashed arrows indicate interactions that we judge to be important, but did not estimate.

RECOMMENDATIONS

Our considerations here are predicated on the notion that the food resources, specifically zooplankton abundances, might limit recruitment of striped bass and other fish with pelagic larval stages in the upper main basin of Lake Marion in spring. The dynamics of zooplankton in this system seem to be governed by advection, phytoplankton abundances, and predation.

Advection is erratically variable and essentially uncontrollable.

Reducing the abundance of *Corbicula* could enhance the abundance of phytoplankton, and thus improve the resource base for zooplankton, in the upper main basin in most years (Chapter 5; in spring seasons with high flushing rates, the effects would be negligible). *Corbicula* populations are vulnerable to drawdown, particularly in warm months (see Chapter 4). However, because most of the *Corbicula* are located at depths >2 m, an effective drawdown would likely have undesirable consequences.

One of the difficulties in analyzing the food web of Lake Marion is the limited knowledge of abundances and diets of the juvenile and adult threadfin shad during spring in the upper main basin. Our analyses suggest that reducing the numbers of threadfin shad could greatly enhance the abundance of zooplankton. Because the numbers of American shad are so low, the effect of increasing passage of American shad into Lake Marion is likely to be negligible.

The options for improving recruitment of key species, particularly striped bass and American shad, by manipulating conditions within the lake appear to very limited. However, strategies for fish stocking and fish passage may offer better opportunities for improvement.

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APPENDIX A. Water Quality in Lake Marion (1997-2014)

Data for pH, specific conductance, hardness, turbidity, secchi transparency, color, total phosphorus, and total nitrogen are summarized by station. Chlorophyll a is summarized by season and station. Samples were collected at near surface (0.3 m or 1 ft) depth at monthly intervals. Years gives the number of years for which data from at least one monthly sample were obtained. Samples were collected by Santee Cooper or by South Carolina Department of Health and Environmental Control; sources for the data are described in Chapter 3.

pH

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	5.40	6.83	7.11	7.06	7.33	8.25	166	16
SC-002	6.15	6.96	7.17	7.15	7.35	8.86	162	17
SC-004	5.86	6.92	7.10	7.06	7.28	7.86	179	17
SC-008	5.74	6.86	7.04	7.04	7.28	8.10	138	13
SC-039	5.80	6.83	7.17	7.11	7.34	8.30	119	12
SC-044	5.67	7.13	7.33	7.37	7.58	9.14	108	12
SC-010	4.57	6.98	7.25	7.21	7.43	8.74	165	18
SC-015	5.79	7.10	7.36	7.36	7.59	8.82	185	18
SC-040	6.10	7.10	7.30	7.31	7.57	8.61	149	15
SC-016	5.63	7.34	7.55	7.60	7.86	8.97	167	18
SC-022	6.20	7.38	7.61	7.63	7.87	8.92	172	18

Specific conductance (µmho cm^{-2})

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	38.0	74.0	82.5	81.7	88.8	123.0	126	14
SC-002	45.0	125.8	153.0	158.1	193.8	281.0	126	14
SC-004	40.0	90.5	109.0	112.8	135.0	251.0	179	17
SC-008	10.1	89.0	110.5	114.2	137.0	253.0	138	13
SC-039	57.0	100.0	118.0	122.4	143.0	206.0	113	12
SC-044	51.0	88.0	103.0	110.2	135.0	199.0	109	12
SC-010	40.0	87.5	105.0	109.4	128.5	222.0	167	18
SC-015	52.0	86.0	105.0	108.0	124.0	199.0	187	18
SC-040	44.0	85.0	101.0	106.8	126.0	184.0	145	15
SC-016	52.0	84.0	100.0	103.9	120.0	168.0	169	18
SC-022	60.0	85.0	95.0	102.0	118.0	169.0	175	18

Hardness (Ca + Mg, mg liter^{-1})

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	10.0	16.0	18.0	18.4	21.0	27.0	47	5
SC-002	12.2	23.3	26.0	26.5	31.0	44.0	47	5
SC-004	9.0	19.0	22.0	21.2	24.0	31.0	94	10
SC-008	7.6	19.0	22.0	21.4	24.0	32.0	93	10
SC-039	10.0	19.0	21.0	21.4	24.0	34.0	93	10
SC-044	11.0	19.0	21.0	20.7	23.0	33.0	90	10
SC-010	10.9	19.0	21.0	22.3	23.6	84.0	95	10
SC-015	8.0	18.0	20.4	21.1	22.7	59.0	98	10
SC-040	7.0	17.0	19.7	20.3	21.0	115.0	100	10
SC-016	7.0	16.0	19.0	18.8	21.0	34.0	96	10
SC-022	9.0	16.0	18.0	18.3	21.0	32.0	97	10

Turbidity (NTU)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	3.3	6.7	10.3	15.7	18.0	76.0	72	7
SC-002	6.0	9.9	16.0	19.1	23.2	61.6	71	7
SC-004	3.7	8.3	12.1	19.6	19.8	138.0	102	10
SC-008	4.2	7.9	11.3	18.7	18.2	140.0	102	10
SC-039	3.8	7.5	10.6	11.7	13.7	30.7	98	10
SC-044	3.0	6.8	9.1	13.0	16.1	75.8	97	10
SC-010	3.7	9.0	12.7	16.3	17.2	122.0	100	10
SC-015	3.1	6.2	8.7	12.4	13.1	54.7	105	10
SC-040	2.7	5.1	7.0	10.0	11.0	55.3	105	10
SC-016	1.1	3.3	4.9	7.9	8.8	44.5	103	10
SC-022	1.2	2.7	3.8	5.7	6.6	29.9	105	10

Secchi transparency (m)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-039	0.3	0.6	0.8	0.8	1.0	1.7	107	12
SC-044	0.1	0.5	0.7	0.7	0.8	1.1	106	12
SC-010	0.1	0.6	0.7	0.7	0.9	2.0	164	18
SC-015	0.1	0.7	0.9	0.9	1.1	2.3	185	18
SC-040	0.2	0.8	0.9	0.9	1.1	2.0	141	14
SC-016	0.3	0.9	1.1	1.1	1.2	2.1	165	18
SC-022	0.4	1.0	1.2	1.3	1.5	2.4	172	18

Color (PCU)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	15.0	25.0	30.0	38.4	40.0	140.0	52	6
SC-002	25.0	35.0	40.0	45.6	50.0	140.0	51	6
SC-004	1.0	30.0	35.0	44.3	40.0	200.0	102	10
SC-008	0.0	30.0	35.0	42.0	40.0	140.0	102	10
SC-039	25.0	35.0	40.0	45.8	50.0	120.0	99	10
SC-044	20.0	35.0	40.0	42.7	50.0	120.0	97	10
SC-010	15.0	30.0	35.0	39.5	40.0	160.0	101	10
SC-015	17.7	30.0	35.0	39.0	40.0	140.0	107	10
SC-040	20.0	30.0	35.0	36.5	40.0	120.0	106	10
SC-016	20.0	30.0	30.0	35.5	40.0	80.0	103	10
SC-022	15.0	25.0	30.0	31.1	35.0	70.0	105	10

Total phosphorus (mg liter-1)   BDL indicates parameter below minimum detection limit of 0.02 mg/liter. Means are shown only if >75% of values were above the minimum detection limit.

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	*BDL*	0.04	0.06	0.07	0.08	0.75	102	12
SC-002	*BDL*	0.06	0.08	0.09	0.10	0.60	102	12
SC-004	*BDL*	0.05	0.07	0.10	0.09	0.92	115	15
SC-008	*BDL*	0.02	0.07	0.09	0.09	1.10	82	11
SC-039	*BDL*	*BDL*	0.05	-	0.08	1.09	74	10
SC-044	*BDL*	*BDL*	0.04	-	0.07	0.16	70	10
SC-010	*BDL*	0.03	0.06	0.06	0.07	0.53	110	15
SC-015	*BDL*	0.02	0.05	0.08	0.07	0.73	122	16
SC-040	*BDL*	*BDL*	0.04	-	0.06	0.26	93	12
SC-016	*BDL*	*BDL*	0.03	-	0.06	0.44	114	16
SC-022	*BDL*	*BDL*	*BDL*	-	0.05	0.46	114	16

Total nitrogen (mg liter^{-1})

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	0.05	0.59	0.75	0.77	0.90	1.62	40	4
SC-002	0.05	0.54	0.69	0.72	0.88	1.65	39	4
SC-004	0.05	0.61	0.71	0.75	0.91	1.73	41	4
SC-008	0.05	0.54	0.70	0.70	0.89	1.31	41	4
SC-039	0.21	0.41	0.58	0.55	0.65	1.02	29	4
SC-044	0.05	0.45	0.56	0.55	0.71	0.98	36	4
SC-010	0.05	0.49	0.60	0.62	0.81	1.51	42	4
SC-015	0.05	0.45	0.64	0.63	0.83	1.23	43	4
SC-040	0.24	0.47	0.60	0.64	0.75	1.37	31	4
SC-016	0.05	0.36	0.54	0.59	0.78	2.00	43	4
SC-022	0.05	0.34	0.45	0.49	0.62	1.07	44	4

Chlorophyll a (winter: December-February)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-039	0.20	0.40	0.90	1.59	2.08	6.70	32	17
SC-044	0.20	1.00	2.75	4.53	4.95	24.90	36	18
SC-010	0.20	0.50	0.80	1.50	1.50	9.90	35	17
SC-015	0.30	0.70	1.10	1.97	2.20	16.90	37	16
SC-040	0.30	1.20	2.00	3.19	3.55	22.50	31	14
SC-016	0.30	1.50	2.50	4.63	5.28	19.00	34	16
SC-022	0.40	3.43	6.00	7.18	9.50	21.80	34	16
Mean of means for 5 main basin stations				3.69				

Chlorophyll a (spring: March-May)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-039	0.30	1.50	3.02	6.28	6.88	30.90	38	17
SC-044	0.60	8.43	14.05	14.86	21.15	31.30	38	18
SC-010	0.60	1.50	2.90	5.12	6.90	28.20	41	18
SC-015	0.30	2.80	5.30	8.36	9.20	58.70	45	18
SC-040	0.60	3.70	5.90	7.87	10.80	23.20	37	15
SC-016	0.30	4.05	7.70	8.05	10.85	26.60	39	16
SC-022	1.70	4.00	6.80	7.48	8.80	18.60	41	17
Mean of means for 5 main basin stations				7.38				

Chlorophyll a (summer: June-August)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	1.26	3.82	3.87	4.41	6.45	6.65	5	2*
SC-002	2.52	2.58	3.61	4.71	6.30	8.54	5	2*
SC-004	0.15	2.02	3.78	3.84	6.41	6.85	5	2*
SC-008	1.60	2.79	3.82	4.53	6.47	7.95	5	2*
SC-039	0.20	3.05	6.50	8.96	13.20	28.30	38	16
SC-044	0.10	12.18	17.30	21.17	25.05	126.70	36	16
SC-010	1.00	3.93	8.30	11.64	15.55	50.60	44	18
SC-015	1.70	5.45	8.60	11.54	12.47	39.90	48	18
SC-040	2.40	5.17	8.25	12.73	13.50	60.90	40	16
SC-016	0.70	6.70	13.05	13.29	16.10	33.20	41	17
SC-022	0.40	3.45	6.80	8.05	9.90	25.40	43	17
Mean of means for 5 main basin stations				11.45				

*2014 & 2015

Chlorophyll a (fall: September-November)

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	0.88	0.98	1.08	2.40	3.17	5.25	3	2*
SC-002	1.92	2.93	3.93	3.49	4.28	4.62	3	2*
SC-004	1.27	1.47	1.67	2.61	3.29	4.90	3	2*
SC-008	1.16	1.58	1.99	1.96	2.37	2.74	3	2*
SC-039	0.30	1.80	2.80	4.90	6.00	25.60	25	14
SC-044	0.90	5.30	9.00	13.48	19.00	50.70	25	14
SC-010	0.20	0.83	2.25	3.32	4.78	18.40	30	15
SC-015	0.20	2.10	4.50	6.52	7.90	34.50	37	16
SC-040	1.10	3.70	5.00	7.14	6.67	28.60	30	13
SC-016	0.72	5.08	8.80	10.66	12.13	32.30	32	14
SC-022	1.00	5.60	8.40	9.70	10.80	27.40	33	14
Mean of means for 5 main basin stations				7.47				

*2014 & 2015

APPENDIX B. Water Quality in Lake Marion (1984-1995)

Total phosphorus is summarized by station. Chlorophyll a is summarized by season and station. Samples were collected at near surface (0.3 m or 1 ft) depth at monthly intervals. Years gives the number of years for which data from at least one monthly sample were obtained. Samples were collected by Santee Cooper or by South Carolina Department of Health and Environmental Control; sources for the data are described in Chapter 3.

Total phosphorus (mg liter^{-1}) (1984-1995). BDL indicates parameter below minimum detection limit of 0.02 mg/liter. Means are shown if >25% of values were above the limit.

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-001	*BDL*	0.05	0.07	0.09	0.12	0.23	115	12
SC-002	*BDL*	0.05	0.08	0.09	0.11	0.60	115	12
SC-004	*BDL*	0.05	0.08	0.08	0.11	0.21	117	12
SC-008	*BDL*	0.05	0.07	0.08	0.10	0.17	118	12
SC-039	*BDL*	0.04	0.05	0.06	0.07	0.22	95	11
SC-044	*BDL*	0.02	0.04	0.04	0.06	0.11	47	6
SC-010	*BDL*	0.04	0.06	0.06	0.09	0.21	114	12
SC-015	*BDL*	0.03	0.05	0.06	0.07	0.17	120	12
SC-040	*BDL*	0.03	0.05	0.05	0.06	0.16	93	11
SC-016	*BDL*	0.03	0.04	0.04	0.05	0.15	97	12
SC-022	*BDL*	0.02	0.03	0.04	0.05	0.14	98	12

Chlorophyll a, 1984-1995, in winter (December-February).

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***n***	***Years***
SC-039	0.30	1.40	2.40	5.01	5.00	24.60	17	8
SC-044	0.50	1.53	2.10	2.23	2.98	4.10	6	3
SC-010	0.70	1.60	2.40	3.76	5.10	14.50	23	10
SC-015	1.20	2.80	4.60	8.23	8.30	63.40	21	10
SC-040	0.64	3.28	5.05	12.14	14.18	54.70	18	9
SC-016	0.60	5.40	9.30	12.85	17.30	34.20	17	8
SC-022	0.90	5.14	9.15	13.79	26.03	31.90	20	8
Mean of means for 5 main basin stations				10.15				

Chlorophyll a, 1984-1995, in spring (March-May).

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***N***	***Years***
SC-039	1.30	3.20	6.05	14.05	18.65	88.90	20	7
SC-044	3.30	12.02	14.00	19.96	23.00	58.50	8	3
SC-010	2.70	6.17	16.85	15.33	22.70	27.20	24	9
SC-015	1.90	14.83	24.10	25.20	33.80	53.90	25	9
SC-040	5.08	10.30	27.70	25.68	36.70	58.00	19	7
SC-016	1.00	13.65	18.70	24.78	32.30	63.60	23	9
SC-022	1.40	9.00	13.30	15.88	24.90	36.80	22	9
Mean of means for 5 main basin stations				21.57				

Chlorophyll a, 1984-1995, in summer (June-August).

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***N***	***Years***
SC-039	0.50	8.10	16.70	17.78	25.70	36.95	21	9
SC-044	5.00	11.35	25.25	24.29	36.13	44.30	8	4
SC-010	1.00	16.50	24.30	24.12	34.00	44.80	25	10
SC-015	7.20	21.05	29.00	27.66	34.48	49.90	23	10
SC-040	10.70	17.50	29.80	35.16	40.20	130.40	19	9
SC-016	2.00	12.46	21.20	23.31	34.80	53.30	21	9
SC-022	4.30	11.28	17.85	17.95	22.78	36.61	18	9
Mean of means for 5 main basin stations				25.23				

Chlorophyll a, 1984-1995, in fall (September-November).

Station	***Min***	***Q1***	***Median***	***Mean***	***Q3***	***Max***	***N***	***Years***
SC-039	3.00	5.20	7.30	10.02	14.16	33.40	17	9
SC-044	12.80	27.15	41.50	36.97	49.05	56.60	3	3
SC-010	0.50	3.25	6.35	9.42	14.00	32.80	22	10
SC-015	1.20	13.70	16.20	24.06	27.90	75.30	23	10
SC-040	2.90	10.70	22.30	30.79	31.36	139.60	19	9
SC-016	2.10	10.35	22.70	22.12	30.69	48.81	19	10
SC-022	4.30	11.28	17.85	17.95	22.78	36.61	18	9
Mean of means for 5 main basin stations				20.87				

APPENDIX C. Chlorophyll a in the Upper Main Basin of Lake Marion (2009)

The water samples for analysis of chlorophyll a were collected in conjunction with the zooplankton samples (see Chapter 6).

Methods

Samples for analysis of chlorophyll a at six open water stations (see Figure 6.1) at two-week intervals from mid-April to early June in 2009. At each station, water samples were collected from 0, 1, 2, 3, and 4 m at 1-m intervals. Subsamples of 100 ml from each sample were combined and placed in a dark bottle on ice. Samples were filtered within 24 hours and analyzed by the SC DNR Chemistry Laboratory according to DHEC-approved protocols.

Results

Mean chlorophyll concentrations at the 6 stations in the main basin of upper Lake Marion increased from 1.2 µg liter^{-1} in mid-April to 1.2 µg liter^{-1} in early June (Figure 2, upper panel). Variation among samples was wide on every date. The April and May values for Santee Cooper station SC-010 were similar to corresponding values for the DNR stations. An exponential function fitted to the first and last points of the time series yielded a growth rate coefficient of $p = 0.044$ day^{-1}.

Table C.1. Chlorophyll a by station in the upper main basin of Lake Marion in April-June 2009.

			Chlorophyll a (µg liter^{-1})			
Date	***M111***	***M123***	***M132***	***M137***	***M142***	***Mean***
10-Apr-09	1.7	0.5	2.8	0.7	0.5	1.2
23-Apr-09	2.6*	1.1*	3.2	0.7	0.9	2.8
07-May-09	2.5	5.8	6.8	2.5	1.7	3.9
21-May-09	3.9	8.0	12.4	3.3	2.4	5.5
04-Jun-09	14.7	20.8	18.2	7.0	5.4	13.2

* Samples may have been exchanged

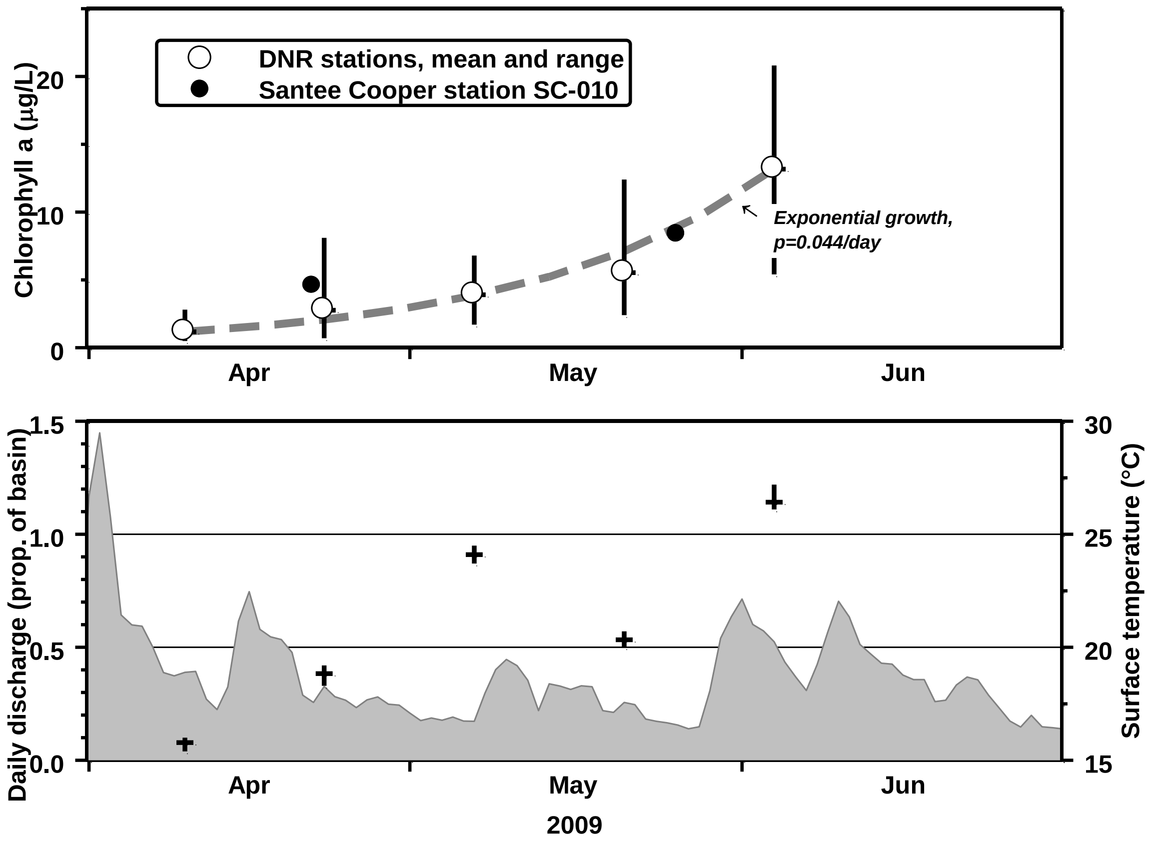

Figure C.1. Chlorophyll a and flushing rate in main basin of upper Lake Marion in April-June 2009. Chlorophyll a values (upper panel) are shown for the six SC DNR stations (five dates) and for SC-010 (two dates only during this period).

APPENDIX D. Zooplankton Abundances by Date and Station in the Upper Main Basin of Lake Marion (2009)

All abundances are reported in animals liter^{-1}.

Date	*Region*	*Station*	*Rotifers*	*Nauplii*	*Copepodids*	*Cladocerans*	*Other*	*Total*
10-Apr-09	Upper main	M111	3.0	3.1	0.3	0.3	0.1	6.8
		M123	1.3	0.7	0.1	0.0	0.3	2.4
		M132	14.9	9.5	2.6	2.8	0.4	30.2
		M137	1.5	1.9	0.1	0.3	0.1	3.9
		M142	1.0	1.6	0.1	0.3	0.1	3.1
		M149	1.0	1.3	0.0	0.1	0.0	2.4
23-Apr-09	Upper main	M111	12.7	2.0	0.2	0.8	0.1	15.8
		M123	7.8	3.3	0.1	0.3	0.4	11.9
		M132	40.1	20.1	1.7	1.3	0.5	63.7
		M137	2.4	2.3	0.0	0.3	0.0	5.0
		M142	2.8	2.6	0.0	0.0	0.2	5.6
		M149	73.3	2.7	0.2	0.9	0.0	77.1
07-May-09	Upper main	M111	53.0	3.7	1.1	3.3	0.2	61.3
		M123	20.9	16.7	1.8	4.6	0.0	44.0
		M132	17.8	25.8	3.9	1.5	0.1	49.1
		M137	22.7	9.4	0.8	1.2	0.0	34.1
		M142	10.5	7.9	0.6	1.9	0.0	20.9
		M149	58.9	3.5	0.2	2.9	0.0	65.5
21-May-09	Upper main	M111	22.8	2.1	0.3	1.1	0.3	26.6
		M123	151.6	45.2	3.2	4.6	0.0	204.6
		M132	84.2	2.3	1.1	0.8	0.1	88.5
		M137	5.9	1.3	0.4	0.8	0.1	8.5
		M142	10.4	3.1	0.6	1.4	0.4	15.9
		M149	130.3	8.0	1.0	1.3	0.5	141.1
04-Jun-09	Upper main	M111	112.3	1.1	0.4	0.8	0.0	114.6
		M123	497.1	11.4	2.2	0.6	0.0	511.3
		M132	307.1	4.8	1.5	2.8	0.2	316.4
		M137	58.1	3.3	0.9	1.7	0.0	64.0
		M142	11.8	2.2	0.5	0.3	0.0	14.8
		M149	16.5	4.0	0.8	1.2	0.2	22.7

APPENDIX E. Zooplankton Abundances by Date, Region, and Station in Upper Lake Marion (2012)

All abundances are reported in animals liter^{-1}.

Date	*Region*	*Station*	*Rotifers*	*Nauplii*	*Copepodids*	*Cladocerans*	*Other*	*Total*
14-Apr-12	Upper main	M111	2.1	6.0	1.1	3.2	0.4	12.7
		M123	0.5	13.0	3.5	1.1	0.2	18.2
		M132	1.4	20.3	8.1	5.4	0.1	35.2
		M137	0.8	7.5	1.6	2.8	0.2	12.8
		M142	3.5	7.3	1.0	2.4	0.1	14.3
		M149	9.6	5.8	2.6	10.0	0.1	28.0
	Backwater	StumpHole	138.8	5.6	0.1	2.6	0.3	147.4
	River	River1	0.0	0.6	0.4	0.8	2.5	4.2
27-Apr-12	Upper main	M111	2.9	5.8	1.8	2.9	0.1	13.6
		M123	2.9	18.4	1.8	2.0	0.1	25.2
		M132	4.7	24.9	2.6	5.5	0.2	38.0
		M137	3.8	5.4	1.0	2.5	0.6	13.2
		M142	1.9	3.3	0.9	1.8	0.0	8.0
		M149	25.1	9.2	1.2	4.1	0.0	39.7
	Backwater	StumpHole	248.5	4.2	0.6	6.8	1.2	261.4
	River	River1	0.6	0.0	0.0	0.1	0.0	0.6
16-May-12	Upper main	M111	149.5	13.6	2.1	2.2	0.2	167.5
		M123	7.4	10.4	7.4	2.9	0.1	28.1
		M132	72.0	12.0	4.6	6.1	0.3	95.0
		M137	37.6	6.0	2.4	2.4	0.2	48.5
		M142	28.0	6.1	1.6	3.5	0.7	39.9
		M149	18.6	1.8	1.1	2.4	0.1	24.1
	Backwater	StumpHole	511.8	3.5	0.9	1.2	0.0	517.4
		PacksFlats	30.3	13.5	1.8	4.2	0.6	50.5
	River	River1	5.2	0.5	0.7	0.1	0.1	6.5
		River2	0.6	0.3	0.9	0.1	4.8	6.6
31-May-12	Upper main	M111	183.3	9.0	1.2	1.3	1.2	195.9
		M123	13.3	5.2	0.8	0.9	0.3	20.4
		M132	56.5	29.8	2.9	13.3	0.6	103.1
		M137	12.3	12.7	1.4	2.5	0.8	29.7
		M142	80.0	3.3	2.8	2.2	0.5	88.7
		M149	27.7	4.8	2.0	1.7	0.0	36.2
	Backwater	StumpHole	615.1	0.8	0.8	1.4	0.5	618.5
		PacksFlats	6.1	2.1	0.9	0.3	0.3	9.7
	River	River1	12.4	0.4	0.1	0.0	0.0	12.8
		River2	2.4	0.1	0.0	0.0	1.2	3.6

Date	***Region***	***Station***	***Rotifers***	***Nauplii***	***Copepodids***	***Cladocerans***	***Other***	***Total***
14-Jun-12	Upper main	M111	116.8	2.5	0.9	3.9	0.6	124.6
		M123	18.9	27.6	2.5	7.3	0.1	56.5
		M132	128.5	35.0	7.6	12.4	1.3	184.9
		M137	20.9	9.7	1.9	4.9	1.4	38.8
		M142	86.7	4.9	0.6	5.3	0.3	97.7
		M149	20.4	4.2	0.8	18.8	0.0	44.2
	Backwater	StumpHole	810.6	12.3	2.0	14.6	0.3	839.7
		PacksFlats	70.3	7.0	2.1	1.1	0.3	80.8
	River	River1	3.1	0.4	0.0	0.5	0.2	4.1
		River2	0.1	0.0	0.1	0.1	2.9	3.2
28-Jun-12	Upper main	M111	84.7	11.7	8.6	37.5	0.5	143.0
		M123	54.1	58.2	15.6	36.6	0.2	164.6
		M132	42.3	66.4	11.4	47.8	1.4	169.2
		M137	20.4	19.4	6.6	20.4	0.6	67.4
		M142	80.7	8.1	2.7	25.9	0.7	118.1
		M149	255.3	14.4	6.1	84.1	0.3	360.1
	Backwater	StumpHole	969.7	20.6	0.9	60.3	0.5	1052.0
		PacksFlats	198.8	2.7	2.6	13.9	0.5	218.5
	River	River1	10.7	0.2	0.2	0.7	0.1	11.9
		River2	0.7	0.1	0.3	0.0	2.0	3.1

APPENDIX F. Zooplankton Abundances by Date, Region, and Station in Lake Marion (2014)

All abundances are reported in animals liter^{-1}.

Date	*Region*	*Station*	*Rotifers*	*Nauplii*	*Copepodids*	*Cladocerans*	*Other*	*Total*
29-Apr-14	Lower main	M044	259.09	10.36	3.91	15.73	0.00	289.09
	Middle main	M069	6.91	2.09	0.36	4.91	0.09	14.27
		M079	4.73	3.73	1.09	3.18	0.09	12.73
	Upper main	M150	0.09	0.18	0.00	1.27	0.00	1.54
20-May-14	Lower main	M044	57.76	13.73	2.64	19.18	0.18	93.31
30-May-14	Lower main	M044	472.73	36.55	3.36	24.91	0.00	537.55
	Middle main	M069	158.59	7.09	0.45	7.18	0.00	173.31
		M079	56.06	1.55	0.36	1.27	0.09	59.24
	Upper main	M150	169.19	0.18	0.09	4.00	0.18	173.46
16-Jun-14	Lower main	M044	82.83	16.73	0.36	14.55	0.18	114.47
	Middle main	M069	71.21	15.00	0.00	0.82	0.00	87.03
		M079	47.95	3.36	0.27	1.18	0.36	52.76
	Upper main	M150	52.53	11.00	0.00	0.91	0.09	64.44
08-Jul-14	Lower main	M044	14.73	37.09	0.82	6.91	0.00	59.55
	Middle main	M069	40.15	7.27	0.00	0.64	0.36	48.06
		M079	4.09	2.36	0.09	0.18	0.18	6.72
	Upper main	M150	32.83	1.00	0.27	2.82	0.00	36.92
30-Jul-14	Lower main	M044	44.70	11.00	0.18	5.55	0.18	61.43
	Middle main	M069	41.86	9.64	0.00	1.18	0.55	52.68
		M079	32.18	5.82	0.09	1.64	0.18	39.73
	Upper main	M150	52.53	2.73	0.36	8.82	0.55	64.44
25-Aug-14	Lower main	M044	23.54	78.84	0.95	5.14	0.86	108.47
	Middle main	M079	32.80	97.88	1.81	6.10	0.38	138.59
	Upper main	M150	33.60	2.95	0.76	1.71	0.10	39.02
29-Oct-14	Lower main	M044	15.67	30.19	2.29	2.10	0.29	50.25
	Middle main	M069	47.62	14.76	0.29	0.48	0.19	63.15
		M079	24.21	13.14	0.48	0.10	0.00	37.93
	Upper main	M150	5.62	3.33	1.62	0.38	0.19	10.95

APPENDIX G. Larval Fish Abundances in the Upper Main Basin of Lake Marion (2009)

Larval fish sampling, conducted by Treye Beyers and others, was scheduled to correspond approximately with zooplankton sampling.

Methods

The larval fish were sampled at 2-week intervals from mid-April to late May 2009. Six transects within the upper main basin main lake (the main nursery area for larval fish) were sampled on each date. The transects were: channel marker 111–112; 122–123 or 123–124; 131–132 or 132–133; 135–137 or 137–139; 141–142 or 142–143; and 146–147; transect locations corresponded approximately to zooplankton sample locations (see Figure 6.1). Samples were collected at night with a 1-m diameter, 0.5-mm mesh net equipped with a flowmeter. Sampled volume for each transect was 130-300 m^3.

Larval fish were identified to species and measured by J. S. Crane. Lengths were converted to weights using a published regression for larval gizzard shad (González, Knoll, and Vanni, 2010).

Results

Abundances of larval fish were initially extremely low, increasing to 0.3-0.4 animals m^{-3} in May (Figure G.1, Table G.1). Except on the first sampling date, threadfin shad made up 75% or more of the populations. Mean biomass estimates ranged from 0.00008 g wet mass m^{-3} (0.0003 g wet mass m^{-2}) in mid-April to 0.016 g wet mass m^{-3} (0.056 g wet mass m^{-2}) in late May.

Table G.1. Abundance of main species of larval fish (<50 mm TL) in Upper Lake Marion in 2009 by species. Other includes striped bass, white perch, cyprinids, and other taxa, as well as a few unidentifiable specimens. Six transects were sampled on each date.

	Mean abundance (number per 1,000 m^3)				
Date	***American shad***	***Inland silverside***	***Threadfin shad***	***Other***	***All***
14 Apr	7	0	2	3	12
28 Apr	3	2	140	4	149
11 May	36	29	271	13	349
26 May	25	20	348	13	406

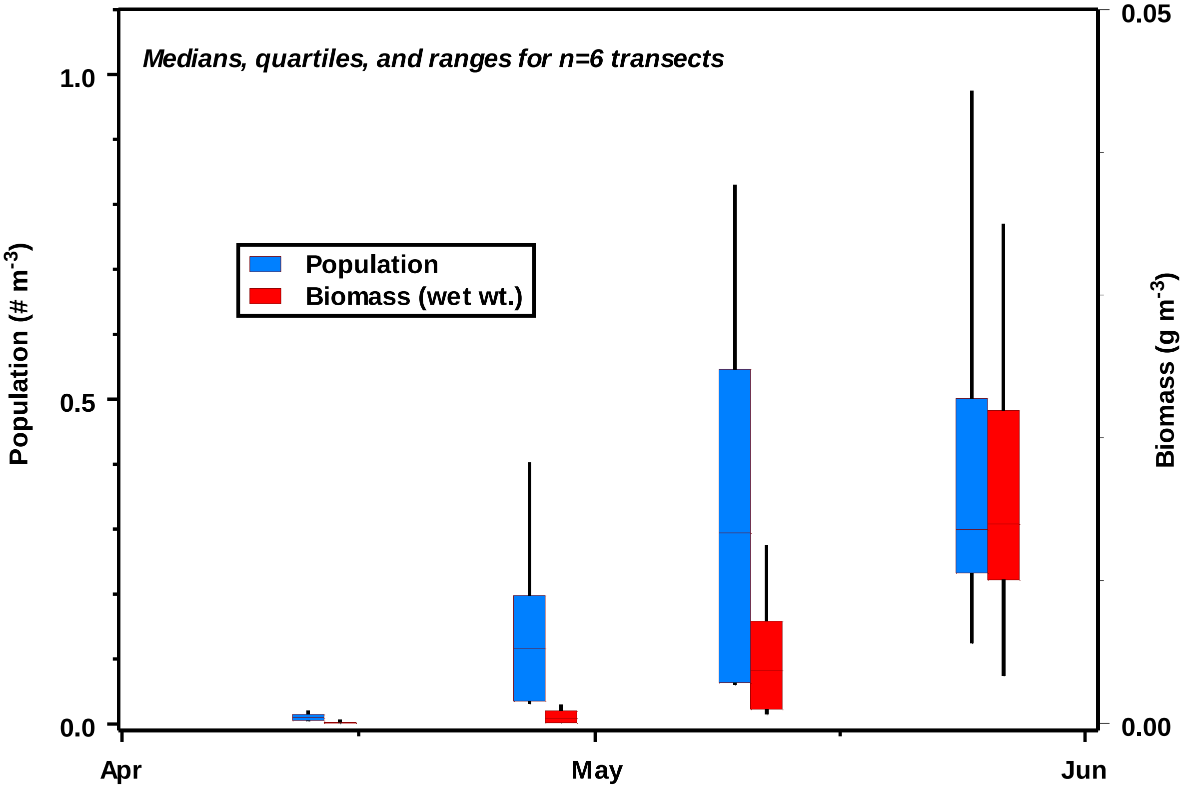

Figure G.1. Abundance and biomass of larval fish in the main basin of upper Lake Marion in April-June 2009.

APPENDIX H. Diets of Threadfin Shad in Pelagic Habitats of Lakes Marion and Moultrie (2012, 2014, and 2015)

Threadfin shad were collected by gill nets or cast nets from pelagic habitats of lakes Marion and Moultrie in May-August of 2012, 2014, and 2015; most of the collections were made in conjunction with hydroacoustic surveys. See Bettinger (2013) for additional details. The stomach contents were analyzed by Hannah Slyce.

Methods

Fish were placed on ice in the field, then identified, weighed, measured, and frozen in the laboratory. Contents of each dissected stomach, preserved in 70% ethanol, were washed onto a 53-micron mesh sieve, then stained with Eosin B. Subsamples were examined microscopically, and a random point count method, based on Wilson (2002), was used to evaluate relative abundance of detritus, phytoplankton, and zooplankton.

Results

Detritus and algae made up the bulk of the gut contents (85% on average for 67 fish collected in 2012-2015). We speculate that the sparsity of zooplankton in the gut contents (15% on average for all fish) reflects typically low abundances of zooplankton in this system. Rotifers and naupliar stages of copepods were preferred by smaller fish (total length <85 mm). Cladocerans (mainly bosminids) and copepodid stages of copepods (mainly cyclopoids) were preferred by larger fish (Figure H.1).

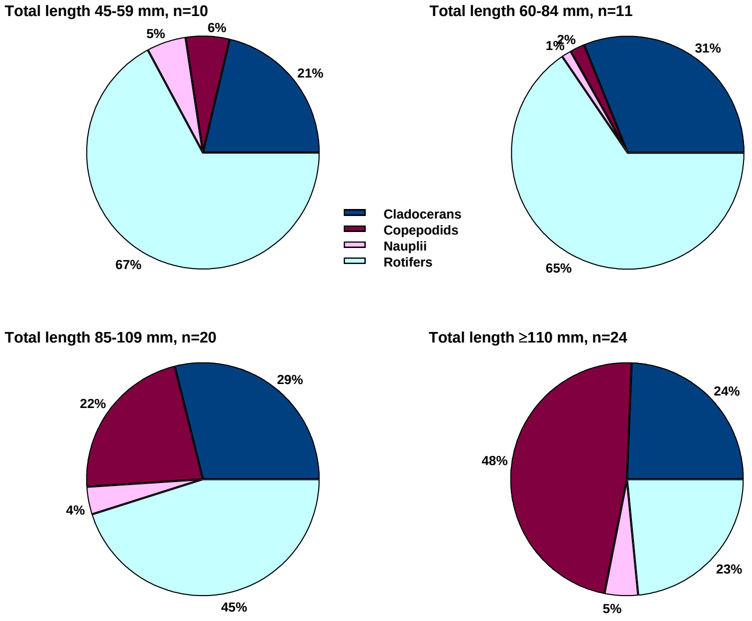

Figure H.1. Composition of zooplankton in stomachs of pelagic threadfin shad from lakes Marion and Moultrie (May-August, 2012, 2014, and 2015). Results are summarized for n = 65 fish; zooplankton were not found in stomachs of two fish.