

Historic nutrient loading and recent species invasions caused shifts in water quality and zooplankton demography in two Finger Lakes (New York, USA)

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Abstract We investigated the paleolimnology of Owasco and Seneca Lakes (New York, USA) and compiled water-quality monitoring data to describe environmental change during the past two centuries. Trophic shifts were detected in the oligotrophic to mesotrophic range and were likely driven by nutrient loading and species invasion. Based on box core reconstructions, primary production increased in both lakes during the last century, which is evidenced by the amount, type and isotopic composition of material preserved in the sediment. Organic matter accumulation and its stable carbon isotopic composition, as well as carbonate abundance, began to increase during the 1960s in Owasco Lake and the 1850s in Seneca Lake. Further, the abundance of phytoplanktivorous

cladocera subfossils increased beginning in the 1910s in Seneca Lake and in the 1960s in Owasco Lake. The different timing and magnitude of the trophic shifts likely resulted from contrasts in lake residence time and species assemblages between the two lakes. The increases in primary and secondary production paralleled, and are interpreted to reflect, increased allochthonous nutrient loading. However, nutrient loading was not detected in the water-quality data, perhaps because of strong uptake of phosphates by phytoplankton or due to limited data collection. Rapid changes in cladoceran subfossils and water quality were also detected during the last decade. Concurrent with the establishment of non-native *Cercopagis pengoi* (fishhook waterflea), phytoplanktivorous cladocera remains declined, and the mucrone length of *Bosmina* increased, consistent with predictions of increased invertebrate predation. Additionally, the post-1990 decline in sediment carbonate, increased Secchi depth and decreased chlorophyll *a* concentrations followed the establishment of filter-feeding *Dreissena* spp. (zebra and quagga mussels). Collectively, paleolimnological data and water-quality monitoring provided a more complete and consistent record of shifts in the productivity of Owasco and Seneca Lakes, which were useful to understand environmental changes over different time scales. Physical, geochemical and biological changes were temporally consistent among three cores collected from different locations in each lake, but differed in magnitude for several variables (e.g., grain size and

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cladoceran subfossils), which could reflect near-shore to offshore gradients.

Keywords Nutrient loading · Invasive species · Finger Lakes · Productivity · Stable isotopes · Cladoceran remains

Introduction

Describing and quantifying the impact of environmental change in lakes requires continuous records of limnological and/or paleolimnological conditions. For example, eutrophication can be measured in situ during long-term monitoring studies, and/or these changes can be inferred from stable isotope measurements of autochthonous organic matter (Hodell and Schelske 1998; Brenner et al. 1999). Likewise, zooplankton, including preserved remains in sediments, can reflect shifts in productivity and food-web composition (Jeppesen et al. 1996; Hall and Yan 1997; Branstrator et al. 2006). Combining paleolimnology and direct monitoring allows for a more complete understanding of how and why a lake is changing (Jankowski and Straile 2003; Manca et al. 2007). In particular, the use of reconstructed and direct histories is appealing to compare multiple perturbations that occur over different time scales.

There has been concern about environmental shifts (e.g., nutrient loading, invasive species establishment, climate change) in the Finger Lakes of New York State (Brown and Balk 2008; Moran and Woods 2009). However, limited water-quality monitoring was published (Birge and Juday 1914; Schaffner and Oglesby 1978; Effler et al. 1987b) and these data are insufficient to evaluate inter-annual trends and document limnological shifts.

Previous paleolimnological approaches in the Finger Lakes used carbonate preserved in sediments to investigate environmental changes. Mullins (1998) documented a parallel rise in carbonate and atmospheric CO₂ since ~1940, and reasoned CO₂, not phosphorous, might limit primary production. In contrast, Lajewski et al. (2003) noted the rapid rise in carbonate was coincident with increased industrialization and acidic rainfall, and concluded that enhanced chemical weathering of deforested landscapes released calcium and bicarbonate to the lakes, promoting calcite supersaturation. Alternatively,

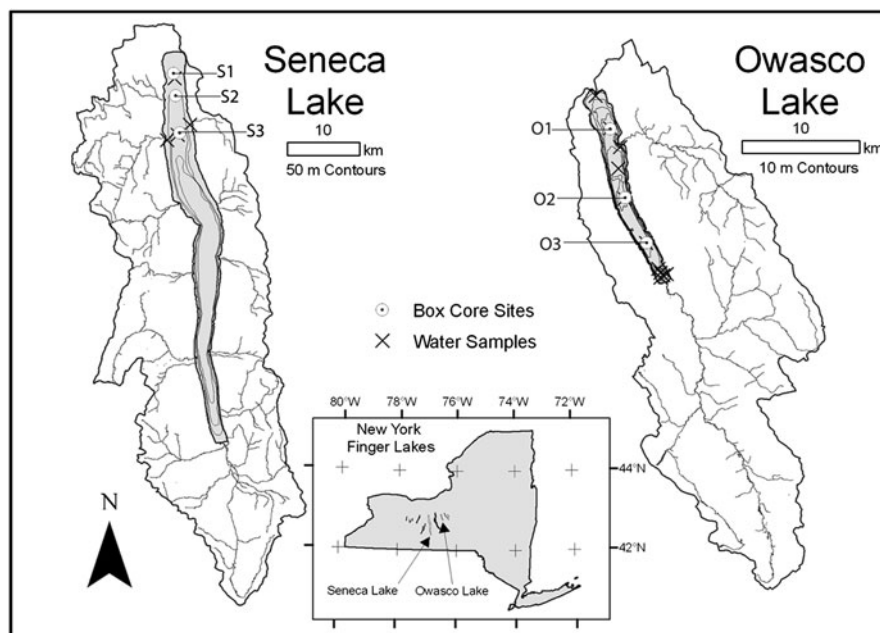
Teranes et al. (1999) suggested the Finger Lakes responded to local changes in nutrient loading. Although at the time there was no evidence for historic nutrient loading in the Finger Lakes, this hypothesis was consistent with documented cultural eutrophication in the Laurentian Great Lakes (Schelske and Hodell 1991, 1995; Hodell et al. 1998; Meyers 2006). The Finger Lakes region experienced similar anthropogenic stresses as the Great Lakes, including population growth, nutrient loading, and species invasions (Schaffner and Oglesby 1978; Lajewski et al. 2003), and these stresses may have played, and continue to play, an important role in changing productivity.

To better contextualize and extend the investigation of environmental change over the last two centuries in the Finger Lakes, we utilized paleolimnology (physical, geochemical, and biological evidence), a literature review of water-quality monitoring data, and our own water-quality data. Our objectives were to: (1) reconstruct trophic status to document primary productivity shifts, (2) characterize pelagic cladocera communities to measure productivity changes at the consumer level, and (3) assess nutrient loading and species invasion as potential drivers that could promote changes in the trophic status and zooplankton assemblages.

Field sites

We focused our study on Owasco and Seneca Lakes (Fig. 1) for which some historic water-quality data existed, and analyzed three cores from different locations in each lake to examine within-lake and inter-lake variability. Owasco and Seneca Lakes share a similar climate and anthropogenic history. Their watersheds are dominated by agricultural and forested land with sedimentary bedrock overlain by till and calcareous soils. Seneca and Owasco Lakes occupy narrow, deep basins. The lakes differ in their annual mixing pattern, mainly due to their contrasting sizes. Owasco Lake (surface area [SA] = 26.7 km², Z_{max} = 54 m, basin SA = 470 km², volume = 0.78 km³) is dimictic, and mixes during spring and autumn. Seneca Lake (SA = 175.4 km², Z_{max} = 186 m, basin SA = 1,181 km², volume = 15.54 km³) is monomictic and mixes completely during winter and spring (Schaffner and Oglesby 1978). The drainage-area to lake-volume ratios result in a shorter water residence time in Owasco Lake (1.5–3 years) compared to

Fig. 1 Location of box core (circles) and water-quality monitoring (crosses) sites in Seneca and Owasco Lakes. For each lake, the watershed is delineated and major tributaries are drawn. Bathymetric contours in Seneca Lake are approximated every 50 m and in Owasco Lake every 10 m. Note that the lakes are shown at different scales. The insert shows the location of Seneca and Owasco Lakes in New York State. Site attributes are given in the captions for Figs. 2 (Owasco Lake) and 4 (Seneca Lake)



Seneca Lake (12–23 years) (Michel and Kraemer 1995).

Materials and methods

Core collection

We used a modified Wildco box corer (internal liner SA: 196 cm²; shaft length: 50.5 cm) to collect three cores from Owasco Lake (cores O1, O2, and O3) and Seneca Lake (cores S1, S2, and S3) in May 2008 (Figs. 1, 2 and 3 provide site attributes). Core sites were chosen to: (1) correspond to deepwater locations where sedimentation rates provided a greater temporal resolution and where hatching stimuli for resting stages of zooplankton were minimal, and (2) overlapped with our water-quality monitoring locations.

Within 24 h of collection, cores (stored at 4 °C) were extruded in 1-cm segments, except near the base (oldest sediment) of cores O2 and S3 where two or three samples, respectively, were 2- to 4-cm thick. To prevent contamination, a 1-cm perimeter was removed from all samples. Samples were split in half, one half for the core chronology and analyses of physical and geochemical variables, and the other for examination of cladoceran subfossils.

Core chronology

Wet homogenized samples from the deepest site in each lake, cores O2 and S3 (Fig. 1), were dated using ¹³⁷Cs and ²¹⁰Pb. Log excess-²¹⁰Pb activities were plotted by depth, and the slope of the best-fit line was used as the mean sedimentation rate. We used the constant rate of supply model (CRS) of Appleby and Oldfield (1978) to construct an age-depth profile for each lake. To confirm our age-depth model we used the ¹³⁷Cs peak (1963–1964). In Seneca Lake, we used the average mass accumulation rate from the lowermost dateable section of core S3 (24 cm) to assign ages before 1850. Within each lake we estimated the age of the two additional, non-dated cores (O1, O3; S1, S2) by comparing carbonate content of these cores with the dated cores (O2 and S3) following the methods of Anderson et al. (1997). For all cores, paleolimnological data are presented relative to age to facilitate comparisons among cores and between lakes.

Physical and geochemical records

Subsamples from each core were freeze dried, and then homogenized for geochemical and physical analyses. Samples were analyzed in duplicate for percent organic matter by weight (%TOC) and carbonate content by weight (%TC) by loss-on-ignition at 550 °C (2 h) and

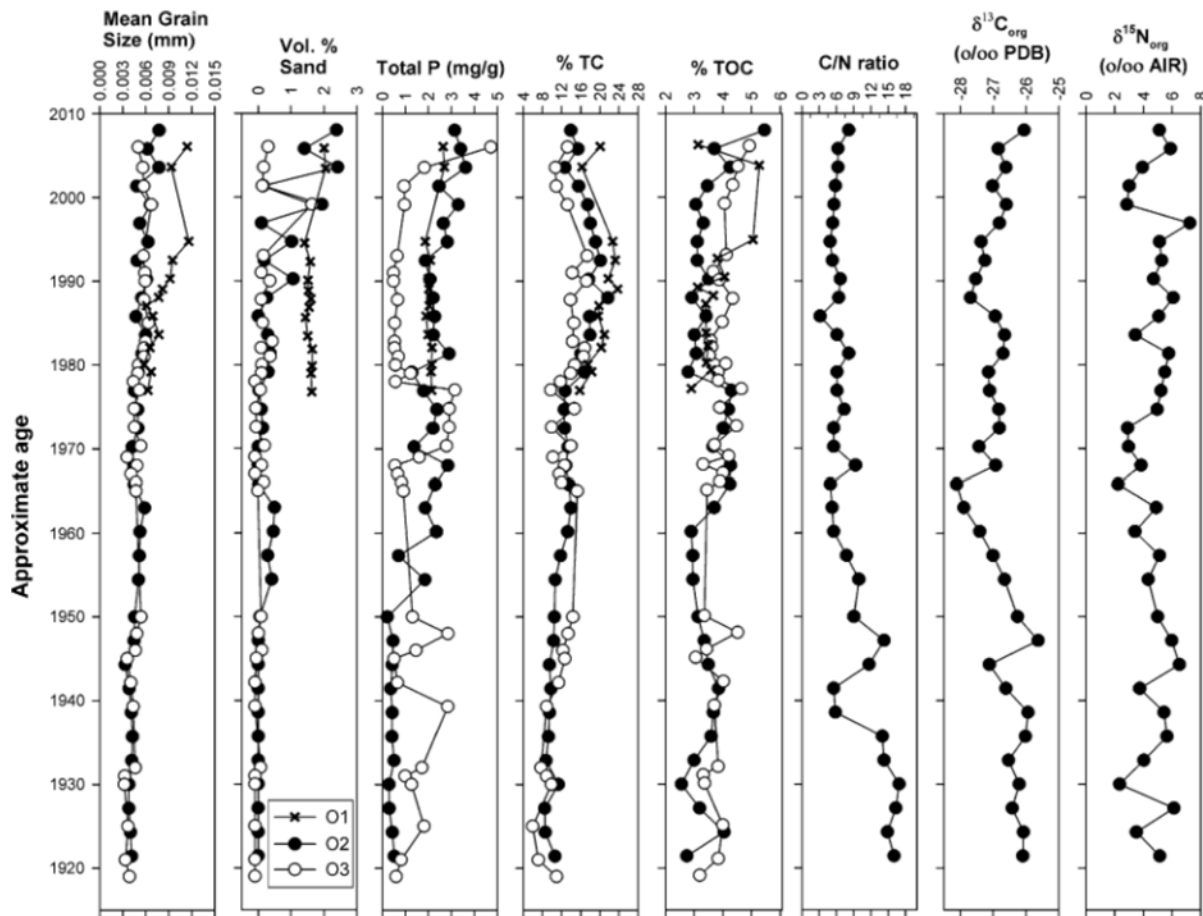


Fig. 2 Downcore variations in physical and geochemical variables for cores collected from Owasco Lake. Crosses represent the shortest core and shallowest site (core O1: Lat. 42°52.383'N, Long. 76°31.331'W, Z = 35 m, core length = 14 cm), *filled circles* are the deepest site (core O2:

Lat. 42°49.195', Long. 76°30.402', Z = 51 m, core length = 36 cm), and *open circles* are an intermediate water depth site (core O3: Lat. 42°47.128', Long. 76°29.062', Z = 45 m, core length = 36 cm)

1,000 °C (2 h), respectively (Dean 1974), and means were reported. The total phosphorous in the sediment (TP) was determined in duplicate using a spectrophotometer (885 nm) after digestion with a 5 % potassium persulfate solution in a hot water bath at 100 °C for 1 h (Wetzel and Likens 2000).

We compared stratigraphic changes in %TOC, %TC and TP with the $d^{13}C$ and $d^{15}N$ of autochthonous sediment organic matter to infer relative changes in lake trophic status. Because hypolimnetic waters in both lakes remain oxic year-round (Schaffner and Oglesby 1978), TP is expected to be retained by surficial sediments (Engstrom and Wright 1984). However, there is no quantifiable relationship between sediment TP and water column phosphorus because

older, deeper sediment may contribute phosphorus to overlying sediments and the water column (Håkanson 2003).

Samples from cores O2 and S3 (deepest sites) were measured simultaneously for their organic carbon and organic nitrogen contents, and stable carbon ($d^{13}C_{org}$) and nitrogen ($d^{15}N_{org}$) isotopic ratios using a Finnigan Deltaplus XL Dual Inlet Stable Isotope Ratio attached to a Costech Elemental Analyzer. Prior to analysis, carbonate was removed using the vapor acidification method of Hedges and Stern (1984). Atomic organic C to total N ratios (C/N) were calculated from total C and N contents. Isotope ratios were expressed in delta notation with respect to deviations from standard reference material (Pee Dee belemnite carbon and

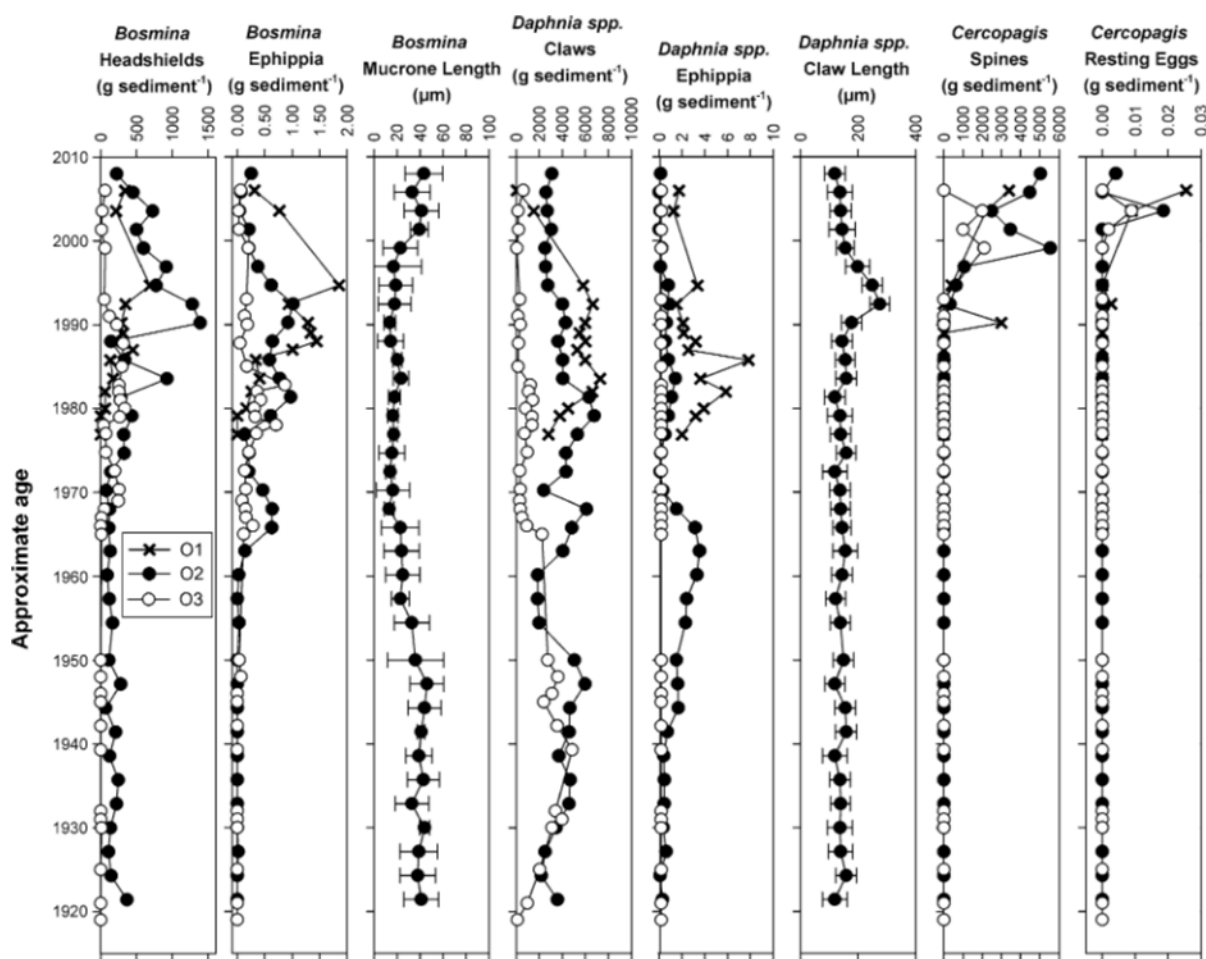


Fig. 3 Downcore variations in biotic variables for cores collected from Owasco Lake. *Bosmina longirostris* abundance reconstruction is based on headshield remains. *Daphnia* spp. abundance reconstruction is based on postabdominal claw remains. *Cercopagis pengoi* abundance reconstructions are

based on caudal-spine remains that contained the ‘s-bend’. Crosses represent core O1, filled circles represent core O2, and open circles represent core O3. Site attributes are given in the caption for Fig. 2

atmospheric nitrogen). Using the equation of Verburg (2007), measured $d^{13}C_{org}$ values were corrected for the Suess effect, which is the change in the abundance of carbon isotopes from burning of fossil fuels and deforestation (Keeling 1979).

To evaluate the amount of erosion in the watershed and potential nutrient loading to the lakes, grain size analysis was performed. Subsamples were pre-treated with 30 % hydrogen peroxide to remove organic matter and 25 % glacial acetic acid to remove calcium carbonate (Jackson 1969). These components were assumed to be autochthonous based on Meyers (2002) and Effler et al. (1987b), and were removed to isolate

terrigenous sediments. We determined the percentage of sand in each sample (averages of duplicates) using a Coulter LS230 Multivariable Laser Diffraction Particle Size Analyzer.

Simple linear regression models between $d^{13}C_{org}$ and C/N or TOC were used to determine if there were relationships between productivity and organic matter accumulating in each lake (cores O2 and S3 only). Regression relationships were also tested between $d^{13}C_{org}$ (primary production) with TP and % sand in each lake (SYSTAT 10.0). For Seneca Lake, dependent variables ($d^{13}C_{org}$, $d^{15}N_{org}$, C/N) were log transformed to meet assumptions of normality.

Pelagic cladoceran subfossils

To assess abundance shifts in major cladoceran zooplankton, subsamples were stained with Rose Bengal and examined for the most common cladoceran subfossils. Based on the methods of Frey (1986), remains of at least 50 and up to 200 *Bosmina longirostris* (hereafter *Bosmina*), *Daphnia* spp. (hereafter *Daphnia*), and *Cercopagis pengoi* (hereafter *Cercopagis*) were identified at 100 \times . The densities of headshields of *Bosmina* and postabdominal claws of *Daphnia* were chosen because these were the most abundant. Remains of *Cercopagis* were identified from caudal-spine segments with the distinctive 's-bend'. Abundance for each taxonomic group is reported as the number of headshields (*Bosmina*), postabdominal claws (*Daphnia*), or caudal-spine segments (*Cercopagis*) per gram of wet sediment to facilitate comparison with physical and geochemical variables.

The mucrone length of *Bosmina* and the postabdominal claw length of *Daphnia* were determined for cores O2 and S3 to assess increased size, which served as a proxy for predation pressure (Manca et al. 2007). For each sample, fifty mucrone lengths and fifty postabdominal claw lengths were measured from magnified digital images (200 \times , Motic Images Plus 2.0.3).

To examine trends in sexual reproduction, resting stages of pelagic cladocerans were enumerated after wet sieving, and the [150 l m fraction was searched in entirety (400–500 ml) for the resting stages of *Daphnia* (ephippia), *Bosmina* (ephippia), and *Cercopagis* (resting eggs) at 50 \times . *Cercopagis* produce clutches of resting eggs that are released from the mother without an ephippium and collect on the lake floor (Yurista 1992). The ratio of *Bosmina* ephippia to the sum of *Bosmina* ephippia and *Bosmina* headshields (modified from Jeppesen et al. 2003) was calculated in cores O2 and S3. Hereafter we refer to this as the *Bosmina* ephippia ratio. *Bosmina* were analyzed because the preservation of their carapaces is superior to other taxa (Frey 1986). For each lake, a simple linear regression between $d^{13}C_{org}$ and the *Bosmina* ephippia ratio was used to test for slopes = 0 (*F*-ratio) to determine relationships between productivity and the accumulation of ephippia (SYSTAT 10.0).

Water-quality monitoring

Averages of water-quality data in the epilimnion during summer were determined for Owasco and Seneca Lakes using a literature review and our own monitoring program. Collection and analytical methodologies for historic data were described in the original sources listed in Tables 1 and 2.

We measured water quality in Owasco Lake beginning in 2005, and in Seneca Lake beginning in 1994. Between two and eleven sites ($Z = 2\text{--}52\text{ m}$) were surveyed in Owasco Lake on a bi-weekly or monthly basis (Fig. 1). Four sites ($Z = 25\text{--}105\text{ m}$) were sampled weekly or bi-weekly in northern Seneca Lake. At all sites, we measured Secchi depth and collected surface samples for chlorophyll *a* (Chl. *a*) and nutrient analyses. Concentrations of Chl. *a*, total phosphorus (from 2006 onward), and soluble reactive phosphate (SRP-P) were determined following Wetzel and Likens (2000). Total phosphorous concentrations were estimated by digesting particulate-bound phosphorous with 5 % potassium persulfate (100 °C for 1 h), and then analyzed as described for dissolved phosphates. Nitrate concentrations ($NO_3\text{--}N$) were determined colorimetrically (504 nm, 1-cm path-length cuvette) using a cadmium reduction technique and potassium nitrate standards (Hach Model NI-14 low range NO_3 test kits).

Results

Owasco Lake (Figs. 2, 3) and Seneca Lake (Figs. 4, 5) preserved distinct spatial and temporal patterns in the physical, geochemical and biological properties of their sediment records. Differences between Owasco and Seneca Lakes included greater $d^{13}C_{org}$ by several per mille in Seneca Lake sediments compared to Owasco Lake (Figs. 2, 4). Contrasts were also observed in the subfossil records for some remains such as *Bosmina* headshields and *Daphnia* ephippia, which were two orders of magnitude less abundant in Seneca (Figs. 3, 5).

Within each lake, there was a similar near-shore to offshore pattern in sediment texture and composition. Shallow water locations (cores O1 and S1) were coarser grained and contained more sand than deep-water locations (cores O2, O3, S2, and S3) (Figs. 2, 4).

Table 1 Water-quality monitoring data for Owasco Lake

Years	Nitrate nitrogen (mg L ⁻¹)	Total phosphorus (1 g L ⁻¹)	Soluble reactive phosphorus (1 g L ⁻¹)	Estimated NO ₃ -N:SRP-P	Secchi disk transparency (m)	Chlorophyll <i>a</i> (1 g L ⁻¹)
1955 ^a	0.8	–	–	–	–	–
1964–1970 ^b	0.64	–	–	–	–	–
1971	0.52 ^b	–	5.3 ^c	100	3.4 ^b	5.3 ^b
1972	0.64 ^c , 0.79 ^c	8.4 ^d	3.7 ^c	≥170	3.3 ^b	2.7 ^b , 5.8 ^c
1973	0.61 ^c , 0.66 ^c	9.4 ^d	1.2 ^c , 4.1 ^c	≥150	2.6 ^b	4.8 ^b
1984 ^e	–	–	–	–	4.0	–
1985 ^d	–	5.4	–	–	3.1	2.3
1986 ^d	–	4.5	–	–	2.7	1.8
1996 ^f	–	7.5	–	–	2.6	5.9
1997 ^f	1.14	14	–	–	3.0	3.2
1998 ^f	–	–	–	–	2.9	2.7
1999 ^f	–	12.4	–	–	3.0	2.6
2005	0.7	–	0.6	1,200	3.8	4.1
2006	0.7	8.6	1.5	470	3.4	2.7
2007	0.7	8.5	0.6	1,200	2.3	2.3

Sources are given as footnotes for either an entire year, if one study was used for multiple variables, or for individual variables, if multiple studies were used. Most values represent the mean of several measurements taken from the epilimnion during summer stratification. Sampling methodology can be found in the original publications. Measurements from 2005 to 2007 are from the present study. Estimated available nitrate nitrogen (NO₃-N) to soluble reactive phosphorus (SRP-P) ratios are based on mass from the reported sources

^a Berg (1963)

^b Oglesby et al. (1973)

^c Mills (1975)

^d Effler et al. (1987a)

^e Miller (1984)

^f Callinan (2001)

Littoral cores had up to 10 % more %TOC than profundal cores in both lakes, which was greater than the overall average increase of ~1–2 % proceeding upwards in the core. In both lakes, %TC decreased by ~6–8 % along a shallow-to-deepwater gradient. Further, shallow sites typically contained greater densities of subfossil remains in Owasco Lake (Fig. 3).

Temporal trends between the two lakes were also distinct. The mean sedimentation rate in Owasco Lake was 0.5 cm year⁻¹ and in Seneca Lake was 0.15 cm year⁻¹ based on the isotopes of ²¹⁰Pb and ¹³⁷Cs (cores O2 and S3; Electronic Supplementary Material, ESM 1). Thus, the cores from Owasco Lake date from ~1920, with each 1-cm core segment representing between ~2 and 4 years (Figs. 2, 3). Because of its low sedimentation rate, Seneca cores date from ~1780, with each 1-cm core segment representing ~5–7 years (Figs. 4, 5). There were dynamic

temporal patterns in most measured paleolimnological variables and these major results are discussed in more detail by lake in the following subsections.

Owasco

Physical and geochemical records

In all three cores, mean grain size and volume percentage of sand increased proceeding upwards in the core (0–7.8 %), although the range in mean grain size (0.003–0.012 mm) was small (Fig. 2). The %TC gradually increased beginning ~1965, peaked at 18–24 % at ~1990, and then declined during the 1990s. Only in cores O1 and O3 did %TC increase slightly post-2000. Organic matter constituted a small fraction of the sediment, ~4 %. By ~1950, the C/N ratios were ~9. Peaks in %TOC were generally concurrent with higher

Table 2 As Table 1 but for Seneca Lake

Years	Nitrate nitrogen (mg L ⁻¹)	Total phosphorus (1 g L ⁻¹)	Soluble reactive phosphorus (1 g L ⁻¹)	Estimated NO ₃ -N:SRP-P	Secchi disk transparency (m)	Chlorophyll <i>a</i> (1 g L ⁻¹)
1910 ^a	–	–	–	–	8.3	–
1927 ^b	–	–	–	–	9.1	–
1965 ^c	–	22.0	–	–	3.1	4.8
1973 ^d	0.2	13.1	0.7	290	3.6	–
1994	–	–	1.2	–	5.7	2.2
1995	–	–	1.5	–	7.8	2.0
1996	–	6.3 ^e	–	–	7.5	1.6
1997	0.1	14.3 ^e	0.5	200	8.3	0.6
1998	0.3	–	2.4	130	6.2	1.5
1999	0.3	8.2 ^e	3.3	90	7.2	1.4
2000	0.2	–	2.1	100	7.3	1.2
2001	0.2	–	1.7	120	6.9	1.7
2002	0.3	–	1.1	270	7.0	0.6
2003	0.4	–	1.4	290	7.1	1.0
2004	0.3	–	0.9	330	6.3	2.3
2005	0.4	–	1.9	210	6.4	1.7
2006	0.4	9.1	1.3	310	6.3	2.0
2007	0.4	8.6	1.5	270	5.5	3.4

Measurements from 1994 to 2007 are from the present study, except for total phosphorus measurements in 1996, 1997, and 1999

^a Birge and Juday (1914)

^b Muenscher (1928)

^c Anonymous (1966), reported by Schaffner and Oglesby (1978)

^d Mills (1975)

^e Callinan (2001)

C/N ratios and TP. In core O2, trends in C/N and d¹³C_{org} paralleled each other. In general, when C/N ratios decreased in the upper portion of the core (e.g., 1920s to 1930s, mid-1940s to mid-1960s), d¹³C_{org} also increased, although increases were small. The d¹³C_{org} increased with C/N ($F_{1,33} = 22.400$, $p < 0.001$) and d¹³C_{org} increased with TP ($F_{1,33} = 6.341$, $p = 0.017$).

The d¹³C of the organic matter ranged from –25.6 to –27.9 ‰. The d¹³C_{org} was higher than average at ~1940, ~1950, between the mid-1960s and mid-1980s, and post-1995. In general, the d¹³C_{org} record mirrored changes in %TOC, except between ~1995 and the mid-2000s when d¹³C_{org} increased and %TOC remained relatively constant. Except between the 1940s and 1960s, the d¹³C_{org} generally increased proceeding upwards in the core. No relationship between d¹³C_{org} and %TOC was detected ($F_{1,33} = 0.0135$, $p = 0.980$). The d¹⁵N_{org} exhibited no systematic trend upcore and ranged from 2.2 to 7.2 ‰.

The most dramatic changes in composition occurred post-1960. Two significant periods of high %TOC occurred between ~1965–1985 (up to 4.1 %) and ~1995–2008 (up to 5.4 %). Periods of elevated %TOC were coincident with periods of low %TC and high TP. TP was highest between ~1965 and 1985 (mean = 1.9 mg g⁻¹) and then again post-2000 (mean = 2.7 mg g⁻¹). The %TC was relatively low between ~1920 and 1960 (mean = 11 %) compared to the period from ~1960 and 2008 (mean = 16 %).

Pelagic cladoceran subfossils

In all three cores, *Bosmina* headshields and ephippia abundance rose gradually beginning in the 1960–1970s, and accelerated during the 1980s (Fig. 3). Also consistent in the cores was a decline in *Bosmina* headshields and ephippia during the 1990s. Subfossils were less abundant in core O3 (deepwater location)

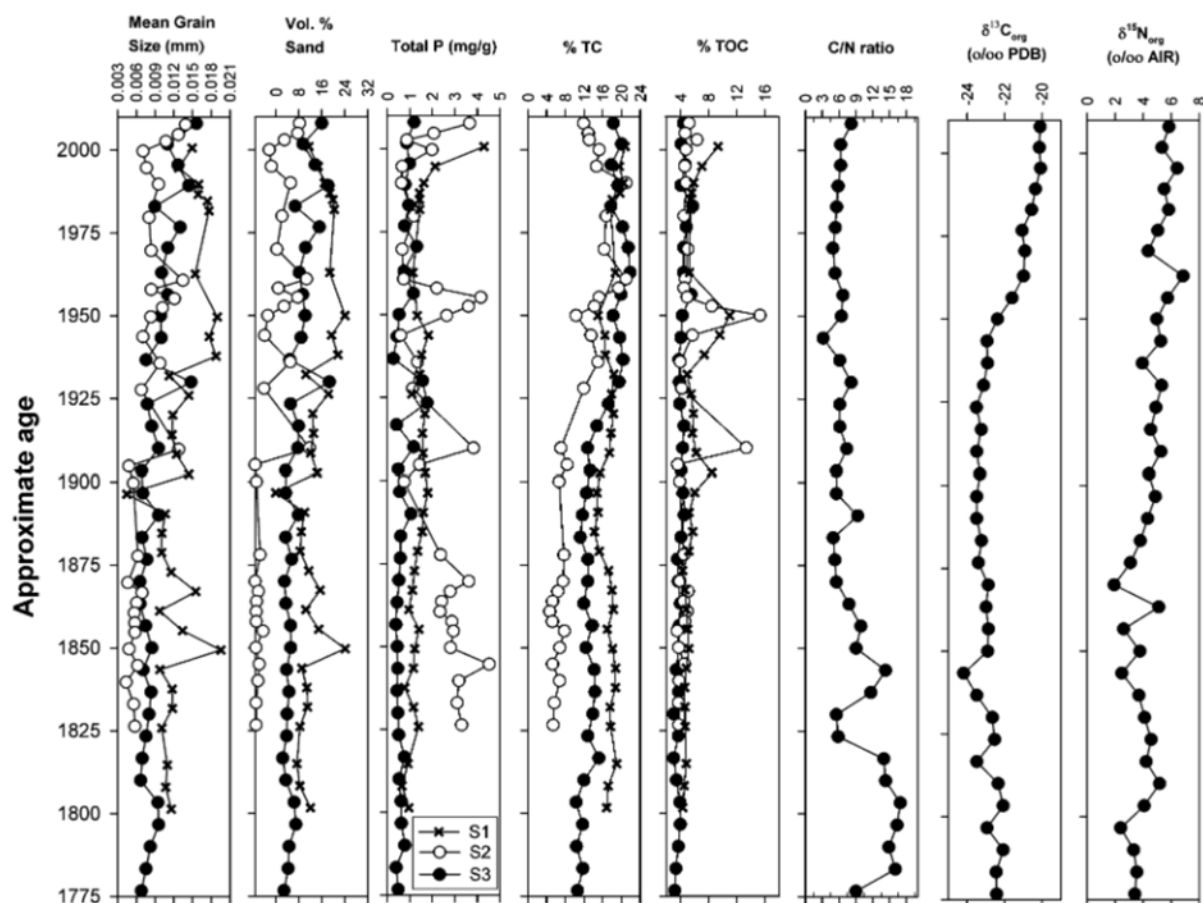


Fig. 4 Downcore variations in physical and geochemical variables for cores collected from Seneca Lake. Crosses represent the shallowest site (core S1: Lat. 42°50.768, Long. 76°57.649', Z = 19 m, core length = 33 cm), open circles are

an intermediate water depth site (core S2: Lat. 42°49.071', Long. 76°57.387', Z = 62 m, core length = 43 cm), and filled circles the deepest site (core S3: Lat. 42°46.296', Long. 76°56.872', Z = 113 m, core length = 36 cm)

compared to cores O1 and O2. Shorter *Bosmina mucrone* lengths were observed during the middle of the core record concurrent with elevated *Bosmina* abundances. The *Bosmina ephippia* ratio decreased with decreasing $\delta^{13}C_{org}$ values ($F_{1,33} = 12.300$, $p = 0.001$).

Daphnia subfossils were an order of magnitude more abundant than those of *Bosmina*, but abundances were more variable among cores. Postabdominal claw and ephippia abundances declined in all cores over the two most recent decades. The highest abundance was in core O1, with elevated abundances of postabdominal claws and ephippia during the 1970s and 1980s. The magnitude of peaks was similar in core O2, with elevated abundances observed during several time periods. Core O3 had lower abundances compared to

other cores, especially post-1970. *Daphnia* postabdominal claw length had a single peak in the early 1990s (~350 μ m), but decreased to previously observed length (< 200 μ m) within the past decade.

The caudal spines and resting eggs of *Cercopagis* were first detected in the mid- to late-1990 in cores O1 and O2, and ~1988 in O3. Both caudal spine and resting egg abundance generally increased in the upper portion of the core.

Water-quality monitoring

Since 1955, ratios of NO_3-N to SRP-P have been consistently [100 by mass (Table 1). SRP-P was nearly an order of magnitude greater during 1971–1973 compared to 2005–2007. Summer Secchi

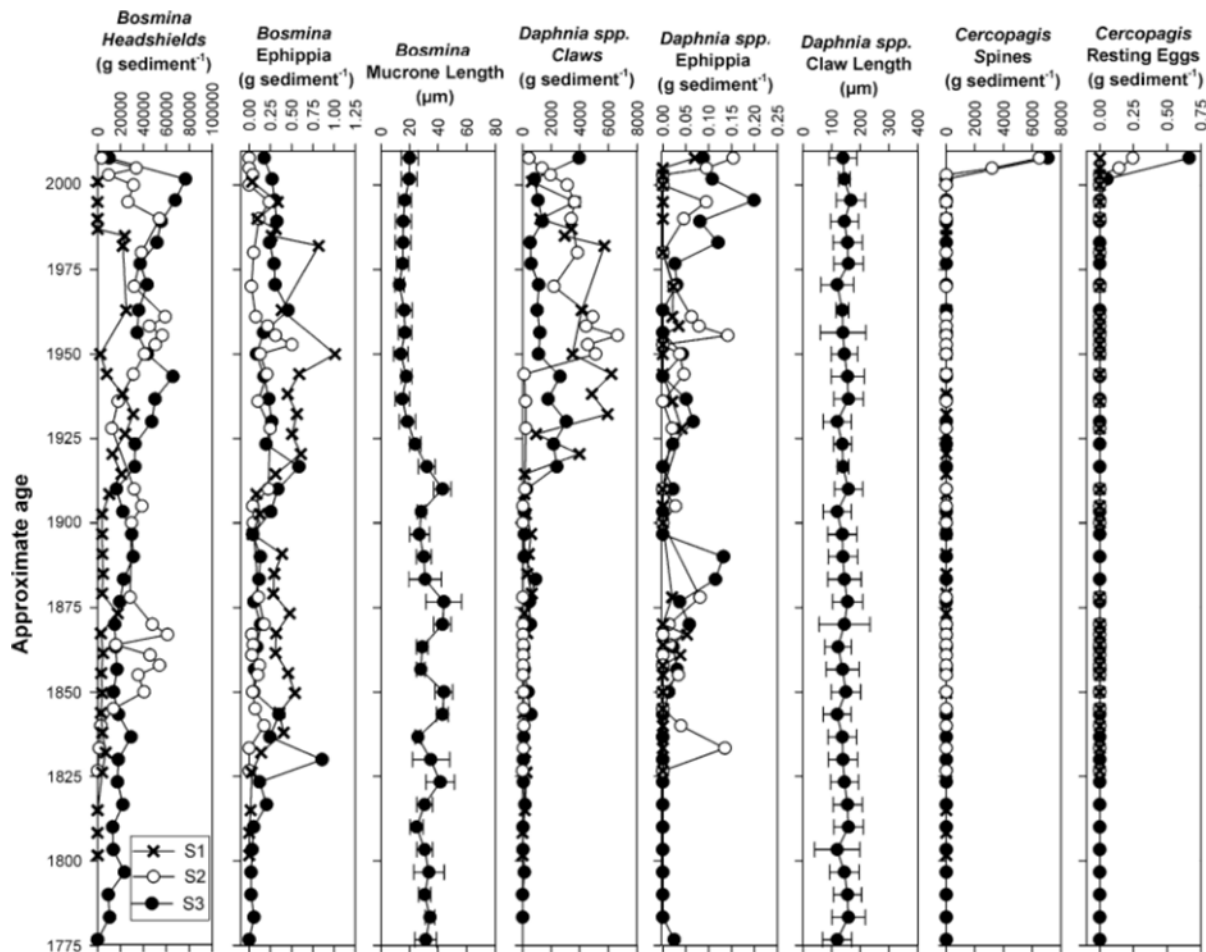


Fig. 5 Downcore variations in biotic variables for cores collected from Seneca Lake. Biotic reconstructions are the same as described in the caption for Fig. 3. Crosses represent

core S1, open circles represent core S2, and filled circles represent core S3. In core S3 no *Cercopagis* resting eggs were detected. Site attributes are given in the caption for Fig. 4

depths ranged between [2 and 4 m and Chl. *a* concentrations ranged between 1.8 and 5.7 g L^{-1} . Three of the four highest Chl. *a* concentrations in Owasco Lake were measured between 1971 and 1973.

Seneca

Physical and geochemical records

Cores exhibited an increase in mean grain size and the volume percentage of sand proceeding upwards in the core (Fig. 4). The range in mean grain size was between 0.003 and 0.019 mm, and contained up to 25 % sand. The shallowest core (S1) was coarser and contained more sand than the deeper cores (S2, S3). The %TC and

%TOC exhibited an inverse relationship upcore (Fig. 3). The %TC ranged from 4 to 22 %, and increased gradually upcore. The average %TOC was low (4 %) in all three cores. Peaks in %TOC occurred more frequently in core S1 (shallow water location) than the other cores. Short-lived peaks in %TOC were concurrent with higher C/N ratios (core S3) and TP. Between ~1780 and 1850, C/N ratios were highest (15), but by 1850, C/N ratios were \backslash 9. The $d^{13}\text{C}_{\text{org}}$ ranged from -23.5 to -20.1 ‰, and were more positive since the mid-1850s. The $d^{13}\text{C}_{\text{org}}$ increased with log TP ($F_{1,33} = 2.964$, $p = 0.094$). The $d^{15}\text{N}_{\text{org}}$ increased from 4.5 to 6.5 ‰ since the 1870s. The $d^{15}\text{N}_{\text{org}}$ increased with log TP ($F_{1,33} = 7.773$, $p = 0.009$) and log % sand ($F_{1,33} = 11.717$, $p = 0.002$).

Pelagic cladoceran subfossils

The vertical profiles of *Bosmina* headshields and ephippia differed depending on location in Seneca Lake (Fig. 5). In cores S2 and S3, headshield abundance began to increase gradually ~1915, but in core S2 it began to gradually decline ~1995, and in core S3 it rapidly declined after 2000. In core S2, elevated abundances of *Bosmina* were also observed between ~1850 and ~1875. Abundances in core S1 were generally lower, with peaks during the 1920–1940s and 1950–1980s. Compared to headshield remains, *Bosmina* ephippia abundances shifted over shorter time periods, with abundances within all cores ranging between 0 and ~1 ephippia per gram of sediment. Consistent among cores was a modest increase in ephippia abundance from ~1900–1975 and a general decrease near the core top.

Mucrone length of *Bosmina* was slightly longer and generally more variable prior to ~1925. The *Bosmina* ephippia ratio was not statistically correlated with $d^{13}C_{org}$ values ($F_{1,33} = 0.776, p = 0.385$), but 5 of the 6 highest ratios occurred when the $d^{13}C_{org}$ values were lowest.

Daphnia postabdominal claws were most abundant after ~1920 in cores S1 and S3 and after ~1950 at core S2. Postabdominal claws remains were rarely detected before 1900, and were much less abundant than *Bosmina*. Compared to the deposition of postabdominal claws, the peaks in *Daphnia* ephippia were more abrupt and more consistent among the cores. There were several periods when *Daphnia* ephippia were abundant in all cores (i.e., ~1850–1880, ~1925, ~1950, and ~1975 to present). Mean daphnid claw length (~200 μ m) was stable over the record.

Cercopagis caudal spines and resting eggs were restricted to the 2000s, and both increased upcore. In core S1 we did not detect any caudal spine segments or resting eggs.

Water-quality monitoring

Over the last 100 years, ratios of NO_3-N to SRP-P were consistently ~90 by mass, mean summer Secchi depths ranged between ~4 and 9 m, and mean summer epilimnetic Chl. *a* ranged between ~1 and 4.8 μ g L^{-1} (Table 2). The two deepest Secchi depths in Seneca Lake occur during the first quarter of the century. During the most recent period in Seneca

Lake, an initial increase in Secchi depth and decrease in Chl. *a* was followed by the opposite trend in both of these variables.

Discussion

Using multiple sediment cores and water-quality data from Owasco and Seneca Lakes, we conclude: (1) primary productivity increased over the last two centuries, (2) pelagic cladocera communities responded to these productivity changes, and (3) nutrient loading and species invasions explained the productivity shifts. Our conclusions are primarily based on sediment records, as these were continuous, and secondarily based on water-quality data to extend beyond the relative changes that could be ascertained from sedimentary evidence.

Analysis of three cores in each lake allowed us to examine spatial differences within the region and further improve our understanding of environmental change in these two lakes. Although the temporal trends in paleolimnological variable for the three cores from each lake were often consistent, actual values were wide ranging among cores. For example, grain size increased proceeding upwards in the cores in both lakes, but grain size variation also increased from offshore to near-shore, and we interpret the latter to reflect sediment focusing. Abundance of biotic remains also increased near-shore and may be due to greater water column densities of zooplankton in shallower water. Previous studies with much greater spatial resolution have shown that location in a lake has strong influence on cladoceran remains preserved in lake sediments (Kattel et al. 2007).

Primary productivity and trophic status

We used %TOC and $d^{13}C_{org}$ to examine relative changes in primary productivity. This was justified because organic matter accumulating in both lakes was algal dominated (C/N ratios ~9) by ~1950 in Owasco Lake and by ~1850 in Seneca Lake, and did not undergo significant diagenesis (Electronic Supplementary Material, ESM 2). The $d^{13}C_{org}$ values were within the expected range for lacustrine plankton (Ortiz et al. 2004), but were distinct between lakes, and could reflect a variety of factors including different carbon sources and dynamics in the lakes

and their watersheds. The different morphometries and mixis types of the lakes could influence how they responded to productivity changes.

During periods of high productivity, $d^{13}C_{org}$ should be more positive because algae preferentially remove ^{12}C during photosynthesis and cause its depletion in the dissolved carbon pool. In Seneca Lake, primary productivity gradually increased from ~1850 to ~2008 (increased %TOC from 3.7 to 5 % and a positive shift in $d^{13}C_{org}$ from -22.9 to -20.1 ‰), with the rate of increase leveling off in recent decades.

In Owasco Lake, although $d^{13}C_{org}$ displayed a trend towards more positive values from the start of the record until ~1940 and after ~1980 to present, during the intervening decades, %TOC and $d^{13}C_{org}$ values did not increase as would be expected if productivity increased. This makes interpreting the paleolimnological record in Owasco Lake more complicated because water-quality data and sediment TP during this time period indicate either no change or increasing productivity. One plausible explanation is that the ^{13}C -depleted carbon may reflect an expansion of microbial communities in response to intensified cultural eutrophication (Hollander and Smith 2001; Teranes and Bernasconi 2005). In their moderate eutrophication model, Hollander and Smith (2001) suggest that as more biogenic methane and ^{13}C -depleted microbial biomass is produced and oxidized, more ^{13}C -depleted CO_2 is added to the water column. Although, methane production in Owasco Lake has not been investigated directly, Mullins and Halfman (2001) hypothesized that methane is responsible for acoustic smears in seismic profiles. They argue that methane originated from Early Holocene sediments, but it is possible that biogenic methane production occurred in recent sediments.

To assess the hypothesis of increased methane, we used stratigraphic variations in the $d^{13}C_{org}$ and $d^{13}C$ of calcite ($d^{13}C_{cte}$) because they should both decline simultaneously. Previous study of the $d^{13}C_{cte}$ in Owasco Lake by Lajewski et al. (2003) allowed us to determine whether both $d^{13}C_{org}$ and $d^{13}C_{cte}$ follow this expected trend. When $d^{13}C_{cte}$ (Lajewski et al. 2003) is corrected for the Suess effect, the $d^{13}C_{cte}$ and the $d^{13}C_{org}$ displayed a parallel decline between ~1960–1980 and then again from ~1990 to 2008, which is consistent with a methane-based carbon source.

In addition to %TOC and $d^{13}C_{org}$, the %TC record is consistent with increased primary productivity over

the last century in both lakes. The rise in %TC in Owasco and Seneca Lakes is similar to other Finger Lakes (Lajewski et al. 2003) and the Laurentian Great Lakes (Hodell et al. 1998). The rise in $d^{13}C_{org}$, %TOC and %TC in Lake Ontario was attributed to enhanced productivity due to nutrient loading (Hodell and Schelske 1998; Meyers 2006).

The Chl. *a*, Secchi depth, and nutrient concentrations indicate that Owasco and Seneca Lakes have been oligotrophic to mesotrophic throughout the past century, and Owasco Lake was consistently more productive than Seneca Lake. Although there was nothing inconsistent between the paleolimnological and neolimnological records, we did not align them because monitoring was limited and methodology differed over time. The paucity of water-quality data before 2000, not the lack of change, is the likely reason that there appeared to be limited or no change in the trophic conditions of these lakes. Only the paleolimnological data were continuous and detailed enough to support the public's perception that these lakes experienced increased productivity over the last two centuries. A limitation of the paleolimnological data was that it revealed relative changes in trophic status, and we required available water quality data to determine actual trophic status. Lake management and policy is often based on water-quality data, and not core records, which may limit the detection and remediation of environmental perturbations.

It is notable that Owasco Lake had greater and more rapid increases in productivity, which could be related to its larger drainage area, smaller volume, and shorter residence time. Alternatively, the potentially contrasting biology of these two lakes, such as zooplankton composition (e.g., abundance of *Bosmina* and *Daphnia*) and demography (e.g., resting egg reproduction, planktonic size), may influence primary production.

Secondary productivity changes at the consumer level

Concurrent with rises in algal productivity, the abundance of phytoplanktivorous cladoceran remains increased in both Owasco and Seneca Lakes. We interpret this as a bottom-up ecological process whereby increased primary production fueled pelagic cladoceran growth and reproduction (Manca et al. 2007; Perga et al. 2010). In Owasco Lake, intensified algal concentrations during the 1970s and 1980s likely

promoted growth of phytoplanktivorous zooplankton. In Seneca Lake, gradually increasing primary productivity over the 1900s was paralleled by steady increases in *Bosmina* abundance, whereas increases in *Daphnia* abundance were more abrupt around 1925. In both lakes, the increase in *Daphnia* abundance occurs shortly before *Bosmina*, which may reflect differences in the ability of these two taxa to capitalize on food resources. In Seneca Lake, *Daphnia* were restricted to the last century, which is consistent with a single study during this period by Birge and Juday (1914), who did not detect *Daphnia* in Seneca Lake in August 1910. An increase in primary productivity during the early 1900s may have shifted conditions to allow *Daphnia* to sustain detectable populations, or remains of *Daphnia* could be better preserved in more recent sediments (Frey 1986).

In Owasco Lake, there were fewer *Bosmina* ephippia produced when the lake was more productive (*Bosmina* ephippia ratio). This may reflect that *Bosmina* were either: (1) less stressed for food as the lake became more productive and invested in parthenogenetic growth over resting stages and/or (2) experiencing decreased predation pressure, as evidenced by a decline in mucrone length during this period (Jeppesen et al. 2003). In general, the *Bosmina* ephippia ratio was nearly two orders of magnitude higher in Owasco Lake compared to Seneca Lake, underscoring that the biota in these two lakes display distinct ecologies.

Direct monitoring of zooplankton in these lakes has been limited, especially at the species level (Birge and Juday 1914; Brown and Balk 2008). Additional research aimed to compare past zooplankton assemblages through paleolimnology with the modern assemblage would extend the work presented here.

Factors affecting productivity changes

Several factors can account for the rise in primary productivity in lakes, including shifting nutrient availability, food-web composition, and thermal conditions (temperature and stratification) (Hodell et al. 1998; Schindler 2001, 2006). We found strong evidence that changes in Owasco and Seneca Lakes resulted from increased nutrient loading and non-native species establishment, which are discussed in the following subsections.

In situ thermal conditions in Owasco and Seneca Lakes were not regularly recorded over the last two

centuries, which prevented us from addressing their role in regulating productivity. Air temperature at Cornell University's research facility in Geneva, NY (National Climatic Data Center, <http://www.ncdc.noaa.gov>) showed a warming trend in the annual average minimum temperature of ~ 1 °C from 1882 to 2008 (data not shown), and thus increased temperature may, in part, enhance productivity in the Finger Lakes.

Nutrient loading

Increased productivity in Owasco and Seneca Lakes is likely due to increased nutrient loading from cultural eutrophication. This interpretation is supported by increasing sediment TP, $d^{15}N_{org}$, mean grain size, the percentage of sand, and water quality data.

The allochthonous input of nutrients, particularly phosphorous and nitrogen, was evident in the sediment records of these lakes. As both Owasco and Seneca Lakes are phosphorous limited, excess phosphorus should result in increased algal productivity. However, no empirical relationship exists between sediment TP and water column TP concentrations (Håkanson 2003). Many environmental factors besides past productivity control how much TP is bound and retained by the sediment (Boström et al. 1982). Therefore, sedimentary TP should be used with caution to infer relative changes in nutrient loading and in conjunction with other evidence.

Overall, TP increased in both lakes, with the most elevated concentrations at or near the core top, typical of TP profiles in lakes undergoing a transition to mesotrophy (Carey and Rydin 2011). In Owasco Lake, the lake bottom sediments may not have been able to store additional TP from ~ 1960 to 1980 and from ~ 1990 to 2008 due to increased allochthonous nutrients. As a result, more phosphorous may have been released into the overlying water column. Water-quality data in Owasco Lake indicated high water-column phosphorus during the same intervals as the high sediment TP concentrations. However, phosphorus concentrations in the water column are not different from the range of measurements within the last century. In contrast to Owasco Lake, sediment TP profiles in Seneca Lake exhibit a steady increase towards the top of the core. Based on the evidence collected, Seneca Lake appears to retain a more oligotrophic character than Owasco Lake, which could

result from its greater volume and smaller drainage-area to lake-volume ratio.

We also examined changes in $d^{15}N_{org}$ to infer potential sources of nutrients. During periods of high productivity, $d^{15}N_{org}$ was most similar to values for soil organic matter and land plants (2–10 %; Peterson and Howarth 1987; Talbot 2001), but increased municipal sewage wastes (10–20 %; Hodell and Schelske 1998) could have also contributed to the $d^{15}N_{org}$ signature. The increase in $d^{15}N_{org}$ paralleled increases in $d^{13}C_{org}$, and could reflect increased nitrate utilization by plankton, but this is unlikely because these lakes are phosphorus, not nitrogen, limited. External inputs of nitrates most likely explained the increase in $d^{15}N_{org}$ and could signal an influx of both nitrogen and phosphorus. Sediment nutrient profiles (TP and $d^{15}N_{org}$) generally mimicked the grain size and % sand trends, providing additional support for an allochthonous source of these nutrients.

Based on water-quality monitoring, it is clear that the lakes remained phosphorus limited. Nutrient concentrations in Owasco and Seneca Lakes were quite stable, especially when considering analytical methods differed among years. The lack of observable change in the water column could be due to limited sampling and averaging over summer months for each year, or it could reflect phytoplankton rapidly sequestering additional phosphate.

Species invasions

Non-native species introductions can shift limnological conditions, including primary and secondary production, through food-web interactions (Mills et al. 1993; Ricciardi 2001). The invertebrate predator *Cercopagis* (fishhook waterflea) was first detected in Owasco and Seneca Lakes in 1999 (Therriault et al. 2002). We detected *Cercopagis* in sediment dated to the late-1990s in most cores, which confirms the establishment of the species proximate with its initial detection. In core O3 we found remains approximately a decade before its first detection in North America (Charlebois et al. 2001). As this was a single egg and caudal spine segment in a single sample, the remains may have been mixed to deeper depths (e.g., bioturbation, recreational disturbance) at this near-shore site, or resulted from contamination from shallower sediment during sampling.

Our reconstructions of the last decade show shifts in the abundance of phytoplanktivorous taxa that were

coincident with the introduction of *Cercopagis* and were of similar magnitude to those attributed to nutrient loading. Following the establishment of *Cercopagis*, *Bosmina* abundances declined in both lakes and *Daphnia* abundances declined in Owasco Lake. Although a cause-effect conclusion is premature, it is consistent with in situ studies that document declines in native cladocerans and potential shifts in primary productivity following establishment of *Cercopagis* (Telesh et al. 2001; Benoît et al. 2002; Laxson et al. 2003; Brown and Balk 2008).

The influence of top-down control by *Cercopagis* is further supported by an increase in *Bosmina* mucrone length, most notably in Owasco Lake. Mucrone length indirectly measures the intensity of predation, as predators selectively prey on shorter morphs (Manca et al. 2007). In Owasco Lake there was an increase in *Daphnia* postabdominal claw length during or just prior to the establishment of *Cercopagis*, which was not sustained, nor observed in Seneca Lake, providing additional evidence that *Daphnia* may not be an important food source for *Cercopagis* (Brown and Balk 2008).

A second genus that established in both lakes by the early 1990s is the filter-feeding bivalve, *Dreissena*. This includes *Dreissena polymorpha* (zebra mussel) that established in the early 1990s in both lakes and *D. rostriformis bugensis* (quagga mussel) that established in Seneca Lake in the early 2000s (J. Halfman and J. Watkins pers. commun.). Dreissenids have consequential effects because they reduce the biomass of primary producers and impact water chemistry and clarity (Strayer 2010).

Shifts in primary production and potentially cladocera dynamics over the last two decades in Owasco and Seneca Lakes could, in part, be due to the establishment of dreissenids. Ingested nutrients are used by mussels for growth and reproduction and then excreted in a bioavailable organic form (Higgins et al. 2008). In both lakes, TP and %TOC in the sediment appear to be greater since the arrival of *D. polymorpha* in the 1990s. Dreissenids could be an important source of dissolved nutrients in these lakes, however, because each sediment sample in Owasco and Seneca Lakes spanned several years, it is difficult to assess the impact.

In Seneca Lake, continuous water-quality monitoring since the establishment of dreissenids showed an initial decrease in Chl. *a* concentration and Secchi

depth, which was reversed in more recent years, and likely reflects the impact of dreissenids on primary production and their changing densities. These shifts are consistent with observations in other northern temperate lakes (Idrisi et al. 2001; Higgins et al. 2008; Higgins and Vander Zanden 2010), but we cannot infer a direct relationship given multiple non-native species introductions and potential shifts in nutrient loading over the same period.

Also potentially attributable to the establishment of dreissenids was the recent decline in carbonate in the sediment of Seneca and Owasco Lakes. The decline is concurrent with the late 1990s proliferation of dreissenids who use calcium and bicarbonate to build their shells. The reduction in %TC in the sediment was as much as 7 % in Owasco Lake and 9 % in Seneca Lake and could be caused by the densities present in these lakes, but chemical weathering in the watershed could also influence carbonate fluctuations in the sediment record. Barbiero et al. (2006) documented that dreissenids in Lake Ontario sequestered enough calcium that concentrations in the lake were reduced to below saturation, preventing calcite precipitation.

Conclusions

Primary and secondary productivity changes following nutrient loading and non-native species establishment in Owasco and Seneca Lakes illustrates that a similar response is possible following bottom-up and top-down perturbations that occur over different time scales (decades versus years). Nutrient loading appears to be an important driver of increased productivity over the last century, which was apparent in the core records, but not detectable in the limited neolimnological data. More rapid limnological changes in the last 20 years were evident in both the neolimnological and the paleolimnological data, which were attributable to the establishment of two invasive species. In our case study, a combined approach using paleolimnology and water-quality monitoring was useful to document shifts in trophic conditions, and we recommend that both approaches be used when possible. Furthermore, using multiple sites in two lakes was advantageous to examine the consequence of anthropogenic stresses in basins with similar geology and landscape attributes, but with several key limnological differences (i.e., lake volume, mixis types).

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