Appendix 8.A. Relationships of Water Flows with Plankton and Water Quality

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2011

I. Introduction

The Plankton Working Group (Chapter 8. Plankton) was charged with the identification and quantification of possible environmental impacts of water withdrawals on plankton communities, established TMDLs, and restoration planning in the Lower and Middle St. Johns River. As part of this assessment, we conducted a literature review of effects of water flows and residence times on plankton communities in aquatic systems. The literature review included studies of rivers, reservoirs, lakes, and estuaries, because of the recognition that distinctions among aquatic system types are irrelevant for plankton communities, and they are better viewed as occupying positions along a continuum ordered by water residence time (Soballe and Kimmel 1987). The literature review focused on effects of water flows on phytoplankton and zooplankton. There was also consideration of flow effects on water quality variables (nutrients, salinity, and oxygen), particularly with regard to their interactions with the plankton communities.

Multiple methods were used to assemble a literature database. Starting from a set of initially known key publications, we did literature searches both backward (examining references cited in those publications) and forward (using ISI Web of Science [Science Citation Index] to locate more recent papers that cited the key publications). We also did retrievals from the SJRWMD Environmental Sciences Division literature database, Cambridge Scientific Abstracts, U.S. EPA online library system, and Wilson Web, using search terms plankton and either residence, retention, or detention. References obtained were entered into an EndNote literature database, which presently contains about 250 references. Complete copies of many of the most relevant publications were obtained for review; presently we have over 110 publications.

II. Flow – Phytoplankton relationships

A number of studies have reported negative relationships between water flow rates and phytoplankton biomass or cell numbers in lakes and reservoirs (Barbiero et al. 1997; Dickman 1969; Kawara et al. 1998; Moss and Balls 1989; Moustaka-Gouni et al. 2006; O.E.C.D. 1982; Pádisak et al. 1999; Perry et al. 1990), and in freshwater-oligohaline rivers (Ahearn et al. 2006; Bertrand et al. 2001; De Cabo et al. 2003; Filardo et al. 1985; Heiskary and Markus 2001; Lionard et al. 2008; Oliver et al. 2010; Paerl 1987; Phlips et al. 2007; Schemel et al. 2004; Soballe and Kimmel 1987; Strayer et al. 2008; Wehr and Thorp 1997). Several of these studies reported water residence times or flushing rates, which are hydrological measures that can be compared across systems to evaluate whether there are general environmental boundaries that limit phytoplankton biomass. However, there are wide ranges of water residence times (1 – 189 days) or flushing rates (0.0053 – 1 per day) reported to limit phytoplankton biomass (Table 1). Since potential doubling times of phytoplankton are on the order of one to a few days (Barbiero et al. 1997; Paerl et al. 2006), these wide ranges indicate that factors other than hydrology play large roles in phytoplankton biomass accumulation (such as nutrients, other water quality factors such as salinity, light, and grazing). As such, there do not appear to be general hydrological boundaries that limit phytoplankton biomass; rather the limiting boundary appears to depend on the specific environmental setting.

Calculations of water residence time generally assume complete mixing of the water body. However, a number of studies have emphasized the importance of heterogeneity of flows for persistence of plankton populations in riverine systems, such as fringing floodplain and slower-moving edges of rivers (Ahearn et al. 2006; Moss and Balls 1989; Reynolds 2000; Saunders and Lewis 1989; Walks 2007; Walz and Welker 1998). As a result, calculated water residence times may substantially underestimate actual plankton residence times.

Although phytoplankton biomass generally increases with water residence time, there are a limited number of studies that did not report such a relationship, also pointing to importance of other factors in determining biomass accumulation. Studies of the Danube River floodplain and the Neuendorfer See reported maximum phytoplankton biomass at intermediate water age (Table 2), attributing a decline at longer water ages to increased grazing. Gosselain et al. (1998) suggest that the phytoplankton community in large rivers may at times be controlled by grazers when discharge is low and other factors allow high zooplankton biomass. Two studies of Canadian rivers reported no significant relationship between water flows and phytoplankton biomass (Table 2). In these cases, phytoplankton biomass was correlated with phosphorus concentrations (Basu and Pick 1996; Chetelat et al. 2006). In two lakes in the Pampa Plain, Argentina, there was an increase in phytoplankton biomass in a summer with lower water residence time, again attributed to increased phosphorus concentrations (Rennella and Quirós 2006). Negative relationships of phytoplankton biomass with retention time in riverine reservoirs have been attributed to rapid sedimentation and other loss processes (Soballe and Bachmann 1984)

The relationship between flow rates and phytoplankton biomass is more complicated in estuaries. While the upper, oligohaline parts of estuaries generally show a negative relationship between discharge and phytoplankton biomass, the lower, more saline parts of estuaries and adjacent coastal areas tend to show a positive relationship (Borsuk et al. 2004; Cloern et al. 1985; Cloern et al. 1983; Howarth et al. 2000; Jordan et al. 1991; Livingston et al. 1997; Mallin et al. 1993; Mortazavi et al. 2000; Sklar and Browder 1998; Valdes-Weaver et al. 2006; Wetz et al. 2011). Lower estuaries and coastal areas tend to have longer residence times under all conditions, and these studies have attributed positive relationships between flow and phytoplankton biomass to downstream displacement of dominant phytoplankton taxa, increased nutrient supplies, greater water column stratification, or reduced zooplankton grazing under higher flow conditions. A series of studies of San Francisco Bay and the Hudson River estuary showed a weakening of flow-plankton relationships after invasion of the systems by exotic grazing bivalves (Alpine and Cloern 1992; Caraco et al. 2006; Jassby 2008; Kimmerer 2002; Strayer et al. 2008).

Lucas et al. (2009) developed a conceptual model to explain the varying relationships between residence time and phytoplankton biomass. In this model, the phytoplankton growth-loss balance determines the response to residence time changes. If phytoplankton growth rates exceed loss rates (e.g. due to grazing or sedimentation), then phytoplankton biomass increases with increasing residence time. Conversely, if loss rates exceed growth rates, then phytoplankton biomass decreases with increasing residence time. As an example of how the growth-loss balance affects responses to residence time, Lucas et al. (2009) further analyzed the data set of Basu and Pick (1996), who reported no relationship between residence time and chlorophyll-*a* in 31 Canadian rivers (Table 2). In one subset of the rivers with highest zooplankton biomass, and therefore expected to have high loss rates, there was a negative relationship between residence time and chlorophyll-*a*. In a second subset of rivers with low zooplankton biomass and high total phosphorus concentrations, and therefore expected to have high growth rates, there was a positive relationship between residence time and chlorophyll-*a*.

Hydrology is also reported to influence phytoplankton composition, with low flow rates or long water residence time favoring blooms of slow-growing taxa such as cyanobacteria and dinoflagellates, while higher flow rates tend to favor faster-growing taxa, such as diatoms (Arhonditsis et al. 2007; Bertrand et al. 2001; Ferreira et al. 2005; Harris and Baxter 1996; Kawara et al. 1998; Moss and Balls 1989; Moustaka-Gouni et al. 2006; Pádisak et al. 1999; Paerl et al. 2006; Perry et al. 1990; Valdes-Weaver et al. 2006). *Cylindrospermopsis*, one of the prominent cyanobacterial genera found in the St. Johns River, appears to be associated with particularly long water residence times (Branco and Senna 1994; Harris and Baxter 1996; Mcgregor and Fabbro 2000).

Low freshwater discharge rates and long residence times can contribute to water column stratification in freshwater and estuarine systems (Paerl 2006; Sherman et al. 1998; Straškraba 1999). Stratified conditions can also lead to dominance by cyanobacteria or dinoflagellates, which can regulate their vertical position in the water column by changing their buoyancy or active swimming (Paerl et al. 2001; Sherman et al. 1998).

The St. Johns River is similar to a number of other large, coastal rivers that are prone to development of severe cyanobacterial blooms in their freshwater-oligohaline sections during low discharge periods (Ha et al. 1999; Jaworski 1990; Jeong et al. 2007; Krogmann et al. 1986; Paerl 1987; Phlips et al. 2007; Sherman et al. 1998). In the Neuse River, North Carolina, the most severe cyanobacterial blooms result from nutrient loading provided by high flows during spring followed by dry, low discharge conditions during summer-fall (Paerl 1987). In Australian Rivers, the development of cyanobacterial blooms has been linked to persistent thermal stratification occurring during low-discharge periods (Maier et al. 2004; Sherman et al. 1998). In the River Darling, Australia, a critical velocity of 0.03-0.05 m/sec was necessary to suppress persistent stratification and development of *Anabaena circinalis* blooms (Mitrovic et al. 2006; Mitrovic et al. 2003). The applicability of this environmental boundary to other riverine systems has not been examined.

Several modeling studies have examined the linkage between hydrology and development of cyanobacterial blooms in lakes and rivers (Jones and Elliott 2007; Lung and Paerl 1988; Maier et al. 2004; Verspagen et al. 2006; Webster et al. 2000). Two modeling studies expressed the hydrology using measures that can be potentially compared across systems. Verspagen et al. (2006) developed a model to predict the magnitude of flushing needed to prevent *Microcystis* blooms in an impounded reservoir. Blooms were suppressed in simulations with year round flushing rate of 0.028/d, or flushing rates of 0.024/d in summer and 0.047/d in winter (these summer flushing rates are equivalent to residence times of 36-42 days), but not with summer flushing rates of 0.0065/d (residence time 154 days). Since these were the only flushing rates simulated, it is not clear if the higher rates represent an environmental boundary necessary to prevent blooms, or whether lower flushing rates would also be sufficient. Jones and Elliott (2007) modeled water residence time effects on phytoplankton in a small lake, with residence time varying from 8.5 to 338.5 days. This paper used the "C-S-R" functional group classification developed by Reynolds (1988), which separates phytoplankton into groups according to their morphology. Modeled R-group algae (including *Oscillatoria*) increased 10-fold over the residence time range, reaching a maximum biomass by about 85 days. Modeled C-S group algae (including *Anabaena* and *Aphanizomenon*) reached maximum biomass at intermediate retention times (40-70 days). The residence times predicted to affect cyanobacterial growth in these two modeling studies are within the ranges reported in empirical studies (Table 1). However, again, the wide ranges reported in empirical studies indicate that hydrological boundaries for cyanobacterial bloom development depend on the specific environmental setting. The relevant boundaries for the lower/middle St. Johns River basin may be better defined from monitoring/modeling data for that system, than from boundaries determined from other systems.

Table 1. Reported relationships between phytoplankton and water residence time or flushing rate. Studies reporting positive relationships with residence time.

Study Area	Residence time (days)	Flushing rate (per day)	Notes	Reference
Hudson River estuary	<1 - 4	0.25 – >1	Phytoplankton blooms become more likely at residence times >1 day	Howarth et al. (2000)
Lakes	3 – 5	0.2 – 0.33	Threshold flushing rates for phytoplankton control	O.E.C.D. (1982) (cited in Barbiero et al. 1997)
Bluestone Lake, West Virginia	3.9 – 9.7	0.1 – 0.26	Water residence time correlated with total algal densities, highly correlated with percent *Microcystis* and *Anabaena*	Perry et al. (1990)

Study Area	Residence time (days)	Flushing rate (per day)	Notes	Reference
Eau Galle Reservoir, Wisconsin	<12	>0.08	Chlorophyll-*a* showed inverse relationship with flushing rate, with pronounced losses when flushing rates exceeded 0.08/d	Barbiero et al. (1997)
Asahi River Dam Reservoir, Japan	14	0.07	Residence time of about 2 weeks required for substantial increase of phytoplankton chlorophyll-a. Cyanobacteria and dinoflagellates dominant during algal blooms.	Kawara et al. (1998)
Schelde estuary, Belgium	10 – 20	0.05 – 0.1	Mean weighted summer chlorophyll *a* concentration in freshwater tidal reaches was negatively correlated to the flushing rate	Lionard et al. (2008)
Lake Pepin, Minnesota	7 – 47	0.02 – 0.14	Mean summer chlorophyll *a* positively correlated with residence time	Heiskary and Walker (1995)
Lowland River Bure and associated Broads, U.K.	2 – 61.5	0.016 – 0.5	Chlorophyll-*a* increases linearly with time for development. Cyanobacteria become more abundant as time for development increases.	Moss and Balls (1989)
Müggelsee, Berlin, Germany	50 – 100	0.01 – 0.02	Flushing pulses in the range of 1–2% of the lake volume per day in a sufficient frequency (20–30 d) considered very effective in breaking cyanobacterial biomass increase.	Pádisak et al. (1999)
126 U.S. rivers	<60 – 100	0.01 – 0.017	Significant correlation between residence time and phytoplankton cell count. Direct effects of flushing on phytoplankton restricted to systems with residence times <60-100 d.	Soballe and (Kimmel 1987)
Lake Kastoria, Greece	189	0.0053	Although the flushing rate was relatively low (0.53% of the lake volume per day), it was effective in eliminating cyanobacteria.	Moustaka-Gouni et al. (2006)

Table 2. Reported relationships between phytoplankton and water residence time or flushing rate. Studies reporting asymptotic, negative, or no relationships with residence time.

Study Area	Residence time (days)	Flushing rate (per day)	Notes	Reference
Danube River floodplain	2 – 6	0.17 – 0.5	Maximum phytoplankton biomass at medium water ages (2-6 days). At water ages greater than 19 days, a decrease of phytoplankton biomass was evident.	Hein et al. (2003)
Danube River floodplain	3 – 10	0.1 – 0.33	Phytoplankton biomass peaks at water ages 3 - 10 days; decreases at higher water ages	Luef et al. (2007)
31 Canadian rivers	3.3 – 19.4	0.05 – 0.3	No significant relationship between chlorophyll-*a* and residence time	Basu and Pick (1996)
Canadian rivers	1 – 39	0.03 – 1	Phytoplankton biomass not related to water residence time	Chetelat et al. (2006)
Neuendorfer See	~ 2 – 53	~ 0.02 – 0.5	Maximum chlorophyll-*a* at residence time 6-8 days	Walz and Welker (1998)
Des Moines River reservoirs	< 5 – 60	0.02 – >0.2	Chlorophyll loss rates decrease as retention time increases; decreases in reservoirs attributed to initial sedimentation of river-borne algae and increases in other losses as retention time increases	Soballe and Bachmann (1984)
Pampa Plain lakes, Argentina	1.6 – 268	0.004 – 0.6	Higher phytoplankton biomass in summer with lower water residence time	Rennella and Quirós (2006)

III. Flow – Zooplankton relationships

As with phytoplankton, zooplankton tend to show a negative relationship with water flow and a positive relationship with water residence time (Basu and Pick 1996; De Cabo et al. 2003; Lair 2006; Pace et al. 1992; Strayer et al. 2008). Zooplankton biomasses increase from rivers to estuaries to lakes, paralleling changes in residence time (Pace et al. 1992). There are few reported quantitative relationships between water residence time and zooplankton biomass. Basu and Pick (1996) found a positive relationship between residence time (range 3.3 – 19.4 days) and zooplankton biomass in 31 Canadian rivers.

The composition of zooplankton in rivers tends to be dominated by rotifers or small-bodied microcrustaceans (cladocerans and copepods), which is generally attributed to their shorter generation times allowing population growth despite advective losses (Basu and Pick 1996; Gosselain et al. 1998; Lair 2006; Pace et al. 1992; Walz and Welker 1998). For example, in the Neuendorfer See, Germany, some rotifers reached maximal densities by a residence time of 10 days, while cyclopoid copepods continued to increase in abundance through residence times of at least 53 days (Walz and Welker 1998). It has also been suspected that turbulence limits zooplankton and affects their composition in rivers. Zooplankton egg ratios have been reported to decrease as current velocities increase (Saunders and Lewis 1989). It has also been shown experimentally that rotifers are favored by high turbulence, while microcrustaceans do better under low turbulence conditions (Sluss et al. 2008).

Three studies reported a shift in zooplankton composition with changes in water residence time. In the Danube River floodplain, microcrustacean biomass increased over a range of water ages from 0 – 39 days, while rotifer biomass increased up to a water age of about 10 days, but decreased at older water age (Baranyi et al. 2002). The decrease in rotifers at greater water age was attributed primarily to competition from the microcrustaceans. Unspecified biotic interactions were suggested to explain decreases of rotifers as crustaceans increased at longer residence times in the Neuendorfer See (Walz and Welker 1998). In two lakes in the Pampa Plain, Argentina, rotifer biomass was not strongly affected by decreased water residence time, but microcrustacean biomass was strongly reduced, particularly that of larger-bodied *Daphnia* (Rennella and Quirós 2006).

Other things being equal, low flows and long water residence times would be expected to lead to increased zooplankton biomass, particularly of larger-bodied cladocerans and copepods, in freshwater-oligohaline sections of the St. Johns River. This, in turn, would be expected to lead to increased transfer of primary production to higher trophic levels, because larger-bodied zooplankton are considered to be more efficient grazers and because larger-bodied zooplankton are generally preferred food for post-larval planktivorous fish (Brooks and Dodson 1965; Carpenter and Kitchell 1993; Elser 1999; Jeppesen et al. 2003; Scheffer 1998).

However, one factor which could prevent low flows from leading to increased trophic transfer is detrimental effects of cyanobacterial blooms. Cyanobacterial blooms are often associated with decreases in abundance of large cladocerans and increases in importance of smaller cladocerans, rotifers and copepods (Leonard and Paerl 2005; Paerl and Fulton 2006; Paerl et al. 2001). Inhibitory effects of cyanobacteria on grazing zooplankton may be due to interference with feeding as a result of awkward size or shape of filaments or colonies, chemical factors (toxicity, poor taste, poor nutritional value), or high abundances (i.e., blooms), which displace more nutritious non-bloom-forming algae or limit the ability of herbivores to utilize coexisting algae. In the Lower St. Johns River, blooms of *Cylindrospermopsis* were associated with low numbers of microcrustaceans, dominance of the zooplankton by rotifers, and high grazing by microzooplankton, although that grazing was apparently primarily on edible algae, not on the

Cylindrospermopsis (Leonard and Paerl 2005). Thus, cyanobacterial blooms stimulated by low flows in the St. Johns River could potentially lead to reductions in zooplankton biomass, size structure, and transfer of primary production to higher trophic levels.

Although there is limited available information, zooplankton-flow relationships are likely to be different in lower estuaries and adjacent coastal areas. Locations of zooplankton in an estuarine system shift upstream or downstream in response to freshwater inflows. In the tidal Alafia River, Florida, abundances of freshwater-dependent zooplankton are reported to decrease during low freshwater flow periods, while the abundances of marine-dependent zooplankton show the opposite trend (Flannery et al. 2002). Estuarine and marine zooplankton may be expected to decrease during prolonged periods of low freshwater inflows, paralleling reductions in phytoplankton biomass and productivity. In a number of estuaries, prolonged droughts have resulted in decreases in phytoplankton, zooplankton and fish populations (Baptista et al. 2010; Bennett et al. 1995; Cloern et al. 1983; Kimmerer 2002; Martino and Houde 2010; Wetz et al. 2011). Thus, reductions in freshwater flows could lead to reductions in productivity at multiple trophic levels in lower estuaries and coastal areas.

IV. Flow – nutrient relationships

Bioavailable nutrient concentrations show opposite trends to plankton populations, tending to decrease as residence times increase (Moss and Balls 1989; Van Den Brink et al. 1994; Walz and Welker 1998). These decreased nutrient levels likely reflect assimilation by increasing phytoplankton populations. Increased denitrification at longer residence times also contributes to reduced nitrogen concentrations and reduced downstream export (Dettmann 2001; Nixon et al. 1996). These decreases in bioavailable nutrient concentrations may contribute to lower phytoplankton growth rates at long residence times. For example, chlorophyll accumulation rates in the Neuendorfer See decreased substantially as residence time increased over a range of about 8 to 50 days (Walz and Welker 1998). Low silicate inputs to Chesapeake Bay in low river flow years are thought to diminish spring diatom blooms (Conley and Malone 1992). Also, as previously noted, a prolonged drought resulted in a decline in diatom populations in San Francisco Bay (Cloern et al. 1983).

Nutrient ratios can change with variations in discharge and residence times, which can affect phytoplankton composition. Nitrogen:phosphorus ratios tend to decrease when residence times are long (Van Den Brink et al. 1994; Walz and Welker 1998). A decrease in available nitrogen as residence times increase can lead to prominence by nitrogen-fixing cyanobacteria (Moss and Balls 1989; Phlips et al. 2007).

Although pristine rivers deliver excess silicate to coastal areas, eutrophication increases inputs of nitrogen and phosphorus relative to silicate, leading to silicate limitation of coastal primary production (Justic et al. 1995). Decreases in silicate inputs resulting from water diversion from coastal rivers could result in shifts in coastal phytoplankton composition from diatoms to potentially toxic flagellates or cyanobacteria (Ittekkot et al. 2000). However, silicate concentrations or silicate to nutrient ratios do not show consistent responses to flows, sometimes increasing with residence time (Moss and Balls 1989; Van Den Brink et al. 1994) or being weakly related to flushing rate (Lionard et al. 2008).

V. Flow – salinity - oxygen relationships

Discharge rates will affect the positioning of the salinity isohalines in estuarine systems. As a result, the locations of the freshwater and estuarine plankton communities will shift up- or downstream as freshwater discharges change (Flannery et al. 2002; Paerl et al. 2006; Valdes-Weaver et al. 2006). Freshwater phytoplankton taxa rapidly disappear near the freshwater-estuarine interface (Filardo et al. 1985). In Danish brackish lagoons, the cladoceran *Daphnia* was replaced above a low salinity threshold by rotifers and estuarine copepods, and there was a parallel increase in chlorophyll concentrations, which was attributed to reduced grazing. It was suggested that improved water quality can be obtained by reducing the nutrient loading or enhancing the freshwater input to a level triggering a shift to *Daphnia* dominance (Jeppesen et al. 2007).

Low freshwater discharge rates can contribute to development of salinity stratification in estuarine systems (Paerl 2006) as well as thermal stratification in freshwater riverine systems (Sherman et al. 1998). Conversely, high freshwater discharges can contribute to salinity stratification in lower estuaries and coastal areas (Cloern et al. 1985; Hagy et al. 2004; Rabalais et al. 2002). Water column stratification can lead to algal blooms and hypoxia or anoxia of bottom waters in rivers and estuaries (Hagy et al. 2004; Paerl 2006; Rabalais et al. 2002; Sherman et al. 1998). Reductions in nutrient loading may be necessary to reduce water column anoxia induced by flow changes (Hagy et al. 2004; Paerl 2006; Rabalais et al. 2002).

VI. Summary

Available literature indicates that effects of low flows on plankton and water quality in the St. Johns River may vary in different parts of the system. In freshwater-oligohaline parts of the system, potential effects of low flows include:

- Increased phytoplankton biomass and algal blooms, primarily of cyanobacteria
- Zooplankton responses dependent on the balance of conflicting effects:
    - Increased zooplankton abundance and compositional shifts from rotifers to larger microcrustaceans due to increases in water residence time and algal biomass
    - Reduced zooplankton abundance and rotifer dominance due to deleterious effects of cyanobacterial blooms
- Higher trophic levels dependent on planktonic production may benefit or be adversely affected, depending on the zooplankton response
- Upstream shifts of salinity isohalines and associated plankton communities
- Increased potential for water column stratification and hypoxia/anoxia

In the lower estuary/coastal zone, potential effects of low flows include:

- Decreased nutrient export (nitrogen, phosphorus, silicon, carbon) from the river
- Reductions in primary production
- Shifts of the phytoplankton community from diatom to flagellate dominance
- Decreased productivity of higher trophic levels dependent on planktonic production or organic carbon exported from the river

VII. References

Ahearn, D. S., J. H. Viers, J. F. Mount, and R. A. Dahlgren. 2006. Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. Freshwater Biology **51:** 1417-1433.

Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography **37:** 946-955.

Arhonditsis, G. B., C. A. Stow, H. W. Paerl, L. M. Valdes-Weaver, L. J. Steinberg, and K. H. Reckhow. 2007. Delineation of the role of nutrient dynamics and hydrologic forcing on phytoplankton patterns along a freshwater-marine continuum. Ecological Modeling **208:** 230-246.

Baptista, J., F. Martinho, M. Dolbeth, I. Viegas, H. Cabral, and M. Pardal. 2010. Effects of freshwater flow on the fish assemblage of the Mondego estuary (Portugal): comparison between drought and non-drought years. Marine and Freshwater Research **61:** 490–501.

Baranyi, C., T. Hein, C. Holarek, S. Keckeis, and F. Schiemer. 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. Freshwater Biology **47:** 473–482.

Barbiero, R. P., W. F. James, and J. W. Barko. 1997. The effects of a change in withdrawal operations on phytoplankton and nutrient dynamics in Eau Galle Reservoir, Wisconsin (USA). Internationale Revue der Gesamten Hydrobiologie **82:** 531-543.

Basu, B. K., and F. R. Pick. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnology and Oceanography **41:** 1572-1577.

Bennett, W. A., D. J. Ostrach, and D. E. Hinton. 1995. Larval striped bass condition in a drought-stricken estuary: evaluating pelagic food-web limitation. Ecological Applications **5:** 680-692.

Bertrand, C., V. Siauve, S. Fayolle, and A. Cazaubon. 2001. Effects of hydrological regime on the drift algae in a regulated Mediterranean river (River Verdon, southeastern France). Regulated Rivers: Research and Management **17:** 407-416.

Borsuk, M. E., C. A. Stowe, and K. H. Reckhow. 2004. Confounding effect of flow on estuarine response to nitrogen loading. Journal of Environmental Engineering **130:** 605-614.

Branco, C. W. C., and P. A. C. Senna. 1994. Factors influencing the development of *Cylindrospermopsis raciborskii* and *Microcystis aeruginosa* in the Paranoa Reservoir, Brasilia, Brazil. Archiv fur Hydrobiologie, Algological Studies **75:** 85-96.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150:** 28-35.

Caraco, N. F., J. J. Cole, and D. L. Strayer. 2006. Top down control from the bottom: Regulation of eutrophication in a large river by benthic grazing. Limnology and Oceanography **51:** 664–670.

Carpenter, S. R., and J. F. Kitchell. 1993. The Trophic Cascade in Lakes. Cambridge University Press.

Chetelat, J., F. R. Pick, and P. B. Hamilton. 2006. Potamoplankton size structure and taxonomic composition: Influence of river size and nutrient concentrations. Limnology and Oceanography **51:** 681-689.

Cloern, J. B., B. E. Cole, R. L. J. Wong, and A. E. Alpine. 1985. Temporal dynamics of estuarine phytoplankton: A case study in San Francisco Bay. Hydrobiologia **129:** 153-176.

Cloern, J. E., B. E. Alpine, R. L. Cole, J. Wong, J. F. Arthur, and M. D. Ball. 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. Estuarine, Coastal and Shelf Science **16:** 415-429.

Conley, D. J., and T. C. Malone. 1992. Annual cycle of dissolved silicate in Chesapeake Bay: implications for the production and fate of phytoplankton biomass. Marine Ecology Progress Series **81:** 121-128.

De Cabo, L., A. Puig, S. Arreghini, H. F. Olguín, R. Seoane, and I. Obertello. 2003. Physicochemical variables and plankton from the Lower Delta of the Paraná River (Argentina) in relation to flow. Hydrological Processes **17:** 1279-1290.

Dettmann, E. H. 2001. Effect of water residence time on annual export and denitrification of nitrogen inestuaries: a model analysis. Estuaries **24:** 481-490.

Dickman, M. 1969. Some effects of lake renewal on phytoplankton productivity and species composition. Limnology and Oceanography **14:** 660-666.

Elser, J. J. 1999. The pathway to noxious cyanobacteria blooms in lakes: the food web as the final turn. Freshwater Biology **42:** 537-543.

Ferreira, J. G., W. J. Wolff, T. C. Simas, and S. B. Bricker. 2005. Does biodiversity of estuarine phytoplankton depend on hydrology? Ecological Modeling **187:** 513-523.

Filardo, M.J., and W. M. Dunstan. 1985. Hydrodynamic control of phytoplankton in low salinity waters of the James River Estuary., Virginia, USA. Estuarine, Coastal and Shelf Science **21:** 653-667.

Flannery, M. S., E. B. Peebles, and R. T. Montgomery. 2002. A percent-of-flow approach for managing reductions of freshwater inflows from unimpounded rivers to southwest Florida estuaries. Estuaries **25:** 1291-1303.

Gosselain, V., L. Viroux, and J.-P. Descy. 1998. Can a community of small-bodied grazers control phytoplankton in rivers? Freshwater Biology **39:** 9-24.

Ha, K., E.-A. Cho, H.-W. Kim, and G.-J. Joo. 1999. *Microcystis* bloom formation in the lower Nakdong River, South Korea: importance of hydrodynamics and nutrient loading. Marine and Freshwater Research **50:** 89-94.

Hagy, J. D., W. R. Boynton, C. W. Keefe, and K. W. Wood. 2004. Hypoxia in Chesapeake Bay, 1950-2001: Long-term change in relation to nutrient loading and river flow. Estuaries **27:** 634-658.

Harris, G. P., and G. Baxter. 1996. Interannual variability in phytoplankton biomass and species composition in a subtropical reservoir. Freshwater Biology **35:** 545-560.

Hein, T., C. Baranyi, G. J. Herndl, W. Wanek, and F. Schiemer. 2003. Allochthonous and autochthonous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. Freshwater Biology **48:** 220–232.

Heiskary, S., and H. Markus. 2001. Establishing relationships among nutrient concentrations, phytoplankton abundance, and biochemical oxygen demand in Minnesota, USA rivers. Journal of Lake and Reservoir Management **17:** 251-262.

Heiskary, S. A., and W. W. Walker, Jr. 1995. Establishing a Chlorophyll a Goal for a Run-of-the-river Reservoir. Lake and Reservoir Management **11:** 67-76.

Howarth, R. W., D. P. Swaney, T. J. Butler, and R. Marino. 2000. Climatic Control on Eutrophication of the Hudson River Estuary. Ecosystems **3:** 210-215.

Ittekkot, V., C. Humborg, and P. Schäfer. 2000. Hydrological alterations and marine biogeochemistry: A silicate issue? BioScience. **50:** 776–782.

Jassby, A. 2008. Phytoplankton in the upper San Francisco Estuary: Recent biomass trends, their causes and their trophic significance. San Francisco Estuary and Watershed Science **6:** 1-24.

Jaworski, N. A. 1990. Retrospective study of the water quality issues of the upper Potomac estuary. Reviews in Aquatic Science **3:** 11-40.

Jeong, K. S., D. K. Kim, and G. J. Joo. 2007. Delayed influence of dam storage and discharge on the determination of seasonal proliferations of *Microcystis aeruginosa* and *Stephanodiscus hantzschii* in a regulated river system of the lower Nakdong River (South Korea). Water Research **41:** 1269-1279.

Jeppesen, E. and others 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: A study of 466 lakes from the temperate zone to the arctic. Ecosystems **6:** 313-325.

---. 2007. Salinity induced regime shift in shallow brackish lagoons. Ecosystems **10:** 47-57.

Jones, I. D., and J. A. Elliott. 2007. Modelling the effects of changing retention time on abundance and composition of phytoplankton species in a small lake. Freshwater Biology **52:** 988-997.

Jordan, T. E., D. L. Correll, J. Miklas, and D. E. Weller. 1991. Long-term trends in estuarine nutrients and chlorophyll, and short-term effects of variation in watershed discharges. Marine Ecology Progress Series **75:** 121-132.

Justic, D., N. N. Rabelais, R. E. Turner, and Q. Dortch. 1995. Changes in nutrient structure of river-dominated coastal waters: Stoichiometric nutrient balance and its consequences. Estuarine, Coastal and Shelf Science **40:** 339–356.

Kawara, O., E. Yura, S. Fujii, and T. Matsumoto. 1998. A study on the role of hydraulic retention time in eutrophication of the Asahi River Dam reservoir. Water Science and Technology **37:** 245-252.

Kimmerer, W. J. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Marine Ecology Progress Series **243:** 39-55.

Krogmann, D. W., R. Butalla, and J. Sprinkle. 1986. Blooms of cyanobacteria on the Potomac River. Plant Physiology **80:** 667-671.

Lair, N. 2006. A review of regulation mechanisms of metazoan plankton in riverine ecosystems: aquatic habitat versus biota. River Research and Applications **22:** 567-593.

Leonard, J. A., and H. W. Paerl. 2005. Zooplankton community structure, micro-zooplankton grazing impact, and seston energy content in the St. Johns River system, Florida as influenced by the toxic cyanobacterium *Cylindrospermopsis raciborskii*. Hydrobiologia **537:** 89-97.

Lionard, M., K. Muylaert, A. Hanoutti, T. Maris, M. Tackx, and W. Vyverman. 2008. Inter-annual variability in phytoplankton summer blooms in freshwater tidal reaches of the Schelde estuary (Belgium). Estuarine, Coastal and Shelf Science **79:** 694–700.

Livingston, R. J., X. Niu, F. G. Lewis, Iii, and G. C. Woodsum. 1997. Freshwater input to a gulf estuary: Long-term control of trophic organization. Ecological Applications **7:** 277-299.

Lucas, L. V., J. K. Thompson, and L. R. Brown. 2009. Why are diverse relationships observed between phytoplankton biomass and transport time? Limnology and Oceanography **54:** 381–390.

Luef, B., F. Aspetsberger, T. Hein, F. Huber, and P. Peduzzi. 2007. Impact of hydrology on free-living and particle-associated microorganisms in a river floodplain system (Danube, Austria). Freshwater Biology **52:** 998–1008.

Lung, W. S., and H. W. Paerl. 1988. Modeling blue green algal blooms in the lower Neuse River. Water Research **22:** 895-905.

Maier, H. R., G. B. Kingston, T. Clark, A. Frazer, and A. Sanderson. 2004. Risk-based approach for assessing the effectiveness of flow managment in controlling cyanobacterial blooms in rivers. River Research and Applications **20:** 459-471.

Mallin, M. A., H. A. Paerl, J. Rudek, and P. W. Bates. 1993. Regulation of estuarine primary production by watershed rainfall and river flow. Marine Ecology Progress Series **93:** 199-203.

Martino, E. J., and E. D. Houde. 2010. Recruitment of striped bass in Chesapeake Bay: spatial and temporal environmental variability and availability of zooplankton prey. Marine Ecology Progress Series **409:** 213-228.

Mcgregor, G. B., and L. D. Fabbro. 2000. Dominance of *Cylindrospermopsis raciborskii* (Nostocales, Cyanoprokaryota) in Queensland tropical and subtropical reservoris: Implications for monitoring and management. Lakes & Reservoirs: Research and Management **5:** 195-205.

Mitrovic, S. M., B. C. Chessman, L. C. Bowling, and R. H. Cooke. 2006. Modelling suppression of cyanobacterial blooms by flow management in a lowland river. River Research and Applications **22:** 109-114.

Mitrovic, S. M., R. L. Oliver, C. Rees, L. C. Bowling, and R. T. Buckney. 2003. Critical flow velocities for the growth and dominance of *Anabaena circinalis* in some turbid freshwater rivers. Freshwater Biology **48:** 164-174.

Mortazavi, B., R. L. Iverson, W. H. Landing, F. G. Lewis, and W. Hwang. 2000. Control of phytoplankton production in a river-dominated estuary: Apalachicola Bay, Florida, USA. Marine Ecology Progress Series **198:** 19-31.

Moss, B., and H. Balls. 1989. Phytoplankton distribution in a floodplain lake and river system. II Seasonal changes in the phytoplankton communities and their control by hydrology and nutrient availability. Journal of Plankton Research **11:** 839-867.

Moustaka-Gouni, M. and others 2006. Plankton food web structure in a eutrophic polymictic lake with a history in toxic cyanobacterial blooms. Limnology and Oceanography **51:** 715-727.

Nixon, S. W. and others 1996. The fate of nitrogen and phosphorus at the land-sea margin of the North Atlantic Ocean. Biogeochemistry **35:** 141-180.

O.E.C.D. 1982. Eutrophication of Waters: Monitoring, Assessment and Control. Organization for Economic Cooperation and Development.

Oliver, R. L., S. M. Mitrovic, and C. Rees. 2010. Influence of salinity on light conditions and phytoplankton growth in a turbid river. River Research and Applications **26:** 894-903.

Pace, M. L., S. E. G. Findlay, and D. Lints. 1992. Zooplankton in advective environments: The Hudson River community and a comparative analysis. Canadian Journal of Fisheries and Aquatic Sciences **49:** 1060-1069.

Pádisak, J., J. Köhler, and S. Hoeg. 1999. The effect of changing flushing rates on development of late summer *Aphanizomenon* and *Microcystis* populations in a shallow lake, Müggelsee, Berlin, Germany, p. 411-423. *In* G. Tundisi and M. Sraškraba [eds.], Theoretical reservoir ecology and its applications. Backhuys Publishers.

Paerl, H. W. 1987. Dynamics of blue-green algal (*Microcystis aeruginosa*) blooms in the lower Neuse River, North Carolina: Causative factors and potential controls. Water Resources Research Institute of The University of North Carolina. The University of North Carolina.

---. 2006. Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations. Ecological Engineering **26:** 40-54.

Paerl, H. W., and R. S. Fulton, Iii. 2006. Ecology of harmful Cyanobacteria, p. 95-109. *In* E. Granéli and J. T. Turner [eds.], Ecology of Harmful Algae. Ecological Studies. Springer-Verlag.

Paerl, H. W., R. S. Fulton, Iii, P. H. Moisander, and J. Dyble. 2001. Harmful freshwater algal blooms, with an emphasis on cyanobacteria. TheScientificWorld **1:** 76-113.

Paerl, H. W., L. M. Valdes, B. L. Peierls, J. E. Adolf, and J. Lawrence W. Harding. 2006. Anthropogenic and climatic influences on the eutrophication of large estuarine ecosystems. Limnology and Oceanography **51:** 448-462.

Perry, S. A., W. B. Perry, and G. M. Simmons, Jr. 1990. Bacterioplankton and phytoplankton populations in a rapidly-flushed eutrophic reservoir. Internationale Revue der Gesamten Hydrobiologie **75:** 27-44.

Phlips, E. J., J. Hendrickson, E. L. Quinlan, and M. Cichra. 2007. Meteorological influences on algal bloom potential in a nutrient-rich blackwater river. Freshwater Biology **52:** 2141-2155.

Rabalais, N. N., R. E. Turner, and D. Scavia. 2002. Beyond science into policy: Gulf of Mexico hypoxia and the Mississippi River. BioScience **52:** 129-142.

Rennella, A. M., and R. Quirós. 2006. The Effects of Hydrology on Plankton Biomass in Shallow Lakes of the Pampa Plain. Hydrobiologia **556:** 181-191.

Reynolds, C. S. 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton, p. 388-433. *In* C. D. Sandgren [ed.], Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press.

---. 2000. Hydroecology of river plankton: the role of variability in channel flow. Hydrological Processes **14:** 3119-3132.

Saunders, J. F. I., and W. M. J. Lewis. 1989. Zooplankton abundance in the lower Orinoco River, Venezuela. Limnology and Oceanography **34:** 397-409.

Scheffer, M. 1998. Ecology of Shallow Lakes. Chapman and Hall.

Schemel, L. E., T. R. Sommer, A. B. Müller-Solger, and W. C. Harrell. 2004. Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, U.S.A. Hydrobiologia **513:** 129-139.

Sherman, B. S., I. T. Webster, G. J. Jones, and R. L. Oliver. 1998. Transitions between *Aulacoseira* and *Anabaena* dominance in a turbid river weir pool. Limnology and Oceanography **43:** 1902-1915.

Sklar, F. H., and J. A. Browder. 1998. Coastal environmental impacts brought about by alterations to freshwater flow in the Gulf of Mexico. Environmental Management **22:** 547-562.

Sluss, T. D., G. A. Cobbs, and J. H. Thorp. 2008. Impact of turbulence on riverine zooplankton: a mesocosm experiment. Freshwater Biology **53:** 1999–2010.

Soballe, D. M., and R. W. Bachmann. 1984. Influence of reservoir transit on riverine algal transport and abundance. Canadian Journal of Fisheries and Aquatic Sciences **41:** 1803-1813.

Soballe, D. M., and B. L. Kimmel. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology **68:** 1943-1954.

Straškraba, M. 1999. Retention time as a key variable of reservoir limnology, p. 385-410. *In* G. Tundisi and M. Straškraba [eds.], Theoretical reservoir ecology and its applications. Backhuys Publishers.

Strayer, D. L., M. L. Pace, N. F. Caraco, J. J. Cole, and S. E. G. Findlay. 2008. Hydrology and grazing jointly control a large-river food web. Ecology **89:** 12-18.

Valdes-Weaver, L. M., M. F. Piehler, J. L. Pickney, K. E. Howe, K. Rossignol, and H. W. Paerl. 2006. Long-term temporal and spatial trends in phytoplankton biomass and class-level taxonomic composition in the hydrologically-variable Neuse-Pamlico estuarine continuum, North Carolina, USA. Limnology and Oceanography **51:** 1410-1420.

Van Den Brink, F. W. B., M. M. V. Katwijk, and G. V. D. Velde. 1994. Impact of hydrology on phyto- and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse. Journal of Plankton Research **16:** 351-373.

Verspagen, J. M. H. and others 2006. Water management strategies against toxic *Microcystis* blooms in the Dutch delta. Ecological Applications **16:** 313-327.

Walks, D. J. 2007. Persistence of plankton in flowing water. Canadian Journal of Fisheries and Aquatic Sciences **64:** 1693-1702.

Walz, N., and M. Welker. 1998. Plankton development in a rapidly flushed lake in the River Spree System (Neuendorfer See, Northeast Germany). Journal of Plankton Research **20:** 2071-2087.

Webster, I. T., B. S. Sherman, M. Bormans, and G. J. Jones. 2000. Management strategies for cyanobacterial blooms in an impounded lowland river. Regulated Rivers: Research and Management **16:** 513-525.

Wehr, J. D., and J. H. Thorp. 1997. Effects of navigation dams, tributaries, and littoral zones on phytoplankton communities in the Ohio River. Canadian Journal of Fisheries and Aquatic Sciences **54:** 378-395.

Wetz, M. S., E. A. Hutchinson, R. S. Lunetta, H. W. Paerl, and J. C. Taylor. 2011. Severe droughts reduce estuarine primary productivity with cascading effects on higher trophic levels. Limnology and Oceanography **56:** 627-638.