

# Influence of Salmonine Predation and Weather on Long-Term Water Quality Trends in Lake Michigan<sup>1</sup>

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Trends in Lake Michigan water quality over 1975–84 appear to reflect reduced nutrient loadings as indicated by gradual declines in spring total phosphorus (TP) and summer epilimnetic chlorophyll *a* (Chl *a*). Deviations from these trends during 1977 and 1983–84 were apparently caused by abiotic and biotic factors, respectively. Prolonged ice cover during 1977 decreased sediment resuspension resulting in lower TP, reduced Chl *a* levels, and increased water clarity. A similar dramatic result occurred in 1983 and to a lesser extent in 1984, but via a different mechanism. Burgeoning populations of stocked salmonines reduced populations of the planktivorous alewife (*Alosa pseudoharengus*), which allowed large *Daphnia* to flourish. Because the *Daphnia* are more voracious and nonselective grazers than the formerly dominant calanoid copepods, they reduced seston concentrations, causing dramatic increases in Secchi disk transparency. These exceptions demonstrate the far-reaching consequences that unusual weather conditions and fish management practices may have on water quality indicators.

Les tendances de la qualité de l'eau du lac Michigan entre 1975 et 1984 reflètent la réduction des charges en matières nutritives indiquée par des déclinés graduels de la teneur en phosphore total (PT) au printemps et en chlorophylle *a* (Chl *a*) de l'épilimnion en été. Les écarts aux tendances notés en 1977 et en 1983–1984 semblent s'expliquer respectivement par des facteurs abiotiques et biotiques. La présence de glace pendant une plus longue période en 1977 a été la cause d'une moins grande resuspension des sédiments, qui s'est traduite par des teneurs en PT et Chl *a* moins importantes et par une augmentation de la transparence des eaux. Un effet similaire très prononcé a été noté en 1983 et, dans une moindre mesure, en 1984, mais le mécanisme était différent. Les populations en expansion des salmonines d'élevage introduits dans le lac ont provoqué une réduction des populations du gaspateau planctivore (*Alosa pseudoharengus*), ce qui a permis aux grosses *Daphnia* de devenir plus abondantes. Les *Daphnia*, brouteurs non sélectifs plus voraces que les copépodes calanoides qui dominaient auparavant, ont réduit les concentrations de seston, ce qui s'est traduit par des augmentations très importantes de la transparence des eaux déterminée au disque de Secchi. Ces exceptions montrent la grande portée des effets que peuvent avoir des conditions météorologiques inhabituelles et certaines pratiques de gestion du poisson sur les indicateurs de la qualité de l'eau.

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It can be difficult to assess a water body's response to altered driving forces. This is especially true for very large water bodies with long residence times. Physical, chemical, and biological forces influence lake trophic status. Physical forces influence lakes through control of their heat content, water movements, and hydraulic loads (Boyce 1974; Denman and Powell 1984). Chemical factors, such as nutrient and organic overenrichment and toxins, also affect water quality and ecosystem structure. More recently, biological factors

have been recognized as potentially important in determining the trophic condition of a lake (Hrbáček 1962; Shapiro et al. 1975; Lampert 1978; Edmondson and Litt 1982; Carpenter and Kitchell 1984). Some of these forces can be controlled or modified through human intervention. Most notable of these actions is nutrient abatement, which may include reduction of nutrient loads by sewage diversion or by treatment. Biological control can be implemented through fish manipulations (e.g. Stenson et al. 1978; Shapiro and Wright 1983). Physical alterations are more difficult to accomplish than biological or chemical alterations; however, in some cases artificial aeration and mixing have been implemented (see references in McQueen et al. 1984). It can also be difficult to separate responses of one

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portion of the ecosystem due to anthropogenic alterations in the watershed from those that are either natural (e.g. meteorological events) or directed at a seemingly distant portion of the ecosystem.

The Laurentian Great Lakes have been the subject of a massive program designed to improve water quality of the lower, more eutrophic lakes — Lakes Erie and Ontario — and to protect the current status of the upper, less productive lakes — Lakes Superior, Huron, and Michigan (Slater and Bangay 1980). The effort has focused largely on reducing the supply of phosphorus (Schelske 1979). This strategy of eutrophication control by nutrient manipulation appears to have improved water quality as measured by the extent of hypolimnetic anoxia, changes in total phosphorus (TP) concentrations, chlorophyll *a* (Chl *a*) concentrations, water transparency, and phytoplankton species composition in Lake Ontario, Lake Erie, Saginaw Bay, and the southern portion of Lake Huron (e.g. International Joint Commission 1984; Dobson 1981).

These lakes are also affected by other management activities (Sonzogni et al. 1983). For example, Lake Michigan is one of the lakes that is managed at the top of the food web through an aggressive salmonine stocking program begun in the mid-1960's. This successful stocking program, continued control of the salmonine predator, the sea lamprey (*Petromyzon marinus*), and largely unsuccessful natural reproduction of stocked lake trout (*Salvelinus namaycush*) (Eshenroder et al. 1984) have produced "a management-dependent system dominated by exotic fish" (Walters et al. 1980; Stewart et al. 1981). Thus, Lake Michigan, the world's fourth largest freshwater lake, sustains an ecosystem that is forced anthropogenically from above (fish stocking) as well as from below (phosphorus control). These anthropogenic forces are superimposed upon natural forces, such as meteorological conditions.

To assess overall trend in water quality, we have analyzed Lake Michigan data accumulated from a region offshore of Grand Haven, Michigan, over the past 10 yr. In general, we found a slight improvement in water quality over the 10-yr period. However, we also detected two periods of dramatic deviation from the overall trend. Certain symptoms of these "outlier" years are similar: lower Chl *a* and clearer water. The suspected causes of these symptoms are dramatically different; one is physical and stochastic, the other is ecological and may be a serendipitous result of changes in fish populations. The data we present below are consistent with two hypotheses concerning these periods of deviation. (1) Severe ice cover in winter 1977 resulted in reduced TP concentration in spring. We suggest that reduced spring TP was manifest further as lower Chl *a* concentrations and clearer water in summer. (2) Cascading effects (Carpenter and Kitchell 1984) of fish manipulations at the top of Lake Michigan's food web have induced changes in planktivorous fish, zooplankton species composition, Chl *a* concentrations, and finally water clarity. Below we outline evidence, primarily from Lake Michigan, that support these hypotheses.

## Methods

Data used in this work have come from various sources. Most were based on samples taken from stations at 70- to 100-m depths in southeastern Lake Michigan approximately 16–30 km offshore of Grand Haven. Except for 1977, 1982, 1983, and 1984, zooplankton were primarily from an offshore station (40 m depth) approximately 105 km south of Grand

Haven (offshore of Bridgman, MI); during those years, collections were also made to the west of Grand Haven.

Total P data are spring values from data files of the Great Lakes Environmental Research Laboratory (GLERL), Rockwell et al. (1980a), EPA Storage and Retrieval System (STORET), and D. Rockwell (Environmental Protection Agency, Chicago, IL). Secchi disk depths are from GLERL data files, Rockwell et al. (1980a), and M. S. Evans and R. A. Moll (University of Michigan, Ann Arbor, MI). Chlorophyll *a* samples were collected on glass fiber filters, ground, extracted in acetone, and processed either fluorometrically or spectrophotometrically (R. A. Moll and GLERL data files) except for Environmental Protection Agency samples (Rockwell et al. 1980a) which were sonicated rather than ground. Data from R. A. Moll for 1977 were from *in vivo* fluorescence corrected by calibration to extracted samples.

Transmissivity measurements were all taken aboard the R/V *Shenelon* with a submersible transmissometer. Because the path length of the system has varied from 1 m to 25 cm over the 10-yr period, all measurements were converted to 1 m following Beer's law. A Kahlsico, Inc., system with an incandescent light source was used during 1975–81, and was then replaced with a Sea Tech, Inc., model 25 transmissometer with a light-emitting diode ( $\lambda = 660 \mu\text{m}$ ). We used wavelength-specific extinction coefficients for Lake Michigan water (G. L. Fahnenstiel, unpubl. data) and spectral characteristics of the light sources and detectors for both systems to normalize data. Because detectors from both systems respond fairly uniformly to light of different wavelengths, the ratio (*R*) of transmissivity measured from a given water mass can be calculated as

$$R = \frac{\sum_i a_{K,i} e^{-k_i}}{\sum_i a_{S,i} e^{-k_i}}$$

where  $k_i$  are the extinction coefficients for Lake Michigan and  $a_{K,i}$  and  $a_{S,i}$  are the fractions of light-energy from the Kahlsico (*K*) and Sea Tech (*S*) light sources for each wavelength interval *i*. The resulting ratio is 1.203 for our instruments used in Lake Michigan water.

The depth of the 1% light level was calculated from extinction coefficients for photosynthetically active radiation (PAR) determined by scalar sensors or by hemispherical (upwelling and downwelling) sensors corrected to scalar estimates following Spigel and Howard-William (1984).

Zooplankton dry weights for 1975–81 were determined from species collected with net hauls from 40 m to the surface (Evans et al. 1980; M. S. Evans, unpubl. data) and individual dry weights as described in Hawkins and Evans (1979). Zooplankton composition for 1983 was determined (J. T. Lehman) from samples pumped through 153- $\mu\text{m}$ -mesh nets. Data for 1984 were again from net hauls from 40 m to the surface (D. Scavia and G. L. Fahnenstiel). Weights for 1982, 1983, and 1984 calculations were based on dry-weight measurements of animals collected in those years. Mean weights were estimated by measuring dry weight of several individuals of the predominant species. *Daphnia pulex* mean weight (13.09  $\mu\text{g}$ ) was based on a weighted average of large and small individuals. Comparisons between net collections from 40 m to the surface and detailed vertical profiles of discrete, pumped samples in 1977 indicated little bias in dominant crustaceans, except for nauplii and mysids (M. S. Evans, unpubl. data). Data on alewife (*Alosa pseudoharengus*) biomass are from

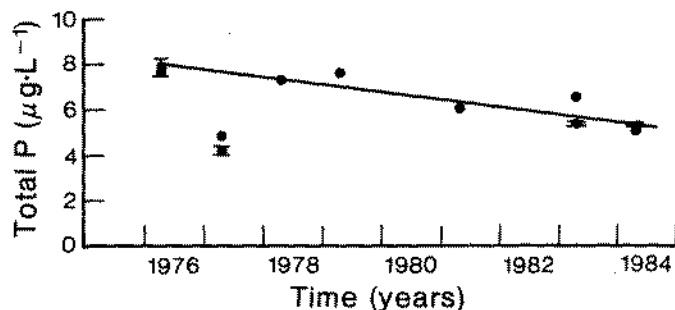


FIG. 1. Total P during spring isothermal conditions for 1976–84. Points represent data from the region off Grand Haven, MI. Bars represent the mean  $\pm 1$  SE for southern basin stations with depths greater than 80 m.

Wells and Hatch (1984) and L. Wells (Great Lakes Fishery Laboratory, Ann Arbor, MI). These abundance estimates are from bottom trawls taken inshore of the 100-m depth contour in autumn at eight index stations from around the lake and represent adult alewife available for midwater planktivory.

Zooplankton grazing experiments conducted in 1983 followed the method described by Lehman (1980). Chlorophyll-based algal net growth rates were measured in rotating 20-L enclosures containing different amounts of zooplankton and incubated at ambient temperature and light for 24 h. The slope of the algal growth rate versus zooplankton abundance curve represents the filtering rate of the zooplankton community.

One must be cautious when using data from different seasons to evaluate changes over years. For Secchi depth, epilimnetic Chl *a*, and transmissivity we present all data and examine detectable signals, as it was not always possible to calculate meaningful averages. Because timing of the onset of stratification is critical and varies from year to year, we delineate critical periods in Fig. 2 by shading from the onset of stratification in late spring to fall when the thermocline passes 15 m and begins to deepen rapidly. For examination of trends, we considered TP prior to the onset of thermal stratification. Chlorophyll *a*, water clarity, and zooplankton biomass trends are viewed through the window of thermal stratification.

## Results and Discussion

### Water Quality Trends

#### Total P

Late winter and early spring TP, generally considered a good indicator of trophic state (e.g. Dillon and Rigler 1974), decreased slowly and systematically from 1975 to 1984 (Fig. 1). These regional data from the isothermal spring period are consistent with data averaged from southern basin stations in 1976, 1977, 1983, and 1984; consequently, at least the southern basin of Lake Michigan has apparently experienced TP reductions. A notable exception to the gradual trend is the outlying datum from 1977, which will be discussed below.

#### Chlorophyll *a*

Surface Chl *a* varied seasonally in a somewhat regular pattern each year (Fig. 2a). Algal blooms prior to thermocline development are generally composed of diatom species (Brooks and Torke 1977; Parker et al. 1977; Bartone and Schelske 1982). Once thermal stratification develops, this major bloom sinks from the epilimnion. Under strong strati-

fication during midsummer, a clear water phase is produced by a growth season minimum of Chl *a*, similar to that of several European lakes (Sommer 1984). The end of this phase in early autumn is often signaled by increases in Chl *a* concentration.

Summer Chl *a* minima did not change dramatically over the decade. From relationships developed between spring TP and Chl *a* (which are typical of the Great Lakes), one might expect little observable change in Chl *a* for a  $2 \mu\text{g}\cdot\text{L}^{-1}$  change in TP. Models by Chapra and Dobson (1981) and Vollenweider et al. (1980) predict, respectively, 0.5 and  $0.3 \mu\text{g}\cdot\text{L}^{-1}$  changes in summer average Chl *a* over the 10 yr, corresponding to a  $2 \mu\text{g}\cdot\text{L}^{-1}$  change in TP. However, Chl *a* minima fell below  $0.5 \mu\text{g}\cdot\text{L}^{-1}$  in 1977 and 1983, which is less than half the typical minimum values in this data set. Reduced Chl *a* concentrations in 1977 and 1983 were also reflected in other indications of a clearer water column.

#### Water clarity

Secchi disk depth followed systematic patterns each year (Fig. 2b). Typically, there was a minimum prior to stratification corresponding with the spring Chl *a* maximum. This was followed by increased transparency during midsummer and then a subsequent dramatic decrease during late summer – early fall, the latter often associated with calcite precipitation (“whittings”). Ladewski and Stoermer (1973) discussed the dramatic seasonal dynamics of Secchi depth as driven by whittings in 1972 in Lake Michigan, and Strong and Eadie (1978) and B. J. Eadie (GLERL, unpubl. data) reported that whittings are a regular phenomenon in Lake Michigan, Lake Ontario, Lake Erie, and southern Lake Huron. The long-term trend in Secchi depth is toward higher values in general. There are again clear signals that maximum midsummer Secchi depths were deeper in 1977 and 1983 than in other years.

Transmissometer data (Fig. 2c) follow a seasonal pattern similar to that of Secchi depth. Maximum transmissivity of surface waters occurs during midsummer. Lower values before and after this period correspond with the spring algal maxima and deepening of the thermocline or whittings, respectively. The long-term trend in this variable also indicates a general improvement in water clarity. Although not as dramatic, the 1983 signal is consistent with lower Chl *a* concentrations; there were no data available to evaluate the 1977 signal. The most dramatic evidence for the increased water clarity in 1983 comes from the 1% light depth (depth of the photic zone) calculated from measured PAR extinction (Table 1). The depth of 1% light penetration reached 32.8 m in July 1983, which corresponds to an extinction coefficient of  $0.14 \cdot \text{m}^{-1}$ .

#### Outlier Year 1977

Spring TP and Chl *a* concentrations were lowest in 1977 and Secchi depths were deeper. Rockwell et al. (1980b) demonstrated that reduced TP and Chl *a* concentrations in 1977 were evident on a lake-wide scale (see also Fig. 1 and 2a) and were not a regional phenomenon.

Winter and early spring winds, under isothermal or weakly stable conditions, typically resuspend deepwater and recently settled particulate material. Analysis of sedimentation and resuspension fluxes via sediment trap collections in Lake Michigan (Eadie et al. 1984) indicates that this winter and early spring resuspension provides the major upward flux of TP and subsequently resets TP conditions prior to the onset of stratification each year. During the severe winter of 1976–77, extensive ice cover developed, ranging up to 90% coverage

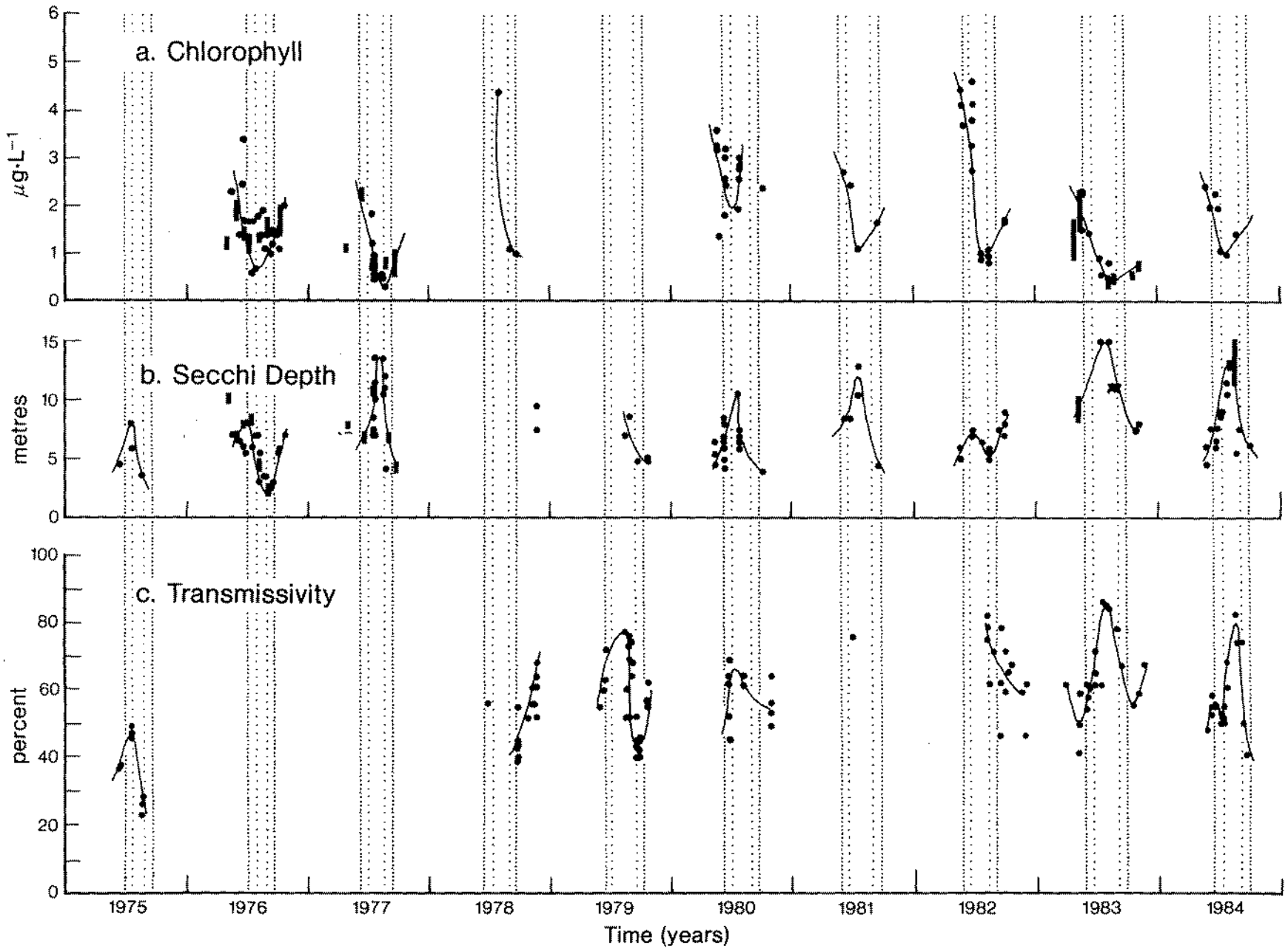


FIG. 2. Chlorophyll *a* and water clarity properties from the southern basin of Lake Michigan for 1975–84. Vertical bars represent means  $\pm 1$  SE from southern basin stations with depths greater than 80 m. Other data are from the region off Grand Haven, MI. (a) Epilimnetic chlorophyll *a*; (b) Secchi disk depth (symbol X represents EPA observations reported as greater than 11 m); (c) epilimnetic average light transmittance through 1-m path. The width of the stippled bars marks the period from the onset of stratification through the time when the thermocline deepens past 15 m.

TABLE 1. Photosynthetically active radiation (PAR) extinction coefficients ( $K_e$ ) and depth of 1% surface irradiance.

Date	$K_e$ ( $m^{-1}$ )	1% light depth (m)
1982		
May 20	0.21	22.0
June 13	0.21	22.0
July 21	0.17	27.0
1983		
May 20	0.18	25.6
June 6	0.19	24.2
June 8	0.17	27.0
July 10	0.14	32.8
July 13	0.14	32.8
1984		
May 21	0.21	22.0
June 4	0.21	22.0
June 18	0.19	24.2
July 25	0.20	23.0
July 30	0.17	27.0
August 24	0.23	20.0

(Quinn et al. 1978). Lake Michigan ice cover typically ranges from 20 to 50% and is restricted mostly to the nearshore area in the southern basin (Assel et al. 1983). Rodgers and Salisbury (1981) reproduced the 1976–77 TP transition in a simulation model by both reducing vertical mixing and increasing the effective sedimentation rate during winter to mimic lower resuspension flux caused by ice cover. While mechanisms relating winter resuspension flux to entrained wind energy and its dissipation by ice are tentative (Lesht and Rockwell 1985), this hydrologic phenomenon may have reduced resuspension, which in turn resulted in lower spring TP concentrations. Approximately 20% of resuspended phosphorus is available for algal production (NaOH extractions (Eadie et al. 1984)). It is not surprising, then, that, as we have shown above, reduced 1977 spring TP concentrations would affect algal production and lead to reduced Chl *a* concentrations (Fig. 2a) and increased water clarity (Fig. 2b) in summer.

#### Outlier Years 1983–84

Winter 1982–83 was not severe and ice cover was not particularly extensive; spring TP also did not vary substantially from the overall trend; therefore the basis for reduced Chl *a* and increased water clarity in 1983 requires further analysis. In addition to nutrient supply, algal abundance is controlled through zooplankton grazing.

#### Zooplankton grazing

Examination of the 10-yr record of total zooplankton biomass during the time of the midsummer Chl *a* minimum (Fig. 3a) shows no particular trend and, more specifically, nothing unusual in 1983. The zooplankton of 1983 and 1984 were, however, different from other years in another important way. Prior to 1983, calanoid copepods (primarily *Diaptomus* spp.) dominated the Lake Michigan summer zooplankton, and in those years, *Daphnia* spp. were a relatively minor component ( $14.1 \pm 6.6\%$  by weight). However, *Daphnia* spp. constituted 50–70% and 40–50% of the zooplankton (0–40 m) biomass during July–August 1983 and 1984, respectively. Furthermore, the numerically dominant *Daphnia* was *D. pulicaria*. This species was first observed in southeastern Lake

Michigan in autumn 1978 but did not become a summer dominant until 1982 (Evans 1985; Evans and Jude 1986). *Daphnia pulicaria* is a relatively large cladoceran, attaining adult body lengths greater than 2.4 mm and dry weights of 39.8  $\mu\text{g}$ . *Daphnia retrocurva* and *D. galeata mendotae*, the previously dominant cladocerans, are smaller, averaging 2.9 and 4.0  $\mu\text{g}$  dry weight, respectively.

Increased water transparency, independent of changes in nutrient status, has been reported for other lakes and has been associated with increased abundance of *Daphnia* (e.g. Shapiro et al. 1975; Lampert 1978; Edmondson and Litt 1982). We measured the grazing pressure exerted by this *Daphnia*-dominated community in August 1983; this experiment yielded a filtering rate of  $7.09 \pm 1.0 \text{ mL} \cdot \mu\text{g}^{-1} \cdot \text{d}^{-1}$ . (Our estimates are conservative because we included in our analysis injured or dead animals whose injuries may have been sustained during incubation.) With total animal dry weight of  $79.0 \pm 21.6 \mu\text{g} \cdot \text{L}^{-1}$ , we calculate that only 1.8 d would be required to clear the epilimnion in August 1983. Comparing this with estimated 3-d turnover times for the algal populations present in August 1983 (G. L. Fahnenstiel and D. Scavia, unpubl. data) indicates the ability of this zooplankton community to clear phytoplankton from the epilimnion.

We also measured grazing pressure in June 1983. Although conditions in June are different from those in mid-summer, zooplankton composition in June 1983 was similar to that found in midsummer of previous years (approximately 75–80% by weight as *Cyclops* spp. and *Diaptomus* spp.). These experiments yielded filtering rates of  $2.46 \pm 0.62 \text{ mL} \cdot \mu\text{g}^{-1} \cdot \text{d}^{-1}$ , which, for zooplankton dry weight of  $79 \mu\text{g} \cdot \text{L}^{-1}$ , would yield epilimnion clearance times greater than 5 d in contrast with 1.8 d for the *Daphnia*-dominated assemblage. In June, copepods were predominantly (approximately 75% by weight) *Diaptomus* copepodites. Adults can be more abundant in summer. Filtering rates determined in the laboratory for adult *Diaptomus* spp. feeding during summer in suspensions of Lake Michigan seston range from 0.2 to 0.3  $\text{mL} \cdot \mu\text{g}^{-1} \cdot \text{d}^{-1}$  (Vanderploeg and Scavia 1979; Vanderploeg 1981; H. A. Vanderploeg, GLERL, unpubl. data). These rates yield a turnover time for the total seston of approximately 50 d! *Diaptomus sicilis* and *D. ashlandi* filtering rates, determined for Lake Michigan by measuring changes in only Chl *a* during feeding bouts (Bowers 1980), are similar (0.1 and 0.5  $\text{mL} \cdot \mu\text{g}^{-1} \cdot \text{d}^{-1}$ , assuming 17.3 and 4.8  $\mu\text{g}$  dry weight per individual (Hawkins and Evans 1979)) to those determined on the total seston, illustrating the selective nature of feeding by these calanoids. Cladocerans, which are less selective than copepods in terms of both particle size and scent (Richman and Dodson 1983; Muck and Lampert 1984; Vanderploeg and Paffenhöfer 1985), will have an even more pronounced effect on the total seston than on Chl *a* concentration only. It appears that the restructured midsummer zooplankton in 1983 and 1984 was capable of reducing seston concentrations below previous midsummer levels, resulting in increased water clarity.

#### Causes for zooplankton species changes

If food quality and quantity are major regulators of zooplankton species composition, then several lines of evidence lead to the conclusion that large cladocerans (e.g. *Daphnia* spp.) should dominate the Lake Michigan assemblage. It has been claimed (Richman and Dodson 1983) that cladocerans such as *Daphnia* occupy niches characterized by moderately abundant high-quality food whereas calanoid copepods dominate in areas

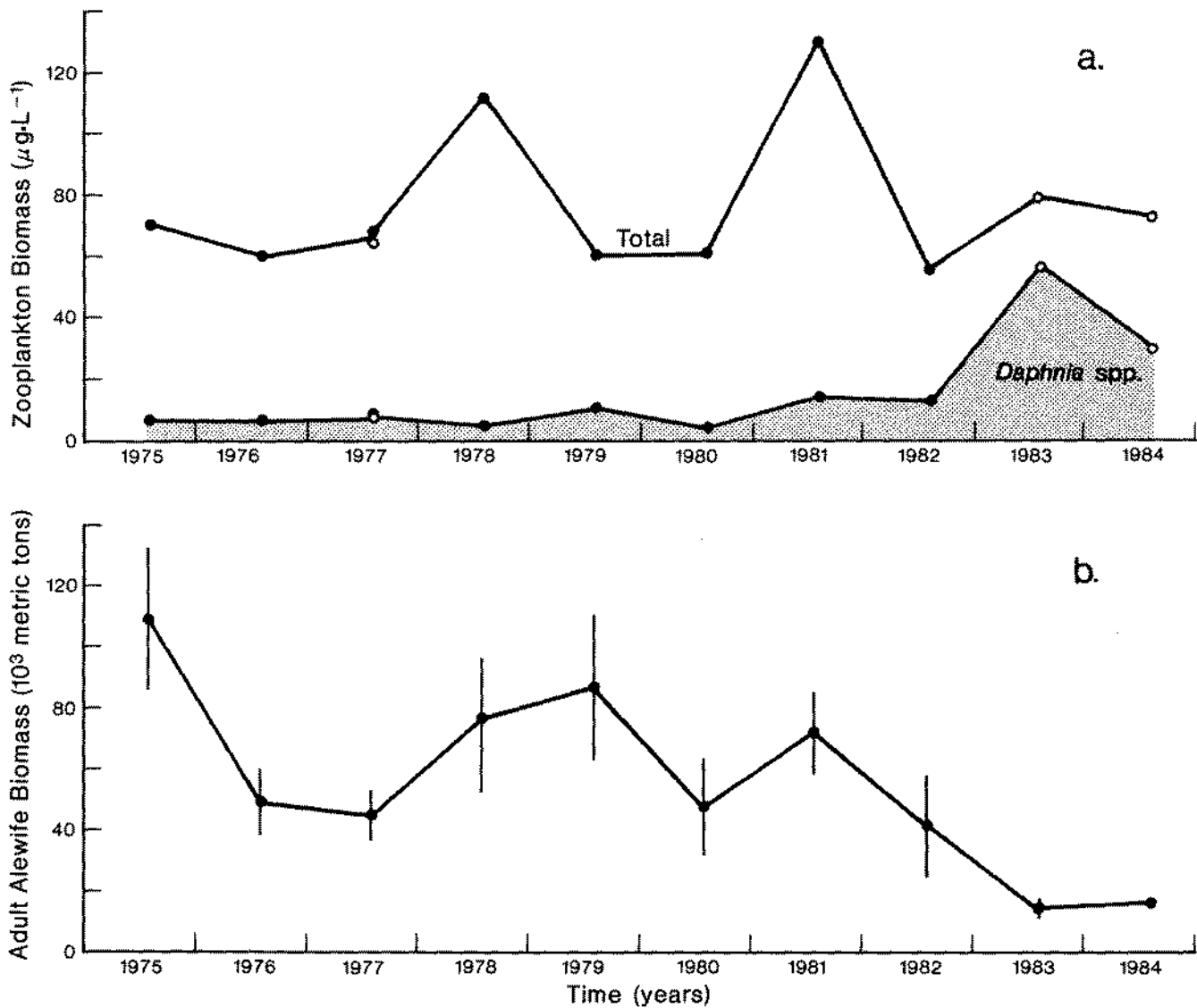


FIG. 3. (a) Dry weight of zooplankton collected during July and August 1975–84. Open points represent data collected from a 100-m station off Grand Haven, MI. Solid points represent data from a 40-m station south of Grand Haven (off Bridgman, MI). (b) Means and SE of estimates of lake-wide averaged adult alewife biomass.

of either lower food quality or lower food abundance. Food quality is a relative measure; however, we suggest that Lake Michigan seston concentration and quality is conducive to a cladoceran advantage. Richman and Dodson (1983) used serial dilutions of southern Green Bay water (mostly species of the algae *Anabaena*, *Aphanizomenon*, *Microcystis*, and *Oscillatoria*) with a mixture of cultured, edible green algae to prepare a gradient of quality for testing the above hypothesis. Vanderploeg et al. (1984) suggested that Lake Michigan seston is of lower quality relative to cultured algae; however, the food quality of open Lake Michigan seston is certainly greater than that of southern Green Bay. In fact, Vanderploeg (1981) explained invariance of measured particle selection by *Diaptomus* by ascribing high quality to the large particles and to at least some small particles of the Lake Michigan seston. Recently, Muck and Lampert (1984) further quantified the competitive regimes of the copepod *Eudiaptomus* and *Daphnia*. At low food concentrations, these two species had very similar weight-specific ingestion rates. Because the calanoid copepod expends

less energy at low food concentrations, it should outcompete *Daphnia*. However, the copepod ingestion rate saturates at a lower value and at a lower food concentration than that of *Daphnia*. Thus, at higher food concentrations, *Daphnia* should be superior. The incipient limiting level, when ingestion rate saturates for *Eudiaptomus*, is approximately  $100 \mu\text{g C}\cdot\text{L}^{-1}$ . A similar level for *Diaptomus sicilis* is apparent from fig. 3 and 10 of Vanderploeg et al. (1984). Particulate organic carbon concentrations in this region of Lake Michigan are typically  $200 \mu\text{g C}\cdot\text{L}^{-1}$  (Eadie et al. 1984), and even if that value is halved to estimate an "effective food concentration" (Vanderploeg and Scavia 1979; Vanderploeg et al. 1984), it appears that food levels are at or above the limiting level for the copepods. If the above hypothesis is correct, then, based on both food quantity and quality, *Daphnia*-like cladocerans should have been abundant in this region of Lake Michigan if resource-based competition is the dominant force shaping the assemblage. They were not.

We suggest that predatory pressure from the planktivorous



alewife suppressed large-bodied zooplankton populations until the early 1980s, when the alewife population decreased to new low levels (Fig. 3b). Alewife, an exotic marine species that invaded the upper Great Lakes through the Welland Canal (Smith 1968, 1970), was first reported in Lake Michigan during the late 1940s (Miller 1957) and has dominated the Lake Michigan fish planktivore population for the past 20 yr. Its population dynamics have been well documented (Brown 1972; Hatch et al. 1981; Jude and Tesar 1985; Eck and Brown 1985), and its impact on Lake Michigan zooplankton is consistent with size-selective predation theories (Hrbáček 1962; Dodson 1974). During periods of great alewife abundance (e.g. 1966), large zooplankton (1.1–5.0 mm) that were previously abundant became rare (Wells 1970). During a massive alewife die-off in 1966–67 (Brown 1972), these large zooplankton increased in abundance.

In the early 1980s alewife abundances again declined (Jude and Tesar 1985), and in 1983 and 1984 they decreased dramatically to their lowest levels since the early 1960s (Wells and Hatch 1984; L. Wells, pers. comm.). This dramatic decrease in alewife abundance has again relieved the larger zooplankton from strong vertebrate predation. Furthermore, a new species, *D. pulicaria*, became the new dominant replacing the smaller *Daphnia* that were most abundant in years before alewife invaded. *Daphnia pulicaria* become reproductive at a body length of 1.6 mm (Edmondson and Litt 1982), and intense size-selective predation pressure from alewife prior to 1982 probably prevented population growth even though the species was observed as early as autumn 1978 in the nearshore region (Evans et al. 1980; Evans and Jude 1986).

#### Alewife decline

Decline of the alewife population as the major forage fish in Lake Michigan was predicted (Smith 1970; Christie 1974; Stewart et al. 1981) and has been linked to management actions involving salmonid stocking. Because the number of stocked salmonines is not linked functionally to their forage base, Stewart et al. (1981) estimated that salmonines would place a demand on prey resources that might outstrip the alewife's reproductive capacity. An alternative view attributes the alewife decline to changes in the physical environment (a series of cold winters) rather than current levels of salmonine predation (Eck and Brown 1985). Salmonine predation, in that case, exerts additional pressure on the alewife population.

The following hypothesis provides the scenario for "outlier" year 1983 and beyond. An aggressive salmonine stocking program (Stewart et al. 1981; Jude and Tesar 1985) and several recent cold winters (Eck and Brown 1985) have contributed to dramatic decreases in the abundance of alewife, the major open-water planktivore. This decrease in vertebrate planktivory allowed *Daphnia* spp. to dominate the summer zooplankton and, because of their higher filtering capacities and less selective feeding, reduce Chl *a* and probably total seston concentrations. This resulted in increased water clarity<sup>2</sup>.

It is not known whether 1983 is an "outlier" year or the beginning of a new sequence of years reflecting a dramatic

reduction in the alewife population and its effect on zooplankton. In either case, it seems reasonable to hypothesize that, for Lake Michigan, management actions at the top of the ecosystem have cascaded (Carpenter and Kitchell 1984; Carpenter et al. 1985; Kitchell and Carpenter 1986) to effects on properties at several lower trophic levels, even to water clarity.<sup>2</sup>

#### General Discussion

We have shown both long-term, gradual changes in TP and water clarity and two periods of deviation from the long-term trend. The long-term data are consistent with expectations of nutrient load control. These gradual changes in TP and barely perceptible changes in Chl *a* are expected (Vollenweider et al. 1980) from consideration of the long hydraulic residence time (Chapra and Sonzogni 1979) and realized nutrient load reductions (International Joint Commission 1984). The observations reported here for the region offshore of Grand Haven are similar to southern basin averages of TP and Chl *a* in 1976, 1977, 1983, and 1984 (see Fig. 1 and 2 and Lesht and Rockwell 1985). These results suggest that, in terms of TP, the management objective of "nondegradation" has been accomplished because concentrations have decreased by about 30% since 1976. Summer Chl *a* concentrations have not decreased in a similar gradual fashion. In fact, little change in the mid-summer, clear phase minimum has been seen except for "outlier" years. However, gradual improvement has been observed in measures of summer water clarity, which are indirect and, at low Chl *a* concentrations, amplified manifestations of Chl *a* changes (Chapra and Dobson 1981). While the gradual trend toward lower TP and clearer water is consistent with the objectives and actions of the phosphorus load reduction program, the latter has not been proven to be the causal mechanism. It would be useful to examine alternative hypotheses (e.g. Brooks et al. 1984). The influence of physical factors on the Great Lakes ecosystems has been recognized for a long time (e.g. Chandler and Weeks 1945) and reiterated recently (Harris and Vollenweider 1982). Analysis of "outlier" year 1977 illustrates the effects that dramatic meteorological events can have on an aquatic ecosystem, even for a lake as large as Lake Michigan. Interestingly, the drop in TP and the lower Chl *a* minimum in 1977 lasted only 1 yr, after which both properties became consistent with long-term trends. Eck and Brown (1985) reported that winters near Lake Michigan have been colder than the 1949–83 mean for all but one of the years between 1976 and 1983. Comparison of the TP trend with the potentially subtle variations in ice cover or winter severity over the past decade would test the hypothesis that winter physics also exerts control over spring TP. It is clear from our analysis that many environmental factors must be considered when evaluating long-term water quality trends.

Results from 1983 and 1984 demonstrate that forces acting at the very top of the Lake Michigan food web may drive the ecosystem in a new direction. The impact of planktivore population dynamics on the zooplankton of this lake has been demonstrated before (Wells 1970; Kitchell and Carpenter 1986), but we now hypothesize that forces at the top of the food web have caused changes in the base, in a clearer water column, and thus have modified one of the most important parameters of perceived water quality.

Stability of this condition is currently uncertain. Data from 1984 suggest that, while alewife populations are still at very low levels, other planktivores (particularly bloater, *Coregonus*

<sup>2</sup>FOOTNOTE ADDED IN PRESS: Conditions in the region off Grand Haven, observed in 1983 and 1984, continued to persist in 1985. Summer Secchi depths were deeper than 14 m, epilimnetic Chl *a* concentrations were as low as 0.5  $\mu\text{g}\cdot\text{L}^{-1}$ , and epilimnetic transmissivity remained very high in 1985. Alewife biomass remained low and *Daphnia* was again abundant during summer.

hoys, and yellow perch, *Perca flavescens*) are still increasing in abundance (L. Wells, pers. comm.). The impact of the alewife decline on invertebrate predators is also unclear at this time; however, one would expect an increase in abundance of the large invertebrates (e.g., *Mysis relicta*, *Limnocalanus macrurus*) that coincide spatially and temporally with the alewife. The impact of these invertebrate predators on other zooplankton may also influence species composition (Lynch 1979), and these predators may also have been responsible for the somewhat reduced relative abundance of *Daphnia* spp. in 1984 (Fig. 3a) and the continued changes in *Daphnia* spp. size and composition in 1984.

Salmonine stocking programs continue to grow in other of the Great Lakes. Given the dramatic changes observed in Lake Michigan in the recent past, we can expect similar response potential in the food webs of other systems. We should take advantage of those opportunities for gaining greater understanding of the mechanisms that control water quality in systems where management activities influence the processes associated with both nutrient loading and food web regulation of nutrient cycles. Weather-related effects remain stochastic and largely uncontrollable, but the prospects for improvement of water quality through food web management remain open to development and testing. Only by continuing evaluation of the dynamics of Lake Michigan and the other Great Lakes during this period of transition will we be able to assess the relative impact of our actions in light of natural variability.

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