Final Report for the N.C. Policy Collaboratory

Assessment of zooplankton- phytoplankton relationships in Falls Lake to guide development of site specific numeric nutrient criteria

3 December 2021

Nathan Hall and Michael Piehler

Introduction: This project examines the trophic relationship between zooplankton and phytoplankton within Falls Lake, North Carolina to provide guidance for development of site-specific numeric nutrient criteria protective of aquatic life uses. Nutrient enrichment of lakes and reservoirs generally stimulates productivity throughout the food web (Bachmann et al. 1996; Hessen et al. 2006; Yuan and Pollard 2018). However, the degree of stimulation of higher trophic levels is often less than at the level of primary producers (Hessen et al. 2006; Yuan and Pollard 2018). Changes in the palatability and nutritional value of primary producers and structural changes to the food web occur as nutrient enrichment progresses that tend to decrease the efficiency of trophic transfer from primary producers to zooplankton (Hessen et al. 2006; other cites). The decreased transfer efficiency of organic matter causes many of the classic symptoms of eutrophication including accumulation of excess phytoplankton in the photic zone with shading of benthic autotrophs, and sedimentation into the hypolimnion leading to hypoxic bottom waters.

The important role that the efficiency of trophic transfer plays in determining the expression of eutrophication has generated significant interest in using trophic transfer efficiency as a metric for establishing regulatory criterion for acceptable levels of phytoplankton biomass in U.S. lakes and reservoirs (EPA 2021). Rates of primary and secondary production required to calculate trophic transfer efficiency are rarely measured, but the ratio of the biomass of zooplankton to phytoplankton can be a useful proxy for changes in transfer efficiency that result from nutrient enrichment (Hessen et al. 2006; Yuan and Pollard 2018). An analysis of summertime zooplankton: phytoplankton biomass ratios for deep (>8 m depth) lakes throughout the United States revealed an inflection point in the slope of the relationship between zooplankton and phytoplankton biomass which has been interpreted as threshold level of P where coupling of zooplankton and phytoplankton production begins to deteriorate (Yuan and Pollard 2018; EPA 2021). The inflection point analysis has been proposed as a way to quantify phytoplankton biomass criterion that are protective of aquatic life uses for U.S. lakes and reservoirs (EPA 2021).

Besides the level of nutrient enrichment, trophic transfer efficiency is also strongly affected by climatic conditions, hydrology, morphometry, fish community structure, and water chemistry (Hesson et al. 2006; Havens and Beaver 2013; Jeppesen et al. 2003). These factors that are largely system-specific result in wide variation in trophic transfer efficiency for a given level of nutrient enrichment, and indicate that a single level of trophic transfer efficiency may not be

appropriate for establishing acceptable levels of phytoplankton biomass across the thousands of disparate lakes and reservoirs in the United States. More effective criterion for phytoplankton biomass levels may be developed by considering site specific information on trophic transfer efficiency.

Since the 1970's, North Carolina's water quality standard for phytoplankton biomass has been based on chlorophyll a (Chl a) concentration and set as a do not exceed value of 40 μg L^{-1} for all surface waters except mountain trout streams. The level of this standard (40 μg L^{-1}) was based largely on best professional judgement with considerations for water clarity and a desire to prevent negative consequences from harmful algal blooms and to protect aquatic life (NCDP SAC 2020). Although the standard has been in place for more than 40 years, the validity of the standard for protection of aquatic life in NC surface waters has rarely been assessed. Many of NC's reservoirs, including Falls Lake, have consistently violated the standard since their creation despite having productive fisheries and heavy recreational use that indicate that violation of the Chl a standard may not be strongly linked to impairment of aquatic life and recreational use in these impoundments (NCDP SAC 2020).

Water quality in Falls Lake is currently managed under the Falls Reservoir Nutrient Management Strategy which has established a plan for meeting the current water quality standards throughout all of Falls Lake by reducing N and P loads by 40 and 77 %, respectively, by the year 2040 at a cost of approximately 1 billion dollars (UNRBA 2019; Stage II of the Falls Reservoir Nutrient Management Strategy). Given the high cost of the nutrient reduction efforts, it is important to use best scientific evidence to establish the linkage between phytoplankton biomass measured as Chl a and designated uses in Falls Lake. This project specifically seeks to understand the relationship between phytoplankton biomass as measured by Chl a and support for aquatic life as indicated by zooplankton biomass. This study examines a three year (2009-2012), approximately monthly record of zooplankton and phytoplankton biomass at 10 sites throughout Falls Lake and compares the plankton of Falls Lake to other southeastern United States reservoirs to address the following questions.

1) Does the spatial temporal distribution of zooplankton and phytoplankton within Falls Lake indicate significant coupling or decoupling between phytoplankton and zooplankton production?
2) How does the trophic transfer efficiency in Falls Lake compare to similar water bodies in the southeastern US?
3) Is there a clear inflection point in the slope of the relationship between zooplankton and phytoplankton biomass for Falls Lake that may guide development of a site-specific criterion?
4) Is there a clear inflection point in the slope of the relationship between zooplankton and phytoplankton biomass for southeastern reservoirs that may help guide development of a region-specific criterion for phytoplankton biomass that could be adopted for use in Falls Lake?

Methods: Zooplankton data from Falls Lake were provided by Dr. Sandra Cooke, Assistant Professor at Greensboro College, who conducted a study of Falls Lake zooplankton in

collaboration with water quality sampling conducted by NC State University's Center for Applied Aquatic Ecology (CAAE). Zooplankton samples were collected at ten CAAE monitoring stations (Fig. 1) with approximate monthly frequency from 2009 to 2012 (Fig. 2). The stations were grouped into three clusters within the upper main arm of the lake, a mid-lake region near the HWY 50 bridge and a lower lake region from HWY 98 to the dam. From each station, duplicate zooplankton samples were collected using a vertical net tow from the bottom to the surface using a 48 μm mesh, 11.5 cm diameter Wisconsin style zooplankton net. Average tow depths for each station are given in Figure 1 and sampling dates for each station are shown in figure 2. Samples were preserved with 90% ethanol and identified microscopically to the lowest possible taxonomic level, most often to genus for cladocerans and rotifers and to the class level for copepods (Table 1). Average organism abundance (animals/L) at each site visit was calculated as the arithmetic mean of the duplicate net tow samples.

During most site visits, hydrographic profiles were conducted and photic zone, depth-integrated water samples were collected for measuring phytoplankton biomass as Chl *a*. Chl *a* was measured using the fluorometry (EPA method 445) on acetone extracts of phytoplankton filtered onto a glass fiber filter according to methods described in Touchette et al (2007). Data on phytoplankton community composition including monthly species-level cell abundances and biovolume were provided by the North Carolina Department of Environmental Quality's Division of Water Resources for the time period 2011 to 2018 at sites in the upper (NEU013B), middle (NEU018E), and lower (NEU019P) reservoir regions (Figure 1).

Biomass of each zooplankton taxa within each sample (μg dry weight m^3) was calculated by multiplying measured organism density by estimates of the dry body weights for each taxa (Table 1). For most taxa, dry body weights for each taxa were gathered from data collected by the 2012 US EPA National Lakes Assessment (US EPA 2017). Zooplankton body weights for a species can vary widely across its range and are influenced by climatic factors such as temperature and mean precipitation, and to a less extent the trophic status of a water body (Yuan and Pollard 2018, and reference therein). To ensure representativeness of the body weights, we used body weights from a subset of lakes from the EPA NLA dataset that were most similar to Falls Lake. This subset of lakes included all the southeast U.S. (EPA region 4) reservoirs that were at an elevation below 500 m. This subset intentionally excluded natural lakes and mountain reservoirs which tend to have very different hydrology and climatic conditions from Falls Lake. Exclusion of natural lakes was particularly important because the majority (19 of 26) within the NLA 2012 dataset were represented by shallow Florida lakes (19 of 26) with a significantly different climate than Falls Lake.

Where body weights could not be found in the EPA NLA dataset, values from published literature were used for those taxa. For many of these taxa, a range of body weights were provided corresponding to different size classes of animal. We chose the size class of each animal based on information provided by Dr. Cooke, or otherwise chose the median body weight provided for each taxa. Body weights and methods used to derive the body weights for 28 taxa identified from Falls Lake are provided in Table 1. Total zooplankton biomass at each site visit was calculated as the sum of the biomass of all taxa observed. Dr. Cooke's zooplankton data

included counts of some unicellular ciliates. These protists constituted less than 1% of the total biomass estimates and were excluded from the zooplankton biomass totals for comparability with zooplankton data from the NLA which does not include protists. Although Dr. Cooke identified and enumerated some rotifers, her primary interest was the crustacean taxa, particularly the exotic water flea, *Daphnia lumholtzi*. Effort spent on identification and enumeration of rotifers was inconsistent over the study period (Cooke, S. pers. comm.). Consequently, we report the rotifer taxa observed by Dr. Cooke and the NLA but only use data for crustacean zooplankton for quantitative comparisons of Falls Lake zooplankton biomass versus zooplankton biomass of other waters within the NLA dataset.

The EPA NLA dataset of southeastern (EPA region 4) reservoirs at elevations less than 500 m was also used to compare relationships between zooplankton and phytoplankton biomass in Falls Lake against similar reservoirs, and to investigate the possibility of deriving a region-specific Chl *a* criteria that might be adopted for use in Falls Lake. The NLA dataset from summer 2012 contained paired measurement of summertime (May-September) zooplankton biomass and Chl *a* from 74 low elevation (< 500 m) reservoirs within EPA Region 4. Most reservoirs (90%) were sampled only once. For reservoirs sampled twice, mean total crustacean zooplankton biomass and Chl *a* concentrations of the two measurements were calculated to provide a single pair of data values for each water body.

Importantly, the sampling methodology used by the EPA NLA and Dr. Cooke's sampling methodology were very similar. The EPA NLA used both a 50 and a 150 mm mesh Wisconsin style net from which the fine and large mesh samples were used to identify and enumerate small and large zooplankton, respectively. Therefore, the combination of taxa enumerated by both nets should have captured almost exactly the same size classes of zooplankton as that collected by Dr. Cooke's 48 mm mesh net. Vertical net tows by the EPA NLA extended from the surface to the bottom or to a depth of 5 m for lakes greater than 7 m deep (Yuan and Pollard 2018). Only a small fraction, 22%, of EPA region 4 reservoirs were deeper than 7 m. So, in the majority of cases, the EPA NLA net tows captured the entire water column like Dr. Cooke's net tows in Falls Lake. Comparisons between the two datasets used only Falls Lake data collected between May and September to match the seasonality of sampling conducted by the EPA NLA.

For deep lakes (> 8 m) within the NLA dataset, Yuan and Pollard (2018) found a pattern of zooplankton biomass (Z) that saturated at high levels of phytoplankton biomass measured as Chl *a*. They fitted this pattern to the piece-wise linear functional model form below that described the observed initial increase and subsequent saturation or declining behavior of log(Z) with increasing log(Chl *a*).

$$\log(Z) = a + b\log(\text{Chl } a) - c\log[1+\exp(d-\log(\text{Chl } a))]$$

Yuan and Pollard estimated the coefficients *a*, *b*, *c*, and *d* from the data using Bayesian inference, and the empirical model was then used to examine changes in the modeled slope (ΔZ: Δ Chl *a*) of the relationship across the observed gradient of Chl *a*. We examined Z and Chl *a* data from low-elevation (< 500 m) EPA region 4 reservoirs using the same empirical model but fit the model using least squares minimization rather than Bayesian inference. We then examined the

model results to determine its usefulness for establishing a region-specific criteria for Chl *a* that could be adopted for Falls Lake.

Results and Discussion: Twenty-five taxonomic categories of zooplankton were identified by Dr. Cooke from the Falls Lake samples. Biomass and abundance of crustacean zooplankton were dominated by copepods with cladocerans with other crustaceans, predominantly ostracods, constituting less than 1%. Seasonally, copepods were dominant in the warm months from May to September but cladocerans dominated biomass during the cooler months from October through April (Fig. 3). At this level of taxonomic resolution, the warm season zooplankton community of Falls Lake appears typical of other southeastern U.S. reservoirs with biomass and abundance dominated by copepods, cladocerans forming about a third of biomass, and other crustaceans constituting a small fraction.

Though the composition of zooplankton in Falls Lake was similar to other southeastern reservoirs, median summer biomass and abundance of zooplankton in Falls Lake was less than a third of those reservoirs (Table 2). Comparatively low zooplankton biomass cannot be explained by lack of fertility because median phytoplankton biomass of Falls Lake quantified by Chl *a* was nearly three-fold higher than the other reservoirs. The combination of low zooplankton biomass and high Chl *a* led to Z:Chl *a* ratios that averaged nearly an order of magnitude lower for Falls Lake than the other reservoirs (Table 2). This indication of poor trophic transfer efficiency in Falls Lake was examined further by assessing correlations between zooplankton and phytoplankton biomass over space and time in Falls Lake.

Analysis of concurrent measurements of zooplankton biomass and Chl *a* which is influenced by both spatial variability in both space and time of zooplankton biomass and Chl *a* throughout Falls Lake exhibited a significant negative rank correlation (R_s = -0.32, p = 0.01). Since the relationship between zooplankton biomass and Chl *a* was consistently negative relationship across the observed range of Chl *a* values, there was no inflection point in the relationship that could be used to develop a site specific Chl *a* criteria. Linear regression analyses of the concurrent measurements grouped by lake region showed that the slope of the negative relationship varied across regions (Fig. 4). The negative slope was strong and statistically significant in the middle and lower regions, but weak and insignificant in the upper region.

Despite the negative relationships of the instantaneous values, when averaged by station, both zooplankton and phytoplankton biomass increased significantly from the lower to upper lake (Fig. 5). Station-averaged zooplankton biomass and Chl *a* increased from ~ 3 µg L⁻¹ and 10 µg L⁻¹, respectively, near the dam to ~ 30 µg L⁻¹ and 70 µg L⁻¹, respectively, at the upper stations near the Interstate 85 bridge. For both zooplankton and Chl *a*, stations located in creek arms of the lake exhibited similar values to main channel stations similarly-distanced downstream in the reservoir. Either the plankton populations of the creek arms are highly connected to the channel through water movements or similar biological/ chemical processes lead to similar biomass levels in both the channel and the creek arms. In either case, these strong spatial gradients of both zooplankton and phytoplankton would give rise to a positive relationship between zooplankton and phytoplankton that is indicative of strong coupling along the downstream to upstream trophic gradient. The positive spatial relationship also indicates that the negative

relationship observed at the scale of individual observations must be driven by temporal variability in the plankton.

Both zooplankton and phytoplankton biomass measured as Chl a exhibited strong seasonality (Figure 6). From a winter minimum of 1-3 μg L^{-1} within all lake regions, zooplankton biomass increased two orders of magnitude during spring and reached a peak in April that ranged from about 100 μg L^{-1} in the lower lake to an average of approximately 500 μg L^{-1} in the upper lake. Following the April peak, zooplankton biomass declined exponentially throughout summer falling 100-fold by July at all stations. The zooplankton decline continued through late fall reaching a stable low concentration by November that persisted through winter.

In both the upper and mid-reservoir regions, phytoplankton biomass measured as Chl a decreased in spring and reached an annual minimum of 10-15 μg/L in April coincident with the annual peak in zooplankton biomass (Figure 6). Chl a levels increased steadily from late spring through summer reaching a maximum in the upper lake of about 120 in August, and an average of about 40 in the middle lake in September. Following the late summer peak, phytoplankton biomass fell in the upper and mid reservoir reaching a winter minimum that ranged 30-50 μg/L in the upper region and 25-30 μg/L in the mid reservoir. In contrast to the summertime peaks of biomass observed in the upper and mid reservoir, Chl a in the lower reservoir reached a peak during the winter of 30-40 μg/L and had a minimum in June of ~10 μg/L.

The strong, and largely opposite seasonal patterns of zooplankton and phytoplankton biomass are obviously the cause of the negative relationship between zooplankton and Chl a in the upper and mid reservoir regions. The similar seasonality of zooplankton despite a very different pattern of phytoplankton biomass in the lower reservoir indicates that the ecological processes that shape phytoplankton biomass differ significantly from the upper to lower regions of the reservoir, and that factors other than total phytoplankton biomass are important for influencing the seasonality of zooplankton biomass.

The seasonality of both zooplankton and phytoplankton biomass in the upper and mid-reservoir regions are entirely consistent with the Plankton Ecology Group's (PEG) conceptual model (Sommer et al. 1986), and has been previously observed in other temperate reservoirs (Chang et al. 2014; Vasconcelos 1990). Alleviation of light limitation through longer day lengths and development of thermal stratification creates conditions conducive for a spring phytoplankton bloom which is allowed to develop under relatively low grazing pressure associated with low zooplankton biomass. With warmer temperatures and plentiful prey, zooplankton biomass rapidly increases and the enhanced grazing pressure results in a rapid decline of phytoplankton biomass. The period in spring leading up to the peak of zooplankton and minimum of chlorophyll a represents a burst of trophic transfer of organic matter that would be poorly characterized by only considering zooplankton and phytoplankton biomass later in the growing season.

According to the PEG model, a combination of summertime seasonal shifts toward largely inedible cyanobacteria, and predation by zooplanktivorous fish causes both the decline of summertime crustacean biomass and a summertime maximum of cyanobacterial biomass due to

low grazing pressure. In southeastern reservoirs, the recruitment of larval gizzard and threadfin shad typically takes place in spring and produces a period of intense zooplanktivory during late spring and summer (Allen and DeVries 1993). Cyanobacterial biomass of Falls Lake also increases significantly from spring to summer (Figure 7). Throughout the lake, cyanobacteria constitute about 50% of cell abundance during the winter and spring and increase to about 90% of abundance during summer. Despite the dominance of cell abundance during summer, cyanobacteria typically constitute only 30-40 % of phytoplankton biomass during summer (Figure 7). The apparent discrepancy between cyanobacterial dominance of abundance and subordinate cyanobacterial biomass is explained by the short and thin (i.e. low biomass) filamentous cyanobacteria (e.g. *Planktolyngbya*, *Pseudanabaena*, and *Cylindrospermopsis*) that dominate the cyanobacterial community of Falls Lake and many other piedmont reservoirs in North Carolina (Touchette et al. 2007).

The relative importance of the increase of inedible cyanobacteria versus zooplanktivory by fish in driving the summertime decline in zooplankton biomass varies between water bodies (Hess et al. 2006; Havens and Beaver 2013; Jeppesen et al. 2003). In shallow Florida Lakes, Havens and Beaver (2013) presented strong evidence that the primary mechanism driving the summertime decrease of the zooplankton: phytoplankton biomass ratio was a decline in zooplankton biomass driven by planktivorous fish. The zooplankton and phytoplankton data from Falls Lake are consistent with this view. First, the major decline in zooplankton biomass each year occurred between April and May throughout the reservoir (Figure 6), while the fastest increases in cyanobacterial abundance and the start of the increase of cyanobacterial biomass occurred a month later (Figure 7), between May and June. Second, the non-cyanobacterial biomass fraction, an indicator of edible prey availability (Havens and Beaver 2013), never constituted more than about half of the total phytoplankton biomass. So, even during late summer when cyanobacterial biomass was at its maximum, there should have been sufficient edible prey to support substantial crustacean zooplankton production (Havens and Beaver 2013). Additionally, if zooplankton were completely unable to prey on cyanobacteria, then one would expect that the approximate 50-75% reductions in total phytoplankton biomass (as Chl *a*) during the April peak of zooplankton biomass (Figure 6) would be accompanied by significant increases in the cyanobacterial fraction of the phytoplankton community. For the upper and mid reservoir where the phytoplankton decline was so pronounced, observed increases in the cyanobacterial fraction were at most, only about 10% for both abundance and biomass (Figure 6). The lack of evidence linking changes in phytoplankton community structure to the summer decline of zooplankton biomass increases the strength of the argument for top-down pressure from planktivorous fish as being the dominant driver for the observed summer decline of zooplankton in Falls Lake.

Chlorophyll *a* criteria from the southeastern U.S., region-specific zooplankton: phytoplankton biomass relationships. For southeastern U.S. reservoirs, the best-fit, piece-wise model of zooplankton biomass increased gradually from a low of about 20 µg L^{-1} zooplankton at 1 µg L^{-1} Chl *a* to a maximum of about 100 µg L^{-1} zooplankton at 51 µg L^{-1} Chl *a*, and then declined with further increases in Chl a (Figure 8). The Chl *a* level where the slope of the zooplankton: phytoplankton relationship reaches zero, (i.e. 51 µg L^{-1}), should be considered as

the upper acceptable level for Chl a (EPA 2021). The EPA found the same 51 μg L^{-1} threshold value for shallow (< 3.8 m) lakes and reservoirs throughout the U.S. Median depth of the southeastern reservoirs was only 4.5 m, and the agreement in thresholds between shallow waters across the U.S. and the southeast reservoirs may relate to the strength of benthic pelagic coupling in shaping plankton communities of shallow water bodies (EPA 2021).

Although the threshold derived here for southeastern reservoirs is consistent with the threshold for waters of similar depth derived by the EPA (2020), the piece-wise model for the southeastern reservoirs explained less than 7% of the variability in zooplankton biomass, and performed only slightly better than a linear model with a weakly-positive slope (Table 4). When the added parameters of the piece-wise model are penalized, comparison of adjusted R^2 values and Akaike criterion for the piece-wise model and the linear model showed that the linear model was actually superior (Table 4). This finding does not prove that either empirical model is correct, but it casts doubt on the underlying assumption that all types of water bodies will exhibit strong bimodal (increase then decrease) responses of zooplankton biomass to increases in phytoplankton biomass. It is important to note, that the range of Chl a values exhibited by the southeastern reservoirs (0.8 – 258 μg L^{-1}) spanned the same orders of magnitude as the full data set examined by the US EPA (0.2 – 800 μg L^{-1}) (EPA 2021). So, the lack of a strong bimodal response is not due to the southeastern reservoirs exhibiting a constrained range (all very low or all very high) of Chl a values which may only display one half (increasing or decreasing) of the bimodal pattern. Strong seasonality of zooplankton and phytoplankton might contribute to the weakness of the observed relationship and zooplankton and phytoplankton biomass in the southeastern reservoirs compared to the larger dataset examined by the EPA (2021) and Yuan and Pollard (2018). If the other southeastern reservoirs are similar to Falls Lake, it appears likely that most of the US EPA's summer-time (May-September) data were collected during a period when zooplankton were strongly top-down controlled, and the zooplankton: phytoplankton biomass ratios during this time period may not strongly reflect trophic status of the reservoirs (Havens and Beaver 2013).

Conclusions:

1) Compared to other southeastern reservoirs the average zooplankton to phytoplankton biomass ratio of Falls Lake is indicative of a poor efficiency of trophic transfer from phytoplankton to zooplankton.
2) In contrast to conclusion 1, a burst of zooplankton production that terminates the spring phytoplankton bloom and a positive correlation of zooplankton biomass with Chl a along the downstream trophic gradient provide evidence for a strong trophic linkage between Chl a and zooplankton biomass in Falls Lake.
3) Strong and opposite seasonal patterns of zooplankton and phytoplankton likely resulted from zooplankton consumption of phytoplankton in spring and fish consumption of zooplankton during summer. The resultant, negative relationship precluded identification

of an inflection point in the zooplankton: phytoplankton relationship that could be used to develop a lake-specific Chl *a* criteria.

4) A region-specific Chl *a* criteria of 51 µg L^{-1} was derived using the US EPA's NLA dataset for southeastern U.S. reservoirs and by identifying an inflection point a unimodal empirical model that related zooplankton biomass and Chl *a*. This criteria value is consistent with criteria determined by the US EPA (2021) for shallow reservoirs similar to those of the southeastern U.S. However, the unimodal empirical model fit the data only slightly better than a positive linear model which casts doubt on the underlying assumption of a unimodal relationship and thus, the validity of the derived Chl *a* criteria.

References:

Allen M.S., DeVries, D.R. 1993. Spatial and temporal heterogeneity of larval shad in a large impoundment. *Transactions of the American Fisheries Society* 122:1070–1079.

Bachmann, R.W., Jones, B.L., Fox, D.D., Hoyer, M., Bull, L.A., Canfield, D.E. Jr. 1996. Relations between trophic state indicators and fish in Florida (U.S.A.) lakes. *Canadian Journal of Fisheries and Aquatic Science* 53: 842-855.

Chang, C., Shiah, F., Wu, J., Miki, T., Hsieh, C. 2014. The role of food availability and phytoplankton community dynamicsin the seasonal succession of zooplankton communityin a subtropical reservoir. *Limnologica* 46: 131-138.

Culver, D.A., Boucherle, M.M., Bean, D.J., Fletcher, J.W. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1380-1390.

Dumont, H.J., Balvay, G. 1979. The dry weight estimate of *Chaoborus flavicans* (Meigen) as a function of length and instars. *Hydrobiologia* 64: 139-145.

Dumont, H.J., Van de Velde, I, Dumont, S. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda, and rotifera from the plankton, periphyton, and benthos of continental waters. *Oecologia* 19: 75-97.

EPA. 2021. Ambient water quality criteria to address nutrient pollution in lakes and reservoirs. United States Environmental Protection Agency. Office of Science and Technology. Office of Water. EPA-822-R-21-005. Washington, D.C., August 2021.

Havens, K.E., Beaver, J.R. 2013. Zooplankton to phytoplankton biomass rations in shallow Florida lakes: an evaluation of seasonality and hypotheses about factors controlling variability. *Hydrobiologia* 703: 177-187.

Hessen, D.O., Faafeng, B.A., Brettum, P., Andersen, T. 2006. Nutrient enrichment and planktonic biomass ratios in lakes. *Ecosystems* 9: 516-527.

Jeppesen, E., Jensen, J.P, Jensen, C., Faafeng, B., Hessen, D.O, Sondergaard, M., Lauridsen, T., Brettum, P., Christoffersen, K. 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.

Rosen, R.A. 1981. Length-dry weight relationships of some freshwater zooplankton. *Journal of Freshwater Ecology* 1: 225-229.

Sommer, U., Gliwicz, Z.M., Lampert, W., Duncan, A. 1986. The PEG* model of seasonal succession of planktonic events in fresh waters. *Archiv fur Hydrobiologie* 106: 433-471.

Touchette, B.W., Burkholder, J.M., Allen, E.H., Alexander, J.L., Kinder, C.A., Brownie, C., James, J, Britton, C.H. 2007. Eutrophication and cyanobacteria blooms in run-of-river impoundments in North Carolina, U.S.A. Lake and Reservoir Management 23: 179-192.

US EPA. 2017. National lakes assessment 2012: Technical report. EPA 841-R-16-114. U.S. Environmental Protection Agency, Office of Water, Office of Research and Development.

US EPA. 2020. Draft ambient water quality criteria recommendations for lakes and reservoirs of the conterminous United States: Information supporting the development of numeric nutrient criteria. EPA 820P20001. Environmental Protection Agency, Office of Water, Office of Science and Technology.

Vasconcelos, V. 1990. Seasonal fluctuation in the zooplankton community of Azibo reservoir (Portugal). *Hydrobiologia* 196: 183-191.

Yuan, L.L., Pollard, A.I. 2018. Changes in the relationship between zooplankton and phytoplankton biomasses across a eutrophication gradient. *Limnology and Oceanography* 63: 2493-2507.

Table 1. Dry body weights for zooplankton taxa identified in Falls Lake

Taxon	Dry Weight (μg/animal)	Reference	Notes
Rotifers			
Asplanchna sp.	2.14	NLA 2012- EPA region 4 reservoirs	
Brachionus sp.	0.064	NLA 2012- EPA region 4 reservoirs	
Kellicottia sp.	0.0022	NLA 2012- EPA region 4 reservoirs	
Keratella sp.	0.010	NLA 2012- EPA region 4 reservoirs	
Keratella taurocephala	0.01	NLA 2012- EPA region 4 reservoirs	
Polyarthra sp.	0.076	NLA 2012- EPA region 4 reservoirs	
Cladocerans			
Bosmina sp.	1.26	Dumont et al. 1975	Median of *Bosmina longirostris*
Ceriodaphnia sp.	2.14	NLA 2012- EPA region 4 reservoirs	
Chydorus sp.	0.22	NLA 2012- EPA region 4 reservoirs	
Chydorus sphaericus	0.81	NLA 2012- EPA region 4 reservoirs	
Daphnia lumholtzi	2.98	NLA 2012- EPA region 4 reservoirs	
Daphnia sp.	7.28	NLA 2012- EPA region 4 reservoirs	
Diaphanosoma sp.	0.90	NLA 2012- EPA region 4 reservoirs	
Holopedium sp.	0.70	NLA 2012- EPA region 4 reservoirs	
Leptadora sp.	1.47	Rosen 1981	Median size
Other Cladocera	0.32	NLA 2012- EPA region 4 reservoirs	
Pleuroxus sp.	1.27	NLA 2012- EPA region 4 reservoirs	
Scapholeberis sp.	6.07	Dumont et al. 1975	Median size
Copepods			
Cyclopoida	2.06	NLA 2012- EPA region 4 reservoirs	
Calanoid copepod	1.94	NLA 2012- EPA region 4 reservoirs	
Calanoid copepodid	1.21	Culver 1985	Mean of class 2 and class 3 diatomid copepodite as recommended by Cooke
Cyclopoid copepod	2.06	NLA 2012- EPA region 4 reservoirs	
Cyclopoid copepodid	1.07	Culver 1985	Class 4 copepodite of *Cyclops vernalis* as recommended by Cooke
Harpacticoid copepod	0.19	NLA 2012- EPA region 4 reservoirs	
Copepod nauplii	1.41	Dumont et al. 1975	Assumed weight was equal to smallest copepodite size class
Other Crustaceans			
Ostracoda	2.32	NLA 2012- EPA region 4 reservoirs	

Table 2. Summary of crustacean zooplankton and chlorophyll *a* in Falls Lake during summer (May-Sep) and spring (March-May) and other southeastern United States reservoirs during summer

	5%	25%	Median	75%	95%
Summer Falls Lake Chl *a* (μg L^{-1})	9.8	22	35	51	72
Summer Falls Lake zooplankton biomass (μg L^{-1})	1.0	3.6	10	39	144
Summer Falls Lake zooplankton abundance (ind. L^{-1})	1.2	4.8	15	46	146
Summer Falls Lake Z: Chl *a* (μg L^{-1}: μg L^{-1})	0.053	0.13	0.26	1.68	10
S.E. Reservoirs Chl *a* (μg L^{-1})	1.8	8.0	12	24	69
S.E. Reservoirs zooplankton biomass (μg L^{-1})	1.7	10	36	83	389
S.E. Reservoirs zooplankton abundance (ind. L^{-1})	12	32	56	125	422
S.E. Reservoirs Z: Chl *a* (μg L^{-1}: μg L^{-1})	0.093	0.77	2.3	6.5	47

Table 3. Results of linear regressions of chlorophyll *a* on log$_{10}$(zooplankton biomass) from concurrent measurements made in the lower, middle, and upper regions of Falls Lake

Lake region	Slope (95% C.I.)	Intercept (95% C.I.)	R^2	p
Upper	-0.0007 (-0.006 – 0.045)	1.60 (1.27 – 1.93)	0.35	<0.001
Middle	-0.029 (-0.040 – -0.017)	2.05 (1.71 – 2.39)	0.31	<0.001
Lower	-0.044 (-0.066 – -0.021)	1.87 (1.44 – 2.30)	0.01	0.78

Table 4. Comparison of piece-wise linear vs linear models of the log-log relationship between zooplankton biomass and chlorophyll *a* from southeastern U.S. reservoirs in summer.

Model type	R^2	R^2_{adj}	AIC_c	AIC weight
Piece-wise	0.065	0.024	102.5	0.16
Linear	0.049	0.036	99.2	0.84
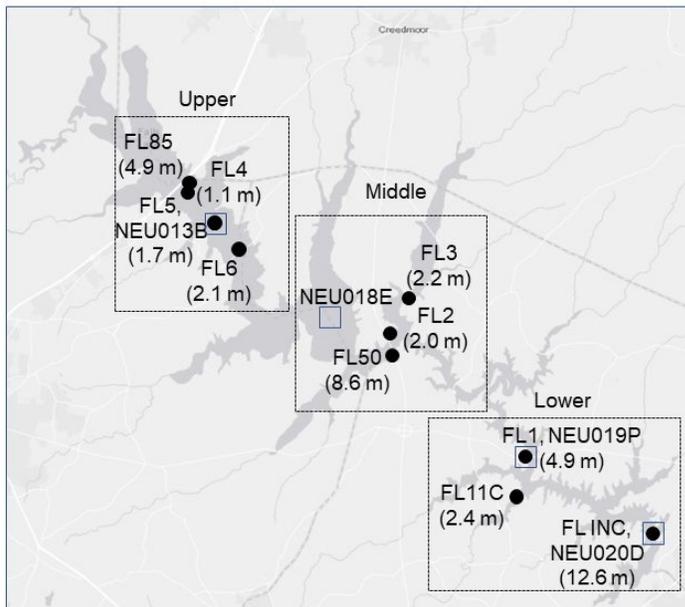
Figure 1. Map of zooplankton sampling stations (stations beginning FL), average net tow depths at those station, and NC DEQ stations where phytoplankton community composition is monitored in Falls Lake (stations beginning NEU0).
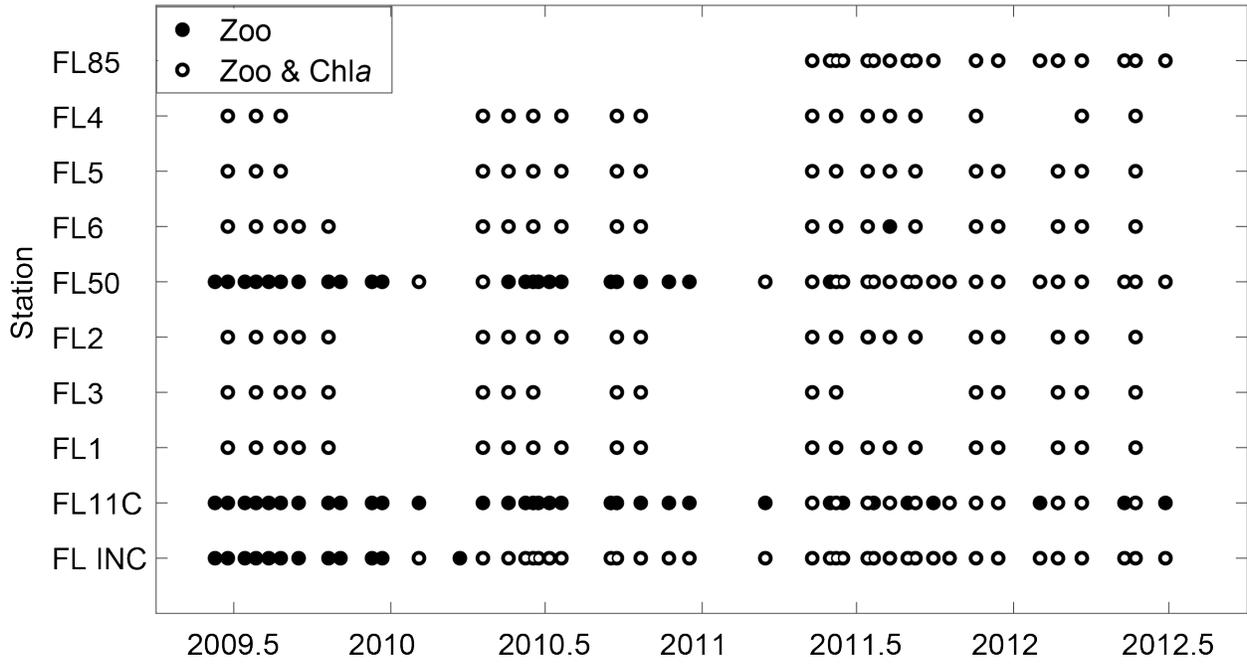
Figure 2. Timing of zooplankton and chlorophyll *a* sample collection at ten sites in Falls Lake.
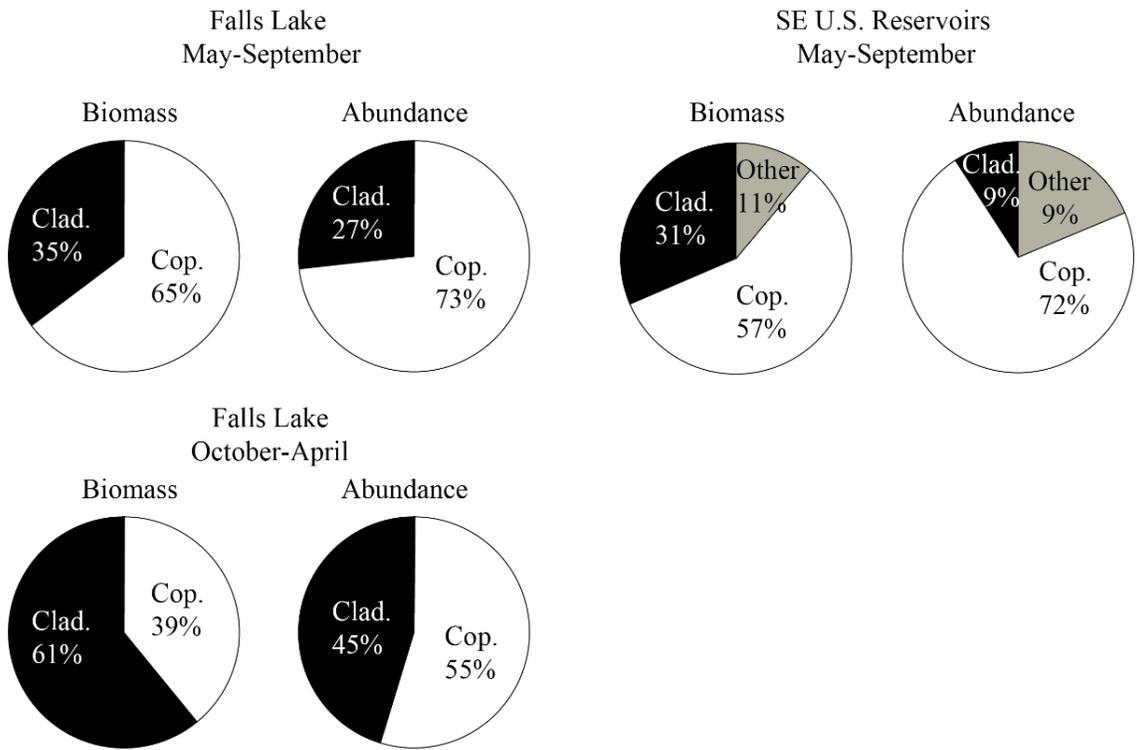
Falls Lake
May-September

Biomass

Clad. 35%
Cop. 65%

Abundance

Clad. 27%
Cop. 73%

SE U.S. Reservoirs
May-September

Biomass

Other 11%
Clad. 31%
Cop. 57%

Abundance

Clad. 9%
Other 9%
Cop. 72%

Falls Lake
October-April

Biomass

Cop. 39%
Clad. 61%

Abundance

Clad. 45%
Cop. 55%

Figure 3. Contribution of cladocerans, copepods, and other taxa to crustacean zooplankton biomass and abundance in Falls Lake and other similar reservoirs in the southeastern United States. For Falls Lake, other taxa constituted less than 1%.
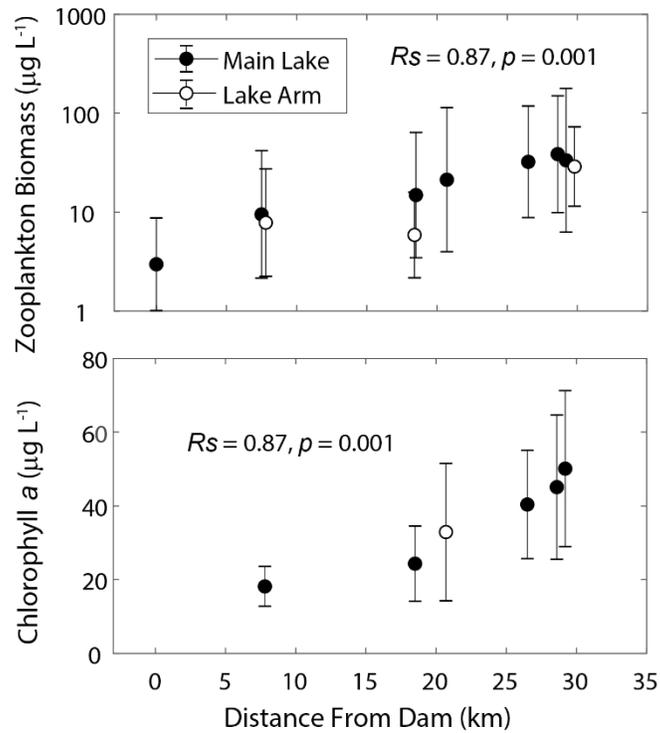
Figure 4. Spatial variability of zooplankton biomass and chlorophyll *a* in Falls Lake. Symbols and error bars represent the mean and standard deviation of log10(zooplantkon biomass) or chlorophyll a at each station during the 2009 to 2012 study period. Open symbols indicate stations located in creek arms off the main reservoir channel. *Rs* and *p* values are results from rank correlations.
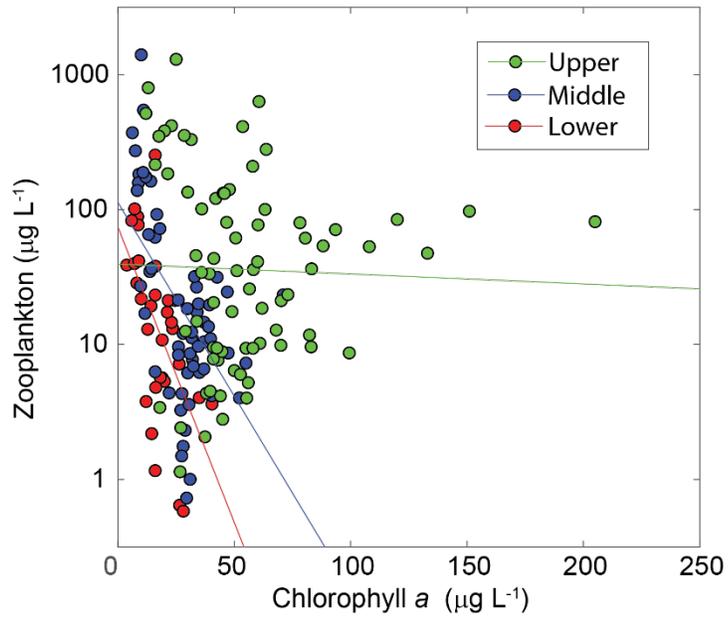
Figure 5. Log linear scatter plot of concurrent measurements of crustacean zooplankton biomass and chlorophyll *a* in the Upper, Middle and Lower regions of Falls Lake. Lines represent linear regressions with coefficients presented in Table 3.
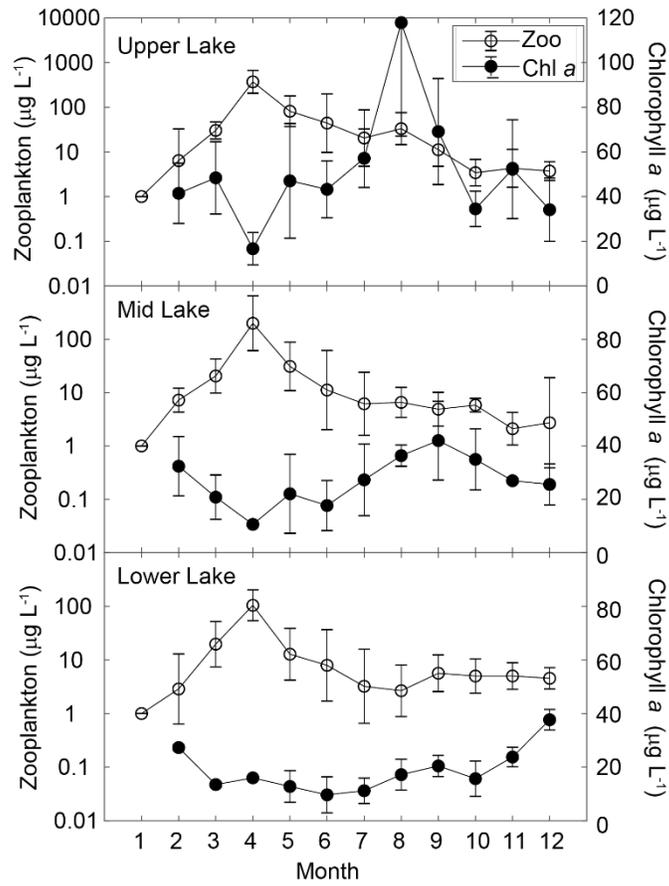
Figure 6. Seasonal variation of log$_{10}$ zooplankton biomass and chlorophyll *a* in the upper, middle, and lower regions of Falls Lake. Circles and error bars represent the mean and standard deviation of all measurements from each month.
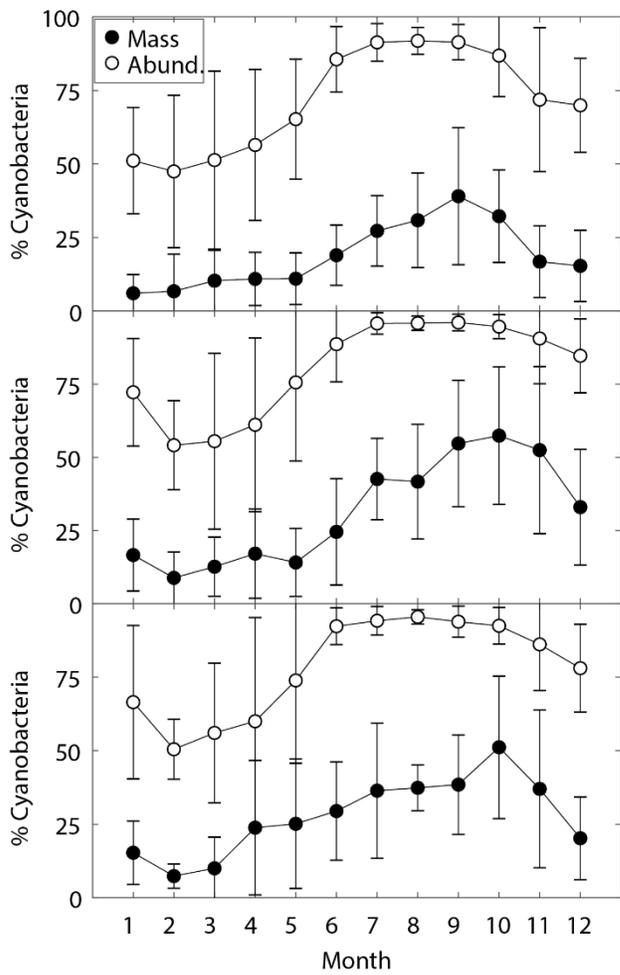
Figure 7. Seasonal variation of the fraction of total phytoplankton biomass (Mass) and cell abundance (Abund) comprised by cyanobacteria over the period 2011 to 2018. Circles and error bars represent the mean and standard deviation of all measurements from each month.
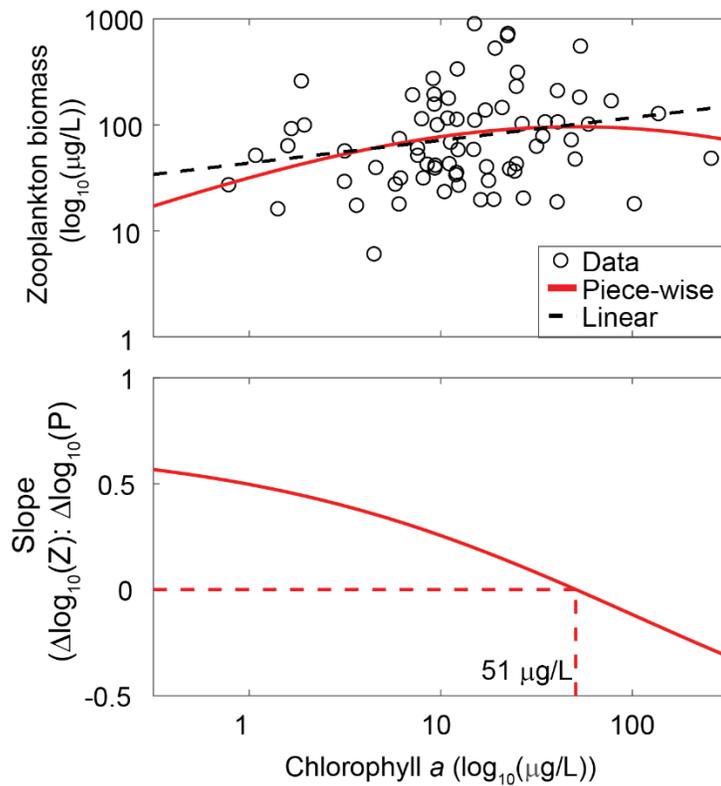
Figure 8. Relationship between summertime (May-September) zooplankton biomass and chlorophyll *a* for low elevation (<500 m), southeastern U.S. reservoirs from the U.S. EPA's 2012 National Lake Assessment dataset. Top panel shows the raw data with piece-wise and linear model fits. Bottom panel shows the derivative of the piece-wise model (solid red line) including and the chlorophyll *a* standard determined at the point where the derivative becomes negative (red dashed lines).