

Phosphorus Regeneration by Lake Michigan Alewives in the Mid-1970s

CLIFFORD E. KRAFT

University of Wisconsin Sea Grant Institute, University of Wisconsin—Green Bay
2420 Nicolet Drive, Green Bay, Wisconsin 54311-7001, USA

ABSTRACT.—A bioenergetics model of fish growth was used to estimate phosphorus (P) cycling by the population of Lake Michigan alewives *Alosa pseudoharengus* in the mid-1970s. The mean annual standing stock of alewives during the mid-1970s contained 1,500 tonnes of phosphorus, representing a substantial pool of particulate phosphorus unavailable to algae. An estimated 12,000 tonnes of phosphorus were egested and excreted annually by the Lake Michigan alewife population. Over half of the alewife-regenerated phosphorus was produced by larvae and age-0 alewives, which inhabit the nearshore epilimnion during summer. Seasonal aggregations of alewives—the dominant component of the Lake Michigan fish community during the mid-1970s—could have served as an important medium of phosphorus regeneration in comparison with more traditionally reported vehicles such as zooplankton. Expressed volumetrically, alewives regenerated $0.22 \mu\text{g P} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ during August, which is comparable to phosphorus regeneration rates previously estimated for Lake Michigan zooplankton. Use of a bioenergetics model provided a means to demonstrate that alewives played a substantial role in Lake Michigan phosphorus regeneration during the mid-1970s.

In this paper, I use a bioenergetics model to explore the potential role of alewives in Lake Michigan nutrient cycling. I hypothesized that fish can provide a major direct source of nutrient regeneration in this large limnetic system.

Bioenergetics estimates of fish consumption can provide key information required for simulation modeling of nutrient cycling. At the spatial scale of the Great Lakes ecosystem, uncertainties regarding fish population size and daily and seasonal patterns of aggregation are inevitable. Previous bioenergetics investigations of the mid-1970s population of alewives *Alosa pseudoharengus* in Lake Michigan (Stewart and Binkowski 1986; Hewett and Stewart 1989) have provided a foundation for the exploration of the role of this Great Lakes fish population in nutrient cycling.

Rates of primary production and the phytoplankton community composition in lakes are influenced by biotically mediated nutrient regeneration during periods when physical processes restrict nutrient inputs. During periods of summer stratification, epilimnetic production in Lake Michigan is limited by the availability of phosphorus and silica (Schelske and Stoermer 1971). Annual phosphorus uptake for primary production in Lake Michigan is estimated to be 100 times greater than estimated soluble reactive phosphorus (SRP) fluxes from lake sediments and 57 times

greater than combined external loads of total phosphorus (Conley et al. 1988). This indicates that internally regenerated phosphorus is necessary to sustain observed rates of primary production. Models examining the dynamics of Lake Michigan phytoplankton (Scavia et al. 1988) and Lake Ontario phosphorus cycling (Scavia 1979) have treated zooplankton as the sole source of internally regenerated phosphorus. This is typical of other published models that examine the effect of food web structure and function on primary production (Carpenter and Kitchell 1987). However, studies showing that fish can provide a major source of nutrients in other systems (Brabrand et al. 1990; Kraft 1992) highlight the need to examine the potential for nutrient regeneration by fish in Lake Michigan.

During the mid-1970s, the fish community of Lake Michigan was dominated by a single forage species, the alewife (Eck and Wells 1987). These fish aggregate in large schools at many stages in their life history. Alewives spawn near shore in late spring (Wells 1968), coincident with the formation of a thermocline in Lake Michigan. This behavior concentrates the adult and larval alewife population in epilimnetic waters during midsummer, a period during which primary productivity most depends on nutrient regeneration. In this paper, I investigate the role that alewives could have

had on phosphorus regeneration in Lake Michigan during the mid-1970s, when the alewife population was very abundant.

Methods

Phosphorus regeneration was estimated according to the mass balance

$$P_R = P_C - P_G,$$

where P_R is phosphorus excreted and egested, P_C is phosphorus consumed, and P_G is phosphorus allocated to growth. This mass balance can be solved for P_R provided estimates are available for consumption, growth, and phosphorus content of the predator and its prey. A P_R estimate can be allocated between phosphorus excretion and egestion if phosphorus assimilation efficiency is known. For the purposes of this paper, P_R was considered as phosphorus elimination without consideration of whether such phosphorus was egested or excreted.

Calculation of phosphorus consumption was based on estimates of prey consumption and prey phosphorus content. Prey consumption was estimated for an average individual with the energetics model developed by Stewart and Binkowski (1986). This bioenergetics model used a mass balance relationship based on calories to estimate consumption for an individual fish, given a known growth and assumed temperature history, as well as information on the caloric content of both the predator and its prey. All estimates of alewife prey consumption presented in this paper rely upon model inputs provided by Hewett and Stewart (1989), who presented detailed tables showing diet proportions (Table 1 in Hewett and Stewart 1989), population numbers (Table 2 in Hewett and Stewart 1989), population numbers (Table 2 in Hewett and Stewart 1989), and growth estimates (Table 2 in Hewett and Stewart 1989) for a mid-1970s population of Lake Michigan alewives. Energy density (calories per unit body mass) and temperature inputs were also described in detail by Hewett and Stewart (1989) and Stewart and Binkowski (1986).

Estimates of daily prey consumption ($\text{g wet weight} \cdot \text{d}^{-1}$) were converted to P_C ($\text{g P} \cdot \text{d}^{-1}$) with the following assumptions.

(1) The total phosphorus contents of cladoceran and copepod prey were assumed to be 0.0012 times wet weight, according to further assumptions that their dry weights are 12% of wet weight and that their total phosphorus contents are 1.0% of dry weight (Harris and Riley 1956; Beers 1966;

Khan and Siddiqui 1971; Andersen and Hessen 1991).

(2) The total phosphorus contents of *Diporeia* and *Mysis* prey were assumed to be 0.0018 times wet weight. This was derived from an estimate for other crustaceans of total phosphorus as 1% of dry weight (Nakashima and Leggett 1980; Galicka et al. 1991) and an estimated dry weight : wet weight ratio of 0.18 for *Diporeia* (Lubner 1979) and *Gammarus* (Galicka et al. 1991).

Changes in alewife mass due to growth were calculated daily with the bioenergetics model and converted to P_G , the equivalent amount of phosphorus incorporated as fish tissue. For this conversion, the phosphorus content of an alewife was estimated to be 0.375% of wet weight on the assumptions that alewife dry weight is 25% of wet weight and that alewife phosphorus content is 1.5% of dry weight, as determined for marine alewives (Durbin et al. 1979). The difference between P_C and P_G provided an estimate of P_R , the amount of phosphorus regenerated by alewives via egestion and excretion. Population-level estimates for P_C , P_R , and P_G were made by multiplying population size of alewives by the corresponding estimate for an average individual of each cohort.

The alewife population structure and diets used in the model were a composite of data available from the mid-1970s. Biomass estimates were a composite of data from 1973–1980 as presented by Eck and Brown (1985), then modified by Hewett and Stewart (1989). The input parameters for the model included (1) annual thermal history for larval, age-0, age-1, and adult (ages 2–7) alewives; (2) annual diet information for larval, age-0, age-1, and adult alewives, and (3) composite population and mortality estimates typical for the mid-1970s. All of these input values were detailed by Hewett and Stewart (1989).

Due to a lack of specific information regarding larval physiology, consumption by larval alewives initially was estimated with two different estimates of respiration rate, as detailed by Hewett and Stewart (1989). The difference in phosphorus elimination between the two larval respiration models was 500 tonnes over a 40-d simulation period, or 4% of the estimated total annual contribution of alewives to phosphorus regeneration. All estimates presented in this paper are based on the most conservative larval model (model A of Hewett and Stewart 1989) to estimate the minimum amount of P regenerated by larval alewives. For these model runs, larval alewives were assumed to hatch on June 20 and to metamorphose

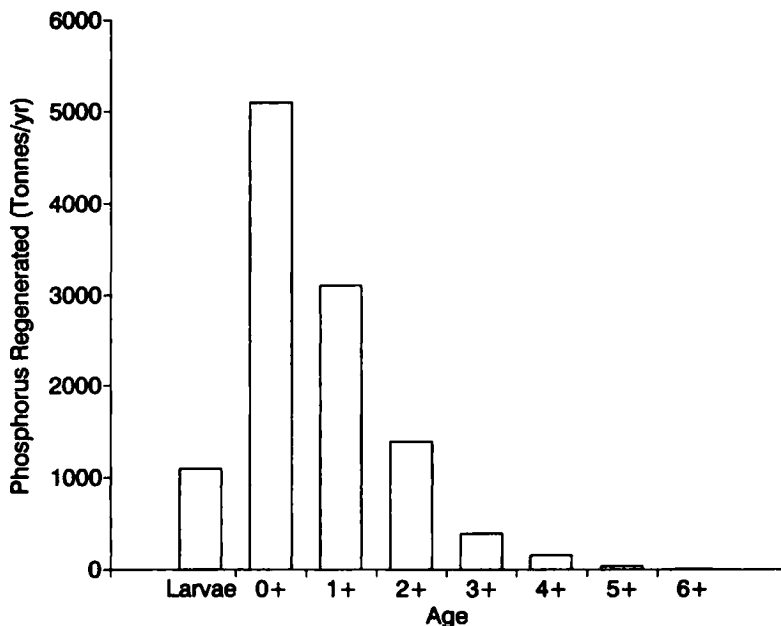


FIGURE 1.—Total annual phosphorus regenerated (egested and excreted) by different age-classes of the mid-1970s population of alewives in Lake Michigan.

40 d later. Hewett and Stewart (1989) demonstrated that the relative effects of alternative larval hatching scenarios on consumption were negligible.

For calculations of volumetric P_R , it was assumed that alewives were distributed throughout the entire Lake Michigan epilimnetic volume of 4.28×10^{14} L (Scavia et al. 1988).

Results and Discussion

Phosphorus contained in the mean annual standing stock of Lake Michigan alewives in the mid-1970s was estimated at 1,500 tonnes. An estimated 12,000 tonnes of phosphorus were annually regenerated through egestion and excretion by the same population. Over half of this phosphorus (56%) was supplied by alewives in their first year of life, including larval alewives (Figure 1; Table 1).

Of the phosphorus regenerated by first-year alewives, 75% was supplied during July–October (Figure 2). Expressed on a volumetric basis, the average epilimnetic concentration of phosphorus egested and excreted by the alewife population peaked during August (Table 2). The amount of phosphorus incorporated in alewife production during periods of thermal stratification was nearly constant at around $0.05 \mu\text{g P} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ (Table 2). Weight-specific regeneration rates during August

were 1.7 , 0.95 and $0.39 \mu\text{g P} \cdot \text{mg dry weight}^{-1} \cdot \text{d}^{-1}$ for age-0, age-1, and adult (age 2–age 7) alewife age-classes, respectively.

These results indicate that age-0 and age-1 alewives dominate nutrient regeneration (Figures 1, 2), suggesting that alewife contributions to regenerated P will be greatest when alewife populations exhibit strong year-classes. These results also suggest another potential link between Lake Michigan alewife abundance and phytoplankton abundance, besides the “top-down” grazing impacts that have been the subject of recent debate (Evans 1992). Positive correlations between nearshore estimates of alewife and phytoplankton abundances in southern Lake Michigan (Evans 1992) during the 1970s could, in part, reflect the effect of alewife-regenerated phosphorus.

The estimated volumetric excretion rate by the alewife population during stratification is of the same order of magnitude as previous phosphorus excretion estimates for Lake Michigan zooplankton in the offshore epilimnion. Busch and Brooks (1988) estimated phosphorus excretion rates using field estimates of zooplankton density from Lake Michigan together with a relationship between zooplankton nutrient excretion, zooplankton weight, and ambient temperature (Korstad 1983). Busch and Brooks (1988) estimated that zooplankton phosphorus excretion ranged from 0.4

TABLE 1.—Annual mean phosphorus mass and mean daily phosphorus regeneration (egestion and excretion), expressed per unit volume, for the mid-1970s Lake Michigan alewife population. Alewives are assumed to have been restricted to the epilimnion. Zero values indicate that estimates equaled zero when rounded to significant digits.

Age	Annual P mass ($\mu\text{g P}\cdot\text{L}^{-1}$)	Daily P regeneration ($\mu\text{g P}\cdot\text{L}^{-1}$)
0	0.9	0.04
1	0.8	0.02
2	0.6	0.01
3	0.3	0.0
4	0.2	0.0
5	0.1	0.0
6	0.0	0.0
7	0.0	0.00
Total	2.9	0.07

to $1.4 \mu\text{g P}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ from mid-June through mid-summer in Lake Michigan. Scavia et al. (1988) estimated that zooplankton phosphorus regeneration rates in Lake Michigan ranged from 0.07 to $0.18 \mu\text{g P}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ over a range of trophic conditions including low to high alewife abundance. Their regeneration rates were estimated with a simulation model, for which they assumed that

TABLE 2.—Daily phosphorus regeneration (egestion and excretion) and incorporation of phosphorus in fish production by the mid-1970s alewife population in the epilimnion of Lake Michigan, expressed on a volumetric basis. Monthly averages during periods when the lake is stratified are shown.

Month	P regeneration ($\mu\text{g P}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	P incorporated in growth ($\mu\text{g P}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)
Jul	0.16	0.04
Aug	0.22	0.06
Sep	0.19	0.05
Oct	0.13	0.02

(1) zooplankton excretion was proportional to respiration ($\text{mg C}\cdot\text{mg C}^{-1}\cdot\text{d}^{-1}$), (2) nutrient fluxes followed a constant "Redfield" mass ratio, and (3) 50% of regenerated phosphorus was available to algae.

Although these zooplankton phosphorus regeneration rates were based on data from offshore zooplankton populations, it is likely that inshore and offshore nutrient regeneration estimates would be of the same magnitude. Both Busch and Brooks (1988) and Scavia et al. (1988) estimated zooplankton phosphorus regeneration as a function of temperature, zooplankton weight, and zoo-

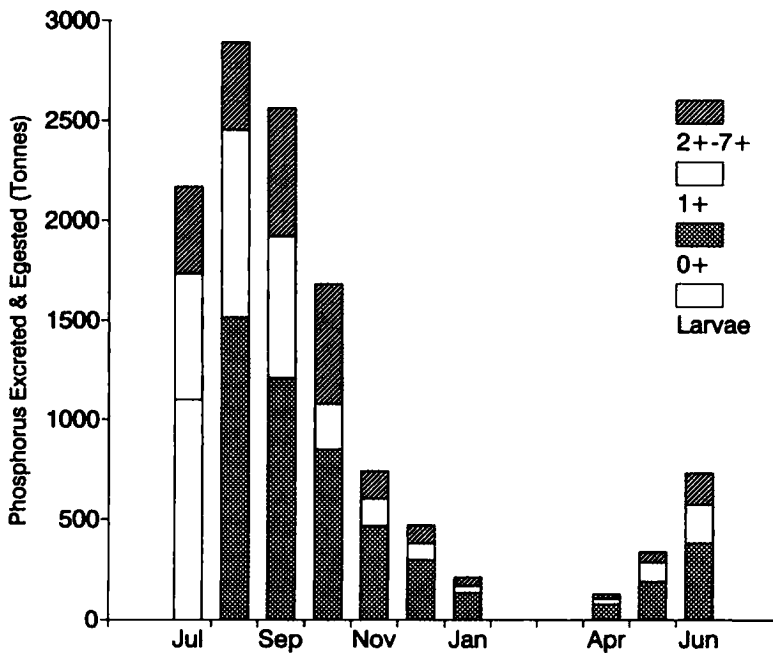


FIGURE 2.—Total phosphorus regenerated (egested and excreted) monthly over an annual period by the mid-1970s population of alewives in Lake Michigan. Proportions of monthly P regeneration due to larvae and to age-0, age-1, and older age-classes are shown.

plankton density. Evans (1990) concluded that summer surface temperatures inshore (4–10-m depths) and offshore (30–45-m depths) in Lake Michigan showed minimal differences over a 10-year period, which suggests that temperature-dependent physiological processes that control zooplankton feeding and excretion would have been similar both inshore and offshore. Mean zooplankton densities over the same interval were consistently lower at inshore regions (Evans 1990), which would result in lower nutrient regeneration rates to the extent that excretion is a function of zooplankton density. This could have been countered, however, by lower mean zooplankton size at inshore stations (Evans 1990), which would increase zooplankton nutrient regeneration due to greater weight-specific feeding rates by smaller zooplankton.

Another way to assess the significance of a component of nutrient regeneration is to calculate how long it would take to regenerate sufficient nutrients to equal ambient levels present in biota. Planktonic components of biotic particulate phosphorus have turnover rates of a few days at most, so total regeneration must be of this order. The regeneration rates provided by alewives in the mid-1970s are important by this criterion.

If the amount of phosphorus accounted for by the mid-1970s alewife biomass (October 1 estimate) was mixed evenly throughout the total volume of Lake Michigan, the average concentration of phosphorus present in alewife biomass would have been $0.3 \mu\text{g P}\cdot\text{L}^{-1}$. The mean total phosphorus present in the Lake Michigan water column during 1976, as measured through conventional chemical analytical methods (i.e., exclusive of fish), was approximately $8 \mu\text{g P}\cdot\text{L}^{-1}$ (Rockwell et al. 1989).

Fahnenstiel and Scavia (1987) reported a 35–70% decline in mixed-layer total phosphorus from the end of spring mixing (May) to the midperiod of stratification (July–August) at an offshore station. If spring total phosphorus were $8 \mu\text{g P}\cdot\text{L}^{-1}$ (Scavia et al. 1986) and 92 d elapsed between final spring mixing and the midperiod of stratification, daily phosphorus losses would have ranged from 0.03 to $0.06 \mu\text{g P}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. Because some of the alewife-regenerated phosphorus is derived from hypolimnetic food sources (e.g., *Diporeia* and *Mysis*), alewives may have slowed the midsummer decline in epilimnetic total phosphorus.

Weight-specific phosphorus regeneration rates were greatest for age-0 alewives, and age-0 alewife rates were similar to the estimated weight-specific

phosphorus regeneration rate ($1.7 \mu\text{g P}\cdot\text{mg dry weight}^{-1}\cdot\text{d}^{-1}$) for zooplankton in Lake Michigan (Scavia et al. 1988). Older alewife age-classes had lower weight-specific phosphorus regeneration rates. Peters and Rigler (1973) cited studies in which weight-specific rates of phosphorus release by zooplankton varied inversely with zooplankton weight by a power ranging from -0.3 to -0.9 . It is surprising that larval alewives, which are several orders of magnitude greater in weight than individual zooplankton, had such large estimated weight-specific regeneration rates. This could be partly a result of the extremely low net conversion efficiency of alewives relative to other fishes (Stewart and Binkowski 1986).

Although the nutrient regeneration rates presented in this paper are subject to several biological assumptions about the alewife population, particularly assumptions about growth and seasonal mortality rates, the assumption most likely in error for volumetric phosphorus regeneration estimates is that alewives were evenly distributed throughout the entire epilimnion during the whole year. Consequently, all volumetric estimates presented in Tables 1 and 2 are conservative. Heufelder et al. (1982) reported that newly hatched larval alewives were found along the shoreline at depths from 0 m to 15 m during July and August. Brandt et al. (1980) observed that age-0 alewives reached maximum abundance in September and occupied water with temperatures greater than 17°C , which corresponded to depths less than 15 m. Jude et al. (1986) reported that age-0 alewives inhabited inshore waters in southeastern Lake Michigan in the vicinity of the 9-m contour throughout summer and began offshore migration in the fall. Although these studies indicate that age-0 alewives aggregate in a smaller volume than that represented by the entire epilimnion, precise information on the extent of such aggregations is unavailable.

Seasonal or daily events not considered as part of the analysis presented here could affect the impact of alewife phosphorus regeneration upon algal production. Age-0 alewives undergo extensive daily vertical migrations from a benthic habitat during the day into the water column at night, when they do most of their feeding. The effect of their released phosphorus on primary production could be influenced by their position in the water column at the time of egestion and excretion. Annual occurrences of postspawning or spring alewife mortality could provide a seasonal nutrient pulse and stimulate algal production, yet no quan-

tified data are available concerning the magnitude and timing of mass alewife dieoffs. For the purposes of the simulations presented in this paper, it was assumed that alewife mortality occurred at a constant rate throughout the year. Changes in the estimated mortality schedule could change the estimated population size at various times through the summer, which might produce changes of similar magnitude in estimated phosphorus cycling rates.

No attempt was made to distinguish between phosphorus egestion and phosphorus excretion when phosphorus regeneration was estimated. A study of phosphorus lability in rainbow trout feces showed that labile organically bound phosphorus constituted 30–50% of the fecal phosphorus when fish were fed commercially prepared food (Pettersson 1988), indicating that up to half of the phosphorus in fish feces may be available for algal production. In experiments with roach *Rutilus rutilus*, Brabrand et al. (1990) found that 85–95% of released phosphorus was soluble molybdate-reactive phosphorus, the remainder sedimenting with fecal pellets. Further information on alewife phosphorus assimilation efficiency, the lability of fecal phosphorus from alewives fed natural prey, and fecal settling rates is needed to assess the proportion of regenerated phosphorus rendered unavailable to primary production as a result of fecal production.

Given the large relative magnitude of the estimated phosphorus regeneration by Lake Michigan alewives in the mid-1970s, it is appropriate to consider scenarios for changes in phytoplankton community structure that could result from changes in fish phosphorus regeneration. It is well documented that for a given total nutrient loading rate, phytoplankton community structure can differ depending on whether nutrient supply is pulsed or constant (Sommer 1989). Reinertsen et al. (1986) invoked this mechanism as a means by which fish excretion can influence phytoplankton community structure, suggesting that fish release phosphorus in larger patches than are released by zooplankton. Because cyanobacteria appear more capable of taking up large pulses of phosphorus than their competitors, Reinertsen et al. (1986) suggested that they have an advantage in the presence of fish. Fahnenstiel and Scavia (1987) reported a shift in the offshore summer Lake Michigan phytoplankton community from green algae and cyanobacteria to phytoflagellates between the 1970s and 1980s, but this can also be attributed

to other processes (Scavia et al. 1988). Alternatively, fish could influence phytoplankton community structure by recycling nutrients in a different nitrogen:phosphorus ratio than zooplankton (Kraft 1992).

Acknowledgments

I thank D. Armstrong, S. Brandt, A. Brooks, K. Hartman, S. Hewett, J. Kitchell, J. Magnuson, W. Porter, R. Ragotzkie, D. Stewart, and two anonymous reviewers for helpful comments on a previous version of this manuscript. This work was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, and from the State of Wisconsin, federal grant NA84AA-D-00065, project A/AS-1.

References

- Andersen T., and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnology and Oceanography* 36:807–813.
- Beers, J. R. 1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. *Limnology and Oceanography* 11: 520–528.
- Brabrand, Å., A. B. Faafeng, and J. P. M. Nilssen. 1990. Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. *Canadian Journal of Fisheries and Aquatic Sciences* 47:364–372.
- Brandt, S. B., J. J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1557–1564.
- Busch, J. L., and A. S. Brooks. 1988. The excretion of phosphate and ammonia from microcrustaceans, and its vertical and seasonal distribution at an offshore station in Lake Michigan. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 23:366–375.
- Carpenter, S. R., and J. F. Kitchell. 1987. The temporal scale of limnetic primary production. *American Naturalist* 129:417–433.
- Conley, D. J., M. A. Quigley, and C. L. Schelske. 1988. Silica and phosphorus flux from sediments: importance of internal recycling in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1030–1035.
- Durbin, A. G., S. W. Nixon, and C. A. Oviatt. 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. *Ecology* 60:8–17.
- Eck, G. W., and E. H. Brown, Jr. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based

- on the status of prey populations in the 1970's. Canadian Journal of Fisheries and Aquatic Sciences 42:449-454.
- Eck, G. W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement 2):53-60.
- Evans, M. S. 1990. Large-lake responses to declines in the abundance of a major fish planktivore—the Lake Michigan example. Canadian Journal of Fisheries and Aquatic Sciences 47:1738-1754.
- Evans, M. S. 1992. Historic changes in Lake Michigan zooplankton community structure: the 1960s revisited with implications for top-down control. Canadian Journal of Fisheries and Aquatic Sciences 49:1734-1749.
- Fahnenstiel, G., and D. Scavia. 1987. Dynamics of Lake Michigan phytoplankton: recent changes in surface and deep communities. Canadian Journal of Fisheries and Aquatic Sciences 44:509-514.
- Galicka, W., M. Grzybkowska, and H. Koszalinski. 1991. Materials for the investigation of calorificity and nutrient contents of chosen groups of invertebrates of the Warta River. Acta Universitatis Lodzianensis Folia Limnologica 5:37-44.
- Harris, E., and G. A. Riley. 1956. Oceanography of the Long Island Sound, 1952-1954. VIII. Chemical composition of the plankton. Bulletin of the Bingham Oceanographic Collection Yale University 15: 315-323.
- Heufelder, G. R., D. J. Jude, and F. J. Tesar. 1982. Effects of upwelling on local abundance and distribution of larval alewife (*Alosa pseudoharengus*) in eastern Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 39:1531-1537.
- Hewett, S. W., and D. J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: ontogenetic, seasonal, and historical patterns. Transactions of the American Fisheries Society 118:581-596.
- Jude, D. J., and seven coauthors. 1986. Impact of the Donald C. Cook Nuclear Plant on fish. Pages 285-351 in R. Rossman, editor. Impact of the Donald C. Cook Nuclear Plant. University of Michigan, Great Lakes Research Division Publication 22, Ann Arbor.
- Khan, J. A., and A. Q. Siddiqui. 1971. Water, nitrogen and phosphorus in freshwater plankton. Hydrobiologia 37:531-536.
- Korstad, J. 1983. Nutrient regeneration by zooplankton in southern Lake Huron. Journal of Great Lakes Research 9:374-388.
- Kraft, C. E. 1992. Estimates of phosphorus and nitrogen cycling by fish using a bioenergetics approach. Canadian Journal of Fisheries and Aquatic Sciences 49:2596-2604.
- Lubner, J. F. 1979. Population dynamics and production of the relict amphipod *Pontoporeia hoyi*, at several Lake Michigan stations. Doctoral dissertation. University of Wisconsin. Milwaukee.
- Nakashima, B. S., and W. C. Leggett. 1980. The role of fishes in the regulation of phosphorus availability in lakes. Canadian Journal of Fisheries and Aquatic Sciences 37:1540-1549.
- Peters, R. H., and F. H. Rigler. 1973. Phosphorus release by *Daphnia*. Limnology and Oceanography 18: 821-839.
- Pettersson, K. 1988. The mobility of phosphorus in fish-foods and fecals. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 23:200-206.
- Reinertsen, H., A. Jensen, A. Langeland, and Y. Olsen. 1986. Algal competition for phosphorus: the influence of zooplankton and fish. Canadian Journal of Fisheries and Aquatic Sciences 43:1135-1141.
- Rockwell, D. C., D. K. Salisbury, and B. M. Lesht. 1989. Water quality in the middle Great Lakes: results of the 1985 USEPA survey of Lakes Erie, Huron and Michigan. U.S. Environmental Protection Agency, Great Lakes National Program Office, Report 4, Chicago, Illinois.
- Scavia, D. 1979. Examination of phosphorus cycling and control of phytoplankton dynamics in Lake Ontario with an ecological model. Journal of the Fisheries Research Board of Canada 36:1336-1346.
- Scavia, D., G. L. Fahnenstiel, M. S. Evans, D. J. Jude, and J. T. Lehman. 1986. Influence of salmonine predation and weather on long-term water quality trends in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 43:435-443.
- Scavia, D., G. A. Lang, and J. F. Kitchell. 1988. Dynamics of Lake Michigan plankton: a model evaluation of nutrient loading, competition, and predation. Canadian Journal of Fisheries and Aquatic Sciences 45:165-177.
- Schelske, C. L., and E. F. Stoermer. 1971. Eutrophication, silica and predicted changes in algal quality in Lake Michigan. Science (Washington, D.C.) 173: 423-424.
- Sommer, U. 1989. The role of competition for resources in phytoplankton succession. Pages 57-106 in U. Sommer, editor. Plankton ecology: succession in plankton communities. Springer-Verlag, Berlin.
- Stewart, D. J., and F. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Transactions of the American Fisheries Society 115: 643-661.
- Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Service Fishery Bulletin 67:1-15.