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Summer water clarity responses to phosphorus, *Daphnia* grazing, and internal mixing in Lake Mendota

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Abstract

Linear models were developed for predicting mean Secchi disk depth readings as a measure of water clarity for the summer months in Lake Mendota, Wisconsin. The 20-yr (1976–1995) data set also included external phosphorus (P) loadings and in-lake April P concentrations as indices of lake nutrient status, and monthly (28 d) water column stabilities and *Daphnia* biomasses as indices of lake mixing and algal grazing potentials, respectively. June Secchi depths were mostly controlled by food web dynamics, which dictated whether the larger-bodied *Daphnia pulicaria* or the smaller-bodied *D. galeata mendotae* dominated during the spring clear-water phase. May *Daphnia* biomasses were significantly greater in *D. pulicaria*-dominated years than in *D. galeata*-dominated years; *D. pulicaria*-year biomasses were also greater during the summer months. The model for the midsummer (July–August) months indicated that Secchi depths were inversely related to April P concentrations and positively related to midsummer *Daphnia* biomasses and lake stabilities. Scenarios for midsummer Secchi depths were tested using the observed minimum and maximum values for each predictor variate. While holding two variates constant, April P, *Daphnia* biomass, and lake stability each resulted in relatively similar Secchi ranges (0.81, 0.81, and 1.17 m, respectively). Our results suggest that summer water clarity in eutrophic Lake Mendota is controlled by interacting ecosystem processes linked to land use activities, lake food web dynamics, and climate.

Excessive phosphorus (P) input to lakes clearly leads to eutrophication, especially affecting summer blue-green algal blooms (Vollenweider 1968; Schindler 1977; Sas 1989). Eutrophication models have linked P loading rates to in-lake P concentrations (Dillon and Rigler 1974b; Vollenweider 1976), which have been used to predict summer algal densities (Dillon and Rigler 1974a; Jones and Bachmann 1976). Although a lake's average P loading can give insights into its trophic status, such an analysis cannot explain the large interannual variability in summer algal densities that is often observed in eutrophic lakes. Factors such as internal P loading and food web dynamics are potential explanations.

In large stratified eutrophic lakes, internal loading supplies much more P to epilimnetic waters during the summer than is delivered from external sources (Stauffer and Lee 1973; Larsen et al. 1981; Effler et al. 1986; Soranno et al. 1997).

Acknowledgments

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Although internal P loading rates may be a function of the history of external P loadings, internal loadings are also mediated by weather. Thus, in a given summer water column stability and the frequency of major wind events control how much P is entrained from the metalimnion and hypolimnion to surface waters. In Lake Mendota, Soranno et al. (1997) showed that P entrainment was highly variable between summers not only because of differences in mixing potential (stability and storm frequency) but also because of differences in the nutrient loading potential (metalimnetic P concentrations). Consequently, interannual variability in algal blooms or water clarity can partly be attributed to interannual variability in internal P loading rates.

Another factor that could cause differences in algal densities between summers is variable grazing rates by *Daphnia* spp. Although the abundance and size structure of *Daphnia* populations clearly are controlled by planktivorous fish (Brooks and Dodson 1965; Shapiro and Wright 1984; Carpenter and Kitchell 1993; Rudstam et al. 1993), it is not clear whether *Daphnia* grazing can control dense growths of blue-green algae in eutrophic lakes where nutrient supply rates are high (McQueen et al. 1986; Benndorf 1990; Elser and Goldman 1991; Reynolds 1994). However, Carpenter et al. (1995, 1996) found that increased piscivory in a nutrient-enriched lake can cause substantially lower summer algal densities than predicted from traditional lake loading models. In Lake Mendota, Lathrop et al. (1996) found that sum-

mer water clarity was significantly greater in years when the larger-bodied *D. pulicaria* dominated during the spring clear-water phase than when the smaller-bodied *D. galeata mendotae* dominated. This difference in clarity may be because *D. pulicaria* can significantly reduce overall summer algal densities, even when the algal community is dominated by filamentous blue-green species (Epp 1996; Kasprzak and Lathrop 1997).

The long-term data that are available for Lake Mendota provide an excellent opportunity to determine the relative importance of P supply rates, lake mixing, and *Daphnia* grazing on summer water clarity in a large stratified eutrophic lake. External P loadings and spring turnover P concentrations, which are an index of overall P supply rates (external and internal), have varied considerably in recent years (Lathrop 1998; Lathrop et al. 1998). *Daphnia* densities and biomasses have also varied considerably (Lathrop and Carpenter 1992b; Rudstam et al. 1993; Lathrop 1998) because of varying planktivory rates (Rudstam et al. 1993; Johnson and Kitchell 1996). Regional climate effects have caused subtle but potentially important differences in lake temperatures among summers (Robertson and Ragotzkie 1990). As a result, summer water clarity as a measure of algal densities has also varied (Lathrop et al. 1996; Lathrop 1998). This natural variability in both predictor and response variates was used to test the hypothesis that P supply rates, lake mixing, and *Daphnia* grazing all affect summer water clarity in Lake Mendota.

Methods

Three main predictors of Secchi disk readings as a measure of summer water clarity in Lake Mendota were evaluated: (1) nutrient status indices using external P loadings or in-lake spring P concentrations, (2) lake mixing index as estimated by Schmidt stabilities, and (3) algal grazing potentials as estimated by *Daphnia* biomasses. A 20-yr data set (1976–1995) of these variates was developed from extensive monitoring data for the lake (Lathrop 1998).

Secchi disk readings—Summer Secchi disk readings were recorded at the central deepest area of the lake during 1976–1995 by the Wisconsin Department of Natural Resources (WDNR) and the University of Wisconsin-Madison Center for Limnology (UWCL) using a 20-cm black/white (B/W) disk (Lathrop 1992, 1998; Lathrop et al. 1996). Additional readings for 1976–1980 were recorded by students of T. D. Brock (unpubl. data) using a 30-cm white disk. These readings were standardized to readings for a 20-cm B/W disk by dividing by 1.129 (Lathrop 1992). Secchi readings were taken at least weekly during 1976–1980 and 1987–1995 and biweekly during 1981–1986.

External P loadings and in-lake P concentrations—External P loadings were developed from extensive monitoring data from the inflowing tributaries, storm sewers, and other loading sources to Lake Mendota (Lathrop 1998; Lathrop et al. 1998). Annual P loading estimates for 1975–1996 were incremented from 16 April. Because most of the lake's 604-km² watershed is rural and because sewage effluents no lon-

ger enter the lake, agricultural runoff delivered by a few major tributaries was the main P loading source to the lake.

In-lake P concentrations for mid-April were derived from long-term monitoring data. Each year's P concentration value was interpolated from data generally obtained on a bi-weekly sampling schedule beginning in early April. Each sampling date's P concentration represented an average for 0- and 4-m water depths, which were representative of the whole water column during spring mixis (Lathrop 1998).

Daphnia biomasses—*Daphnia* spp. enumerations and biomass estimates were determined from vertical tow samples collected with conical zooplankton nets during 1976–1995. Details of field sampling and laboratory procedures are available elsewhere (Lathrop 1998). Sampling was conducted biweekly during the open water period and at least once through the ice at the deepest region of the lake in water depths of ~23–24 m. In 1976–1994, zooplankton samples were collected by the WDNR using a net with a 15-cm diameter opening (small net). Beginning in 1991, 30-cm-diameter closing-style nets (large net) have been used by the WDNR and the UWCL for routine zooplankton sampling on Lake Mendota. The nets were made of Nitex screening with a mesh size of 75–80 μm (No. 20 net) for all years except 1976, when the mesh size was about 153 μm (No. 10 net). Direct comparisons between samples obtained with the small versus large nets showed that *Daphnia* density, biomass, and species composition were not discernibly different (Lathrop 1998). For our analyses, *Daphnia* data for the small net were used for 1976–1994; only large net data were used for 1995 when no small net data were available.

For the small net, a vertical tow sample was taken from approximately 0.5 m off the lake bottom; the depth of the large net tow was standardized to 20 m. For each zooplankton sample, *Daphnia* were later identified under a microscope to species and enumerated in three or four separate 1-ml subsamples. For the small net samples, individual body lengths for all *Daphnia* encountered were recorded. For the large net samples, the first 30 *Daphnia* of each species were measured. Based on specified size criteria, juvenile and adult *Daphnia* of each species were recorded separately. Dry weights for both juveniles and adults of each species were computed from the average length (L) data (in millimeters) based on the following equations (Lynch et al. 1986) for *D. galeata mendotae* and *D. pulicaria*, the two major *Daphnia* species encountered in Lake Mendota:

$$D. pulicaria \text{ mass } (\mu\text{g}) = 10.674 L^{2.093}$$

$$D. galeata mendotae \text{ mass } (\mu\text{g}) = 5.48 L^{2.200}$$

On the few occasions when *Daphnia retrocurva* were present, the equation for *D. g. mendotae* was used for estimating *D. retrocurva* weights. These average weights were then multiplied by their respective densities to compute raw biomass concentrations (mg dry weight liter⁻¹). In the final analysis, juvenile and adult data were combined for each *Daphnia* species.

To supplement the summer 1977 record, *Daphnia* densities from Woolsey (1986) were also used. Biomasses corresponding to the Woolsey density data were computed using

a mean length of 1.4 mm, which was the average of the WDNR *Daphnia* length data for the same time period.

Because Lake Mendota's hypolimnion is generally anoxic by early July, the majority of *Daphnia* (and grazeable algae) are restricted to the epilimnion and oxic portion of the metalimnion during the late summer months (Lathrop 1998). To convert the raw density and biomass data computed for the entire tow depth (TOW) to data based on the oxygenated water depth (DO), the raw data were multiplied by TOW/DO. DO for each sampling date was determined from dissolved oxygen vertical profile data as the depth where a concentration of 1 mg liter⁻¹ dissolved oxygen occurred. Thus, *Daphnia* density or biomass concentration data for mid to late summer dates could be more directly compared with data for periods when *Daphnia* inhabited the entire water column.

Another factor that affected *Daphnia* biomass determinations was zooplankton net efficiency. Both the small and large nets used for sampling *Daphnia* had reduced net efficiencies when algal densities were high as compared with periods of clear water (Lathrop 1998). Although there are interseasonal differences in net efficiency (range, 0.4–0.6 for the small net), this variability is small compared with the >10 times range in *Daphnia* biomasses that we observed. Because net efficiency is roughly constant, it would have negligible effect on the regression models. Therefore, biomasses were not corrected for net efficiency.

Lake mixing index—Schmidt stability (S) is a lake mixing index that describes the relative potential for entrainment of P-rich hypolimnetic and metalimnetic waters to the epilimnion. S (g cm⁻¹) is the amount of work required to mix the lake to a uniform temperature and represents the susceptibility of the entire water column to mixing by the wind (Likens 1985; Robertson and Imberger 1994):

$$S = A_z^{-1} \sum (z - z^*)(\rho_z - \rho^*) A_z \Delta z \quad (1)$$

where A_z is the lake area at depth z , ρ_z is water density at depth z , ρ^* is the lake's mean density, and z^* is the depth where the mean density is found. The summation is taken over all depths at interval $\Delta z = 1$ m. Low stability means that little work is needed to mix the water column and indicates that a relatively high potential for entrainment is present if the metalimnetic gradient of P is large, which is the situation in Lake Mendota (Soranno et al. 1997; WDNR unpubl. data).

Stabilities were calculated using WDNR/UWCL lake temperature profile data for 1976–1995. Additional water temperature data from Fallon (1978) were used to supplement the 1977 summer record. The S calculated for each sampling date was used as the daily value until a new value could be calculated from another temperature profile. An average of these daily values was used for each month's stability value.

Another index of lake mixing that was examined was lake number (LN), which incorporates the stability of the water column and the destabilizing force of the wind (Robertson et al. 1990; Robertson and Imberger 1994). S and LN had similar capabilities for predicting water clarity (Lathrop 1998). This similarity was due to the high correlation ($r = 0.83$) between the two indices, which is not unexpected giv-

en that S is used in the calculation of LN . Because LN is an index of realized mixing and S is an index of potential mixing, we initially expected LN to be a superior predictor. However, the actual extent of mixing (low LN values) was reflected in the calculated average monthly S values; mid-summer wind events produced temperature profile changes that in turn produced lower water column stabilities. For simplicity, we present only models using S as a mixing predictor.

Data analyses—Summer (June–August) is comprised of two distinctly different periods in Lake Mendota. June normally has clear water for much of the month because of the clear-water phase that coincides with a late spring increase in *Daphnia* populations (Luecke et al. 1990; Lathrop 1992; Lathrop et al. 1996). July and August generally are the months when blue-green algal blooms are most dense (Lathrop and Carpenter 1992a).

Because of the biweekly lake sampling schedule, we divided the summer into three 28-d time periods: June (1–28 June), July (29 June–26 July), and August (27 July–23 August). For each of these 28-d periods in each year during 1976–1995 (20 yr), *Daphnia* biomass means, the mean daily value for S , and mean Secchi disk readings were calculated. Because conditions in the previous month could greatly influence water clarity for any summer month, mean Secchi disk readings and *Daphnia* biomass concentrations for May (28 d, 4–31 May) of each year were also computed. *Daphnia* data were not available for May 1978; results were based on 19 yr of data when May *Daphnia* values were included in the analyses.

All statistical analyses were performed using SYSTAT. Stepwise multiple linear regression was used to test for significant predictive models of summer water clarity. The P -value to enter and remove a variate was set at 0.10. Multiple regressions were also run with backwards elimination to determine any differences in model outcomes, but identical models were generated. Separate analyses were conducted for each summer monthly period and for July–August combined.

For each regression model, mean Secchi disk depth (in meters) for the given month was the response variate. Predictor variates for each year were external P loading (megatons yr⁻¹), in-lake April P (mg liter⁻¹), and *Daphnia* spp. biomass (mg liter⁻¹) and lake water column stability (S) for the corresponding month(s) of that year. In addition, analyses were conducted using 1-month lagged variates for *Daphnia* biomass, lake stability (excluding May), and Secchi depth as well as the current month's predictor variates. An extra sum-of-squares F -test (Draper and Smith 1981) was used to determine if the inclusion of an extra predictor variate in a model was warranted ($\alpha = 0.10$). For each model presented here, the residuals were normally distributed and not autocorrelated.

Results

***Daphnia* biomasses**—*Daphnia galeata mendotae* and *D. pulicaria* exhibited strong seasonal patterns in Lake Mendota during 1976–1995 (Fig. 1, Table 1). From 1978 through

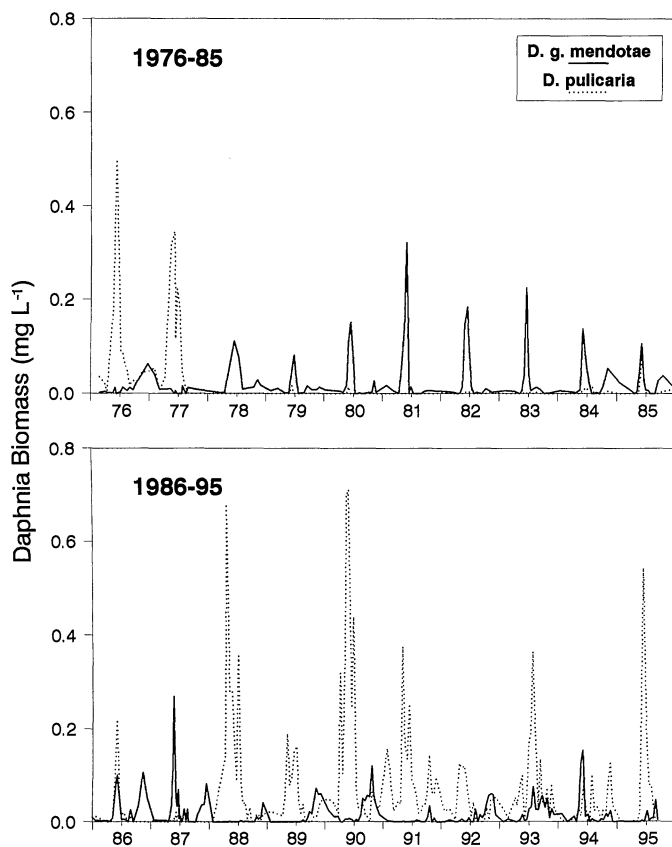


Fig. 1. Biomass concentrations ($\text{mg dry weight liter}^{-1}$) for *Daphnia galeata mendotae* (solid line) and *D. pulicaria* (dotted line) during 1976–1995 in Lake Mendota. Concentrations were adjusted for water depths where dissolved oxygen was $\geq 1 \text{ mg liter}^{-1}$. Concentrations were not adjusted for net efficiency.

1987 when planktivory was high because of abundant cisco (Rudstam et al. 1993; Johnson and Kitchell 1996), the smaller-bodied *D. g. mendotae* dominated most of the spring clear-water periods. The larger-bodied *D. pulicaria* dominated in 1976–1977 prior to the development of a strong year class of cisco and again in 1988–1995 following the massive cisco die-off in late summer 1987. Only during 1985, 1986, and 1994 did both *Daphnia* species coexist during the late spring period. In 1985–1987, planktivory rates had been declining following a peak in 1980 (Rudstam et al. 1993). In 1987, a year when lake temperatures warmed very rapidly in the spring, *D. g. mendotae* with its higher temperature requirements for growth (Burns 1969; Threlkeld 1980) may have been able to increase in numbers before *D. pulicaria* could reduce the spring algal densities. In 1994, planktivory (primarily from yellow perch and white bass) had increased again to levels only slightly less than those in 1986–1987 (Johnson and Kitchell 1996). Planktivory rates are not available for 1995, but the predominance of *D. pulicaria* in that year suggests that planktivory had declined somewhat from 1994.

In years when *D. pulicaria* dominated at the time of the spring clear-water phase, *Daphnia* biomasses increased earlier in the spring and remained higher into July than in years when *D. g. mendotae* dominated or when both species co-

existed (Fig. 1). Maximum peak biomasses also tended to be higher in years dominated by *D. pulicaria*. In 1988 and 1990, *D. pulicaria* biomasses were particularly high from early spring to midsummer. In 1995, biomasses also reached a peak, but *D. pulicaria* did not increase until June.

Overall, mean *Daphnia* biomasses were significantly greater in May and marginally greater in June during *D. pulicaria*-dominated years (when *D. pulicaria* represented more than half of the total *Daphnia* biomass) than during *D. g. mendotae*-dominated years (Table 2). These greater *D. pulicaria* biomasses in May and June generally carried through to July and August. In July, mean *Daphnia* biomasses in *D. pulicaria* years were significantly greater than the mean biomasses in *D. g. mendotae* years. Mean biomasses were also greater in August in *D. pulicaria* years than in *D. g. mendotae* years, although not significantly. In general, mean *Daphnia* biomasses declined from June to August in both *D. pulicaria* and *D. g. mendotae* years.

April P concentrations and external P loadings—April P concentrations varied during 1976–1995, particularly following periods of both drought and high runoff (Table 1). Minimum and maximum concentrations occurred in 1988 ($0.070 \text{ mg liter}^{-1}$) and 1994 ($0.177 \text{ mg liter}^{-1}$), respectively. External P loadings also varied considerably during the same time period. Minimum and maximum loadings were 16 and 67 metric tons yr^{-1} , respectively. Because April P had a significant lag-1 (year) autocorrelation, concentrations in a given spring were a function of the P loading from both runoff earlier in that spring and lake P concentrations carried over from the previous year(s). Annual P loadings were not autocorrelated and did not reflect any carryover effect. Regardless of when P loading occurred, April P was a good predictor of blue-green algal blooms later the same summer in Lake Mendota (Stow et al. 1997; Lathrop et al. 1998).

Lake water column stabilities—Schmidt stabilities were generally much lower in June than during July or August (Table 1). Stabilities were particularly high in August of 1983, 1987, 1988, and 1995, which were summers with above-average air temperatures. High stabilities occurred in July of those years, but also in 1989 and 1991 when maximum values occurred. June stabilities were very high in 1987 and 1991. In 1987, spring warming occurred earlier than usual. In 1991, rapid warming occurred late in May, causing thermal stratification with very cold hypolimnetic temperatures ($<10^{\circ}\text{C}$). Stabilities were very low during the summer of 1985 as a result of unusually warm hypolimnetic water temperatures.

Summer Secchi disk depths—Mean Secchi disk depths for the June through August monthly periods were highly variable in eutrophic Lake Mendota (Fig. 2, Table 1). In general, mean depths were deeper in June than later in the summer. June Secchi depths in *D. pulicaria* years were only slightly deeper than those in *D. g. mendotae* years (Table 2). However, June Secchi depths exceeded May Secchi depths in *D. g. mendotae* years, whereas Secchi depths were deeper in May in *D. pulicaria* years. Only in 1979 and 1990 were Secchi depths relatively shallow in June (Fig. 2). The deep-

Table 1. Annual P loadings, lake April P concentrations, and monthly means of Secchi disk depth readings, *Daphnia* biomasses, and water column stabilities for Lake Mendota, 1976–1995. Months are 28-d periods: May = 4–31 May; June = 1–28 June; Jul = 29 June–26 July; Aug = 27 July–23 August.

Year	P load (MT yr ⁻¹)*	April P (mg li- ter ⁻¹)	Secchi depth (m)				<i>Daphnia</i> biomass (mg liter ⁻¹)				Stability (g cm ⁻¹)		
			May	Jun	Jul	Aug	May	Jun	Jul	Aug	Jun	Jul	Aug
1976	56.5	0.130	6.83	3.71	1.40	1.46	0.185	0.457	0.100	0.061	326	460	456
1977	23.6	0.150	6.10	3.05	0.83	1.30	0.326	0.229	0.120	0.034	371	562	475
1978	15.5	0.160	1.67	4.31	1.73	1.10		0.111	0.077	0.009	381	548	557
1979	49.3	0.110	1.77	2.02	1.33	1.45	0.001	0.085	0.018	0.001	258	543	524
1980	31.1	0.140	1.10	4.13	0.90	1.02	0.016	0.141	0.043	0.001	282	620	609
1981	44.6	0.100	2.84	3.88	1.38	1.17	0.106	0.164	0.008	0.000	390	560	490
1982	39.3	0.091	1.25	3.45	1.60	1.35	0.008	0.171	0.060	0.001	279	501	668
1983	25.1	0.091	1.75	4.75	2.85	2.00	0.003	0.133	0.025	0.015	212	623	851
1984	15.9	0.072	1.15	4.00	1.55	1.40	0.007	0.120	0.059	0.009	303	543	646
1985	51.7	0.091	1.65	3.30	1.30	0.85	0.023	0.128	0.007	0.000	155	379	429
1986	39.3	0.090	2.25	4.80	2.30	1.80	0.092	0.209	0.023	0.007	281	464	633
1987	24.2	0.088	4.45	3.07	1.80	2.30	0.116	0.078	0.007	0.040	604	687	726
1988	21.8	0.070	8.62	3.57	3.82	2.81	0.280	0.137	0.226	0.040	453	669	855
1989	25.6	0.093	8.70	5.48	2.88	2.02	0.134	0.125	0.104	0.030	370	749	608
1990	26.1	0.113	2.77	1.93	1.88	1.71	0.524	0.487	0.263	0.039	261	520	512
1991	26.0	0.107	7.98	4.12	1.95	2.60	0.272	0.192	0.087	0.041	604	765	643
1992	23.4	0.098	7.56	2.89	1.91	1.94	0.121	0.071	0.027	0.018	383	466	527
1993	51.7	0.151	5.21	5.25	1.74	1.81	0.095	0.027	0.207	0.327	261	504	579
1994	67.0	0.177	3.34	2.92	1.21	1.77	0.098	0.135	0.008	0.065	508	601	494
1995	22.7	0.125	4.10	6.98	2.08	1.70	0.012	0.428	0.137	0.065	385	616	808

* MT = metric tons.

est June Secchi depth during the 20-yr period (1976–1995) occurred in 1995.

The generally shallower mean Secchi disk depths during July and August of 1976–1995 (Fig. 2) can be attributed to blue-green algal blooms in Lake Mendota (Lathrop and Carpenter 1992a). Secchi depths were deeper on average in *D. pulicaria* years than in *D. g. mendotae* years, although the differences were not statistically significant for July (Table 2). The deepest Secchi depths for July and August occurred during 1988 at the end of a prolonged drought period when P loadings and concentrations were low (Lathrop et al. 1996,

1998). Planktivory rates were also much lower in 1988 because of the massive die-off of cisco the previous year (Vanni et al. 1990; Rudstam et al. 1993). The deepest July–August Secchi depths during a *D. g. mendotae* year was in 1983. The shallowest July Secchi depths occurred in 1977 and 1980, when mean Secchi readings were <1 m. The shallowest August Secchi depths occurred in 1985 when stabilities were low.

Predictive models for summer water clarity—Summer water clarity varied greatly during 1976–1995. At the same

Table 2. Means and standard deviations (SD) for monthly Secchi disk readings and *Daphnia* spp. densities and biomasses in Lake Mendota during 1976–1995 (20 yr). Months are defined as 28-d lunar months: May = 4–31 May; June = 1–28 June; Jul = 29 June–26 July; Aug = 27 July–23 August. Years are grouped as *D. pulicaria* ($n = 10$) or *D. g. mendotae* ($n = 10$ except for May *Daphnia* densities/ biomasses, where $n = 9$) depending on which species had the greatest biomass during the late spring clear-water phase in a given year. Independent *t*-tests were used to determine differences in means between year groupings.

Measure	May		Jun		Jul		Aug	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Secchi (m)								
<i>D. pulicaria</i> years	6.01***	2.36	4.18	1.48	2.08	0.81	1.92**	0.47
<i>D. g. mendotae</i> years	2.10	1.10	3.58	0.80	1.57	0.52	1.44	0.46
<i>Daphnia</i> density (liter ⁻¹)								
<i>D. pulicaria</i> years	10.8	7.1	11.5	8.1	5.7**	4.0	3.2	3.8
<i>D. g. mendotae</i> years	6.5	7.6	15.9	7.0	2.5	2.1	1.2	1.6
<i>Daphnia</i> biomass (mg liter ⁻¹)								
<i>D. pulicaria</i> years	0.204***	0.149	0.236*	0.165	0.129***	0.081	0.066	0.093
<i>D. g. mendotae</i> years	0.042	0.049	0.127	0.030	0.031	0.026	0.014	0.022

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$.

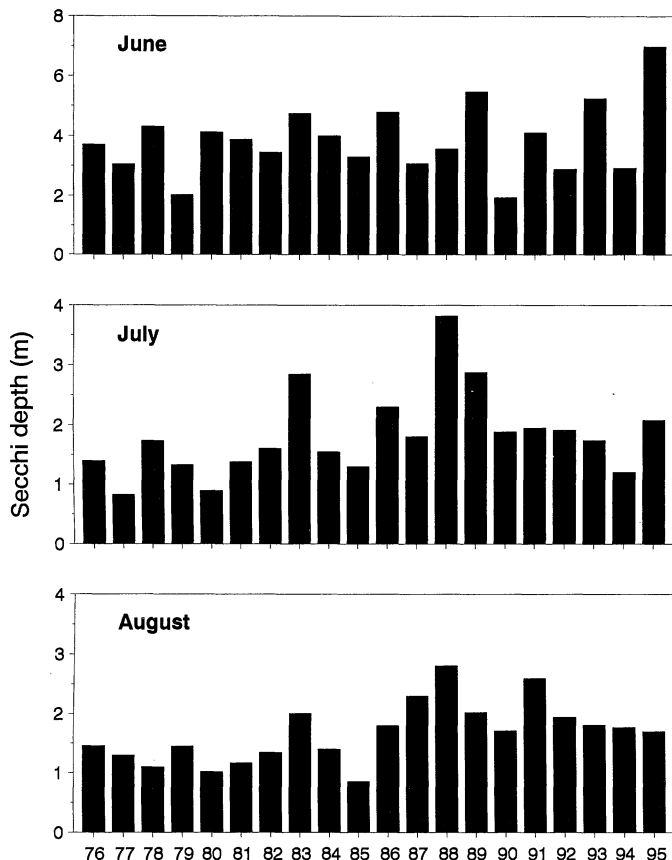


Fig. 2. Mean Secchi disk depths for the June (1–28 June), July (29 June–26 July), and August (27 July–23 August) 28-d periods for 1976–1995 in Lake Mendota. (Note the greater Secchi depth scale in June.)

time, the three main groups of predictor variates (i.e., P loadings or April P concentrations, *Daphnia* biomasses, and lake stabilities) also varied considerably but for the most part independently of one another, as indicated by nonsignificant correlation coefficients (for correlation matrix, see Lathrop 1998). Monthly Secchi depths were significantly correlated with a number of predictor variates.

Stepwise linear regression revealed different results for each month. For June, if no lagged variates were included in the stepwise procedure, the only significant predictor of June Secchi depth was the June mean. With the inclusion of the lagged variates in the model development, then May Sec-

Table 3. Linear model predicting June (1–28 June) mean Secchi disk depth from mid-April lake P concentration, monthly mean *Daphnia* biomass, and daily Schmidt stability for Lake Mendota.

Variate	Coeff.	SE	<i>t</i>	<i>P</i>
Constant	3.01	0.563	5.34	<0.001
May <i>Daphnia</i>	−7.56	2.319	−3.26	0.005
May Secchi	0.239	0.104	2.30	0.036
Jun <i>Daphnia</i>	4.38	2.157	2.03	0.060

Predictor variates tested: P loading, Apr P, Jun *Daphnia*, Jun stability, May Secchi, May *Daphnia*

Model: $r = 19$ yr; SE estimate = 1.013; $R^2 = 0.428$, $P = 0.034$

Table 4. Linear model predicting July–August (29 June–23 August) mean Secchi disk depth from mid-April lake P concentration, and July–August mean *Daphnia* biomass and daily Schmidt stability for Lake Mendota.

Variate	Coeff.	SE	<i>t</i>	<i>P</i>
Constant	0.496	0.667	0.74	0.468
Jul–Aug stability	0.00328	0.000845	3.88	0.001
Apr P	−7.61	2.878	−2.64	0.018
Jul–Aug <i>Daphnia</i>	3.07	1.291	2.38	0.030

Predictor variates tested: P loading, Apr P, Jul–Aug *Daphnia*, Jul–Aug stability, Jun Secchi, Jun *Daphnia*, Jun stability

Model: $n = 20$ yr; SE estimate = 0.3407; $R^2 = 0.702$, $P < 0.001$

chi depth and May and June *Daphnia* biomasses were significant predictors of June Secchi depth (Table 3). An extra sum-of-squares *F*-test verified that June *Daphnia* was a significant predictor. P loading, April P, and June stability were not significant predictors of June Secchi depth.

Significant models were also found that predicted both July and August mean Secchi depths (Lathrop 1998). Because similar ecosystem processes appeared to control water clarity in both months (although August clarity was affected by July clarity), we present a combined model for the July–August (midsummer) months. Variate values for Secchi depths, *Daphnia* biomasses, and stabilities listed in Table 1 were averaged for the 2 months.

A significant model predicted July–August mean Secchi depths from April P, and midsummer *Daphnia* biomasses and water column stabilities (Table 4, $P < 0.001$, $R^2 = 0.70$; Fig. 3). No lagged variates including June Secchi depth were significant predictors. Thus, lake P concentrations from the

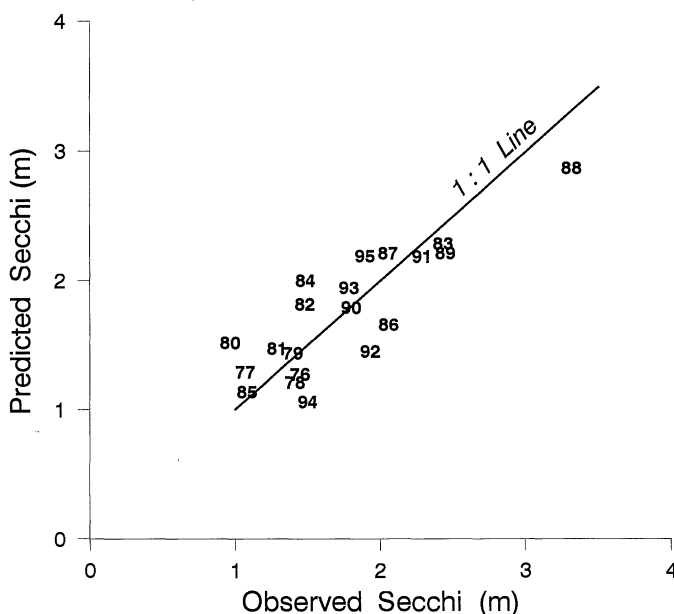


Fig. 3. Observed versus predicted mean Secchi disk readings for July–August 1976–1995 for Lake Mendota. Predicted readings for each year were based on the linear model presented in Table 4. The unusually clear water recorded during the summer of 1988 is highlighted.

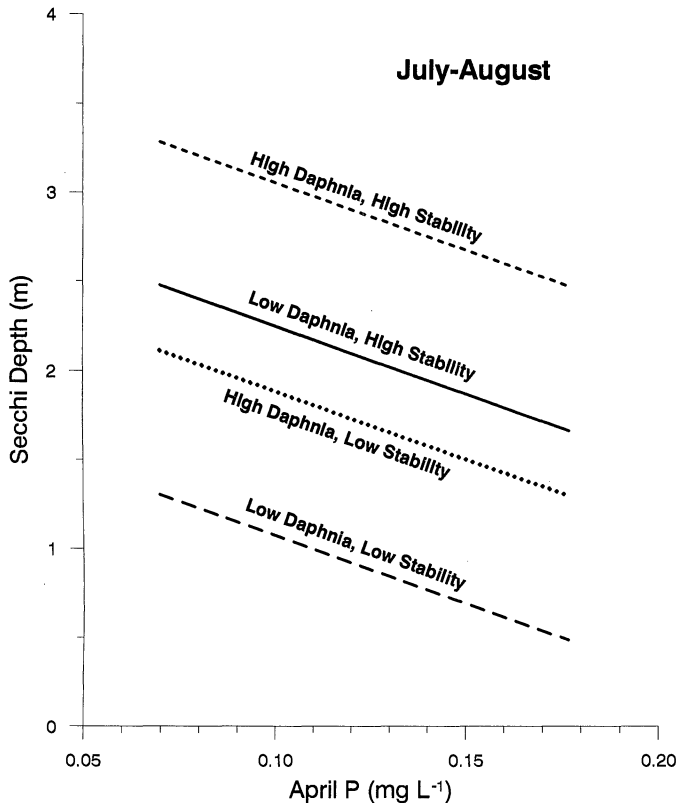


Fig. 4. Scenarios for July–August mean Secchi disk depths based on the range of April P concentrations (0.070–0.177 mg liter⁻¹), the minimum and maximum values of July–August mean *Daphnia* biomasses (0.004 and 0.267 mg liter⁻¹), and July and August mean stabilities (404 and 762 g cm⁻¹, respectively) recorded during 1976–1995 for Lake Mendota.

previous spring, *Daphnia* grazing during midsummer, and internal P loading resulting from lake mixing by wind all affected water clarity in midsummer. April P was a more useful predictor than external P loading because April P incorporates the loading “memory” from previous years. In addition, April P influences summer metalimnetic P concentrations and therefore the potential for internal nutrient loading.

Scenarios for July–August water clarity—Relative impacts of P, *Daphnia* grazing, and lake mixing are illustrated using the July–August regression model (Fig. 4). Predicted mean Secchi depths for July–August were plotted against the range of April P concentrations observed in Lake Mendota during 1976–1995. The four scenario lines were calculated from combinations of the observed minimum and maximum values for both July–August *Daphnia* biomasses and water column stabilities. Secchi depths for all scenarios combined ranged between 0.49 and 3.29 m. The linear model predicted that the range of April P concentrations observed during 1976–1995 in Lake Mendota would result in a 0.81-m difference in mean Secchi depths when the other variates were held constant. Similarly, Secchi differences of 0.81 m and 1.17 m would result from the range in observed *Daphnia* biomasses and water column stabilities, respectively. Even

though stability was predicted to have the greatest effect on July–August Secchi depths, the effects of the three factors (April P, *Daphnia* biomass, and stability) would not be significantly different given the standard error of the regression model (0.34, Table 4).

Discussion

Summer water clarity in Lake Mendota is affected by diverse factors. In June, water clarity is governed mostly by food web interactions that result in a regular clear-water phase in late spring, a phenomenon observed in many eutrophic lakes (Lampert et al. 1986; Sommer et al. 1986). The larger-bodied *D. pulicaria*, with its lower temperature requirements for growth (Burns 1969; Threlkeld 1980) can reduce algal densities earlier in the spring and hence prevent *D. g. mendotae* from obtaining sufficient food resources to grow. Although May water clarity is much greater in *D. pulicaria* years, June water clarity is not significantly different when either species dominates because *D. g. mendotae* also reduces algal densities, resulting in a clear-water phase in June.

During the 20-yr record evaluated for Lake Mendota, 2 years (1979 and 1990) did not have a June clear-water phase. The first year coincided with the highest level of planktivory during 1976–1995, which was caused by a strong year class of cisco and to a lesser extent yellow perch (Rudstam et al. 1993; Johnson and Kitchell 1996) and crappies (Lathrop et al. 1992). In that year, planktivory was apparently so high that even *D. g. mendotae* densities were suppressed. The second year occurred when planktivory was very low (Johnson and Kitchell 1996). Poor water clarity was the result of an unusual spring bloom of *Aphanizomenon flos-aquae*, which occurred even though *D. pulicaria* populations were dense. The apparent resistance of this blue-green alga to grazing by *D. pulicaria* (or *D. pulex*) has been observed in many lakes (Hrbáček 1964; Lynch 1980; Ganf 1983; Andersson and Cronberg 1984; Pechar and Fott 1991).

One other factor that may affect June water clarity, especially in *D. g. mendotae* years, is water temperature. In 1987, a year when spring warming occurred unusually early, the clear-water phase peaked by late May (Luecke et al. 1990). By early June, Secchi disk depths had declined to <4 m, which coincided with a precipitous decline in *D. g. mendotae* caused by their overexploitation of food resources (algae of edible size). Given the starvation intolerance of *D. g. mendotae*, the role of temperature in determining the timing of the short-lived spring clear-water phase could be important in determining early summer water clarity in *D. g. mendotae* years. Blue-green algal blooms should begin earlier in those summers, which did happen in 1987 in Lake Mendota (Lathrop and Carpenter 1992a). Such events may become more common if the climate warms (Arnell et al. 1996; Magnuson et al. 1997).

Midsummer (July–August) water clarity in Lake Mendota is associated with three factors that are largely independent: (1) April P concentrations, which are a measure of past external P loadings and summer internal P loading potentials, (2) *Daphnia* grazing, which is mediated by planktivory lev-

els, and (3) internal mixing, which is dictated by water column stabilities that are affected by air temperatures, solar radiation, and frequency of wind events. April P levels respond to the recent history of external loadings, although there is a strong carryover effect from previous years. *Daphnia* biomasses are significantly greater in the summer during years dominated by *D. pulicaria* in the spring months. Unusually high or low water column stabilities occur in years when air temperatures depart from normal with additional effects from wind events. Water clarity is higher in August when water column stabilities and/or unusually warm air temperatures delay metalimnetic deepening. However, August water clarity can also be poor when lower than normal summer stabilities allow substantial metalimnetic deepening to occur, as in 1985.

Our analyses identified reasons why exceptional water clarity (relative to other years) can occur in certain summers in Lake Mendota. The greater clarity in the summer of 1988 (July–August mean Secchi disk reading of 3.3 m) was originally attributed to increased *Daphnia* grazing that resulted from the massive cisco die-off the previous summer (Vanni et al. 1990). Although summer *Daphnia* biomasses were exceptionally high in 1988 (especially in July), they were also very high in 1990 (Fig. 1, Table 1), a year of *Aphanizomenon* blooms and average clarity. Furthermore, downstream Lake Monona also had exceptional water clarity in 1988 (July–August mean Secchi disk reading of 3.1 m) but did not experience unusually high *Daphnia* biomasses (Lathrop 1998). However, in both lakes April P concentrations were low and epilimnetic temperatures were high in 1988. The exceptional water clarity in Lake Mendota in 1988 resulted from an interaction of all three factors: low P availability, low internal mixing, and high *Daphnia* grazing. Without the drought-induced lower spring P concentrations and greater water column stabilities, the exceptional water clarity in both lakes likely would not have occurred. The somewhat greater clarity in Lake Mendota during July (Mendota Secchi = 3.8 m; Monona Secchi = 3.2 m) can be attributed to the enhanced grazing that month. These same interacting factors may also explain the exceptional water clarity that was recorded in Lake Mendota in 1939 and 1947, years associated with massive fish kills, hotter than normal summer temperatures, and low P availability compared with more recent years (Lathrop 1998).

Significance for lake eutrophication—Although all three factors—P availability, *Daphnia* grazing, and lake mixing—had similar potential impacts on summer water clarity in Lake Mendota, only P availability can be realistically controlled by management actions in this large urban lake. Lathrop et al. (1998) predicted that a 50% reduction in external P loadings (a goal being pursued as part of a recently initiated watershed management project) would result in two-thirds of the years having spring P concentrations below the 1988 drought-induced minimum. Although these in-lake concentrations are outside the predictive range of our July–August model (Table 4), water clarity should be substantially greater than without P control.

Although *Daphnia* grazing can significantly increase summer water clarity in Lake Mendota, food web manipulations

to control *Daphnia* populations are difficult to sustain in an urban setting where fishing pressure on piscivores is heavy (Johnson and Staggs 1992; Johnson and Carpenter 1994). At present, planktivory remains low in Lake Mendota because of the cisco die-off of 1987 (Johnson and Kitchell 1996); the larger *D. pulicaria* continues to dominate during the spring and summer months. If cisco populations were to increase again, a shift to the smaller *D. g. mendotae* with less grazing potential would probably occur along with a significant decline in water clarity. Although it has been suggested that food web manipulations are incapable of producing desirable improvements in summer water clarity in eutrophic lakes (McQueen et al. 1986; Benndorf 1990; Reynolds 1994), our results from Lake Mendota suggest that the constraints are more social than limnological. In other eutrophic lakes, sustained food web manipulations may be possible.

Lake mixing (and hence internal P recycling) is a major factor controlling summer water clarity in Lake Mendota. Water column stabilities usually cannot be increased by management in natural lakes, although internal water currents sometimes can be managed for increased stabilities in reservoirs. On a larger scale, global warming is expected to increase surface water temperatures and their seasonal rate of increase in temperate lakes, but bottom water temperatures are not expected to change much (Robertson and Ragotzkie 1990; Stefan et al. 1993; DeStasio et al. 1996). As a consequence, water column stabilities in Lake Mendota could increase and stay high for longer periods of time, causing internal P loading rates to decline. Alternatively, longer periods of summer stratification could also lead to a build-up of higher hypolimnetic P concentrations that could lead to higher P concentrations at fall turnover, which would then carry over to the following spring (Lathrop 1992). This carryover could lead to higher metalimnetic P concentrations and thus higher internal P loading. The duration of blue-green algal blooms could also be extended as a result of global warming. Further research on the effects of global warming on lake thermal structure and responses in P recycling rates and in phytoplankton and zooplankton dynamics will occur as the global climate continues to change (Arnell et al. 1996; Magnuson et al. 1997).

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