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RESEARCH ARTICLE

Seasonal shifts in the relative importance of local versus upstream sources of phosphorus to individual lakes in a chain

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Abstract Water quality in the Yahara chain of lakes in southern Wisconsin has been degraded significantly since European settlement of the region, primarily as a result of anthropogenic nutrient inputs. While all four main lakes (Mendota, Monona, Waubesa, and Kegonsa) have undergone eutrophication, elevated phosphorus and chlorophyll concentrations are particularly pronounced in the smaller lakes at the bottom of the chain (Waubesa and Kegonsa). Due to their short water residence times (2–3 months), these lakes are more responsive to seasonal variability in magnitude and source of phosphorus loading compared with the larger upstream lakes. In 2014, more than 80 % of the phosphorus load to Lake Waubesa passed through the outlet of Lake Monona (situated immediately upstream). However, between mid-May and late October when phosphorus concentrations in Lake Monona were reduced as a result of thermal stratification the upstream load dropped to ~40 % of the total, with the majority of loading during this period coming from Lake Waubesa's local watershed. Correspondingly, seasonal phosphorus trends in Lake Waubesa during summer are correlated with precipitation, rather than phosphorus concentrations leaving upstream lakes. While phosphorus export from the local watersheds of Lakes Waubesa and Kegonsa is relatively small on an annual time scale, targeted loading reductions in these areas during the summertime will most effectively reduce summertime phosphorus concentrations in these fast-flushing lakes. Understanding the interaction of landscape position, water residence time, and mixing regime can help guide watershed management for water quality improvements in lake chains.

Keywords Lake chain · Landscape limnology · Phosphorus · Eutrophication

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Introduction

Many regions of the world contain lake chains—lakes and rivers connected in a series of alternating lentic and lotic reaches (Jones 2010). The position of a lake within the regional flow system determines the relative importance of various hydrologic inputs to the lake (Kratz et al. 1997). The water chemistry of lakes in chains is also often related to landscape position (e.g., Kling et al. 2000; Leavitt et al. 2006; Sadro et al. 2011). In general, downstream lakes in lake chains have been observed to contain greater amounts of nutrients and chlorophyll, higher levels of conductivity and acid neutralizing capacity, and lower clarity (Soranno et al. 1999; Riera et al. 2000).

Efforts to understand lake chains often focus on identifying longitudinal patterns and temporal coherence among lakes (i.e., synchrony). From a management perspective, however, understanding the drivers of spatial heterogeneity in these systems is an equally important goal (Steinman and Denning 2006). Studies of lake chains have indicated that in contrast with conservative solutes such as calcium or magnesium, those influenced by in-lake processes tend to exhibit the lowest degree of synchrony (Webster et al. 2000; Kling et al. 2000). Constituents influenced by in-lake processes include those most relevant to management of eutrophication in fresh water systems, such as phosphorus and chlorophyll.

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Water residence time is a major factor controlling nutrient residence time, and in turn nutrient concentrations, in lakes. In lakes with water residence times of greater than 1 year, water column concentrations are influenced by at least the full annual cycle of hydrologic and nutrient loading. In lakes with water residence times of only a few months, however, water column concentrations during certain times of the year may not be linked to loading at other times. It has been observed that as systems, lakes in chains exhibit the highest degree of synchrony when water residence times are short (Soranno et al. 1999). Greater water residence time has also been associated with a lower degree of allochthony within a chain (Queimaliños et al. 2012). In lake chains containing lakes with significant variability in water residence times among lakes there may be corresponding in-chain variability in the connectivity of each lake to local watersheds (and conversely, to the upstream river system).

In general, the biogeochemistry of lakes in series is more closely related to landscape position and catchment characteristics than it is to lake morphometry (Kling et al. 2000; Sadro et al. 2011). Nonetheless, the influence a lake has on the chemistry of an outflowing river is dependent on, among other factors, lake size and shape (Jones 2010). In particular, thermal stratification, which is largely a function of lake morphometry, plays a pronounced role in seasonal nutrient cycling within lakes (and consequently, in their outflows). During the stratified period, phosphorus settling tends to lead to a buildup of phosphorus in the hypolimnion, accompanied by a seasonal decrease in epilimnetic P concentrations (Vollenweider 1969; Chapra 1975; Sonzogni et al. 1976); much of this temporarily sequestered phosphorus is recirculated throughout the lake following fall mixis. It follows that the phosphorus concentrations in the outflows of dimictic lakes, which typically contain epilimetic water, follow this same seasonal trend. Because this strong seasonal P sink is not present in mono- or polymictic lakes, transitions between deep and shallow lakes (or vice versa) in a chain of lakes may result in discontinuities along the chain.

The Yahara chain of lakes—Mendota, Monona, Waubesa, and Kegonsa—near Madison, Wisconsin (Fig. 1a) have undergone dramatic cultural eutrophication since the mid-1800s (Lathrop 2007). Initial declines in water quality were driven largely by sewage and wastewater effluent discharges, while ongoing elevated phosphorus levels can be attributed primarily to non-point source nutrient inputs. Very high levels of productivity and blue-green algal blooms are common (Lathrop 2007; Lathrop et al. 1998). The lower two lakes in the chain (Waubesa and Kegonsa) are polymictic and have short water residence times (2–3 months), and typically exhibit the poorest water quality in the system (Table 1). In contrast, the upper two lakes in the chain (Mendota and Monona) have longer water residence times, and lower levels of phosphorus and chlorophyll in the surface waters during the summer (Table 1). While there exists an extensive history of limnological research in the Yahara lakes (Magnuson 2002), these efforts have been mainly focused on Lakes Mendota and Monona, and the factors driving the considerably poorer water quality downstream are not yet fully understood.

It is commonly assumed that due to their shallow depth, rapid recycling of phosphorus in Lakes Waubesa and Kegonsa is responsible for maintaining the high surface concentrations. Lathrop (2007) found low and constant concentrations of phosphorus in sediment cores from the lower lakes, and noted that low iron availability may be a factor in reduced phosphorus retention. Phosphorus concentrations appear to be sufficient to regularly induce seasonal nitrogen limitation in the system; measurable soluble reactive phosphorus (SRP) in conjunction with non-detectable levels of dissolved inorganic nitrogen (DIN) is common during the late summer in the lower lakes (Lathrop and Carpenter 2013; Lathrop 2007), and low DIN:DIP has been implicated in nitrogen-limited cyanobacterial blooms in Lake Mendota during the late summer (Beversdorf et al. 2013).

Recent modeling and data synthesis efforts have characterized phosphorus loading to the Yahara Lakes using annual time steps (Carpenter and Lathrop 2013; Lathrop and Carpenter 2013), and have concluded that the upper lakes will respond more quickly to reductions in non-point source phosphorus loading while the lower lakes are expected to exhibit muted responses to management efforts (Carpenter and Lathrop 2013). The lower lakes receive the bulk of their annual phosphorus loading from the upstream lakes (i.e., through the Yahara River); 83 % for Waubesa and 76 % for Kegonsa (Lathrop and Carpenter 2013). At the same time, Lakes Mendota and Monona have relatively low phosphorus pass-through factors (27 and 59 %), as compared with 94 % in Lake Waubesa and 78 % in Lake Kegonsa (Lathrop and Carpenter 2013). The higher pass-through factors in the lower lakes are consistent with the observed low phosphorus retention in their sediments (Lathrop 2007). The implication for management strategies is phosphorus export from Lake Mendota's watershed must be reduced in order for phosphorus loading to Lakes Waubesa and Kegonsa to be significantly reduced. Unfortunately, however, the lower pass-through factors of the upper lakes also imply that the benefit of such reductions will be significantly attenuated in downstream lakes. For example, a loading reduction of 1 kg P to Lake Mendota might only result in a $1 \times 0.27 \times 0.59 \times 0.94 = 0.15$ kg P corresponding reduction to Lake Kegonsa.

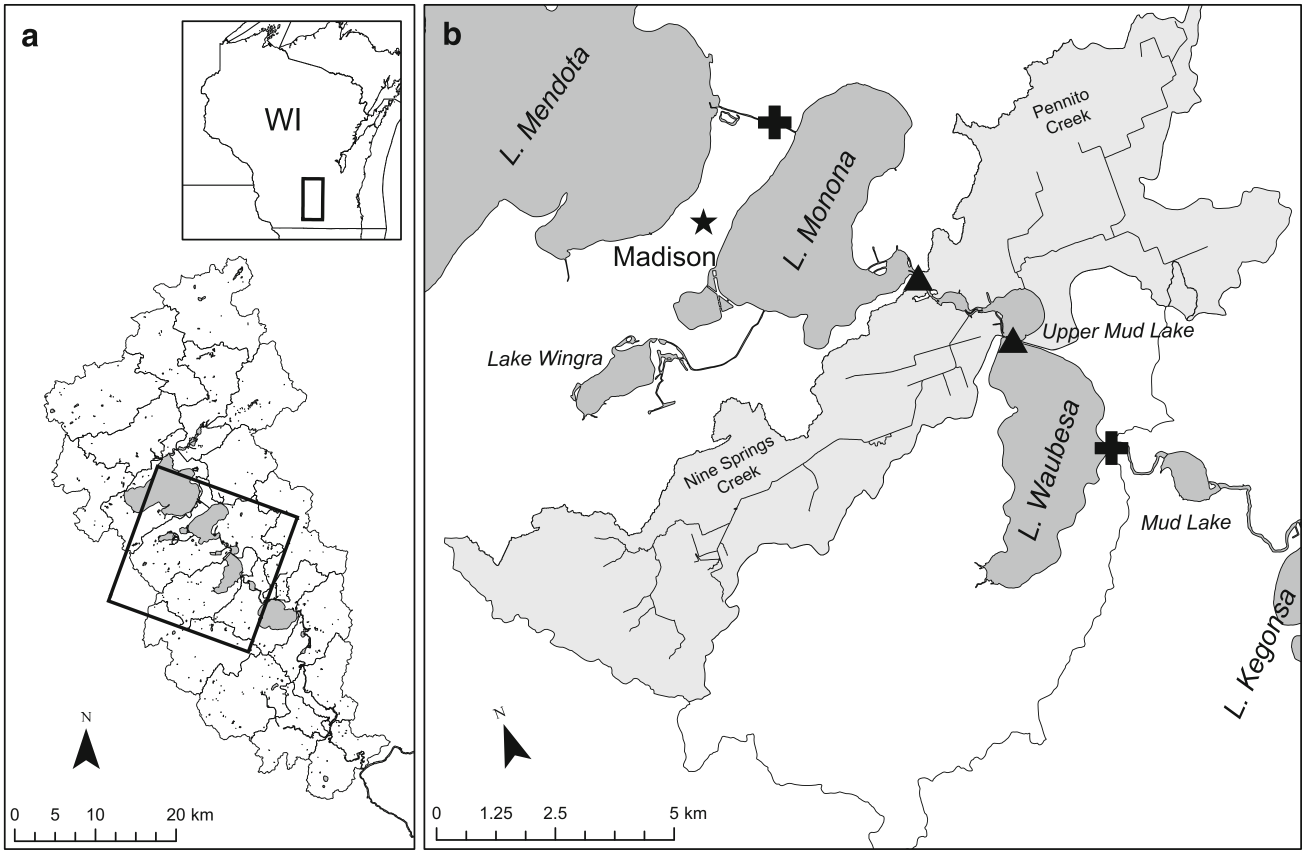

Fig. 1 Yahara River Watershed (**a**) and Lake Waubesa watershed (**b**). Sampling locations are indicated by *triangles*, upstream and downstream USGS gaging stations are indicated by *crosses*. The *shaded area* in (**b**) indicates the direct drainage area contributing to the total load at the inlet to Lake Waubesa (Nine Springs Creek to the west and Pennito Creek to the east)

Table 1 Characteristics of the Yahara Lakes

Lake	Area (km^2)	Volume (10^6 m^3)	Max. depth (m)	Mean depth (m)	Water residence time (year)	Total Phosphorus ($\mu g\ L^{-1}$)[a]	Chlorophyll *a* ($\mu g\ L^{-1}$)[a]
Mendota	39.9	505	25.3	12.7	4.3	56	8.7
Monona	13.3	110	22.6	8.3	1.3	51	10.8
Waubesa	8.4	40	11.6	4.7	0.23	68	15.8
Kegonsa	13.0	67	9.8	5.1	0.33	79	17.6

[a] May–September surface mean, 1995–2014, calculated from NTL-LTER data

Surface phosphorus concentrations follow distinctly different seasonal trajectories in the two downstream lakes (Waubesa and Kegonsa) than in the upstream lakes (Mendota and Monona) (Fig. 2a). Concentrations tend to decrease throughout the growing season in Mendota and Monona before increasing following fall mixis, typical behavior for large stratified lakes. Concentrations in Waubesa and Kegona, on the other hand, peak in mid-summer. Given the short residence time of Lake Waubesa, and the fact that most of the inflow to the lake comes from Lake Monona, it is surprising that seasonal trends in phosphorus are so different in these two adjacent lakes. The seasonal trend of surface TP in Lakes Waubesa and Kegonsa closely mimics the seasonal trend in precipitation (Fig. 2b), with a time lag of about 1 month, suggesting that these lakes are actually closely linked to their watersheds (i.e., watershed inputs represent a major source of phosphorus to the lake) during this period.

We hypothesize that the shorter water residence time of Lakes Waubesa and Kegonsa, coupled with the transition from dimictic Lake Monona to polymictic Lake Waubesa, are important factors controlling seasonal variability in phosphorus sources to the lakes, producing the discontinuity illustrated in Fig. 2. To explore this hypothesis, we

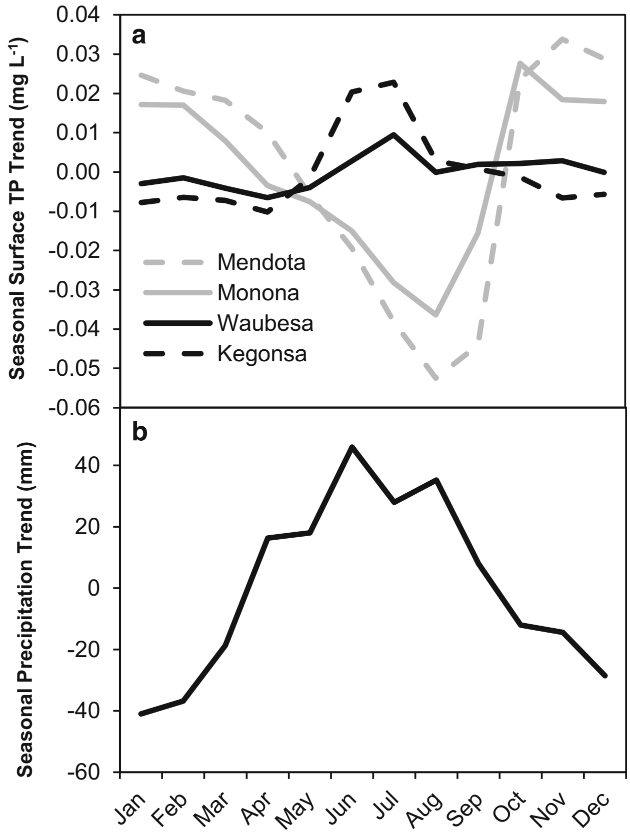

Fig. 2 Seasonal trends in TP in the Yahara Lakes (**a**), and precipitation (**b**), 1980–2015, as determined by time-series decomposition (see "Methods")

examined the seasonal progressions of phosphorus export from Lake Monona and loading from Lake Waubesa's local watershed. Our findings have important implications for identifying effective management strategies to improve water quality in the Yahara chain of lakes, and more broadly to the management of any physically dissimilar lakes in series.

Methods

Study site

The Yahara River watershed (930 km^2) is located in south-central Wisconsin, and is situated primarily in Dane County (Fig. 1a). The river flows south to the Rock River, a tributary of the Mississippi. Lake Mendota's basin comprises a majority of the watershed and is primarily agricultural. The city of Madison is situation between Lakes Mendota and Monona, and Lake Monona's watershed is a mixture of urban and agricultural land uses. The areas of direct drainage to Lakes Waubesa and Kegonsa, as well as the region below Lake Kegonsa, are predominantly agricultural. Characteristics of the lakes and their associated watersheds are summarized in Tables 1 and 2.

In this study, we differentiate between "upstream" and "local" sources of phosphorus, where upstream is defined as the watershed above the Lake Monona outlet, and local is defined as the subwatersheds below Lake Monona that drain to Lake Waubesa. Sampling was performed at a site on the Yahara River just downstream of Lake Monona; this was considered to fully capture the upstream component. Sampling was also performed where the Yahara River enters Lake Waubesa. This reach of the Yahara River receives drainage from the Nine Springs Creek watershed to the west and the Pennito Creek watershed to the east; these two watersheds combined comprise approximately 50 % of the total local drainage area to Lake Waubesa (Table 2). Just upstream of Lake Waubesa lies Upper Mud Lake, a small, shallow embayment created by a railroad crossing in the mid-1800s (Fig. 1b). A large wetland complex is situated at the bottom of the Nine Springs Creek watershed (Owen 1995, 1998), and Upper Mud Lake and the river are surrounded by fringing wetlands. Nine Springs Creek discharges directly into the river, while Pennito Creek discharges into the northeast corner of Upper Mud Lake.

Sample collection and analysis

Samples were collected on 10 dates between late January and late October 2014. Samples at the downstream site were collected from a railroad trestle bridge spanning the river, consisting of four main piers creating three channels. On 2 May, evidence of incomplete mixing in the outflow was first observed at the railroad trestle bridge, and confirmed with in situ measurements of conductivity, pH, and dissolved oxygen. Each channel was sampled individually on this date and subsequently. The flow in the eastern channel represents primarily outflow from Upper Mud Lake, while the center and western channels are typically Yahara River flow. While there is some mixing between upper Mud Lake and the river along the entire western side of Upper Mud Lake (Fig. 1b), it appears to be minimal; navigational dredging of the river channel maintains higher flows through this portion of the system while dense macrophyte growth helps to maintain relatively stagnant conditions in the lake basin. Samples were retrieved from 0.5-m below the surface using a Kemmerer bottle. A subsample for total phosphorus (TP), acidified with sulfuric acid and an unpreserved subsample for orthophosphate were transported on ice to the Wisconsin State Lab of Hygiene (Madison, WI, USA) within 24 h for analysis. Total phosphorus (TP) was determined according to EPA method 365.1 on a Beckman DU-650 spectrophotometer.

Table 2 Watershed characteristics of the Yahara Lakes and tributaries included in this study

	Area (km^2)	Developed (%)	Forested (%)	Agricultural (%)	Wetlands (%)
Lake Mendota	604	19.9	4.5	63.9	3.5
Lake Monona	117	61.9	4.5	16.3	2.9
Lake Waubesa	116	33.9	11.0	37.5	8.4
Lake Kegonsa	160	15.3	7.3	59.8	6.6
Nine Springs Creek	32	51.0	12.7	25.9	9.1
Pennito Creek	22	52.8	9.3	30.1	7.0

Flow and load estimation

Daily TP loads were calculated for each sampling location and date as a simple product of estimated flow and measured concentration. Flows were estimated daily at the two sampling stations based on measured flows at USGS gages above and below our study area, between Mendota and Monona and at the outflow of Lake Waubesa, respectively (Fig. 1b). Interpolation of flow at the two sampling stations was performed based on available, fine-scale statewide streamflow modeling (Diebel et al. 2013). Modeled flows indicate that flow at the outlet of Lake Monona is equivalent to, on average, 48 % (range 43–52 %) of the flow gained between the gaging stations, and the inlet of Lake Waubesa is equivalent to 75 % (range 72–77 %) of the flow gained between the gaging stations. The estimated flow at the Lake Waubesa inlet (trestle bridge) was then divided between the three channels proportional to cross-sectional area as estimated based on a 2004 survey completed by the Dane County Land and Conservation Division. The east and west channels each contain approximately 21 % of the flow, while the remaining 58 % passes through the center channel.

Extrapolation of calculated phosphorus loads from sampling dates to the annual scale was performed differently at each station. Because phosphorus concentrations in outflow from Lake Monona reflect the surface water in the lake they are not significantly correlated with flowrates. Concentrations between sampling dates at this location were therefore estimated by linear interpolation. These interpolated concentrations were then multiplied by daily flow rates to arrive at load estimates. At the Lake Waubesa inflow, however, loads are influenced by the local watersheds (Nine Springs Creek and Pennito Creek); calculated loads were observed to be correlated with flow rate. A log-linear regression was developed to relate the estimated increase in flow between Lake Monona and Lake Waubesa (a proxy of tributary direct runoff inputs) and the concurrent increase in calculated loads between these sites ($R^2 = 0.88$; Fig. 3). The model was then used to extrapolate to daily loads over the entire year using daily flow data.

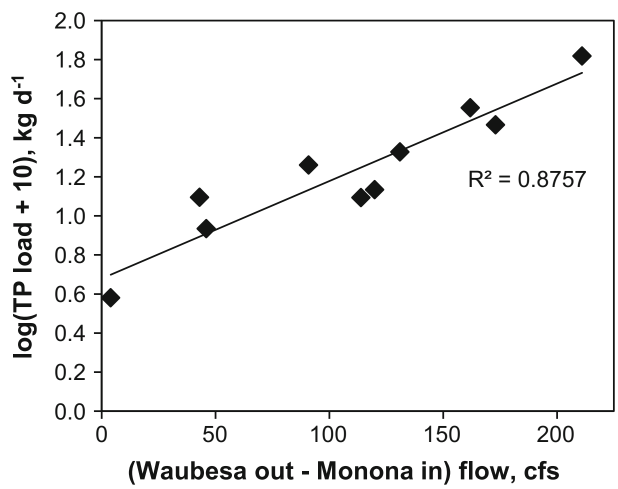

Fig. 3 Modeled relationship between the difference in modeled flows at gages and increase in calculated load between sampling stations

Lake and climate data

Surface phosphorus concentrations in the deepest part of all four lakes are routinely measured by the North Temperate Lakes Long-Term Ecological Research project at the University of Wisconsin-Madison (http://lter.limnology.wisc.edu). Data were retrieved for the period 1995–2014. Precipitation data for Madison, Wisconsin for this time period were also retrieved from the National Climatic Data Center (http://www.ncdc.noaa.gov). Observations were binned by month and time series were decomposed by LOESS using R (v.2.14) to extract the seasonal components of each signal (Fig. 2).

Results

Inlet/outlet phosphorus concentrations and flows

Total phosphorus concentrations in the outflow from Lake Monona (upstream) were highest during the late fall and winter (January, March, and October), approximately 0.06 mg L^{-1} (Table 3). Concentrations dropped coincident with ice-out, which occurred on 10 April (Wisconsin State

Table 3 Measured concentrations and interpolated flows at sampling sites

	24 Jan	6 Mar	9 Apr	2 May	29 May	25 Jun	23 Jul	27 Aug	26 Sep	30 Oct
TP (μg L^{-1})										
Monona out	63	57	25	47	38	43	46	30	30	65
Waubesa in	54[a]	59[a]	47[a]	46[a]	67	114	60	66	34	54
Measured flow (cfs)										
Mendota out	111	130	60	251	187	131	104	50	83	232
Waubesa out	157	173	151	365	349	342	235	223	203	236
Estimated flow (cfs)										
Monona out	133	151	104	306	265	232	167	133	141	234
Waubesa in	146	162	128	337	309	289	202	180	173	235

TP values presented at the Waubesa inlet are volumetrically weighted means (see text), unless otherwise noted

[a] Value from a single sample collected on the east side of the channel

Climatology Office, http://www.aos.wisc.edu/), and then rebounded in early May. From May to September there was a fairly consistent decline to around 0.03 mg L^{-1}, followed by a greater than twofold increase following fall mixis in October.

Total phosphorus concentrations in the Yahara River at the inlet to Lake Waubesa (upstream + Nine Springs Creek/Pennito Creek) were comparable to or slightly less than concentrations in the outflow from Lake Monona in January, March, early May, September, and October. However, in April and late May through August TP concentrations increased substantially (170–300 %) between the two stations. TP concentrations at the inflow to Lake Waubesa did not exhibit the same seasonal trend as was observed in the outflow from Lake Monona. Rather, they were correlated with precipitation, with the highest concentrations coinciding with wet periods in June and August (Table 3).

Recorded flows at the outflows of Lakes Mendota and Waubesa spanned a broad range of hydrologic conditions; 50–251 cfs for the former and 151–365 cfs for the latter (Table 3). The flow gained between these two stations was also highly variable, ranging from 2 to 350 %. Modeled flows at the outflow of Lake Monona and the inflow to Lake Waubesa ranged from 104–306 cfs to 128–337 cfs, respectively. The flow gained between these two stations ranged from less than 1 % to more than 35 %.

Estimated total phosphorus loads

There was considerable variability in calculated loads, both across sampling dates and between sampling sites (Fig. 4; Table 3). Loads were similar between the two locations during winter, early May, and following turnover (October), suggesting little net P was added to the system from the Nine Springs Creek and Pennito Creek watersheds and Upper Mud Lake (the travel time between the two sites is typically less than 1 day). In some cases the system actually appeared to be functioning as a net P sink, with lower loads estimated at the Lake Waubesa inlet than at the Monona outlet on 24 January and 30 October. However, in April and from late May through September, TP loads were substantially greater at the downstream station. On 25 June and 27 August (wet periods), the load entering Lake Waubesa was more than double the load leaving Lake Monona (Fig. 4).

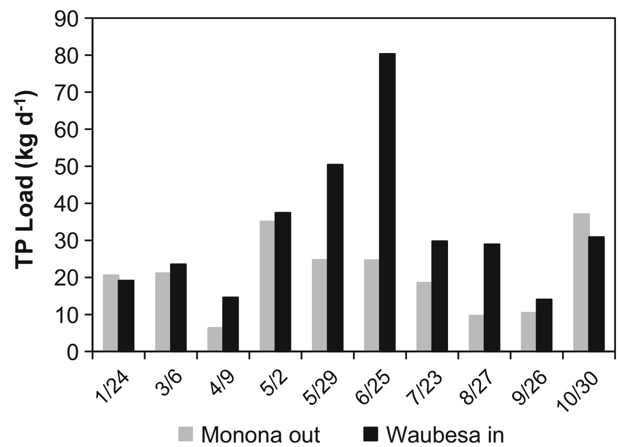

Fig. 4 Calculated TP loads below Lake Monona (upstream) and at the inlet to Lake Waubesa. The difference represents inputs from Nine Springs Creek and Pennito Creek plus direct drainage (~50 % of Waubesa's local watershed). From May through September considerable increases were observed between the two stations

Upstream sources (i.e., the outflow from Lake Monona) comprised the majority of loading at the inlet to Lake Waubesa on an annual scale, representing 72 % of the year's load (Fig. 5). This upstream source dominates the total load prior to stratification (May) and following turnover (October), during which time it actually represents 92 % of the total. However, during the summer stratified period, loading to the system from local watersheds is comparable to or greater than upstream loading,

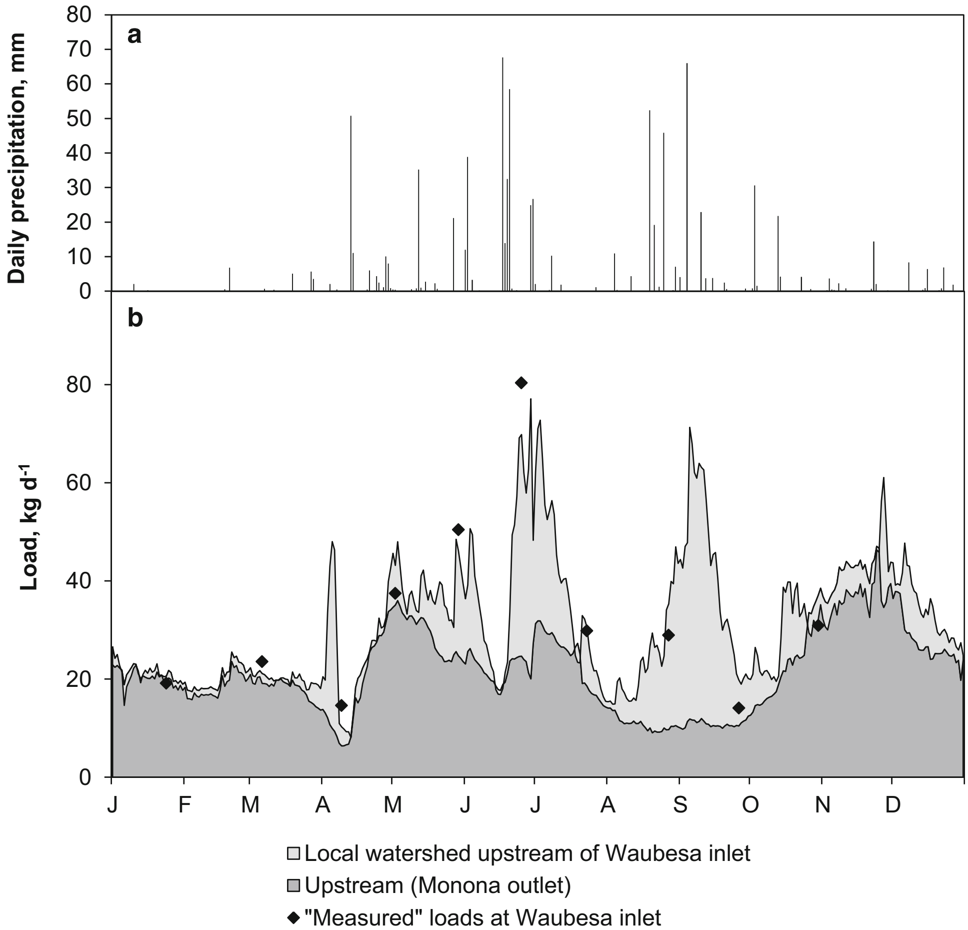

Fig. 5 Daily precipitation (**a**) and extrapolated TP loads for 2014 (**b**). The *plot* in **b** is stacked, so that the *top* of the *lightly shaded area* represents the total load at the lake Waubesa inlet; *symbols* represent loads calculated at this location on sampling dates, and correspond to the *black bars* in Fig. 2

particularly during the wet period in June/July and in late summer/early fall (August–October). Between 1 May and 15 October, the upstream load only represents 55 % of the load at the Lake Waubesa inlet.

In-lake phosphorus concentrations

Historically, phosphorus concentrations in Lake Waubesa track well with those in Lake Monona in the winter, but diverge during the summer, when they follow opposite trajectories (Fig. 2). Measurements made in the lakes during the summer of 2014 were consistent with this historical trend. Beginning in May, TP concentrations in Lake Monona (and therefore its outflow) began to decrease and remained low until fall turnover (Fig. 6; Table 3). In contrast, TP in Lake Waubesa increased from ice-out through July (Fig. 6).

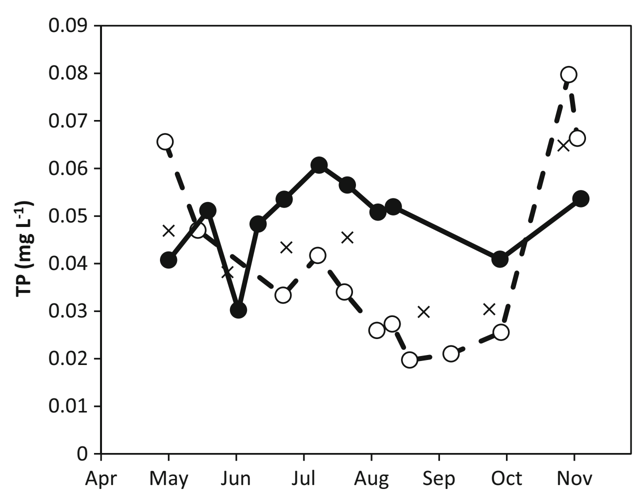

Fig. 6 Surface TP measured at the deepest part of Lake Waubesa (*filled circles*) and Lake Monona (*open circles*), and in the outflow of Lake Monona (×) during 2014

Discussion

Given the short water residence time in Lake Waubesa, it would be expected that seasonal trends in phosphorus concentrations in the lake would track those in the outflow of Lake Monona if upstream loads were dominant. As demonstrated by both historical and recent data (Figs. 2, 6), however, phosphorus concentrations generally continue to increase in Lake Waubesa for several months during the summer while concentrations in the outflow from Lake Monona are decreasing. This suggests significant additional loading to Lake Waubesa occurs during this period, from either internal or external sources.

Internal phosphorus loading is common in shallow, polymictic systems (Søndergaard et al. 2003; Nürnberg and LaZerte 2016; Orihel et al. 2015), and likely occurs in Lake Waubesa (and likewise, in Lake Kegonsa). Internal loading may indeed be an important factor in controlling water quality in the lower Yahara lakes. Turnover following intermittent stratification has been shown to deliver bioavailable phosphorus to the photic zone during periods of low nutrient availability, leading to increased productivity and cyanobacterial blooms (e.g., Orihel et al. 2015). However, considering the external loads estimated in this study, it is clear that internal loading alone cannot explain the timing or magnitude of the summertime increase in total phosphorus in this system. A simple mass-balance calculation, treating TP as conservative, suggests that given the estimated flows and loads for 2014 (Fig. 5) surface TP concentrations in Lake Waubesa would be between 0.06 and 0.09 $\mu g\ L^{-1}$ by late summer, greater than the approximately 0.045 $\mu g\ L^{-1}$ observed (Fig. 6). In other words, external loading is more than sufficient to explain observed TP concentrations, and in fact the lake is acting as a net sink for P during the summer. In other words, net settling is greater than internal and external loads combined.

The relative magnitude of phosphorus loads to Lake Waubesa from upstream and local watersheds varies considerably throughout the year, and there is a clear distinction between fall and winter when the majority of TP loading to Lake Waubesa is originating from upstream sources and the spring and summer when a large fraction of loading is also from local sources (Fig. 5).

Between May and August, TP concentrations at the inlet to Lake Waubesa are approximately double those at the outlet of Lake Monona due to loading from the Nine Springs Creek and Pennito Creek watersheds. The Nine Springs Creek and Pennito Creek watersheds represent only approximately half of the direct drainage area to Lake Waubesa (Table 1), and SWAT modeling conducted in the watershed has suggested that these two watersheds represent approximately 60 % of the annual TP loading to Lake Waubesa (The Cadmus Group 2011). It is clear that if the entire local watershed is considered local loads would dominate the total during this period, on the order of 60 % of the total. It is worth noting, however, that upstream loading still comprises the majority of loading at the Lake Waubesa inlet during periods of low flow in summer (Fig. 5). Thus, comparatively few high flow events may have a large impact on overall phosphorus budgets. This has also been observed to be the case in Lake Mendota, where nearly three-quarters of the annual load is delivered, on average, over only 29 days (Carpenter et al. 2015).

Viewed as summertime averages, TP and chlorophyll data exhibit a steadily increasing pattern with lake position that might be expected to result from the effects of increasing catchment area and processing of materials along the chain (Kling et al. 2000; Sadro et al. 2011). Analysis of seasonal patterns, however, reveals a distinct discontinuity between the upper two and lower two lakes during the summer months (Fig. 2). This leads to the general observation that the degree of synchrony between lakes in chains can vary over time, or as a function of the time scale on which it is assessed. The discontinuity is the result of two simultaneous phenomena: (1) net TP settling reduces concentrations in the surface waters of the upstream stratified lakes during the summer, resulting in reduced downstream delivery during this time, and (2) the downstream lakes respond more strongly to seasonal variability in loading due to a combination of their short water residence times and lack of stratification. It has been recognized that flushing rates are important factors when assessing system-scale dynamics in lake chains (Soranno et al. 1999); this study provides evidence that thermal dynamics can play a key role as well.

Implications for management

The seasonal variability in the importance of upstream and local sources of phosphorus documented here is critical to understanding how proposed efforts to control phosphorus export throughout the watershed will affect phosphorus concentrations in the lakes. While TP loading from the upstream lakes dominates the *annual* loading to Lake Waubesa (Fig. 5), reductions in upstream loads will be expressed primarily as reductions in loading to this system during the fall and winter months. Given the fast flushing rate of the lake, reductions in fall and winter loading will likely have little effect on the summertime water quality of the lake.

Reducing phosphorus loading from local watersheds, which make up approximately 60 % of the total load to the lake between May and October, will most efficiently reduce the TP load to Lake Waubesa during this time period. TP loads from the upstream lakes represent approximately 40 % of the summertime total load, which is still a considerable portion. However, given that (on an annual time scale) Mendota and Monona retain 73 and 41 % of P inputs, respectively (Lathrop and Carpenter 2013), upstream load reductions will be significantly attenuated moving further downstream, with a corresponding reduction in potential water quality improvement.

Summertime TP and chlorophyll concentrations in Lake Kegonsa are typically the greatest in the chain (Table 1).

Because it is hydrologically similar to Lake Waubesa, we can infer that Lake Kegonsa similarly receives a large pass-through load of phosphorus during the fall and winter from upstream lakes, and is strongly connected to its watershed during the summer months. This is corroborated by the similarities in seasonal TP trends in these two lakes (Fig. 2). In contrast with Waubesa, however, Kegonsa is not situated directly downstream from a stratified system and therefore does not receive the relatively low-P river water during the summer, but rather receives the high-P outflow from Lake Waubesa. The significance of local loading, relative to total summertime loading may be somewhat diminished in Kegonsa as compared with Waubesa. Nonetheless, the greater summertime TP concentrations in rapidly-flushing Kegonsa must again be attributed to local loads, either internal or external—and the morphometric and hydrologic similarity of these two lakes would suggest it likely acts as a seasonal net P sink. While reductions in TP loading to Kegonsa will likely reduce summertime concentrations in the lake more dramatically than annual modeling has predicted (Carpenter and Lathrop 2013), reductions in TP loading to Waubesa from its local watershed should be of significant benefit to both of the lower lakes; these watersheds may therefore be an ideal location to focus management efforts.

In this system, annual modeling has indicated that major reductions in loading the upstream lakes will be required in order to significantly improve water quality in the lower lakes, and that loading reductions in the lower part of the watershed will have the greatest impact on downstream export; a balanced approach to load reduction between upstream and downstream watersheds has therefore been recommended (Lathrop and Carpenter 2013; Carpenter and Lathrop 2013). The findings of this study support that recommendation, but the additional insight gained through the seasonal analysis presented here further suggests that this course of action will lead to a more rapid recovery of Lakes Waubesa and Kegonsa than is currently anticipated.

In addition to landscape position and system-wide properties of lakes (Soranno et al. 1999), we suggest that *transitions* between (a) stratified and unstratified lakes and (b) long and short water residence times play a critical role in defining the system-scale dynamics of lake chains. These transitions should be taken into account specifically when targeting non-point source nutrient loading reductions to chain of lakes. It is possible to identify a unique management-relevant timescale, defined as the period during which nutrient loading has the greatest impact on growing-season water quality, for each lake (or group of lakes) and prioritize management strategies accordingly.

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