

The Effect of Whole-Lake Fish Community Manipulations on Daphnia Migratory Behavior



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Limnology and Oceanography, Vol. 36, No. 2 (Mar., 1991), 370-377.

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Limnol. Oceanogr., 36(2), 1991, 370-377
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The effect of whole-lake fish community manipulations on *Daphnia* migratory behavior

Abstract—A four-summer study of vertical migration by *Daphnia* was conducted in two neighboring lakes during a two-stage fish community manipulation. This manipulation produced discrete periods of low and high planktivory by fish. The migration pattern was variable and weak during the low predation stage, but became consistent and intense within weeks of the change to high levels of predation, confirming the pre-eminence of predation avoidance among several extant hypotheses.

Many planktonic organisms exhibit day-night differences in vertical distribution. Several mechanisms, based on differences in vertical stratification of light, temperature, or food resources, have been proposed to account for the adaptive significance of diel vertical migration by zooplankton. A nonexhaustive list finds darker waters at depth providing a refuge from daytime fish predation (Hutchinson 1967; Zaret and Suffern 1976; Gliwicz 1986), cooler waters at depth causing energy-saving metabolic shifts (McLaren 1974), especially when food is limiting (Geller 1986), and various schemes involving heterogeneous vertical distributions of algal abundance, quality, or size (Johnsen and Jakobsen 1987; Pijanowska and Dawidowicz 1987). Most recently, interactive hypotheses involving two or more of these mechanisms have been proposed (Clark and Levy 1988; Gabriel and Thomas 1988). They involve tradeoffs between the adaptive optima of various mechanisms as, for example, between optimal protection from predation in deep water and optimal

growth rate in surface waters (Lampert 1989).

To date, field experiments to test these hypotheses directly have been lacking. Here we report a two-stage, whole-lake manipulation in which planktivorous fish were removed from and later reintroduced to a lake. During the period of reduced planktivory, migratory behavior of *Daphnia* in the lake was inconsistent and variable, as previously reported (Dini and Carpenter 1988). Here we show that the reintroduction of planktivorous fish was associated with a persistent pattern of nocturnal vertical migration by *Daphnia*. These results are best explained by the predation-avoidance hypothesis.

Tuesday and Paul are kettle lakes within 1 km of each other at the University of Notre Dame Environmental Research Center near Land O'Lakes, Wisconsin. Tuesday Lake's area, maximal depth, and mean depth are 0.79 ha, 18.5 m, and 10.0 m. The same measures for Paul Lake are 1.2 ha, 12.2 m, and 5.0 m. A two-stage manipulation permitted us to monitor migratory behavior under different predation intensities. The reduced-predation stage began in May 1985 when 90% of the biomass (56.4 kg) of planktivorous fish (88% *Phoxinos eos*, 6% *Phoxinos neogaeus*, 6% *Umbra limi*) was trapped out of Tuesday Lake and replaced with 55.8 kg of piscivorous largemouth bass, *Micropterus salmoides* (see Carpenter et al. 1987). The ensuing reduction in planktivory allowed *Daphnia* to dominate the plankton within 3 months (Carpenter et al. 1987). In September 1986, all fish were removed from Tuesday Lake with rotenone. The increased-predation stage began in May 1987 with the reintroduction of planktivorous fish (in the same ratio as those removed) to 2% of their former biomass.

Migration studies in Paul Lake occurred on 15 dates across four summers. In Tuesday Lake, there were 13 migration studies;

Acknowledgments

We thank J. Kitchell, T. Frost, and S. Dodson for comments on earlier versions of the manuscript, X. He and J. Hodgson for data on fish assemblages, and J. and M. Elser, N. MacKay, P. Soranno, A. St. Amand, P. Leavitt, C. Blanchette, and M. Bremigan for encouragement and assistance in the field. We thank C. Hughes for the drafting.

This work was funded by NSF grants BSR 83-08918 and BSR 86-06271.

A contribution from the University of Notre Dame Environmental Research Center.

the scarcity of daphnids in Tuesday Lake in early-midsummer 1985 precluded migration studies at that time. Studies were conducted at midday and midnight (preliminary studies indicated maximal diel displacement at those times). A 12-liter Schindler-Patalas trap was deployed in duplicate casts at 5–6 depths at each of 2–5 horizontal stations (the 9-liter trap referred to in our 1988 paper was actually a 12-liter trap). Animals were preserved in sugared, buffered Formalin at a final concentration of ~4%. Samples with ≤ 100 animals were counted in their entirety with a dissecting microscope at 7 \times . Denser samples were subsampled with a Folsom plankton splitter to facilitate counting (Dini and Carpenter 1988). Throughout this time we monitored daphnid migration as day–night difference in the average depth of the assemblage at each station (Plew and Pennak 1949); values from all stations were then averaged to arrive at “lakewide” means.

Biweekly measurements of planktivore catch per unit effort (CPUE) made with minnow traps set for 24 h in both littoral and pelagic zones (Carpenter et al. 1987) allowed us to estimate predation intensity. We emphasize that CPUE is only an approximation of predation pressure. It is an indirect measure of fish density and includes no direct observations on predation. Recapture data from angling and electroshocking of the tagged bass populations during August indicated densities of juvenile and adult bass. Egg ratios (the product of mean brood size and proportion of adult females bearing broods) were calculated biweekly from 10 to 300 individuals (actual number depended on daphnid abundance in the samples) and allowed us to estimate daphnid reproductive potential. Weekly Chl *a* concentrations were determined fluorometrically for 6–8 samples distributed vertically through the photic zone (Carpenter et al. 1987). Mean daphnid length (base of tail spine to most anterior part of helmet) was measured weekly at 250 \times on 10–15 randomly chosen individuals. Species composition of the assemblage was determined by identifying these same individuals (Carpenter et al. 1987). The same measurements were performed in Paul Lake, which was

Table 1. Epilimnetic temperature ($^{\circ}\text{C}$), depth to thermocline (m), depth to 1 mg liter $^{-1}$ dissolved oxygen (m), and depth to 1% of surface irradiance (m) during the diel migration studies. Means and ranges (in parentheses) for all dates of diel migration measurements from 1985 to 1988 are reported.

Lake	Epilim- nion temp.	Depth to		
		thermocline	1 mg liter $^{-1}$ O $_2$	1% irradiance
Paul	19.8	3.6	6.1	5.4
	(14–24)	(2.5–4.2)	(4.8–10.0)	(4.9–6.0)
Tuesday	20.3	2.6	3.9	3.1
	(16–24)	(2.0–3.5)	(2.4–8.7)	(2.5–3.5)

not manipulated, and which contained largemouth bass, few planktivores, and abundant *Daphnia* throughout the study (Carpenter et al. 1987).

Daphnia is sensitive to rotenone (Rach et al. 1988), although recent studies indicate the effect to be short lived (Gilderhus et al. 1988). In Tuesday Lake, live *Daphnia* were common in net tows taken 2 d after the rotenone application on 23 September 1986 (S. R. Carpenter pers. obs.). In water at 23–27 $^{\circ}\text{C}$, the half-life of rotenone applied at the maximal recommended dosage (0.225 mg liter $^{-1}$) is 22.6 h. In water at 0–5 $^{\circ}\text{C}$, the same dosage is reduced to <0.002 mg liter $^{-1}$ in 57 d (Gilderhus et al. 1988), a level at which there are only minimal fecundity and survivorship effects on *Daphnia* (Rach et al. 1988). About 240 d elapsed between the rotenone application in September 1986 and migration studies in May 1987, so rotenone was no longer present in a concentration that could have affected *Daphnia* during the studies reported here.

Statistical tests for changes in migratory amplitude and other variates after the minnow introduction were performed with randomized intervention analysis (RIA; Carpenter et al. 1989). We chose RIA over conventional parametric alternatives because RIA requires no assumptions about the underlying distributions, and the effects of serial autocorrelation on the *P* value can be readily determined by Monte Carlo simulation. Power curves and the effects of serial autocorrelation were reported by Carpenter et al. (1989). *P* values reported here were corrected for the effects of autocorrelation by Monte Carlo analysis with the au-

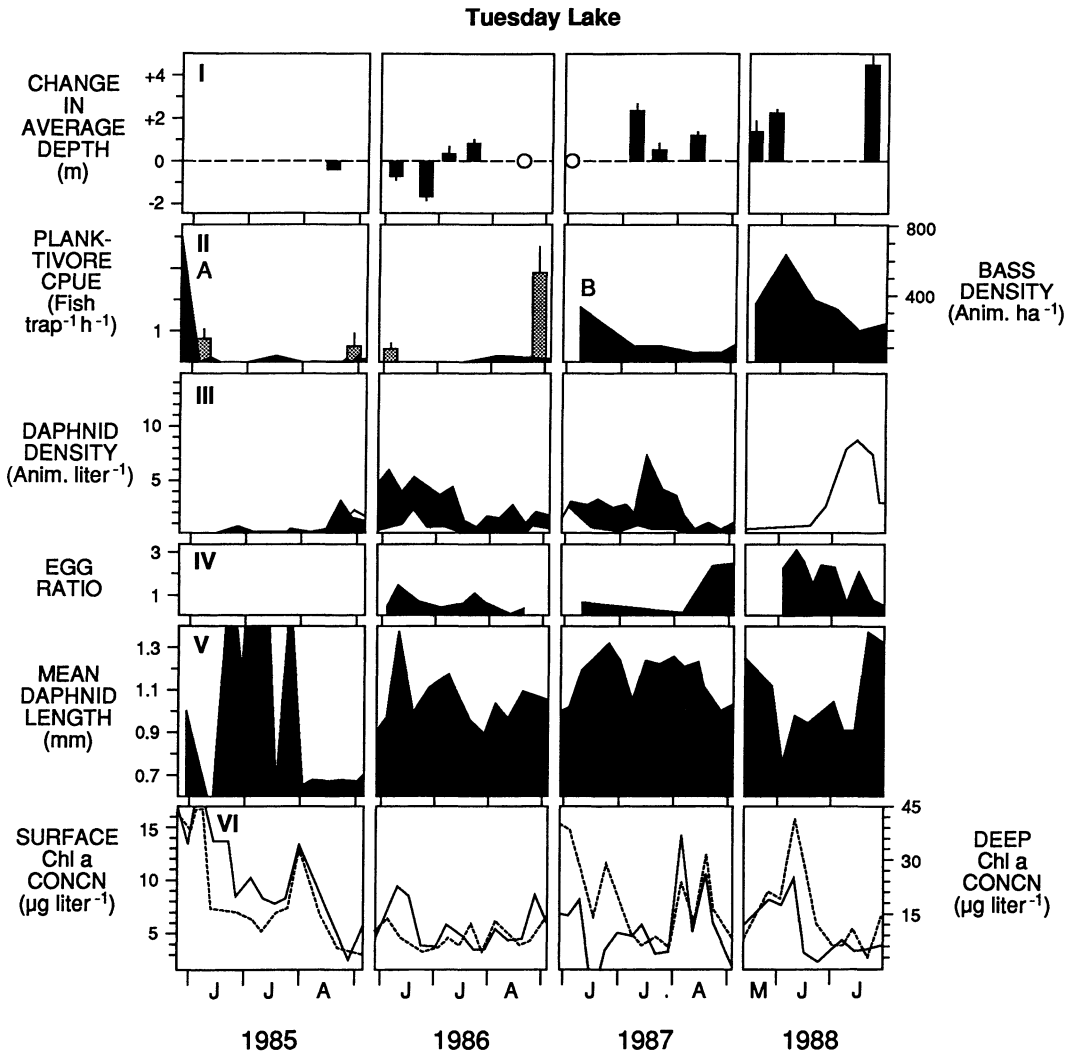


Fig. 1. I. Change in lakewide average depths calculated from the difference between midday and midnight average depths, with standard error bars. II. Planktivore catch per unit effort, CPUE (left scale). In Tuesday Lake, A indicates time of minnow removal and bass addition, B minnow reintroduction. Small peaks in 1985 and 1986 consisted of young-of-the-year bass. Shaded bars represent juvenile (left) and adult (right) bass densities during August, with standard deviation error bars (right scale). III. Daphnid densities and relative abundances; black portions indicate *Daphnia pulex* densities, clear *Daphnia rosea*. IV. Egg ratios (the product of mean brood size and proportion of adult females bearing broods). Throughout most of summer 1985, daphnids in Tuesday Lake were too rare to calculate egg ratios. V. Mean daphnid length (base of tail spine to most anterior part of helmet). VI. Chl *a* concentrations; solid line—pooled mixed layer (left scale), dashed line—depth of 1% light transmission (right scale).

toregressive model described by Carpenter et al. (1989). Autocorrelation and partial autocorrelation functions of our data indicated that the autoregressive (1) model was in fact appropriate (Chatfield 1980).

Depths to the thermocline and 1% of sur-

face irradiance were relatively constant in both lakes during the four summers of diel migration studies (Table 1). During June, epilimnion temperatures were cooler and the water column was oxygenated to greater depth than in July and August.

Paul Lake

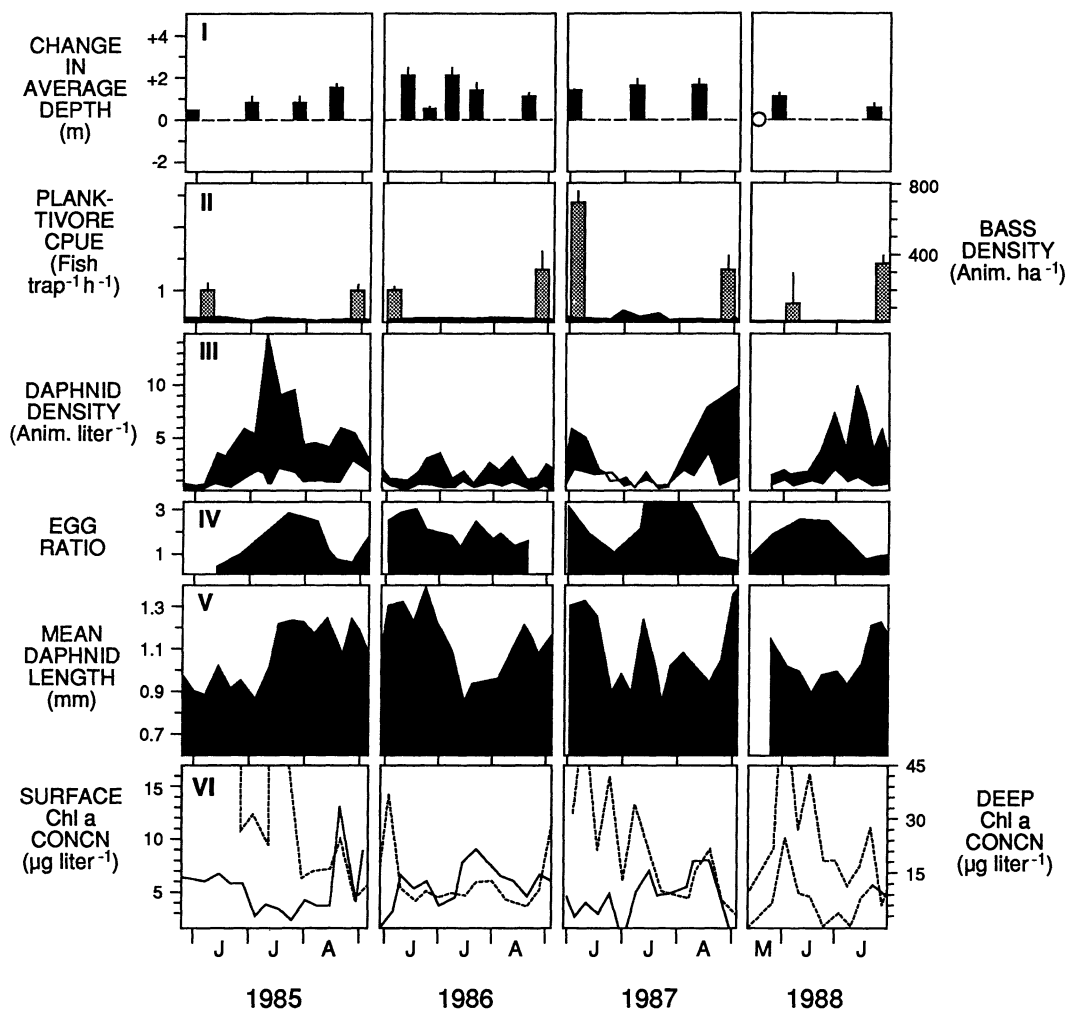


Fig. 1. Continued.

Daphnia became sufficiently abundant to measure vertical migration in August 1985 (Carpenter et al. 1987). Daphnid migration was highly variable in Tuesday Lake during 1985 and 1986 when minnows were absent (Fig. 1). Daphnids twice performed a weak nocturnal migration (up after sunset, down before dawn). Twice they did not migrate. Three times, migration was reversed (up at day, down at night; e.g. Fig. 2)—a relatively rare phenomenon among daphnids (Hutchinson 1967). During 1985 and 1986, day and night mean depths were above the thermocline (Fig. 3). Even though several of the

migrations had relatively small amplitudes, the small size of the standard error bars compared to the mean changes in average depth indicates significant differences between midday and midnight mean depths on most occasions (Fig. 1).

Within 6 weeks after the reintroduction of minnows in 1987, nocturnal migration was pronounced (Fig. 1). Daytime vertical profiles from 1987 and 1988 contrast sharply with the nocturnal ones from those years and both the day and night profiles from 1985 and 1986 (Fig. 2). During the day in 1987 and 1988, daphnid mean depth was

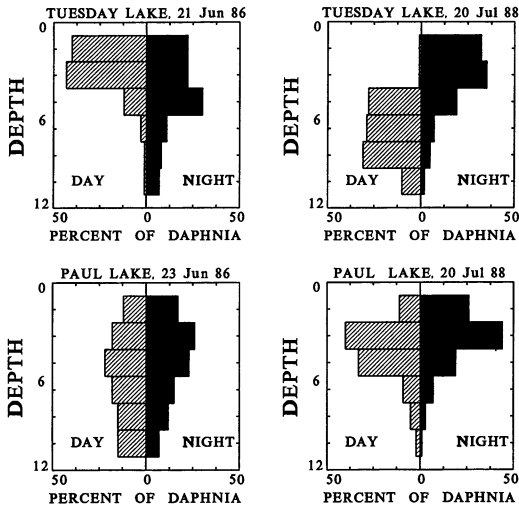


Fig. 2. Above—depth distribution of *Daphnia* assemblages in Tuesday Lake when reverse migration was strongest and when nocturnal migration was strongest; below—on similar dates in Paul Lake. Data for 1986 are combined abundances at five horizontal stations in each lake; 1988 data are from three horizontal stations. Abundances are reported as percent of total catch.

at or below the thermocline (Fig. 3). Most of the animals were therefore in relatively cool (and sometimes hypoxic) water.

Meanwhile, *Daphnia* in Paul Lake underwent normal nocturnal migration throughout the study despite high natural variabilities in daphnid density, relative species abundance, egg ratio, mean body length, and Chl *a* content of the water column (Fig. 1). Planktivore CPUE and adult bass densities remained relatively constant throughout this period.

Statistical analyses confirm the patterns that are visually apparent in Fig. 1 (Table 2). Migration intensity, as measured by change in mean depth, increased significantly following reintroduction of minnows. Egg ratio also increased significantly following the reintroduction. There is no evidence of nonrandom change in chlorophyll concentration, the ratio of epilimnetic chlorophyll to metalimnetic chlorophyll, total *Daphnia* density, the proportion of total *Daphnia* represented by *Daphnia pulex*, or *Daphnia* length. Power curves for RIA indicate that *P* values depend only weakly on sample size when 40 or more observa-

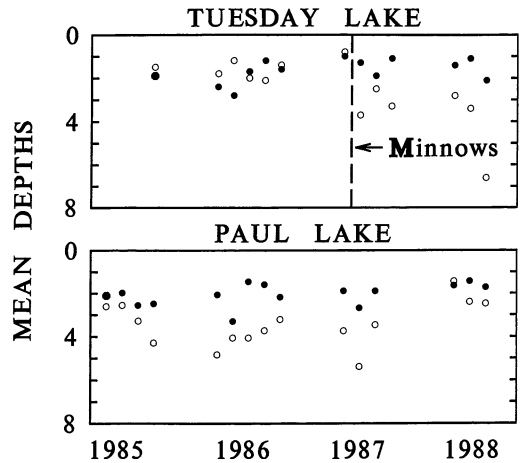


Fig. 3. Mean midday depths (○) and mean mid-night depths (●) of *Daphnia* assemblages in Tuesday Lake (13 dates) and Paul Lake (15 dates) across four summers.

tions are available (Carpenter et al. 1989). Therefore, our nonsignificant RIAs with $n = 50$ provide strong evidence that these variates did not change following minnow reintroduction.

Diel vertical migration was closely associated with the presence of minnows in Tuesday Lake. These fish are extremely effective planktivores. Minnow predation was sufficient to exclude *Daphnia* from Tuesday Lake before the bass introduction in May 1985 (Carpenter et al. 1987). By 1989, minnow predation had eliminated *Daphnia* from Tuesday Lake (Carpenter et al. unpubl. data).

The fact that our results are fully consistent with the predation-avoidance hypothesis does not exclude the possibility that other factors were involved. For example, differences in thermocline depth and penetration of light and oxygen may have contributed to the differences in migration between the lakes in the presence of bass. Bass predation is not capable of eliminating *Daphnia* in these lakes. On the other hand, *Daphnia* is a major component of bass diets in Paul Lake and was present in bass diets in Tuesday Lake (Hodgson and Kitchell 1987; Carpenter et al. 1987). Therefore, diel vertical migration may reduce predation on *Daphnia* by bass. Variable migratory behavior in Tuesday Lake during 1985–1986 may have been due to weak predation on a

Table 2. Results of randomized intervention analysis testing for nonrandom changes after reintroduction of minnows to Tuesday Lake. For each variate, we present the premanipulation mean interlake distance, post-manipulation interlake distance, pooled standard deviation, lag-1 autocorrelation coefficient, number of observations, and *P* value corrected for serial autocorrelation.

Variate	Premanip.	Postmanip.	SD	<i>r</i> (1)	<i>n</i>	<i>P</i>
Change in mean depth	-1.60	1.50	1.124	0.25	12	0.008
Epilimnetic Chl	7.92	5.91	3.71	0.54	50	0.16
Epilimnion : metalimnion Chl ratio	1.75	2.77	1.37	0.27	50	0.081
<i>Daphnia</i> density	1.76	3.05	2.46	0.75	50	0.36
<i>Daphnia pulex</i> : total <i>Daphnia</i> ratio	0.497	0.390	0.430	0.91	50	0.42
<i>Daphnia</i> length	1.00	1.04	0.427	0.19	50	0.80
<i>Daphnia</i> egg ratio	0.227	1.06	0.791	0.39	50	0.009

daphnid population that was highly heterogeneous with respect to migratory behavior (Dini and Carpenter 1988) or to other factors. Our study was not designed to resolve this question.

We considered several alternative hypotheses that might explain the abrupt change in the migratory behavior of daphnids in Tuesday Lake. They include a shift in species composition (Stich and Lampert 1981), increase in daphnid size (Hutchinson 1967), onset of thermal stratification (McLaren 1974; Geller 1986), and several hypotheses relating migratory behavior to food availability. One of them proposes that migration occurs only when food availability is low (Geller 1986), another only when food is abundant (Johnsen and Jakobsen 1987), and a third only when food distribution is vertically heterogeneous (Pijanowska and Dawidowicz 1987).

There was no significant change in daphnid density after minnow reintroduction compared to the period before it, nor was there any change in the relative proportions of *Daphnia pulex* and *Daphnia rosea*. *Daphnia pulex* dominated the Tuesday Lake assemblage before, during, and for an entire summer after the dramatic change in migratory behavior. Moreover, there was no difference in the character of migration between summer 1987, when *D. pulex* was predominant, and summer 1988 when *D. rosea* completely replaced *D. pulex*. The change in daphnid species is probably explained by *D. rosea*'s inconspicuousness relative to *D. pulex* at a time of rebounding minnow populations (see Kitchell and Kitchell 1980). A study conducted in summer 1988 in Long Lake, 3 km away, dem-

onstrated nearly identical migratory behavior by *D. pulex* and *D. rosea* on five different dates (Dini 1989).

It is generally accepted that larger daphnids migrate more consistently and with greater amplitude than smaller daphnids (Hutchinson 1967), and this disparity has been confirmed for the daphnid assemblage in this suite of lakes (Dini et al. 1987). Body lengths after the reintroduction were not significantly different, however, from those before. We conclude that the shift in migratory behavior cannot be accounted for by a shift in body size.

Migrating, cold-acclimated zooplankters may gain an "energy bonus," translated via shifts in enzyme pathways into increased growth and fecundity (Geller 1986). We used egg ratio to monitor daphnid reproductive potential and found this measure to be significantly higher following minnow reintroduction. Higher egg ratios may indicate a metabolic advantage acquired by daphnids spending a considerable portion of each day in deeper, colder water (McLaren 1963, 1974; Geller 1986), as they consistently did following minnow reintroduction. The question becomes one of timing: since Tuesday Lake had similar temperature stratification in all years, why did *Daphnia* not take consistent advantage of the purported energy-saving value of cold water at depth in 1986? Geller (1986) proposed that migration is a starvation-avoidance mechanism and should most likely occur when food resources are limiting. The very low egg ratios of Tuesday Lake's 1986 daphnid assemblage, relative to those in subsequent summers and those in Paul Lake (Fig. 1), indicate that these daphnids were starving.

According to the metabolic-advantage hypothesis, then, these daphnids should have undertaken consistent migrations into deep water. Instead, when they migrated at all, they undertook very weak migrations that rarely exposed them to cold water.

Rather than indicating a metabolic advantage achieved by migrating into cold water, the higher egg ratios in Tuesday Lake daphnids in 1987 and 1988 were maybe the result of the increased Chl *a* content of the water column, especially at depth (Fig. 1). Johnsen and Jakobsen (1987) proposed that migratory behavior results from a tradeoff between the need to obtain sufficient food and the need to avoid visual predators. They identified starvation avoidance as the more important of the two and asserted that when food is limiting and predators are present, animals will reduce migratory behavior and feed in surface waters, thereby increasing their vulnerability to predation. Only when food is not limiting should zooplankters migrate—presumably to reduce vulnerability to predation. They associated reverse migration with periods of starvation. The general trends in Tuesday Lake are consonant with Johnsen and Jakobsen's hierarchy. Yet, individual cases do not fit as well. For example, the two strongest nocturnal migrations by daphnids in Tuesday Lake in 1987 and 1988 corresponded to times when algal abundance was extremely low—as low, in fact, as during the instances of reversed migration. Moreover, reduced algal abundance throughout the water column in Paul Lake in 1986—a reduction similar to that in Tuesday Lake—was not accompanied by reverse migrations or even by cessation of migration but, rather, by the strongest migrations in that lake during the four-summer study (Fig. 1).

Pijanowska and Dawidowicz (1987) proposed that migratory behavior hinges on a combination of vulnerability to visual predation and the vertical distribution of food resources, with vertical differences in size of food particles being an important consideration. Chl *a* data from both lakes indicated no pattern between the ratio of surface:metalimnetic Chl *a* content and the direction or intensity of migration (Fig. 1). Our data are insufficient to evaluate their

hypothesis, however, as we have no information about vertical distribution of variously sized food particles.

Our data strongly support predation avoidance as the primary factor behind the dramatic introduction of consistent nocturnal migration among daphnids of Tuesday Lake. They do not, however, indicate the means by which fish were able to effect change in *Daphnia's* migratory behavior, whether by selective elimination of non-migrating clones (Dini and Carpenter 1988), by chemical induction (Dodson 1988), or by mechanical contact with fish (Bollens and Frost 1989). Determining the nature of the fish effect is a crucial area for future research.

Neither do our data eliminate alternative hypotheses based on food availability. And it is not likely that they would, since it has been well established that the predation-avoidance hypothesis cannot account for all the different migratory patterns (Geller 1986). Further research will also be needed to explore the interplay of predation avoidance and food availability in bringing about and controlling diel vertical migration.

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References

- BOLLENS, S. M., AND B. W. FROST. 1989. Predator-induced diel vertical migration in a planktonic copepod. *J. Plankton Res.* **11**: 1047–1065.
- CARPENTER, S. R., T. M. FROST, D. HEISEY, AND T. K. KRATZ. 1989. Randomized intervention analysis and the interpretation of whole-lake experiments. *Ecology* **70**: 1142–1152.
- , AND OTHERS. 1987. Regulation of lake primary productivity by food web structure. *Ecology* **68**: 1863–1876.
- CHATFIELD, C. 1980. The analysis of time series. Halstead.
- CLARK, C. W., AND D. A. LEVY. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* **131**: 271–290.

- DINI, M. L. 1989. The adaptive significance of diel vertical migration by *Daphnia*. Ph.D. thesis, Univ. Notre Dame. 108 p.
- , AND S. R. CARPENTER. 1988. Variability in *Daphnia* behavior following fish community manipulations. *J. Plankton Res.* **10**: 621–635.
- , AND OTHERS. 1987. *Daphnia* size structure, vertical migration and phosphorus redistribution. *Hydrobiologia* **150**: 185–191.
- DODSON, S. I. 1988. The ecological role of chemical stimuli for the zooplankton: Prediction-avoidance behavior in *Daphnia*. *Limnol. Oceanogr.* **33**: 1431–1439.
- 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.
- GILDERHUS, P. A., V. K. DAWSON, AND J. L. ALLEN. 1988. Deposition and persistence of rotenone in shallow ponds during cold and warm seasons. U.S. Fish Wildl. Serv. Invest. Fish Control 95. 7 p.
- GLIWICZ, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* **320**: 746–748.
- HODGSON, J. R., AND J. F. KITCHELL. 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). *Am. Midl. Nat.* **118**: 323–335.
- HUTCHINSON, G. E. 1967. A treatise on limnology. V. 2. Wiley.
- JOHNSEN, G. H., AND P. J. JAKOBSEN. 1987. The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnol. Oceanogr.* **32**: 873–880.
- KITCHELL, J. A., AND J. F. KITCHELL. 1980. Size-selective predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes. *Limnol. Oceanogr.* **25**: 389–402.
- LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**: 21–27.
- McLAREN, I. A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *J. Fish. Res. Bd. Can.* **20**: 685–722.
- . 1974. Demographic study of vertical migration by a marine copepod. *Am. Nat.* **108**: 91–102.
- PIJANOWSKA, J., AND P. DAWIDOWICZ. 1987. The lack of vertical migration in *Daphnia*: The effect of homogeneously distributed food. *Hydrobiologia* **148**: 175–181.
- PLEW, W. F., AND R. W. PENNAK. 1949. A seasonal investigation of vertical movements of zooplankters in an Indiana lake. *Ecology* **30**: 93–100.
- RACH, J. J., T. D. BILLS, AND L. L. MARKING. 1988. Acute and chronic toxicity of rotenone to *Daphnia magna*. U.S. Fish Wildl. Serv. Invest. Fish Control 92. 5 p.
- STICH, H.-B., AND W. LAMPERT. 1981. Predator evasion as an explanation of diel vertical migration by zooplankton. *Nature* **293**: 396–398.
- ZARET, T. M., AND J. S. SUFFERN. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**: 804–813.

Submitted: 12 February 1990

Accepted: 23 August 1990

Revised: 12 October 1990

Limnol. Oceanogr., 36(2), 1991, 377–383

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Bioerosion of coral reefs—A chemical approach

Abstract—We measured total alkalinity changes as a direct clue to the rate and mechanism (chemical or mechanical) of boring of the bivalve *Lithophaga lessepsiana* in colonies of the coral *Stylophora pistillata*, the most abundant coral-borer association in the reefs of the northern Gulf of Elat (Aqaba), Red Sea. Our experiments included comparison between total alkalinity measurements of seawater surrounding colonies of *S. pistillata* free of *L. lessepsiana* and colonies infected

with it. It is suggested that *L. lessepsiana* is able to redissolve chemically up to 40% of the CaCO₃ deposited by *S. pistillata*.

Buildup of the primary framework on coral reefs is accompanied by continuous biological, physical, and chemical destruction. The net rate of CaCO₃ deposition on the reef is the sum of these processes (MacGeachy and Stearn 1976). Biological weathering, or bioerosion (Neumann 1966), destroys and removes the calcareous substrate by the direct boring or rasping action of organisms.

Boring organisms, rather than rasping organisms, have a significant effect on the mechanical stability of the reef framework,

Acknowledgments

We thank J. Erez for laboratory facilities; Ruth Ben-Hillel, A. Nehorai, and T. Neuwirth for technical assistance; N. Chadwick, J. Erez, Y. Shlesinger, and O. Mokadi for critical discussions; and M. J. Risk for review of the manuscript.

This research was supported by grants 86-00174 and 85-00036 from the United States-Israel Binational Science Foundation (BSF) Jerusalem, Israel.