

- KILLINGLEY, J. S., AND W. A. NEWMAN. 1983. O-18 fractionation in barnacle calcite. A barnacle paleotemperature equation. *J. Mar. Res.* **40**: 893–902.
- MCCREA, J. M. 1950. On the isotopic chemistry of carbonates and paleotemperature scale. *J. Chem. Phys.* **18**: 849–857.
- MIKKELSEN, N., L. LABEYRIE, JR., AND W. H. BERGER. 1978. Silica oxygen isotopes in diatoms: A 20,000 yr record in deep-sea sediments. *Nature* **271**: 536–538.
- MOORE, T. C., JR., AND OTHERS. 1980. The reconstruction of sea surface temperatures in the Pacific Ocean of 18,000 B.P. *Mar. Micropaleontol.* **5**: 215–247.
- REDFIELD, A. C., AND I. FRIEDMAN. 1969. The effect of meteoric water, melt water and brine on the composition of polar sea water and of the deep waters of the ocean. *Deep-Sea Res.* **16**: 197–214.
- SCHUMACHER, J. D., K. AAGAARD, C. H. PEASE, AND R. B. TRIPP. 1983. Effects of a shelf polynya on flow and water properties in the northern Bering Sea. *J. Geophys. Res.* **88**: 2723–2732.
- STERNBERG, L. D. S. L. O., AND M. J. D. DENIRO. 1983. Biogeochemical implications of the isotopic equilibrium fractionation factor between the oxygen atoms of acetone and water. *Geochim. Cosmochim. Acta* **47**: 2271–2274.
- TAN, F. C., AND P. M. STRAIN. 1980. The distribution of sea-ice melt-water in the eastern Canadian arctic. *J. Geophys. Res.* **85**: 1925–1932.
- USHAKOV, P. V. 1955. Subphylum Tunicata, class Ascidiaceae, p. 307–312. *In* E. N. Pavlovskii [ed.], *Atlas of the invertebrates of the far eastern seas of the USSR*. Akad. Nauk SSSR. Zool. Inst. [Isr. Program Sci. Transl., 1966.]
- VETSHTSEYN, V. Y., G. A. MALYUK, AND V. P. RUSANOV. 1974. Oxygen-18 distribution in the central arctic basin. *Oceanology* **14**: 514–519.
- WALSH, J. J., AND OTHERS. 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: Source regions for organic matter effecting AOU demands of the Arctic Ocean. *Prog. Oceanogr.* **22**: 279–361.
- WHITE, M. G. 1977. Ecological adaptations by Antarctic poikilotherms to the polar marine environment, p. 197–208. *In* G. A. Llano [ed.], *Adaptions within Antarctic ecosystems*. Gulf Publ.
- WISE, L. E. 1944. *Wood chemistry*. Reinhold.

Submitted: 12 April 1989

Accepted: 4 December 1989

Revised: 17 April 1990

*Limnol. Oceanogr.*, 35(5), 1990, 1195–1200

© 1990, by the American Society of Limnology and Oceanography, Inc.

## Predicting diel vertical migration of zooplankton

**Abstract**—Amplitude of diel vertical migration is predicted by water clarity measured by Secchi depth. The model assumes that vertical migration serves to minimize mortality from visually feeding fish and to maximize grazing rate within this predation context. Three of the 24 observations of diel vertical migration are outliers which are either ultraoligotrophic, or have minimal populations of plankton-eating fish, or both. The other 21 observations in lakes with average photosynthetic rates  $\geq 300 \text{ mg C m}^{-2} \text{ d}^{-1}$  and more than  $\sim 2 \text{ g m}^{-2}$  of plankton-eating fish showed diel vertical migration proportional to Secchi depth, with a correlation coefficient of about

0.880. The residual of the migration–water clarity relationship is significantly and inversely correlated with percent illumination of the moon. Water clarity and moon intensity together account for 84% of the variation in migration amplitude for the 21 observations.

The usual behavior pattern of diel vertical migration is for a population of zooplankton to spend the daylight hours deep in a lake and then to rise toward the surface for a few hours at night. This behavior has been studied for nearly two centuries (Lampert 1989). Several recent reviews identify a few factors as important causes of the behavior in both marine and freshwater habitats: intensity of visual predation on zooplankton, light intensity, temperature, and food levels (e.g. Clark and Levy 1988; Gabriel and Thomas 1988; Lampert 1989; Wurtsbaugh and Neverman 1988). Although differing in details, a common theme runs through these studies. Diel vertical migration is thought of as being primarily determined by a com-

### Acknowledgments

I thank Virginia Dodson, Ken Parejko, Charles Ramcharan, Bart DeStasio, and Peter Jumars for comments on the manuscript. Thanks to Charles Ramcharan (Licht Pond), Trevor Downie (Muskellunge Lake), and the 1987 University of Wisconsin summer limnology class (Lake Mendota), who helped sample these lakes. I especially thank Steve Carpenter who allowed me to use unpublished data from Long Lake, Michigan, Arni Litt who went out and sampled Lake Washington when I asked if there were any data, and Jane and Wes Licht, who allowed me to sample their pond in Wisconsin.

promise between predator avoidance and foraging opportunities. Because light flux diminishes exponentially as it penetrates into water, the resulting vertical gradient of light means that photosynthesis and visual predation (especially on prey  $\geq 1$  mm, cf. O'Brien 1987) are most intense near the surface during daylight. Zooplankton can avoid fish predation by moving deeper during the day, but they also leave their food behind. They can then compensate by returning to graze in the upper waters at night.

Migration is costly because it reduces population growth rate in several ways: reduces the total time spent feeding, diverts energy to swimming from growth and reproduction, and slows growth and reproduction by exposure to cooler (deeper) waters during the day. Physiological studies by Dagg (1985) and Lampert (1989) support the hypothesis that zooplankton migrate only if they are not severely food limited.

Diel vertical migration is probably possible only if light intensity fluctuates daily. Bogorov (1946) and Buchanan and Haney (1980) found no migration in arctic waters during the constant light of the arctic summer.

If one knows that zooplankton in a specific lake experience a daily light-dark cycle, intense fish predation, and lack severe food limitation, is it possible to correctly predict vertical migration? For example, Madison, Wisconsin, lakes fulfill the first criterion and probably the second two criteria in summer, but zooplankton show little or no migration (Table 1). On the other hand, zooplankton of a small, shallow pond (Licht Pond) in the same region show migration through most of the available water column. At least three recent models (Clark and Levy 1988; Gabriel and Thomas 1988; Gliwicz and Pijanowska 1988) use the predator-avoidance scenario as the basis for making quantitative predictions of vertical migration intensity. These models are general and make precise predictions but require extensive knowledge of factors such as light penetration, algal distribution, predator distribution, and prey size and swimming behavior. This information is expensive and time consuming to gather and is not available in the vertical migration literature. I see a need

for a simpler model that predicts vertical migration intensity, perhaps with less precision and generality, and is easy to use.

*Daphnia* is probably the most commonly studied genus of the appropriate size zooplankton (generally  $\geq 1$  mm). Surprisingly few studies of *Daphnia* diel vertical migration report both Secchi depth (or any measure of light penetration, such as the depth of the 10% light level) and thermocline depth. Table 1 includes data from all such studies done since 1931. I excluded only studies, such as those of Worthington (1931) in which zooplankton were collected with a closing net over large depth intervals, because this technique shows large variations in capture efficiency in different strata (Langford 1938).

Migration intensity can be measured as the amplitude of vertical migration ( $M$ ).  $M$  refers to the extent of diel oscillation of the average depth of the population. In the *Daphnia* example given here, I used data from the original literature for all species and ages of *Daphnia* to calculate  $M$  (Table 1). Typically, not all individuals of a species, or all species participate in migration to an equal extent, but the available data on *Daphnia* migration often do not make these distinctions. Certainly, precision of the relationship could be improved by restriction of migrating classes.

Even for lakes with high populations of plankton-eating fish, predation intensity is not high throughout the year. Fish predation is most intense in north temperate lakes between May and October, both because of the temperature-dependent increase in feeding rate and the enormous recruitment of young fish (e.g. Hairston et al. 1983; Threlkeld 1979; Hewett and Stewart 1989). For this reason, all the estimates of  $M$  analyzed here (Table 1) are taken from May to October.

The predator-avoidance scenario suggests migration intensity is proportional to water clarity, which is proportional to the Secchi depth ( $D_s$ ): the deeper light penetrates into a lake, the deeper the zooplankton must sink during the day to avoid fish predation. In order to compare habitats of different depth (e.g. Licht Pond and Lake Michigan), it might be necessary to scale  $M$

Table 1. Data for 25 instances of diel vertical migration. When data for more than one species of *Daphnia* were given, the vertical distributions were combined. The residual is that of the linear model, Eq. 1, for  $M$  vs.  $D_s$ .

Lake	Location	$M$ (m)	$D_s$ (m)	$D_t$ (m)	Residual	Moon (% full)	Reference*
Bull Shoals	Arkansas, 7 Jun 67	6	4	14	1.54	0	1
Czos	Poland, 4 Jul 86	0.6	0.8	7	-1.23	7	2
Constance	Germany, 20 Jul 82	7.4	5	9	2.12	0	3
Kuc	Poland, 4 Jul 86	8.6	6.2	7	2.33	7	2
Lampackie	Poland, 4 Jul 86	4.6	1.8	5	1.95	7	2
Licht	Wisconsin, 29 Aug 88	0.73	1.8	2.5	-1.92	87	4
Long	Colorado, 6 Sep 41	5.8	9.2	9	-2.93	98	5
Long	Michigan, 10 Jul 88	5.5	3.4	2.75	1.54	15	6
Long	Michigan, 21 Jun 88	5	3.4	3	1.04	47	6
Long	Michigan, 1 Jul 88	4.6	4	3.3	0.14	92	6
Long	Michigan, 21 Jul 88	2.5	2.85	3.75	-1.01	51	6
Long	Michigan, 30 Jul 88	2.1	2.75	4	-1.33	94	6
Mendota	Wisconsin, 26 Jun 87	0.1	1.4	12	-2.22	0	4
Michigan	Michigan, 7 Aug 54	9.6	9.1	14	0.95	63	7
Michigan	Michigan, 27 Aug 54	10.9	6.4	18	4.47	7	7
Michigan	Michigan, 7 Oct 54	5.6	3.6	27	1.47	79	7
Muskellunge	Wisconsin, 21 Jul 87	2.35	6	9.5	-3.75	15	4
Pilanko	Poland, 4 Jul 86	3.1	2.2	6	0.12	7	2
Probarskie	Poland, 4 Jul 86	10.7	5.1	5	5.34	7	2
Schöhsee	Germany, 1 Jul 82	3	3.5	8	-1.05	83	8
Washington	Washington, 28 Sep 89	2.04	8	14.5	-5.71	1	9
Wintergreen	Michigan, 21 Jun 76	0.64	1.25	3.75	-1.56	30	10
Wintergreen	Michigan, 6 Jul 76	1.25	0.75	4.25	-0.54	77	10
Three Lakes	Michigan, 21 Jun 72	5.5	5	4	4.33	81	11

\* 1—Applegate and Mullan 1969; 2—Gliwicz and Pijanowska 1988; 3—Geller 1986; Müller 1985; 4—Dodson unpubl. data; 5—Pennak 1944, 1955; 6—Dini 1989; Carpenter unpubl. data; 7—Wells 1960; 8—Lampert and Taylor 1985; 9—Litt and Edmondson unpubl. data; 10—Threlkeld 1979, unpubl. data; 11—Haney and Hall 1975.

by some appropriate measure of depth. I chose the depth of the thermocline ( $D_t$ ) as the scaling factor because it defines the lower limit of the region of greatest biological activity.

Of the 24 observations, some are single observations from a lake and some are multiple observations from the same lake (Table 1). This leads to problems in the statistical analysis. Namely, are the observations independent? The observations are a collection of different studies and are not organized to test the independence of within-lake samples compared to between-lake samples. The within-lake samples are likely to be independent at least to the extent that they, being at least 11 d apart, are not measurements on the same animals. The data were analyzed in two ways. First, the observations were treated as independent ( $N = 24$ ); second, the data from lakes with multiple samples were averaged, and the average values were used in place of the multiple observations ( $N = 17$ ). In terms of statistical

significance ( $\alpha = 0.05$ ), the two approaches gave the same results. In the following analyses, only the results of the first approach (full data set) are given.

The correlation coefficient for  $M$  vs.  $D_s$  for the 24 observations in Table 1 is 0.629, which is significant ( $df = 22$ ,  $P < 0.01$ ). Adding the thermocline depth in a multiple linear regression increases the correlation coefficient to 0.633, and  $D_t$  is not significantly correlated with  $M$  (correlation coefficient = 0.300,  $P > 0.05$ ). Thus, the Secchi depth, but not the thermocline depth, has predictive power for the amplitude of diel vertical migration.

When the relation between  $M$  and  $D_s$  is plotted, there appear to be three points (O, Fig. 1) which do not fit the general pattern (Lakes Washington, Muskellunge, and Long in Colorado). These outliers are similar in that they all have low or minimal populations of plankton-eating fish (Table 2). Planktivorous fish biomass in Long and Muskellunge is probably well below  $1 \text{ g m}^{-2}$ ,

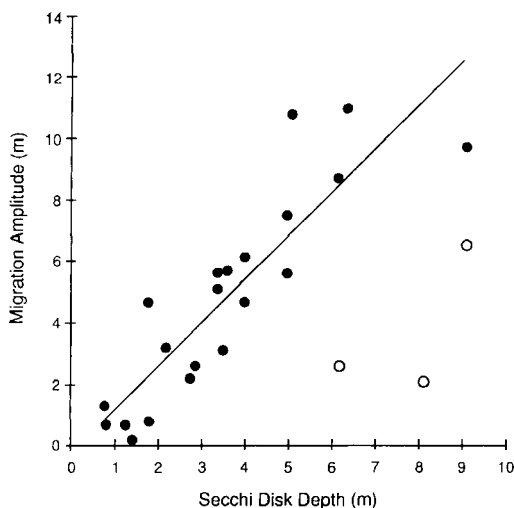


Fig. 1. The linear relationship between amplitude of diel vertical migration and Secchi disk depth. The statistics are calculated for ● only.  $Y = 1.41X - 0.32$ ;  $r^2 = 0.775$ .

and the biomass in Lake Washington is  $\sim 1.5 \text{ g m}^{-2}$  planktivorous juvenile sockeye salmon and longfin smelt. However, the bulk of the Lake Washington planktivores occur below 10 m (day) to 15 m (night), while over half the *Daphnia* live above 8 m day and night, in a region with lower fish predation (Beauchamp pers. comm.). A minimal level of effect of fish on the Lake Washington *Daphnia* is suggested by a lack of correlation between *Daphnia* population dynamics and annual variation in fish numbers (Edmondson pers. comm.).

Two of the three outliers are ultraoligotrophic; the third (Washington) is oligotrophic (Table 2). All the other lakes have higher levels of predation intensity and none are ultraoligotrophic: they have average photosynthetic rates of  $\sim 288 \text{ mg C m}^{-2} \text{ d}^{-1}$  (Schöhsee) or greater and  $\sim 2 \text{ g m}^{-2}$  (Long Lake, Michigan) or more of plankton-eating fish. Thus, the three outliers in Fig. 1 are least likely to fit the assumptions of the model (intense fish predation and not se-

Table 2. Productivity and plankton-eating fish. Fish data are given for the year of the diel vertical migration study, except for Lake Michigan, which is an estimate for 1987. The average rates of photosynthesis are not necessarily for the same year. Photosynthetic flux per  $\text{m}^3$  was estimated by dividing the per  $\text{m}^2$  rates by the average depth of the lake. Annual average rates of photosynthesis below  $\sim 300 \text{ mg C m}^{-2} \text{ d}^{-1}$  may be considered oligotrophic; rates above 1,000, eutrophic (Wetzel 1983). Relative predation intensity was estimated by comparing all quantitative and qualitative data given by the investigators, in consultation with two fisheries biologists (J. Kitchell and J. Baylis).

Lake	Avg photosynthesis		Major planktivorous fish species predation	Predation intensity ( $\text{g m}^{-2}$ )	Reference*
	( $\text{mg C m}^{-2} \text{ d}^{-1}$ )	( $\text{mg C m}^{-3} \text{ d}^{-1}$ )			
Bull Shoals	Eutrophic		Threadfin, gizzard shad	High	1
Czos	Highly eutrophic		Vendace, roach, smelt, perch	600, high	2
Constance	822	8.22	Whitefish, perch	Moderate	3
Kuc	Highly eutrophic		Vendace, roach, smelt, perch	600, high	2
Lampackie	Highly eutrophic		Vendace, roach, smelt, perch	600, high	2
Licht	Eutrophic		Sunfishes	High	4
Long (Colorado)	429	2.23	Few benthic trout	Minimal	5
Long (Michigan)	Oligotrophic		Yellow perch	2, low	6
Mendota	938	75.6	Cisco, yellow perch, sunfish	15, low	7
Michigan	550	6.5	Bloater, alewife, smelt	4.9, low	8
Muskellunge	Oligotrophic		Few yellow perch	Minimal	9
Pilanko	Highly eutrophic		Vendace, roach, smelt, perch	600, high	2
Probarskie	Highly eutrophic		Vendace, roach, smelt, perch	600, high	2
Schöhsee	288	22.1	Vendace, roach, bream, perch	High	10
Washington	263	8.0	Longfin smelt, sockeye salmon	2, low	11
Waubesa	Eutrophic		Yellow perch, sunfish	Moderate	7
Wintergreen	1,010	289	Yellow perch, sunfish	200, high	12
Three Lakes	Mesotrophic		Bluegill, brook silversides	Moderate	13

\* 1—Applegate and Mullan 1969; Applegate et al. 1966; 2—Gliwicz and Pijanowska 1988; 3—Geller 1986; Stich and Lampert 1981; 4—Dodson unpubl. data; 5—Keefer and Pennak 1977; 6—Carpenter and Kitchell unpubl. data; 7—Brock 1985; Rudstam pers. comm.; 8—Fahnenstiel pers. comm.; Sprules pers. comm.; 9—Frost pers. comm.; McLain and Magnuson 1988; 10—Lampert et al. 1986; Lampert and Taylor 1985; 11—Lehman 1988; Beauchamp pers. comm.; 12—Threlkeld 1979; Hall and Ehlinger 1989; 13—Tessier pers. comm.

verely food limited). Note that Lake Michigan, which is also borderline for both criteria (it has an especially low average photosynthetic flux per  $\text{m}^3$ ), has one point that is somewhat of an outlier and two points that are in the cloud of the remaining 21 points. The linear model predicting  $M$  from  $D_s$  is

$$M = 1.409D_s - 0.317. \quad (1)$$

The correlation coefficient is 0.880 ( $df = 19$ ,  $P < 0.01$ ). The  $Y$ -intercept ( $-0.317$ ) is not significantly different from zero (no migration with  $D_s = 0$ ), and the slope of the relationship (1.409) is a species-specific constant for *Daphnia*. The coefficient of determination ( $r^2$ ) for the 21 observations is 0.775. Vertical migration literature suggests that the remaining 23% of the variation in  $M$  not explained by Secchi depth could be due to factors such as variation in predation intensity and food limitation, varying responses among different *Daphnia* species to fish predation and food limitation, responses to invertebrate predators, variation among studies in the diel pattern of trap avoidance, and other within- and between-study sampling error. Also, diel vertical migration can be masked by diel horizontal migration or diel patterns in *Daphnia* population dynamics. For example, the average population depth can rise and fall with no movement of any of the constituent individuals: if fish feed near the surface during the day, the *Daphnia* population may appear to sink; if *Daphnia* reproduction is then highest near the surface at night, the population may appear to rise again.

Moonlight is also thought to influence the amplitude of diel vertical migration (e.g. Gliwicz 1986). The percent of illumination of the moon at midnight for each location can be used as an index of the effect of moonlight. This index and the Secchi depth have a multiple correlation coefficient with  $M$  of 0.916 ( $n = 21$ ,  $P < 0.001$ ). There is a significant negative correlation between the residual of the  $M$  vs.  $D_s$  correlation and the moon index (correlation coefficient =  $P < 0.05$ , Fig. 2). Full moonlight appears to depress  $M$  by  $\sim 2$  m (Fig. 2).

This linear model (Eq. 1) leads to several predictions. First, it can be used to predict

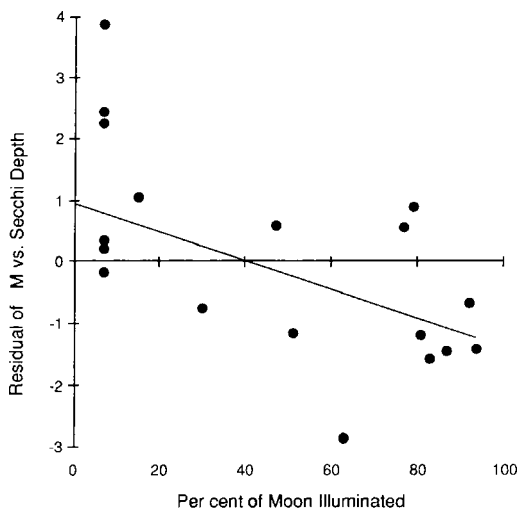


Fig. 2. The linear relationship between the residual values from Fig. 1 (diel vertical migration amplitude vs. Secchi disk depth) and the percent of the moon illuminated (percent full) when each observation of migration was done.  $Y = -0.021X + 0.93$ ;  $r^2 = 0.29$ .

the intensity of *Daphnia* vertical migration in north temperate lakes or ponds that have a diel light-dark cycle and contain visually oriented predators and sufficient food for the migrating animals. Departures from predictions indicate possible food limitation or unusually low levels of fish predation. Second, the model predicts that turbidity of whatever source, including glacial flour or suspended clay, should inhibit diel vertical migration. It supports the wisdom of doing diel vertical migration studies during the dark of the moon.

This predictive model, based on what is known of the biology of migrating *Daphnia* and calibrated from previous studies, provides a tool which can be generalized to the comparative study of zooplankton diel vertical migration in lakes of various size, trophic status, and fish abundance. Its strengths are that only the simplest data are required for prediction and that (at least for *Daphnia*) the relationship explains  $\sim 84\%$  of the variation in migration intensity for a wide range of lakes.

Stanley Dodson

Department of Zoology  
University of Wisconsin  
Madison 53706

## References

- APPLEGATE, R. L., AND J. L. MULLAN. 1969. Ecology of *Daphnia* in Bull Shoals Reservoir. U.S. Fish Wildl. Serv. Res. Rep. 74. 23 p.
- , AND D. I. MORAIS. 1966. Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir, p. 469–482. In Southeastern Assoc. Game Fish Comm. 20th Annu. Conf.
- BOGOROV, B. G. 1946. Peculiarities of diurnal vertical migrations of zooplankton in polar seas. J. Mar. Res. 6: 25–32.
- BROCK, T. D. 1985. A eutrophic lake: Lake Mendota, Wisconsin. Springer.
- BUCHANAN, C., AND J. F. HANEY. 1980. Vertical migrations of zooplankton in the arctic: A test of the environmental controls. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3: 69–79. New England.
- CLARK, C. W., AND D. A. LEVY. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am. Nat. 131: 271–290.
- DAGG, M. J. 1985. The effects of food limitation on diel migratory behavior in marine zooplankton. Ergeb. Limnol. 21: 247–256.
- DINI, M. L. 1989. The adaptive significance of diel vertical migration in *Daphnia*. Ph.D. thesis, Univ. Notre Dame. 108 p.
- GABRIEL, W., AND B. THOMAS. 1988. Vertical migration of zooplankton as an evolutionarily stable strategy. Am. Nat. 132: 199–216.
- GELLER, W. 1986. Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): A starvation avoidance mechanism? Arch. Hydrobiol. Suppl. 74, p. 1–60.
- GLIWICZ, M. Z. 1986. A lunar cycle in zooplankton. Ecology 67: 883–897.
- , AND J. PUANOWSKA. 1988. Effect of predation and resource depth distribution on vertical migration of zooplankton. Bull. Mar. Sci. 43: 695–709.
- HALL, D. J., AND T. J. EHLINGER. 1989. Perturbation, planktivory, and pelagic community structure: The consequence of winterkill in a small lake. Can. J. Fish. Aquat. Sci. 46: 2203–2209.
- HANEY, J. F., AND D. J. HALL. 1975. Diel vertical migration and filter-feeding activities of *Daphnia*. Arch. Hydrobiol. 75: 413–441.
- HEWETT, S. W., AND D. J. STEWART. 1989. Zooplanktivory by alewife in Lake Michigan: Ontogenetic, seasonal and historical patterns. Trans. Am. Fish. Soc. 118: 581–596.
- KEEFER, V. M., AND R. W. PENNAK. 1977. Plankton and seston of a Colorado (U.S.A.) alpine lake: The winter anomaly and the inlet-outlet budget. Int. Rev. Gesamten Hydrobiol. 62: 255–278.
- LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3: 21–27.
- , W. FLECKNER, H. RAI, AND B. E. TAYLOR. 1986. Phytoplankton control by grazing zooplankton: A study of the spring clear-water phase. Limnol. Oceanogr. 31: 478–490.
- , AND B. E. TAYLOR. 1985. Zooplankton grazing in a eutrophic lake: Implications of diel vertical migration. Ecology 66: 68–82.
- LANGFORD, R. R. 1938. Diurnal and seasonal changes in the distribution of the limnetic crustacea of Lake Nipissing, Ontario. Univ. Toronto Stud. Biol. Ser. 45: 1–142.
- LEHMAN, J. T. 1988. Hypolimnetic metabolism in Lake Washington: Relative effects of nutrient load and food web structure on lake productivity. Limnol. Oceanogr. 33: 1334–1347.
- MCLAIN, A. S., AND J. J. MAGNUSON. 1988. Analysis of recent declines in cisco (*Coregonus artedii*) populations in several northern Wisconsin lakes. Finn. Fish. Res. 9: 155–164.
- MÜLLER, H. 1985. The niches of *Bosmina coregoni* and *Bosmina longirostris* in the ecosystem of Lake Constance. Int. Ver. Theor. Angew. Limnol. Verh. 22: 3137–3143.
- O'BRIEN, W. J. 1987. Planktivory by freshwater fish: Thrust and parry in the pelagia, p. 3–16. In W. C. Kerfoot and A. Sih [eds.], Predation. New England.
- PENNAK, R. W. 1944. Diurnal movements of zooplankton organisms in some Colorado mountain lakes. Ecology 25: 387–403.
- . 1955. Comparative limnology of eight Colorado mountain lakes. Univ. Col. Stud. Ser. Biol. 2. 75 p.
- STICH, H., AND W. LAMPERT. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 293: 396–398.
- THRELKELD, S. T. 1979. The midsummer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. Ecology 60: 165–179.
- WELLS, L. 1960. Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. Fish. Bull. 60: 343–368.
- WETZEL, R. G. 1983. Limnology, 3rd ed. Saunders.
- WORTHINGTON, E. B. 1931. Vertical movements of fresh-water macroplankton. Int. Rev. Gesamten Hydrobiol. 25: 394–436.
- WURTSBAUGH, W. A., AND D. NEVERMAN. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333: 846–848.

Submitted: 9 October 1989

Accepted: 19 December 1989

Revised: 26 April 1990