**Daphnia** grazings, the clear water phase, and implications of minerogenic particles in Onondaga Lake

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**Abstract**

We evaluated the influence of *Daphnia* grazing on water clarity in Onondaga Lake, New York, by testing 2 related hypotheses: (1) that the high clarity (Secchi disk depth [SD]) events observed in 18 years of a 27-year record were occurrences of the clear water phase (CWP) associated with elevated levels of *Daphnia* grazing, and (2) that reductions in minerogenic (i.e., inorganic) particle concentrations and the accompanying reductions in light scattering (quantified by $b_m$) due to grazing contributed importantly to the SD signatures of the CWPs. Our analysis is based on a 27-year record of the *Daphnia* population, SD, and the concentration of chlorophyll $a$ (Chl-$a$), as well as shorter-term characterizations of minerogenic particle concentrations in the lake and application of an optical theory-based SD model previously tested for the lake. The first hypothesis is supported by (a) the consistency of seasonal patterns of Chl-$a$, SD, and *Daphnia* biomass, (b) the consistency of *Daphnia* biomass maxima with literature values associated with the CWP, (c) the positive relationships demonstrated between interannual differences in *Daphnia* biomass (and estimated grazing rates) and peak SD and duration of high clarity events, and (d) because during CWPs, estimated grazing rates exceed by a wide margin reasonable maximum values of phytoplankton growth rates. The second hypothesis is supported by (a) demonstration that the minerogenic particle sizes responsible for $b_m$ (and so its influence on SD) are within the size range subject to *Daphnia* grazing, and (b) application of the SD model, in the context of SD and Chl-$a$ observations, showing that a reduction in $b_m$ is necessary to explain the high SD values observed during CWPs. Finally, a review of the growing literature on the contribution of $b_m$ to the overall particle scattering coefficient in various lakes suggests that minerogenic particles are often important to the SD signature of CWPs.

**Key words:** clear water phase, *Daphnia*, grazing, minerogenic particles, optics model, Secchi depth

**Introduction**

Decreases in phytoplankton biomass and accompanying increases in clarity (Kirk 2011) are observed in response to a number of drivers, including increases in zooplankton grazing (Reynolds 2006). *Daphnia*, nonselective filter feeding cladocerans, are the most prominent in this regard because their grazing potential generally exceeds that of other zooplankton taxa in temperate lakes (Vanni and Temte 1990, Kasprzak et al. 1999). Dense populations of *Daphnia* can graze at rates faster than phytoplankton can grow (Lampert 1988, Hambright et al. 2007) and so can cause decreases in phytoplankton biomass, with accompanying increases in water clarity. A period of particularly high clarity, described as the clear water phase (CWP), is observed in response to this grazing in many temperate lakes, usually in spring to early summer (Lampert et al. 1986, Sommer et al. 1986, Lampert 1988). High clarity events (i.e., CWPs) are now commonly attributed to *Daphnia* grazing, although other consumers have also
been implicated (Tirok and Gaedke 2006). The evidence that supports this cause-and-effect relationship has varied. As a minimum, this relationship has been based on paired distributions of *Daphnia* biomass, phytoplankton biomass (or a proxy), and Secchi disk depth (SD; Lampert 1988, Hairston et al. 2005). More detailed studies have included *in situ* grazing rates, primary production measurements, and enclosure experiments (Lampert et al. 1986). The large-bodied daphnids, *D. pulex* and *D. mendotae*, are particularly effective at producing CWPs in North American lakes (Lathrop et al. 1996, Kaspriak et al. 1999, Hairston et al. 2005).

Although the most conspicuous signature of the CWP is optical (water clarity), the interplay between the nonselective nature of *Daphnia* grazing and the implications for SD observations has received little attention. *Daphnia* filter feeding extends to particle diameters from 0.5 to 70 µm (Lampert 1987, Hambright et al. 2007). Although differences in efficiencies have been reported within this size range (Knoechel and Holtby 1986b), members of this genus are generally unselective with regard to composition of ingested items, removing both food and nonfood particles of similar size with the same efficiency (Lampert 1987). Observations of *Daphnia* gut contents with a high ratio of mineral to organic solids (300:1; G-Tóth 1984) indicate the potential for removal of substantial amounts of minerogenic (i.e., inorganic) particles through *Daphnia* grazing.

SD, an apparent optical property (AOP, dependent on the geometry of the ambient light field), is determined primarily by the light-attenuating process of scattering caused by particles, as quantified by the particulate scattering coefficient (*b*<sub>p</sub>, m<sup>-1</sup>). Coefficient *b*<sub>p</sub> is an inherent optical property (IOP, an intrinsic property of the medium; Kirk 2011). Accordingly, the magnitude and variations in SD are driven by those of *b*<sub>p</sub>. SD has an inverse dependency on *b*<sub>p</sub> (SD<sup>-1</sup>) µ m<sup>2</sup>; Davies-Colley et al. 2003, Effler and Peng 2014). Minerogenic particles have increasingly been reported to make noteworthy contributions to *b*<sub>p</sub> in lacustrine waters (Peng et al. 2007, Peng and Effler 2007, 2012) and thereby exert an important influence on SD (Peng and Effler 2011, Effler and Peng 2014). Coefficient *b*<sub>p</sub> can be partitioned according to the summation of 2 components (Peng et al. 2009, Peng and Effler 2011, Effler and Peng 2012),

\[
b_p = b_m + b_o,
\]

where *b*<sub>m</sub> and *b*<sub:o</sub> are the scattering coefficients associated with minerogenic and organic particles (phytoplankton and its retinue; e.g., bacterioplankton and organic detritus), respectively. Increases in SD from *Daphnia* grazing are mediated by decreases in *b*<sub>p</sub>, which may be associated with reductions in both *b*<sub>m</sub> and *b*<sub:o</sub>. The magnitudes of both *b*<sub>m</sub> and *b*<sub:o</sub> depend on the light-scattering attributes of the respective particle populations, including their number concentrations, particle size distributions, compositions, and shapes (Wozniak and Stramski 2004, Peng et al. 2007, 2009, Peng and Effler 2011). The dependence of *b*<sub>m</sub> on *Daphnia* grazing and its implications for the SD signature of the CWP have not been considered.

In this study we evaluated the role of *Daphnia* grazing in influencing SD in Onondaga Lake, New York. Two hypotheses were tested: (1) that high clarity events observed were occurrences of the CWP; and (2) that reductions in *b*<sub>m</sub> from grazing contributed importantly to the magnitude of the SD signature of the CWP. Our analysis is based on a 27-year record of the *Daphnia* population, SD, and the concentration of chlorophyll *a* (Chl-*a*), as well as characterizations of minerogenic particle populations of the lake and application of a previously tested optical theory-based SD model. The dynamics of *Daphnia* species composition, population densities, body size, and estimates of biomass and filtering rates were used to support quantitative testing of the first hypothesis. Evaluation of paired Chl-*a* and SD observations over the record in the context of predictions of the SD model and system-specific *b*<sub>m</sub> information support testing of the second hypothesis. The extent to which decreases in *b*<sub>m</sub> from grazing contributes to the SD signature of the CWP elsewhere was considered.

## Methods

### Study system and background information

Onondaga Lake is an alkaline, hard-water, dimictic lake located (43°6′54″N, 76°14′34″W) in metropolitan Syracuse, New York (USA), with a volume of 131 × 10<sup>6</sup> m<sup>3</sup>, an area of 12.0 km<sup>2</sup>, and a maximum depth of ~20 m. The lake flushes ~4 times per year on a completely mixed basis and thus responds rapidly to changes in external loading (Effler 1996). Onondaga Lake was oligo-mesotrophic before European settlement (Rowell 1996) but became severely degraded from inputs of industrial and domestic wastes that accompanied development of the watershed (Effler 1996).

A single point-source input, the regional domestic wastewater treatment facility (Metro), has been the dominant source of phosphorus (P) to the lake (Effler et al. 2013). The lake was hypereutrophic in the 1950s (Rowell 1996), extending into much of the period considered in this study (1987–2013; Fig. 1). Despite the mostly progressive decreases in the summertime epilimnetic total P concentration (TP) over much of our study period in response to treatment upgrades at Metro (Fig. 1a), the response in primary production was distinctly nonlinear.
over the study period, with hypereutrophy persisting through the early 2000s. The most recent decrease in loading achieved substantial reductions in primary production, consistent with the kinetics of the limiting nutrient physiology of algal growth (Effler et al. 2008a). Contemporary conditions for the trophic state metrics of TP$_e$, the summer average epilimnetic Chl-a concentration (Chl$_a$), and SD support the position that the lake has been transformed to mesotrophy (Effler and O’Donnell 2010). Wide within-year variations in Chl$_a$ (Fig. 1b) and SD (Fig. 1c) have been observed in many years (extending into spring, not shown), however, with long-term trends that are far less progressive than for TP$_e$ (Fig. 1a).

A recurring feature of the spring to early summer phytoplankton assemblage since the early 1970s has been the dominance of forms edible by *Daphnia*, primarily cryptomonads and diatoms (Effler 1996, Onondaga County 2013). The spherical equivalent diameter of the phytoplankton assemblage, weighted according to the contributions to total biovolume, ranged from 4 to 10 μm over the spring to early summer interval for the 2004–2009 period (Perkins et al. 2014).

The dynamics of light-scattering attributes of minerogenic particles in the upper waters of the lake were characterized over the April–September interval of 2010 with scanning electron microscopy interfaced with automated image and X-ray analyses (SAX; Effler and Peng 2012). These SAX results were used to estimate $b_m$ through Mie theory calculations (Bohren and Huffman 1983) using protocols described previously (Peng et al. 2009, Peng and Effler 2010, 2011). Good optical closure for the 2-component scattering model (equation 1) with bulk measurements of $b_p$ was reported, with $b_o$ estimated with an empirical Chl-$a$-based bio-optical model (Effler and Peng 2012). The contribution of $b_m$ to $b_p$ was estimated to be 25%, on average. Allochthonous clay minerals were the dominant minerogenic component, with autochthonous calcium carbonate particles making secondary contributions (Effler and Peng 2012).

**Zooplankton sampling, and biomass and filtering estimates**

Zooplankton samples were collected April through October biweekly during 1987–1989 and weekly during 1990–2013 at a 20 m deep site centrally located in the south basin of the lake, as vertical net hauls extending from a depth of 15 m to the surface. This site is generally representative of conditions in the pelagic zone (Effler 1996). Samples were subjected to a preliminary analysis for the presence of noteworthy *Daphnia* densities; those with densities $>\sim$10 animals L$^{-1}$ received more detailed analysis. A conical net (75 µm mesh) was used through 1999, and a Wisconsin net (64 µm mesh) was used starting in 1999 (the 2 nets yielded comparable results for 1999). Samples were preserved with formalin (8%) through 2000 and with ethanol (70%) thereafter.

*Daphnia* individuals were identified to species, enumerated, and their body lengths (L, in mm) measured (top of the eye to the base of the tail spine) for 25 specimens for each of the important species, a subset of the enumerated individuals.

Dry-weight (dw) biomasses for individual *D. mendotae* ($M_{D/m}$; μg individual$^{-1}$) and *D. pulicaria* ($M_{D/p}$; μg individual$^{-1}$), the 2 dominant taxa in Onondaga Lake when high SD events occurred, were calculated from L according to (Lynch et al. 1986):

$$M_{D/m} = 5.48 L^{2.200}$$

$$M_{D/p} = 10.674 L^{2.093}$$
Mass estimates for *D. ambiguа* and *D. retrocurva* (only observed in relatively low concentrations) were made using equation 3. The areal dry weight biomass (e.g., Lampert 1988), $B_{dw/a}$ (g dw m$^{-2}$), was calculated according to

$$B_{dw/a} = \frac{\overline{M}_B \cdot N_h}{A_n \cdot K_f}, \quad (4)$$

where $\overline{M}_B$ is the average mass of *Daphnia* individuals, $N_h$ is the number of *Daphnia* collected in the net haul, $A_n$ is the area of the net opening, and $K_f$ is the net efficiency. A value of $K_f = 0.5$ was adopted, consistent with the range of values (0.4–0.6) reported for eutrophic Lake Mendota (Wisconsin, USA) with similar equipment (Rudstam et al. 1993, Kasprzak et al. 1999).

We estimated *Daphnia* filtering rate (mL animals$^{-1}$ d$^{-1}$) in 2 different ways to represent variations that accompany selection of specific algorithms. The first depends only on $L$, as developed by Knoechel and Holtby (1986a):

$$F_{KH} = 11.695 \text{ L}^{2.48}. \quad (5)$$

This simple model (designated KH) has been reported to perform well (Knoechel and Holtby 1986a, 1986b), providing reasonable approximations (Lampert 1988), and is widely used (e.g., Sarnelle 1992). The other expression, which depends on both $L$ and temperature ($T$), was reported by Burns (1969; designated B/T):

$$F_{B/20} = 4.992 \text{ L}^{2.8}, \quad (6)$$

where $F_{B/20}$ is the filtering rate at 20 °C (mL animal$^{-1}$ d$^{-1}$). The rate at the ambient $T$ is calculated according to an Arrenhius relationship:

$$F_{B/T} = F_{B/20} \Theta^{T-20}, \quad (7)$$

where the coefficient $\Theta$ was specified as 1.1048 for *D. mendotae* and 0.9938 for *D. pulicaria*, corresponding to values reported for *D. galeata* and *D. pulex* (Burns 1969), respectively.

The hypolimnion (i.e., depths >8 m) is mostly anoxic from late spring to early fall (Matthews and Effler 2006), often restricting *Daphnia* to the epilimnion and upper oxic portions of the metalimnion, and always within the 15 m haul depth interval. The overall filtering by *Daphnia* per unit volume of oxic lake water ($F_x$, mL L$^{-1}$ d$^{-1}$), was calculated as:

$$F_x = \frac{\overline{F}_{Da} \cdot N_h}{V_{nDO} \cdot K_f}, \quad (8)$$

where $\overline{F}_{Da}$ is the average filtering rate of *Daphnia* individuals, and $V_{nDO}$ is the volume of the net haul for the portion of the water column for which the dissolved oxygen concentration (DO) was ≥1 mg L$^{-1}$. The adjustment for the fraction of the net haul volume that was oxic, from the paired DO profile (Matthews and Effler 2006), was generally consistent with the observations of Haney (1973) for eutrophic Heart Lake (Ontario, Canada) and with protocols adopted by Lathrop et al. (1999) in representing long-term *D. pulicaria* and *D. mendotae* concentrations for Lake Mendota.

Implications of the *Daphnia* populations for clarity (SD) were evaluated using long-term paired measurements of SD and epilimnetic Chl-$a$, with methods described by Effler et al. (2008b). These datasets have been extended (2008–2013) in support of this analysis. More frequent SD and Chl-$a$ measurements (i.e., >1 wk$^{-1}$) were made in some years, without zooplankton monitoring, to improve temporal resolution of these features during high SD events.

**Mineralogic particle size contributions to $b_m$**

In this study we focused on the methods that support resolution of the particle size distributions (PSDs) of the mineralogic particle populations and the associated size dependencies of $b_m$ for Onondaga Lake. We characterized ~1500 individual mineralogic particles with SAX for each of 32 weekly samples, collected from the upper waters at the same pelagic monitoring site over the April–September interval of 2010 (Effler and Peng 2012). SAX provides both the morphometric and X-ray composition information necessary to support forward Mie theory-based estimates of $b_m$ and partitioning of contributions of chemical and size classes to $b_m$, as described elsewhere (Peng and Effler 2007, 2010, Peng et al. 2009). SAX protocols with respect to sample preparation and instrument methodology have been described (Peng and Effler 2007, Peng et al. 2009), including specifically for these samples (Effler and Peng 2012).

Mie scattering theory provides an exact solution to Maxwell’s equations that describe the scattering of an electromagnetic wave (light) by a homogeneous sphere (macroscopic particle). One of the important outputs of the calculation is the scattering efficiency factor for a single sphere, which depends on size, composition, and wavelength. The forward Mie theory-based estimates of $b_m$, based on SAX information for multiple mineralogic particles, were made according to Peng and Effler (2007) and Peng et al. (2009):

$$b_m(\lambda) = \frac{1}{V} \sum_{i=1}^{N_4} Q_{bm,j}(m_i, \lambda, d_i) PA_{m,j}, \quad (9)$$

where $\lambda$ is the wavelength of light (specified as 660 nm here; Effler and Peng 2012), $V$ is the sample volume, $N_m$ is...
the number of minerogenic particles in the sampled volume of water, \( Q_{bm} \), is the scattering efficiency of minerogenic particle \( i \), and \( PA_{mi} \) is the projected area of minerogenic particle \( i \) determined by SAX. The value of \( Q_{bm} \) depends on particle size \( d \), the complex refractive index \( m \), function of particle composition), and \( \lambda \). Values of \( m \) were specified according to the X-ray composition of the particles (Peng and Effler 2010) based on literature listings for various minerals (e.g., Wozniak and Stramski 2004).

PSDs are presented as a density function, \( F(d) \) (Peng and Effler 2007, Peng et al. 2009):

\[
F(d) = \frac{1}{V} \frac{\Delta N}{\Delta d},
\]

(10)

where \( \Delta N \) is the number of minerogenic particles in size interval \( \Delta d \). The size dependencies of \( b_m \) for the various samples are presented in a cumulative format (Peng and Effler 2007, Peng et al. 2009). PSDs and size dependencies of \( b_m \) are presented for all 32 samples; 2 have been presented previously (Effler and Peng 2012).

Secchi depth (SD) model and application

The clarity (SD) model is mechanistic in that it implements the contrast transmittance theory expression (Tyler 1968, Preisendorfer 1986) that represents the effects of light-attenuating processes \( (b_p \) dominant for SD) and partitions these according to the contributions of individual attenuating constituents through summations (Babin et al. 2003a, 2003b; Effler et al. 2008b). The model was fully described and tested for Onondaga Lake previously (Effler et al. 2008a) and evolved from 2 earlier versions (Effler et al. 2001, 2005). The model considers spectral average values of attenuating components over the 510–540 nm wavelength interval (Effler et al. 2008b) to accommodate the effect of the eye’s photopic response on SD measurements. Specification of model coefficients was based on the results of independent system-specific optical studies (Perkins et al. 2010, 2014). Estimates of \( b_o \) were based on the following empirical Chl-\( a \)-based expression (Loisel and Morel 1998):

\[
b_o (660) = 0.347\cdot[\text{Chl}–a]^{0.766},
\]

(11)
as described by Peng and Effler (2011). The good closure of the summation of \( b_o + b_m \) with bulk measurements of \( b_o \) demonstrated for Onondaga Lake (Effler and Peng 2012) further supports the overall SD model for the lake (Effler et al. 2008a).

The model has a probabilistic framework that represents the effects of uncertainty and variability of inputs (e.g., variations in the dependence of \( b_o \) on Chl-\( a \); see equation 11) on model predictions through specified distributions and Monte Carlo calculations (Effler et al. 2008b). The model was applied here to generate a nomograph that describes the dependence of SD (y-axis) on Chl-\( a \) (x-axis) and \( b_o \) (different values as a family of curves), with model predictions presented here as means. The nomograph could instead be presented with \( b_o \) (equation 11) as the x-axis, but Chl-\( a \) is preferred here to make its interplay with SD and \( b_o \) more meaningful to a broader audience. This application of the model focuses on relatively low Chl-\( a \) levels (\( \leq 5 \mu g\ L^{-1} \)) consistent with occurrences of a high SD event for this lake.

Results

Seasonal patterns of Daphnia and related features

Seasonal patterns are illustrated for 2 years with high SD events, 1991 (Fig. 2a–f) and 2008 (Fig. 2g–l), representative of periods of eutrophy and mesotrophy, respectively. Two distinct population peaks of \( D. mendota \) occurred in 1991, in late May and late June (Fig. 2a). No other species of \( Daphnia \) were observed in that year. Average body length increased from ~0.9 to 1.3 mm from early May to early June, then decreased to ~0.75 mm at the time of the second population density peak, and increased thereafter (Fig. 2b). The patterns of the estimates of biomass (Fig. 2c) and filtering rates (Fig. 2d) had single major peaks coincident with the first peak in population density. The peak \( Daphnia \) areal biomass was ~25 g dw m\(^{-2}\). Filtering rates estimated by the KH method were about twice those of the B/T method in 1991, and the respective maxima in late May were ~4000 and 2000 mL L\(^{-1} \) d\(^{-1}\). Levels of Chl-\( a \) were at the seasonal minimum (0.65 \( \mu g\ L^{-1} \); Fig. 2a), and SD values were conspicuously higher (a high SD event), spectra, and seasonal maximum (Fig. 2f) when \( D. mendota \) were at the seasonal minimum (0.65 \( \mu g\ L^{-1} \); Fig. 2a), and SD values were conspicuously higher (a high SD event), including the seasonal maximum (Fig. 2f) when \( Daphnia \) biomass (Fig. 2c) and filtering (Fig. 2d) were near maximal. A Chl-\( a \) minimum and a second, although diminished, high SD event coincided with the second \( Daphnia \) population density (Fig. 2a) and estimated filtering (Fig. 2d) peaks in late June. Much higher Chl-\( a \) concentrations and low SD levels prevailed over the mid-July through September interval.

While intervals of low Chl-\( a \) and high SD in 2008 also coincided with elevated \( Daphnia \) densities, there were several noteworthy differences from the 1991 patterns. \( D. mendota \) was dominant, but \( D. retrocurva \) was also present for most of the same interval (Fig. 2g). Maximum densities of \( Daphnia \) occurred in late summer in 2008 instead of late spring to early summer (1991), and densities did not reach the levels reported for 1991 (Fig. 2g and 2a, respectively). Except for an early August peak in body length (\( L = 1.2 \) mm), mean length in 2008 (Fig. 2h) was
lower than in 1991 (Fig. 2b). Peak biomass (~6 g dw m\(^{-2}\); Fig. 2i) and filtering rates (Fig. 2l) were lower than in 1991 (Fig. 2l). The KH and B/T filtering rate estimates were more similar in 2008 (Fig. 2j). The differences for these 2 years with the B/T relationship were not as great as those obtained with the KH algorithm because of the differences in T during the intervals of elevated Daphnia populations. The Ts at the times of estimated peak grazing were 18 and 23.5 °C in 1991 and 2008, respectively (Fig. 2j). Chl-a levels (Fig. 2k) were lower and SD (Fig. 2l) decidedly higher outside of the Daphnia interval in 2008 compared with 1991, consistent with the shift in trophic state.

**Long-term patterns for Daphnia and high clarity events**

Strong interannual differences in the Daphnia population, features of its timing, and the concurrent SD levels occurred over the 27-year record (Fig. 3). Peak areal Daphnia biomass levels were <0.5 g dw m\(^{-2}\) in 9 years when the lake was mesotrophic (Fig. 1), the 2002–2007 and 2010–2013 intervals (Fig. 3a), and in certain years, Daphnia was virtually absent. Noteworthy Daphnia biomass maxima occurred in each of the 2 intervening years of 2008 and 2009. The annual peak Daphnia areal biomass in the other 18 years exceeded 4 g dw m\(^{-2}\) (Fig. 3a). Daphnia maxima were particularly high (>20 g dw m\(^{-2}\); e.g., Lampert 1988) in 1990, 1991, 1993 (nearly 60 g dw m\(^{-2}\)), and 1995–1997. The long-term pattern of the annual maxima of the filtering (or grazing) rate estimates (Fig. 3b) was strongly correlated with the pattern for biomass maxima (Fig. 3a; r = 0.9 and 0.8 for KH and B/T expressions, respectively), consistent with their shared dependencies on population density and individual body length. The peak grazing rates ranged from ~0.5 × 10\(^{3}\) mL L\(^{-1}\) d\(^{-1}\) (0.5 d\(^{-1}\)) in 2002 to ~8 × 10\(^{3}\) mL L\(^{-1}\) d\(^{-1}\) (8 d\(^{-1}\)) in 1996 according to the KH expression, and from 0.15 to 3.4 d\(^{-1}\) according to the B/T relationship (Fig. 3b). During the 2 years (2008–2009) of mesotrophy when Daphnia were relatively abundant, both the biomass and filtering rate maxima were nevertheless lower than in all but 2 of the earlier years of hypereutrophy.

![Fig. 2. Within-year times series for Onondaga Lake for 2 years: (a) Daphnia density, 1991; (b) Daphnia length, 1991; (c) Daphnia biomass, 1991; (d) Daphnia filtering rate and temperature, 1991; (e) Chl-a, 1991; (f) SD, 1991; (g) Daphnia density, 2008; (h) Daphnia length, 2008; (i) Daphnia biomass, 2008; (j) Daphnia filtering rate and temperature, 2008; (k) Chl-a, 2008; and (l) SD, 2008. Shading shows intervals of high SD events. Two estimates of filtering rates in (d) and (j).](image-url)
Annual SD maxima were significantly \((p < 0.001)\) lower for the 9 years when *Daphnia* biomass levels remained below the 0.5 g dw m\(^{-2}\) threshold (Fig. 3c). The SD maxima in those years were all <3.5 m, representing a system-specific empirical threshold for the presence of dense populations of *Daphnia* that was not exceeded in the 2010–2013 interval, despite the shift in trophic state. SD \(\geq 3.5\) m was generally not exceeded in the absence of a substantial *Daphnia* population (>0.54 g dw m\(^{-3}\)). The only exception encountered for the coupling of SD \(\geq 3.5\) m and *Daphnia* was in late June 2008 (Fig. 2l) when an observation of SD = 3.8 m was instead associated with a dense population of *Bosmina* (~1500 animals L\(^{-1}\)), with an estimated filtering rate of 750 mL L\(^{-1}\) d\(^{-1}\) (0.75 d\(^{-1}\)). The 3.5 m threshold was used as a diagnostic in describing timing features of the high SD events that accompanied substantial *Daphnia* populations, such as their onset and duration. For example, in some years the annual biomass maximum occurred at the same time as the onset of the CWP, while in others the *Daphnia* peak occurred at a different time and was much greater than when the CWP started (Fig. 3a). The SD maxima for years with the *Daphnia*-based SD events ranged from 4.9 m (1987 and 2009) to 7.8 m (1993; Fig. 3c). A cause-and-effect relationship between the *Daphnia* biomass and associated grazing rate estimates and the high clarity signature is supported by linear least-squares regression analyses. Variation in the annual peak biomass explained 49% \((p = 0.0026)\) of the interannual differences in the SD maximum (1/SD format; Davies-Colley et al. 2003; Fig. 4a). Variation in the estimated annual peak grazing rate explained 66% \((p = 0.0025)\) and 63% \((p = 0.002)\) of the interannual differences in the maximum SD based on the KH and B/T relationships, respectively (Fig. 4b). Two distinct, high SD events, separated by a short-term increase in Chl-a and decrease in SD as described for 1991 (Fig. 2e and f), were observed in 8 consecutive years during 1988–1995 and again in 1999, 2001, and 2009 (Fig. 3c).

*Daphnia mendotae* was dominant at the biomass maxima in all years with high SD events except in 1993 and 1995, when *D. pulicaria* dominated (Fig. 3d). Average body lengths (L) at the time of peak biomass ranged from \(~1\) to 1.65 mm (Fig. 3e). The highest biomass values were observed in the years *D. pulicaria* dominated. Low densities were observed for 2 smaller *Daphnia* species, *D. retrocurva* (2007 and 2008) and *D. ambigua* (2009). The timing of the peak *Daphnia* biomass varied from late May to early July during 1988–2002 but occurred in mid-July in 1987 and August in 2008 and 2009 (Fig. 3f). In 7 years the onset of the high SD interval (adopting the SD = 3.5 m threshold) preceded the peak biomass by \(>20\) d. Wide differences in ambient T accompanied the variation in the onset of the events, ranging from \(~10\) to \(>20\) °C. No
significant relationships between these T differences and *Daphnia* biomass levels were observed. The duration of the high clarity (SD > 3.5 m) events ranged from ~1 week (1987, 2000, and 2002) to 6 weeks (1993) for the 1987–2002 period and extended to 7 weeks in 2008 (Fig. 3g). The 2 years of the earlier period with the longest duration were those in which *D. pulicaria* dominated. The duration of the high SD events during 1987–2002 was significantly positively related to the peak *Daphnia* biomass. Variations in the annual peak biomass explained 45% (p = 0.0047) of the interannual differences in the duration according to linear least-squares regression (Fig. 4c).

**Particle size distribution (PSD) of minerogenic particle populations and size dependencies of \( b_m \)**

The minerogenic particles in 2010 varied widely in concentration among sampling dates but exhibited a distinct PSD that was generally recurring in overall shape (Fig. 5a). More than an order of magnitude variation in concentrations was observed throughout the particle size diameter (d) range of 0.2 to 10 µm. Peak F(d) values occurred mostly at a d ~0.4 µm. No PSDs consistent with the Junge function, monotonic increases in F(d) with decreasing d, were observed.

Despite the high concentrations of minerogenic particles with d <0.5 µm, these small particles did not make noteworthy contributions to \( b_m \) in any sample (Fig. 5b). Contributions by submicron particles were minor, representing <10% of \( b_m \) and much less (~1%) for several samples. The upper size limit of noteworthy (>1%) contributions ranged from ~7 to 30 µm; for 38% of the samples the limit was ≤10 µm.

**Secchi depth (SD) and Chl-a observations in the context of the SD model, and the effect of *Daphnia***

Predictions of the previously validated (Effler et al. 2008b) SD model of the dependence of SD on both Chl-a (e.g., \( b_o \); equation 11) and \( b_m \) are presented in the form of a nomograph (Fig. 6a), with the SD threshold (3.5 m) for a high SD event included for reference. Two hypothetical trajectories (cases D and E) are included for illustration of the effects of the 2 components of scattering (Chl-a and \( b_m \)). At a Chl-a = 2 µg L\(^{-1}\) and an initial \( b_m = 5 \text{ m}^{-1} (D) \), the SD would be about ~1.3 m (Fig. 6a). A 5-fold decrease of \( b_m \) at the same Chl-a level would be necessary to reach the 3.5 threshold, and a 10-fold decrease to reach an SD of...
Daphnia grazing, the clear water phase, and implications of minerogenic particles in Onondaga Lake

~4.7 m ($D_3$, Fig. 6a). The other case (E) instead tracks a curve of constant $b_m$ and considers a trajectory moving from an initial Chl-$a = 4$ µg L$^{-1}$ ($E_1$, Fig. 6a). This trajectory also moves from below (~2.7 m) to above (~4.3 m) the threshold. More likely trajectories from grazing effects would reflect concurrent decreases in both $b_m$ and Chl-$a$.

Paired observations of SD and Chl-$a$ were added to the same nomograph for the 1987–2002 period for cases of SD meeting the high SD event threshold (SD ≥ 3.5 m), with designations of the levels of Daphnia biomass included (Fig. 6b). In this format, the position of points of the paired SD and Chl-$a$ observations corresponds to the $b_m$ value predicted by the SD model. This format is illustrated for 2 selected sets of observations designated “f” and “g” (Fig. 6b). The SD = 5.6 m and Chl-$a = 0.6$ µg L$^{-1}$ that correspond to “f” are predicted to be accompanied by a $b_m$ ~ 0.65 m$^{-1}$ (see position among family of $b_m$ values; Fig. 6b). The conditions of the “g” observations are predicted to correspond to an even lower $b_m$ value (~0.25 m$^{-1}$). Values of $b_m < 1$ m$^{-1}$ were predicted to be necessary in most cases to explain the exceedance of the threshold for the high SD events. A robust array of combinations of Chl-$a$ and $b_m$ levels were apparently responsible for the high SD values of the events (Fig. 6b). Particularly high Daphnia biomass levels coincided with many of the highest SD values and associated low levels of Chl-$a$ and $b_m$ (Fig. 6b).

The population of paired SD and Chl-$a$ observations and associated predictions of $b_m$ for the case of Chl-$a ≤ 5$ µg L$^{-1}$, but with no or low (<0.5 g dw m$^{-2}$) Daphnia (Fig. 6c; 2003–2007, 2010–2013), presents a strong contrast to the conditions during the high SD events (Fig. 6b). All the SD observations were less than the threshold. The value of $b_m$ was predicted to be >1 m$^{-1}$ in all cases, and >2 m$^{-1}$ for most cases. Despite occurrences of similarly low Chl-$a$ levels to those observed during the earlier high SD events when Daphnia were prominent, SD remained below the 3.5 m threshold. Review of the differences in SD between the Daphnia (Fig. 6b) and no-Daphnia (Fig. 6c) cases for similarly low Chl-$a$ levels establishes that the much higher SD observations of the Daphnia case were a result of lower $b_m$ levels.

Discussion

The clear water phase (CWP) and minerogenic particles

Analysis of the monitoring record for Chl-$a$ and SD for Onondaga Lake, considered in the context of accepted optical theory for SD (Fig. 6; Effler et al. 2008b), shows that co-occurring decreases in both Chl-$a$ (i.e., $b_o$) and $b_m$ were necessary to explain the observed major increases in SD (the high clarity events). Furthermore, there is strong indication that the low Chl-$a$ and $b_m$ of the high SD events were caused by Daphnia grazing; that is, these were classic CWP events. These conclusions have both empirical and mechanistic support.

We consider the empirical evidence first. Seasonal patterns within years when Daphnia populations were substantial (Fig. 2) are consistent with the widely reported CWP signatures of minimum Chl-$a$ and maximum SD occurring at the time of peak Daphnia biomass (Lampert et al. 1986, Sommer et al. 1986, Lampert 1988, Kasprzak et al. 1999). Peak Daphnia biomasses are consistent with
levels reported as adequate to cause the CWP. The *Daphnia* biomass necessary to cause a CWP is expected to be greater as the rate of phytoplankton growth increases (Lampert 1988, Kasprzak et al. 1999, Schalau et al. 2008). Lampert (1988), reviewing the literature, found that a *Daphnia* biomass of 1.5 g dw m\(^{-2}\) could cause a CWP in oligotrophic lakes, but that at least 4 g dw m\(^{-2}\) was necessary for eutrophic systems. That eutrophic threshold (4 g dw m\(^{-2}\)) was exceeded in Onondaga Lake in all the years with high clarity events (Fig. 3a), and by a wide margin in most of the years of eutrophy. Whereas the highest *Daphnia* biomass maximum during a CWP that Lampert (1988) found in his review was 26.9 g dw m\(^{-2}\) in eutrophic Greifensee (Bürgi et al. 1985), the biomass peaks in Onondaga Lake exceeded this Greifensee maximum in 1993, 1995, and 1996. Although the number of years with a CWP when mesotrophy prevailed was small (2008 and 2009), we note the consistency of the lower *Daphnia* biomass levels in those years with Lampert’s (1988) hypothesis of trophic state dependence. Finally, the central role of *Daphnia* in regulating the clarity events is seen in the strong positive relationships between maximum *Daphnia* biomass and grazing rates as well as the peak SD values and the duration of the CWP events (Fig. 4). We believe this is the first case of resolution of these dependencies from a long-term record for a single system.

Establishing that grazing rates during the CWPs exceeded reasonable upper bounds of phytoplankton growth rates represents mechanistic evidence (Lampert 1988) that the periods of high clarity were in fact CWP events. Although the absence of direct rate measurements and limitations of certain protocols (e.g., constant net efficiency and representativeness of 25 individual subset for sizing) introduces uncertainties, we suggest that the evidence is nevertheless compelling because the margin by which the grazing estimates exceed reasonable levels of phytoplankton growth is large. Lampert (1988) found that grazing estimates by the KH method were correlated with, but about 50% lower than, direct grazing measurements in Schöhee (Germany). Algorithms to estimate grazing rates, as adopted here, have been widely used (Lampert 1988, Sarnelle 1992, Kasprzak et al. 1999), particularly for long-term and cross-sectional datasets where the conduct of direct measurements throughout the study period has practical limitations. Moreover, the performance of the peak grazing rate estimates for both algorithms in explaining peak SD for the various years (Fig. 4c) supports these estimates as meaningful. Maximum specific growth rates for phytoplankton vary within the range of ~0.2–1.8 \(d^{-1}\), depending on the species (Reynolds 2006). In-lake rates are substantially diminished (e.g., several-fold: \(<0.5\ d^{-1}\)), however, due to the effects of non-ideal temperature(s), light, and nutrient conditions (Chapra 1997, Reynolds 2006). Moreover, there are respiration and sinking losses for phytoplankton in addition to grazing (Lampert 1988, Chapra 1997). All of the estimated peak KH grazing rates (range 0.55–8.2 \(d^{-1}\)) and all but one of the B/T rates (exception, 0.15 \(d^{-1}\) in 2002) exceed reasonable upper bounds of phytoplankton growth rates (Fig. 3b), supporting the conclusion that *Daphnia* grazing was responsible for the observed accompanying decreases in Chl-a to low levels.

The application of the mechanistic SD model (Fig. 6), together with the paired SD and Chl-a observations both when the lake was hypereutrophic and more recently since mesotrophy has prevailed, establishes that the coincident reduction in \(b_m\) (e.g., from the levels in Fig. 6c to those in Fig. 6b) was responsible for the dramatic increases in SD (Fig. 3c) that characterize the CWP in Onondaga Lake. In other words, the decreases in \(b_m\) (i.e., Chl-a) alone cannot explain the high SD values observed during the CWP. Concurrent decreases in \(b_m\) were also required (Fig. 6b). The subsequent failure to exceed the 3.5 m CWP threshold, despite low Chl-a levels, can only be explained by the maintenance of high \(b_m\) levels (Fig. 6c) that prevail in the lake in the absence of *Daphnia* grazing (Effler and Peng 2012). Moreover, the particle size dependency of \(b_m\) for the lake (Fig. 5b) shows that minerogenic particles responsible for \(b_m\), an important component of \(b_b\) (and thereby SD), are in the size range that would be removed by *Daphnia* grazing (Lampert 1987, Hambright et al. 2007). The numerous smaller (<0.5 µm) minerogenic particles that would not be influenced by grazing are not important to SD because of their much lower scattering efficiencies (Peng and Effler 2012) and small contribution to overall projected area (equation 9). Further, the sizes contributing to \(b_m\) (Fig. 5b) are generally similar to those for edible algae (Perkins et al. 2014), eliminating the possibility of a secondary effect of differences in filtering efficiencies of phytoplankton versus minerogenic particles based on size differences (Knoechel and Holtby 1986b).

A similarly important role of grazing of minerogenic particles for the SD signature of the CWP is expected in other *Daphnia* lakes where \(b_m\) makes substantial contributions to \(b_b\) (represented by the ratio \(b_m:b_b\)). The growing list of lakes for which minerogenic particles have been characterized by SAX, and the reported substantial \(b_m:b_p\) values (Table 1), suggests the important effect of these particles found here occurs widely. Multiple lakes characterized by SAX were found to have similar or higher \(b_m:b_p\) ratios to that reported for Onondaga Lake (Table 1). A number of features of the minerogenic particle population described for Onondaga Lake are recurring, including (1) the dominance of clay mineral (i.e., allochthonous) particles, (2) the general shape of the PSDs (Fig. 5a; Peng and Effler 2007, 2010, 2011), and (3) particles in the size range of 1–10 µm, sometimes extending up to 20 or 30 µm, responsible for \(b_m\).
Autochthonously produced calcite (whiting events; Homa and Chapra 2011), another source of $b_{\text{in}}$, is expected to have a similar interplay with Daphnia grazing because the responsible particles are also well within the 1–10 μm size range (Peng et al. 2007, Peng and Effler 2011).

Drivers of variation in the Daphnia population and other ecological signatures of the CWP

The parallel datasets for fish for the 27-year period of this study are uneven with regard to monitoring protocols and coverage. Hydroacoustic surveys commenced in 2003. These data provide compelling evidence that the virtual absence of Daphnia in certain recent years (2003–2007 and 2010–2013; Fig. 3a) was due to large populations of the alewife (Alosa pseudoharengus; 1600–2300 fish ha$^{-1}$; Wang et al. 2010, Onondaga County 2013). The alewife preferentially and efficiently feeds on large Daphnia (Brooks and Dodson 1965). Such top-down food effects (planktivores → Daphnia → phytoplankton biomass → SD) have been described as a “trophic cascade” (e.g., Carpenter et al. 1985, Carpenter and Kitchell 1993). The return of Daphnia and the CWP in 2008 and 2009 apparently was a result of the substantial diminishment of the alewife population in those years (~110 fish ha$^{-1}$; Wang et al. 2010). Alewife had a strong year class in 2002 (Wang et al. 2010), a year with one of the weakest CWP signatures.

Monitoring of the fish community from the late 1980s through the mid-1990s with different methods indicated that relatively inefficient planktivores, including white perch and gizzard shad, were common whereas the alewife was rare (Ringler et al. 1996). Poorly resolved variations in the level of planktivory likely contributed to the variability in the Daphnia populations over the 1988–2001 period, including peak biomass (Fig. 3a), size (L; Fig. 3e), and composition (D. pulicaria vs. D. mendotae; Fig. 3d). Daphnia pulicaria is generally favored by low planktivory (Rudstam et al. 1993, Lathrop et al. 1999). The systematic increase in the alewife population in recent years has been attributed to reductions in free ammonia concentrations in the lake (Wang et al. 2010) in response to decreases in loading of ammonia from the domestic wastewater treatment facility (Effler et al. 2013). Given the widely observed large fluctuations of alewife populations, in part related to their sensitivity to particularly cold winter temperatures (Ridgeway et al. 1990, Dunlop and Riley 2013), the irregular return of substantial Daphnia populations in the future is likely. The first year of this study, 1987 (small CWP signature; Fig. 3a, 3c, and 3g), represents the transition from an extended period of high lake salinity (from industrial discharges), which eliminated Daphnia species common to the region, to lower contemporary salinity levels (Hairston et al. 2005).

Daphnia populations can have important effects on the cycling of various materials (Lampert et al. 1986, Pitsch et al. 2012). Other conspicuous signatures of Daphnia metabolism beyond clarity (SD) have been reported for Onondaga Lake for portions of this study period. For example, short-term increases of the concentration of soluble reactive P have been documented during CWPs (Effler and O’Donnell 2010), associated with excretion by Daphnia (Lampert et al. 1986, Urabe 1993, Urabe et al. 1995, Hambright et al. 2007). Recurring short-term decreases in downward flux (assessed with sediment traps) of particulate organic carbon, nitrogen, P, and Chl-a were reported for the lake during CWPs (Effler et al. 2012).

SD signature of the CWP

Water clarity (SD) is closely coupled to the public’s perception of water quality (Effler 1985, Smith and Davies-Colley 1992). Improvements in SD are both sought and expected as part of rehabilitation programs for cultural eutrophication (Cooke et al. 2005). Earlier bio-maniipulation (top-down) approaches focused on improved clarity, without substantial changes in trophic state, through increasing the populations of large daphniids (Shapiro and Wright 1984, Carpenter et al. 1985).

Temporal variations in the top-down effect of the CWP have complicated the SD signature of the nutrient-based (bottom-up) rehabilitation program for Onondaga Lake (Fig. 1d; Effler et al. 2008b, 2013). The CWP offered varying degrees of short-term relief from the generally low SD conditions that accompanied hypereutrophy during 1987–2002. The extent of the relief depended on the biomass of Daphnia that developed in each of those years (Fig. 4a and 4c). The absence of the CWP in most of the recent years of mesotrophy has resulted in some deterioration of SD levels, as seen in annual summary metrics (worse when based on historic means instead of median values; Fig. 1d), particularly when compared with much of the earlier period of hypereutrophy. This counter-intuitive pattern demonstrates the need for recognition of the implications of Daphnia grazing (top-down effects) in interpreting typical monitoring data. Resolution of the clarity benefits (SD) of the bottom-up rehabilitation program associated with systematic reduction of Chl-a (i.e., $b_{\text{in}}$) requires grouping of years according to the occurrence of the CWP. For example, average SD values in 2010–2013 are nearly twice those that prevailed before 1987 when the CWP was also absent (Hairston et al. 2005, Effler et al. 2008b). Evaluations within the population of years that experience the CWP are more imperfect because of the wide interannual variations in the extent of the event (e.g., peak biomass and duration; Fig. 3a, 3c, and 3g), not because of variations in the extent of the bottom-up effects (Effler et al. 2008a).
The SD threshold of ≥3.5 m to identify periods of substantial grazing effects has been demonstrated to be 100% effective when all cladocerans are considered and 98% effective (423 of 424 weekly observations) for *Daphnia* alone for Onondaga Lake over a wide range of trophic state. The optical signature of increased SD has a rigorous optical basis (Davies-Colley et al. 2003, Effler et al. 2008b), reflecting the effects of reductions in both $b_m$ and $b_p$ (equation 1) from the nonselective feeding by daphnids on both phytoplankton and minerogenic particles. The SD threshold established here demonstrates the diagnostic value in characterizing features of the CWP (Fig. 3c, f, and g); however, the 3.5 m value is system-specific, and values for other lakes would be influenced primarily by ambient levels of $b_m$ (e.g., Table 1). Long-term monitoring datasets that include paired SD, Chl-a, and appropriate *Daphnia* observations (e.g., Fig. 2a–c) could support establishment of such system-specific threshold values.

Several features make our analysis for Onondaga Lake a valuable addition to the case studies of CWP events and the associated SD signatures: (1) the long-term monitoring record supporting the analysis, (2) the major variations in *Daphnia* population densities and occurrences of the CWP

### Table 1. Contributions of minerogenic particles to scattering ($b_m:b_p$) in multiple lakes, with references.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Date</th>
<th>No. of Samples</th>
<th>$b_m : b_p$ (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross Lake, NY</td>
<td>July 2005</td>
<td>2</td>
<td>24.9 and 37.0</td>
<td>Peng et al. 2007</td>
</tr>
<tr>
<td>Onondaga Lake, NY</td>
<td>July 2005</td>
<td>1</td>
<td>30.2</td>
<td>Peng et al. 2007</td>
</tr>
<tr>
<td>Otisco Lake, NY</td>
<td>July 2005</td>
<td>2</td>
<td>31.0 and 57.6</td>
<td>Peng et al. 2007</td>
</tr>
<tr>
<td>Owasco Lake, NY</td>
<td>July 2005</td>
<td>1</td>
<td>22.2</td>
<td>Peng et al. 2007</td>
</tr>
<tr>
<td>Skaneateles Lake, NY</td>
<td>July 2005</td>
<td>1</td>
<td>20.0</td>
<td>Peng et al. 2007</td>
</tr>
<tr>
<td>Seneca River, NY</td>
<td>July 2005</td>
<td>3</td>
<td>63.5 (45.2–94.2)</td>
<td>Peng et al. 2007</td>
</tr>
<tr>
<td>Lake Superior, Keweenaw Bay</td>
<td>July 2006</td>
<td>5</td>
<td>35.6 (21.8–46.6)</td>
<td>Peng et al. 2009</td>
</tr>
<tr>
<td>Lake Erie, central basin</td>
<td>Sep 2007</td>
<td>1</td>
<td>22.9</td>
<td>Peng and Effler 2010</td>
</tr>
<tr>
<td>Western Lake Erie</td>
<td>Sep 2007</td>
<td>10</td>
<td>82.4 (57.2–94.4)</td>
<td>Peng and Effler 2010</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>Aug 2007</td>
<td>7</td>
<td>31.8 (16.3–53.6)</td>
<td>Peng and Effler 2010</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>Apr 2008</td>
<td>9</td>
<td>14.0 (6.2–25.9)</td>
<td>Peng and Effler 2010</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>Summer 2008</td>
<td>6</td>
<td>29.9 (11.8–54.3)</td>
<td>Peng and Effler 2010</td>
</tr>
<tr>
<td>Onondaga Lake, NY</td>
<td>Apr–Sep 2010, weekly</td>
<td>24</td>
<td>26.3 (3.4–76.7)</td>
<td>Effler and Peng 2012</td>
</tr>
<tr>
<td>Lake Huron</td>
<td>Aug 2008</td>
<td>4</td>
<td>17.0 (12.7–19.6)</td>
<td>unpub.</td>
</tr>
<tr>
<td>Lake Michigan</td>
<td>Aug 2008</td>
<td>6</td>
<td>4.8 (3.3–8.8)</td>
<td>unpub.</td>
</tr>
<tr>
<td>Cayuga Lake, NY, pelagic</td>
<td>Apr–Oct 1999–2006, biweekly</td>
<td>104</td>
<td>23.7 (5.8–84.0)</td>
<td>Effler and Peng 2014</td>
</tr>
</tbody>
</table>

† mean and range in parentheses for more than 2 samples.
over the period of the long-term dataset, (3) the changes in environmental factors that influence the Daphnia population over this period, and (4) the multiple lines of evidence used to establish the occurrences of the CWP. An even more valuable contribution, however, is the new insights we have provided concerning the important effect of minerogenic particles on the SD signature of the CWP. The inclusion of minerogenic particles in the long-term monitoring program for the lake will expand these contributions related to the CWP and the SD signature.

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