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Evidence from the Recent Sediments of Manipulated Lakes**



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Size-selective predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes¹

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Abstract

In an experiment maintained since 1951, half of a divided lake was limed, resulting in a significantly expanded euphotic zone. In both basins native fish were removed and rainbow trout introduced. Quantitative analysis of zooplankton remains preserved in the sediments of both lakes provides evidence of the selectivity of a visually dependent predator at natural and enhanced transparency and oxygen concentrations.

The sediment record effectively documents the known manipulations and the expected responses. In the control lake, no significant changes in zooplankton species composition, species dominance, or size-frequency distribution are recorded. In the alkalized lake, a succession in zooplankton dominance from *Daphnia pulex* to *Daphnia rosea* to *Bosmina* is recorded, as is a reciprocal change in mean size of *D. pulex* and *D. rosea*. The relative position of the thermocline with respect to the oxygen minimum barrier and the light transmission curve accounts for the observed differences in selective predation intensity.

Some of the earliest studies in experimental limnology were conducted in bog lakes of northern Wisconsin and Michigan (Hasler et al. 1951; Johnson and Hasler 1954). These lakes are characteristically brown-stained, dystrophic, and acidic, with continual depletion of oxygen due to the oxidation of humic organic matter. Zooplankton was dominated by species of *Daphnia*. The experimental objective was to make dystrophic lakes into suitable habitats for rainbow trout

(*Salmo gairdneri*) by adding hydrated lime to precipitate the humic colloids so that the depth of the euphotic zone would be substantially increased.

We believed that simultaneous tests of the interaction of fish predation, light intensity, and oxygen stratification in structuring a zooplankton community might be recorded in the sediments of such manipulated lakes. We here provide evidence of vertebrate predation effects under conditions of natural and of experimentally enhanced transparency and oxygen concentrations. By analyzing the concomitant responses of the zooplankton community to the introduction

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Table 1. Summary of morphometric and limnological data for Peter and Paul Lakes: 1951-1978.

	Area (ha)	Max depth (m)	pH	Secchi depth (m)	Min DO (ppm) (summer thermo- cline)
Paul L.	1.21	12.0	4.7-6.6	0.7-2.8	0.2
Peter L.	2.43	19.0	6.5-7.5	2.5-4.7	5.8

of an exotic predator following removal of indigenous predators and to an expanded euphotic zone, we can assess selective predation intensity as a function both of predatory efficiency and of prey adaptive mechanisms aimed at reducing this efficiency.

Because the experimental manipulation of the study site has been continued for 27 years, a paleoecological approach affords the opportunity of long term observations within the sediment record. The variability in prey species composition and size during the premanipulation period provides a measure of the dynamic equilibrium condition.

We are indebted to A. D. Hasler, W. E. Johnson, and R. G. Stross, whose early work on these lakes provided us with a suitable system to test our predictions, and to the personnel of the Trout Lake Biological Station and the University of Notre Dame Environmental Research Center, who have maintained the experimental condition and monitored the lakes for the last two decades. We thank E. Werner, T. Zaret, and S. Dodson for discussions of selective predation. We also thank A. Swain, H. Wright, M. Adams, L. Maher, and M. Davis for advice on coring and processing procedures. L. Crowder and J. Breck provided useful discussions of the manuscript. C. Hughes drafted the figures.

Materials and methods

Site selection: Historical data—Peter-Paul Lake is located within the University of Notre Dame's Environmental Research Center in the Upper Peninsula of Michigan. The lake originally consisted of two deep basins connected by a shallow channel. In 1951 it was separated

into two units by an earthen dam built at the constriction so that one basin could function as a control (Paul Lake) and the other as an experimental basin (Peter Lake). Pertinent morphometric data are given in Table 1.

The original lake was a seepage kettle lake with a small catchment basin restricted on three sides by moraine ridges. This attribute of a semiclosed system in which the effects of immigration and emigration of fish species could be minimized was an important criterion in selecting the site originally. The native fish species, common to dystrophic lakes in this region, consisted predominantly of stunted yellow perch (*Perca flavescens*) and largemouth bass (*Micropterus salmoides*). Because the zooplankton was dominated by *Daphnia* (70-90%), one procedure carried out was to remove the indigenous species of fish and to introduce a species that relied on a zooplankton diet throughout its life. Rotenone was applied to both basins, and juvenile (15-18 cm) rainbow trout were introduced annually in equal densities ranging from 370 to 740·ha⁻¹. Analyses of stomach contents showed that the trout fed almost exclusively on zooplankton throughout their growing season (from May through October: Johnson and Hasler 1954).

Peter Lake received an experimental addition of hydrated lime. Its alkalinity increased, humic colloids precipitated, and the euphotic zone was extended from 2.7 to 4.3 m. Later additions of hydrated lime effectively tripled the depth of the euphotic zone to 7.0 m (Stross and Hasler 1960; Hasler 1964). Successive additions of hydrated lime over the past 27 years have maintained significant differences in transparency (Secchi), pH, and dissolved oxygen (Table 1). Although pH went down, significant differences in light transmission (4.4 m in Paul vs. 7.5 m in Peter) were maintained despite a 4-year lapse in liming (Malueg 1963).

There was no increase in rainbow trout production in the experimental lake and Johnson and Hasler (1954) assumed that zooplankton density determined zooplankton availability as food items for

trout; there was as yet no understanding of the mechanisms of size-selective predation. However, there were changes in the zooplankton. By 1954, *Daphnia pulex*, originally dominant, remained dominant in the control lake, but *Daphnia rosea* (formerly termed in these studies *Daphnia longispina*), originally present in low densities, became dominant in the experimental lake (Stross et al. 1961). *Holopedium* remained in the control lake, but was replaced by *Diaptomus* in the experimental lake. *Epischura* and *Diaphanosoma* were only occasionally present in small numbers in the experimental lake. *Cyclops*, *Bosmina*, and *Chaoborus* were reported as minor constituents of the plankton in both lakes. Stross (1958) observed an inverse relationship during 1955 sampling between the number of *Daphnia* collected and mesh size in the experimental lake only, indicating that *Daphnia* in the control lake was larger, an observation he attributed to *D. pulex* being larger than *D. rosea*.

Stross (1958) could not detect any permanent change in the phosphorus concentration of Peter Lake after liming. Two phytoplankton surveys (Johnson 1954; Malueg 1963), indicated a greater diversity of phytoplankton in Peter Lake. The increased diversity generally was the result of the appearance of species characterized by protective projections, indicating more intensive herbivory (L. Graham pers. comm.). There was a single *Aphanizomenon* bloom in 1954 in Peter Lake.

In summary, Peter and Paul Lakes provided a unique opportunity for us to contrast the effectiveness of size-selective predation by an introduced planktivore under conditions of natural and enhanced transparency and oxygen concentrations. The control and experimental systems were as closely similar as field conditions permit, and such problems as cultural eutrophication, species reinvasion, and sediment mixing by bioturbation were minimal.

Coring and processing—To sample the sediments with minimal disturbance, we

used a freeze-coring technique (Swain 1973). Replicate 1.5-m cores were taken in August 1978 from the deepest parts of the lakes. Sediment thickness along the coring device ranged from about 1–2 cm. The Peter Lake core is varved throughout its length, and the undisturbed nature of the varved laminae attests to the lack of disturbance by the coring operation. Construction of the earthen dam in 1951 resulted in the deposition of a layer of clay at a depth of 7.5 cm in Peter Lake and about 5 cm in Paul Lake. The experimental addition of hydrated lime to Peter Lake over the past 27 years has obviously increased its rate of sedimentation and the varves above the clay horizon are thicker than those below it. This horizon can be used as a time marker.

The cores were kept frozen until processed. They were then sectioned with an electrical bandsaw. Two 5-cm core sections were selected in sequence from just beneath the clay horizon. A narrow 0.75-cm subsample was cut along the clay horizon to represent the time immediately after the first manipulation. The remaining postmanipulation sediment was divided into three subsamples, representing successive time since the experiment began.

The samples were weighed, dried at 70°C for 72 h, reweighed, and then boiled in 10% KOH and subjected to repeated centrifuging and rinsing at 1,200 rpm. The final residue was diluted to 50 ml with distilled water. Quantitative subsampling followed Schrader's (1973) technique. To disperse the residue, we added 5 ml of 5% sodium hexametaphosphate (used to disperse fine particles for analysis with a Coulter Counter) to each subsample. The quantitative subsamples were mounted as permanent slides with piccolyte in xylene.

Slides were examined from each sampling interval until a minimum of 100 postabdominal claws of *Daphnia* had been measured or, in the uppermost interval where daphnid remains are rare, until a minimum of 100 *Bosmina* and daphnid remains had been measured. Cladoceran remains were counted at

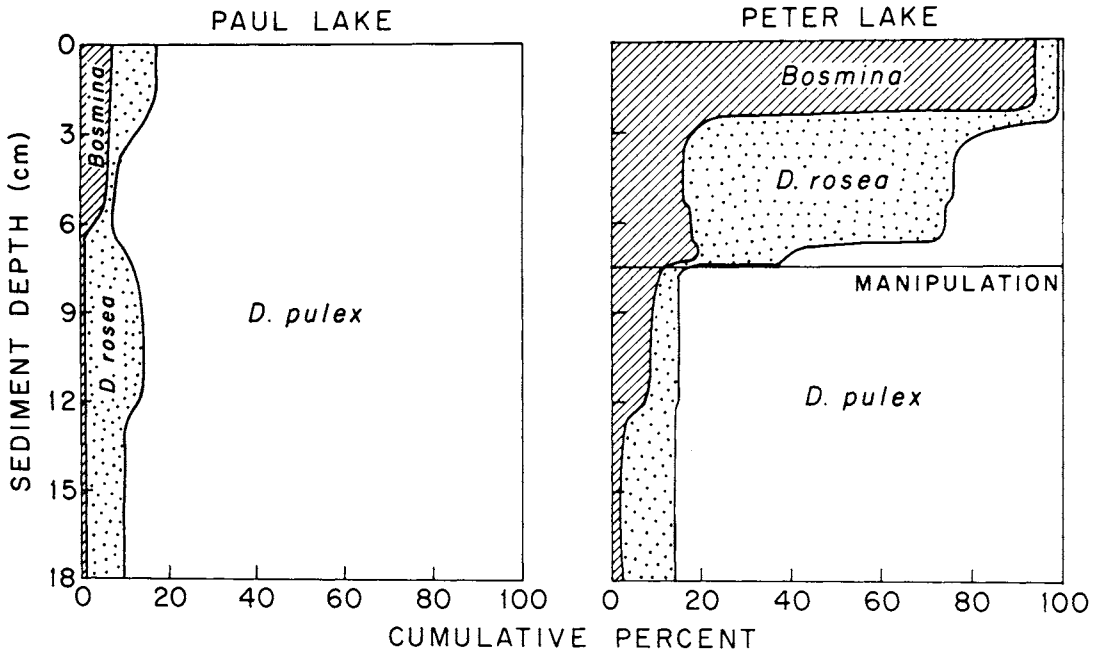


Fig. 1. Relative abundance of *Daphnia pulex*, *Daphnia rosea*, and *Bosmina* in sediments of the lakes.

100 \times . Postabdominal claws were measured with an ocular micrometer at 400 \times ; mandibles and *Bosmina* half-carapaces were measured at 100 \times . Species identification from postabdominal claws follows Brooks (1959). A Datagrid digitizer was used to measure postabdominal claw length and total body length of the plankton samples. Plankton identifications were confirmed by S. I. Dodson. Both parametric and nonparametric statistics were used to analyze the data; similar conclusions were reached.

Results

Empirical evidence from many other case histories (e.g. Hrbáček 1962; Hall et al. 1970; Hutchinson 1971; Nilsson and Pejler 1973; Northcote and Clarotto 1975; Stenson 1976) as well as theoretical predictions (Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976) suggest that in Peter and Paul Lakes we could expect a shift in zooplankton dominance toward smaller species and the possible elimination of large species after

the introduction of rainbow trout. The actual results, however, are more complex.

Removing the indigenous fish population and introducing an efficient zooplanktivore resulted in no changes in species composition or species dominance of the *Daphnia* in Paul Lake nor in any significant shifts in the size-frequency distribution of individuals within species. By contrast, in Peter Lake, which received the same predator manipulation, changes were extensive and significant.

In Paul Lake (the control), *D. pulex* was the dominant zooplankton species before the introduction of trout, its postabdominal claw comprising 86–98% of the total remains (total refers to combined daphnid and *Bosmina* remains; other zooplankton remains were too rare for analysis). *Daphnia pulex* remained dominant after the introduction of trout, comprising 83–95% of the total (Fig. 1). *Daphnia rosea* in the control lake remained the subordinate species both before (2–13%) and after (2–10%) the intro-

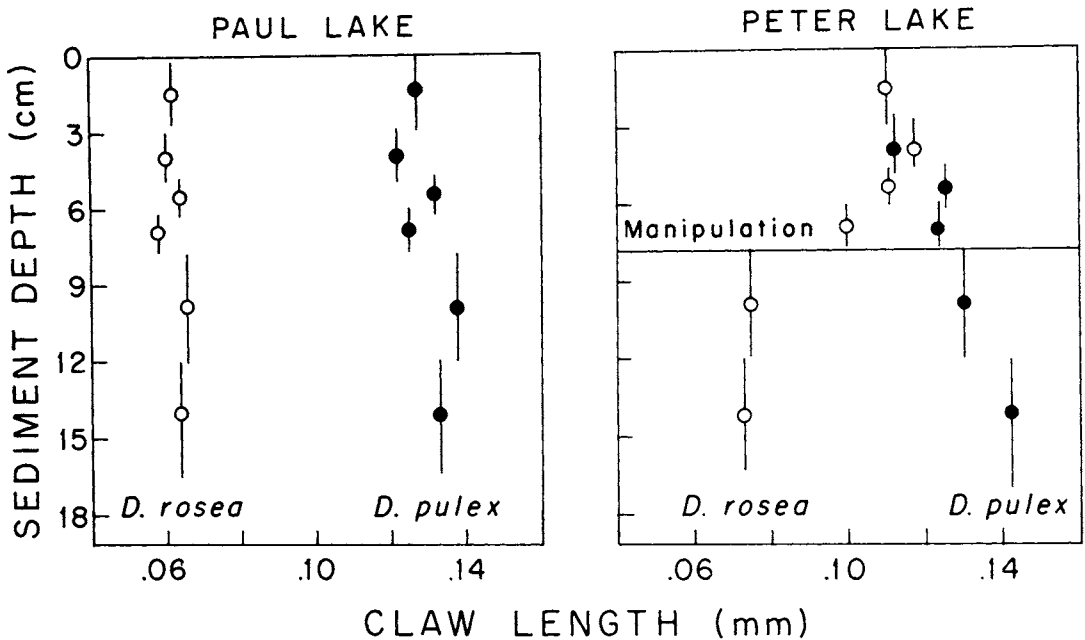


Fig. 2. Mean postabdominal claw length of *Daphnia pulex* and *Daphnia rosea* as a function of sediment depth in the lakes.

duction of trout (Fig. 1). *Bosmina*, as evidenced by rostra and half-carapaces, similarly showed no significant changes in abundance, constituting only up to 7% of the total (Fig. 1).

Before the introduction of trout to Peter Lake (the experimental lake), *D. pulex* was similarly the dominant species, comprising 88–92% of the total remains. Immediately after the initial manipulations however, *D. pulex* abundance declined to 62%, and then to 26–24%, until its almost complete elimination (1%) in the uppermost sampling interval (Fig. 1). *Daphnia rosea*, the subordinate species before manipulation, increased to 60%, followed by a precipitous decline to 5% in the uppermost interval (Fig. 1). *Bosmina* comprised only about 5% of the total remains before manipulation and after manipulation accounted for a modest 16–19% of the population. However, *Bosmina* remains dominate in the uppermost sampling interval, comprising 94% of the total (Fig. 1).

Equally dramatic were the reciprocal changes in mean size of *D. pulex* and *D.*

rosea that occurred concurrently with the shift in species dominance. Again, in the control lake, there was no significant size response to the manipulation. Mean claw length of *D. pulex* consistently ranged from 0.12–0.13 mm, of *D. rosea* from 0.06–0.07 mm, indicating that these two species remained segregated along a size axis (Fig. 2). But in the experimental lake, after manipulation, mean claw length of *D. pulex* decreased from 0.14 to 0.11 mm, whereas mean claw length of *D. rosea* increased from 0.07 to 0.12 mm (Fig. 2). Previously, as in the control lake, both species had been separated along a size axis.

Our discussion will be based on prey body length, which is well correlated with claw length. Hrbaček (1969) documented a good correlation between postabdominal claw length and body length of several daphnid species, not including *D. pulex* or *D. rosea*. Dodson (1970), in feeding experiments of *Chaoborus*, used postabdominal claw length of *D. pulex* as a measure of its body length and found a good linear correlation. In two sedi-

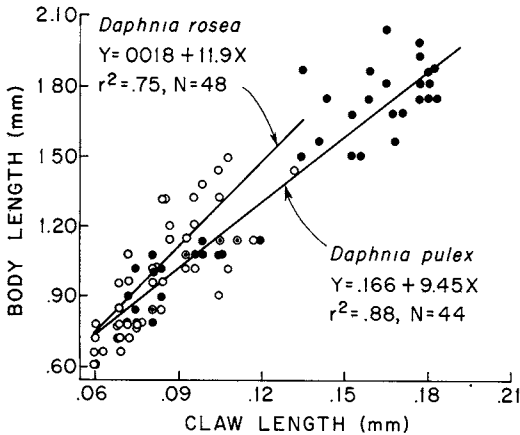


Fig. 3. Relationship between postabdominal claw length and body length of *Daphnia pulex* and *Daphnia rosea*.

ment studies, Kerfoot (1974) relied on measurements of mandible lengths as evidence of changes in the size-frequency distribution of Cladocera, and Brugam (1978) relied on relative abundance of both postabdominal claws and mandibles to assess the intensity of fish predation. It is also of interest that >90% of cladoceran remains collected in sediment traps in Wintergreen Lake were in the form of fish fecal pellets (Threlkeld 1979).

Plankton samples from Peter and Paul Lakes collected during August–October 1978 yielded a linear relationship between postabdominal claw length (X) and body length (Y) for *D. pulex* of $Y = 0.166 + 9.45X$ and for *D. rosea* of $Y = 0.0018 + 11.9X$ (Fig. 3). Making use of these regression equations, we can see that mean body size of *D. pulex* in Peter Lake declined from 1.5 to 1.2 mm, while the mean length of *D. rosea* increased from 0.9 to 1.4 mm.

Figure 4 illustrates the composite responses of species abundance, dominance, and size as a function of time (core depth) for both lakes. The height of each curve corresponds to relative abundance read along the y -axis. The x -axis value corresponding to peak height is a measure of mean body length. The width of each curve is a measure of size variability: the lower and upper x -intercepts cor-

respond to 2 SD above and below the means of body length. We can clearly see that before manipulation (lowermost panels), species composition, relative abundance, and size distribution of the dominant zooplankton were essentially identical in the two lakes. In the control lake (Paul), there were no subsequent changes of significance. By contrast, Peter Lake showed an immediate response and a long term trend of species succession, as well as a significant decrease in size of the dominant species and an increase in size of the subordinate species. More recently in the experimental lake, *D. rosea* remained large relative to pre-experimental conditions and rare, *D. pulex* remained small relative to pre-experimental conditions and even rarer, and *Bosmina* became very abundant.

Analysis of covariation in mean size between *D. pulex* and *D. rosea* in the control lake yielded a significant positive relationship ($r^2 = +0.93$), indicating that any perturbation resulting in a size shift of one species elicited a size shift in the same direction and of the same approximate magnitude in the other species, while there was a significant inverse relationship ($r^2 = -0.93$) in the experimental lake (Fig. 5).

Discussion

The introduction of a highly planktivorous fish to Paul Lake, dominated by large zooplankton, resulted in surprisingly minor responses and no observable disruption of the equilibrium conditions previously established between *D. pulex* and *D. rosea*. We interpret this lack of a size-selective predation response to indicate either no enhancement of planktivory or, conversely, no diminution of effective avoidance strategy by the prey after the replacement of indigenous predators.

Introduction of the same planktivore to Peter Lake, similarly dominated by large zooplankton, resulted in a dramatic decline of the larger species and a simultaneous increase of the smaller species. For both *D. pulex* and *D. rosea*, relative abundance and size responded as cou-

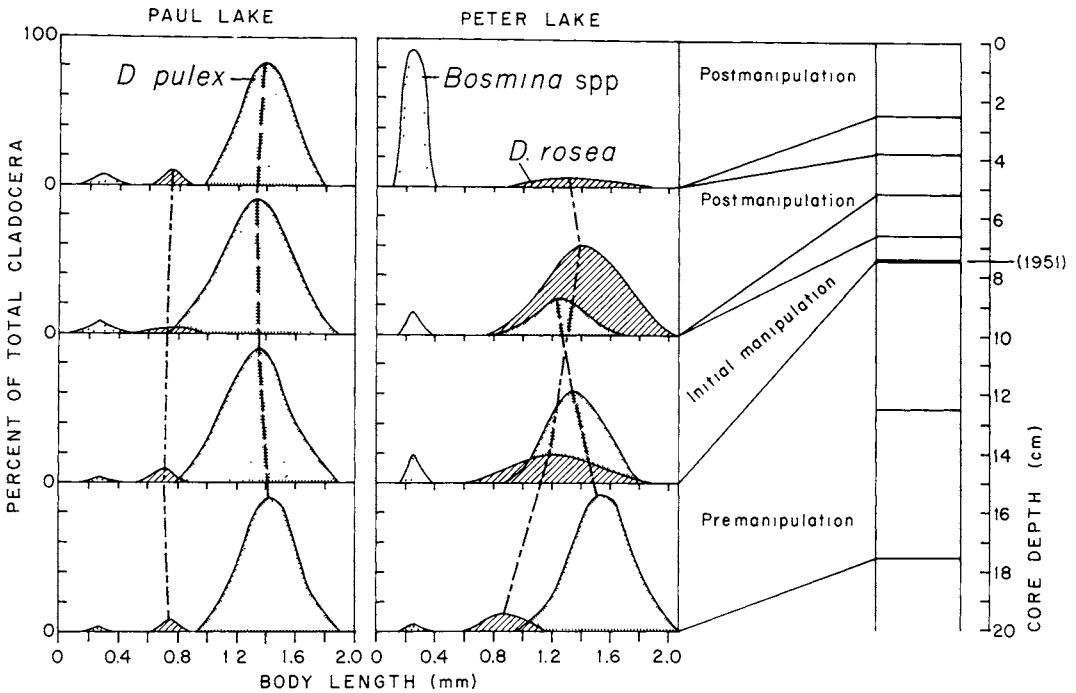


Fig. 4. Schematic representation of species abundance, mean body length, and variability in body length of *Daphnia pulex*, *Daphnia rosea*, and *Bosmina* before and after experimental manipulations in the lakes.

pled variables. The obvious conclusion is that the additional experimental manipulation of Peter Lake (i.e. the addition of hydrated lime and the subsequent increases in transparency and oxygen content of an expanded euphotic zone) either greatly enhanced the reactive distance of the predator, severely reduced the effectiveness of the prey's defensive strategy, or both.

It is also possible that the experimental liming of Peter Lake, independent of its effect on fish-zooplankton interactions, altered the zooplankton community by causing changes in primary production and phytoplankton abundance. However, the available data do not support this hypothesis. For example, Peter Lake was limed in 1976. Two years later, T. Parkin (unpubl. data) measured algal productivities in both lakes directly by radioactive tracer methods; he concluded that productivity in Peter Lake was not significantly increased, although transmission

measurements indicated significantly increased light penetration in Peter Lake. Earlier work by Stross et al. (1961), based on calculations of biomass and turnover rates for *Daphnia* in both lakes, indicated no significant differences (that were unrelated to turnover rates) in production as a function of the observed species shift from *D. pulex* to *D. rosea* in Peter Lake. Hence, although competitive mechanisms play a role in structuring zooplankton communities (e.g. see Lynch 1977a,b, 1978, 1979), our discussion will focus on changes that might have been affected by visibility.

Prey selection processes include both detection and handling of prey. Werner and Hall (1974), however, suggested that due to the minimal expenditure of energy associated with prey handling by planktivorous fishes, the dominant energetic cost factor is search time. Any mechanism that minimizes prey visibility in effect minimizes prey accessibility. This is par-

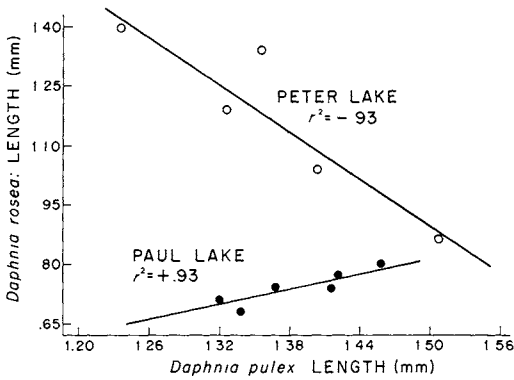


Fig. 5. Covariation in mean length of *Daphnia pulex* and *Daphnia rosea* in control (Paul) vs. experimental lake (Peter).

ticularly true for Cladocera which, once detected, has a capture probability approaching 1.0 (Drenner et al. 1978).

Even minor increases in reactive distance, because it is three-dimensional, should significantly increase the probability of prey detection (O'Brien et al. 1979). Laboratory measurements of reactive distance under optimal illumination indicate a positive relationship with prey size (e.g. Ware 1973; Confer and Blades 1975; Vinyard and O'Brien 1976). On the basis of the work of Confer et al. (1978), reactive distance for rainbow trout offered 1-mm *D. pulex* should be 8–10 cm.

Werner and Hall (1974) suggested that decreased light intensity could also provide a refuge from visually dependent planktivores because of the attenuation of contrast. Laboratory measurements of reactive distance have shown a sharp decline at light intensities below 50 lux for lake trout, brook trout, pumpkinseed (Confer et al. 1978), and white crappie (Wright and O'Brien unpubl.). Vinyard and O'Brien (1976) reported a lower threshold intensity of 10 lux for bluegill.

Laboratory prey are larger than those encountered in either Peter or Paul Lake, and in these laboratory trials fish are tested after acclimation to a certain light intensity, whereas in the field, light intensities change fast, particularly at dawn and dusk. Consequently, increased light

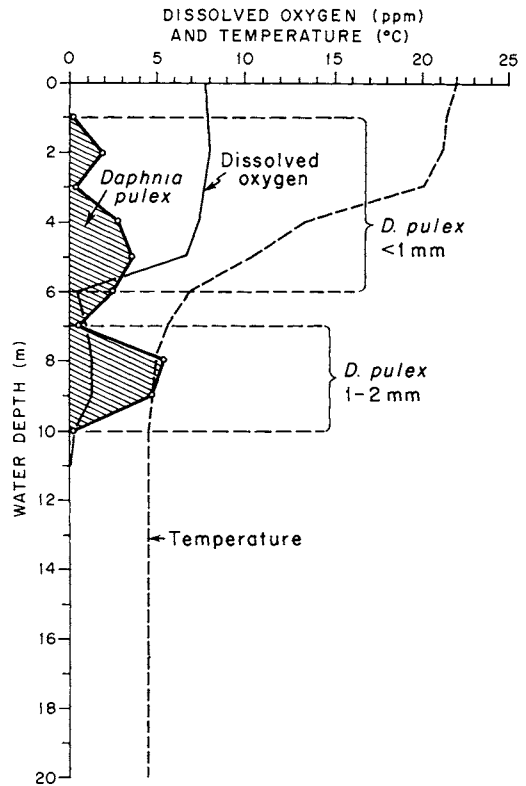


Fig. 6. Distribution, abundance (No. liter⁻¹), and size of *Daphnia pulex* as related to summer temperature and midday oxygen profiles in dystrophic Riley Lake, Wisconsin (after Brynildson 1958).

transmission in Peter Lake should have discernible effects on the intensity of size-selective predation. The behavioral refugium that reduced selective predation on *D. pulex* in Peter-Paul Lake before its experimental separation and continued to reduce selective predation in Paul Lake was probably vertical migration of the prey, which allows them to remain at ambient light intensities below the threshold necessary for the predator (Confer et al. 1978). Zaret and Suffern (1976) have presented evidence that vertical migration can function as an adaptive response to predator avoidance.

If low light intensities operate as a prey refuge, then both large species and larger individuals of a species should be found at relatively greater depths than coexist-

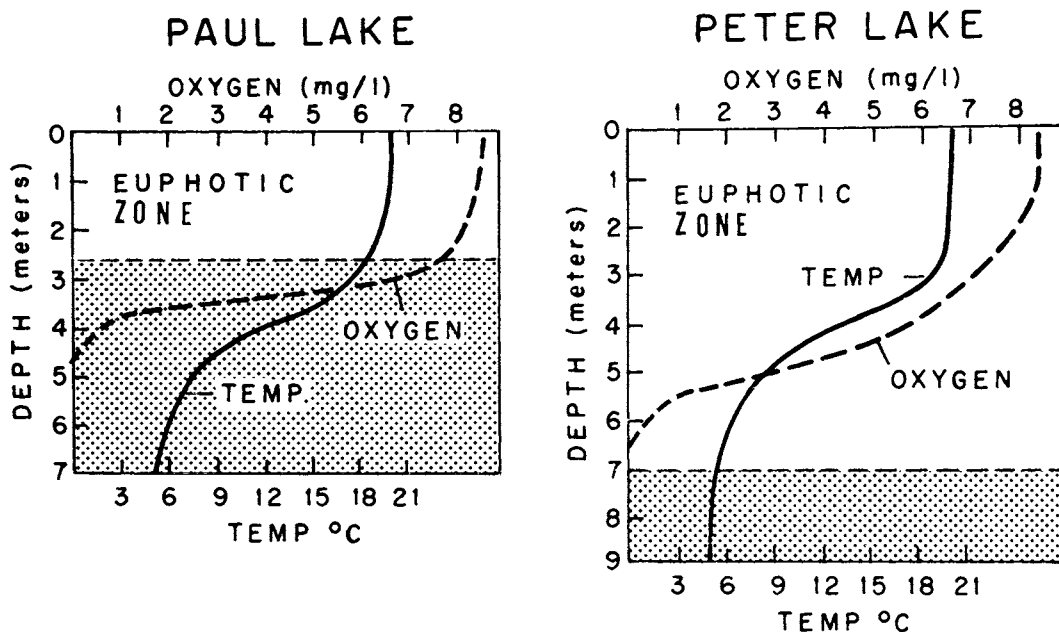


Fig. 7. Typical midsummer oxygen and temperature profiles and depth of euphotic zone in the lakes showing relative position of thermocline with respect to euphotic zone.

ing small species (Vinyard and O'Brien 1976). Brynildson (1958) observed that in Riley Lake, Wisconsin (a brown-stained lake similar to Peter-Paul Lake), specimens of *D. pulex* ranging in size from 1-2 mm inhabited depths below 7 m, whereas animals <1 mm long comprised 80% of that species above 6 m. His data also show (Fig. 6) that the zone of refuge was made secure from intensive predation by trout because of its low oxygen content, 1.2 mg·liter⁻¹; trout requires at least 3 mg·liter⁻¹. In nearby Nebish Lake, dominated by planktivorous perch, large specimens of *D. pulex* inhabit depths of 10 m where dissolved oxygen is only 1 ppm (Brynildson and Kempinger 1973). Shapiro (1978) has also noted the relationship between low oxygen and predation-free refuges for *Daphnia*. *Daphnia pulex* sustains feeding at low oxygen levels by producing hemoglobin; this synthesis can be retarded during high ambient light levels (Kring and O'Brien 1976).

We have calculated from Brynildson's data the depth at which, assuming a day-

light surface illumination of 75,000 lux, the critical light intensity threshold of 50 lux would be located. According to the equation

$$\mu z = \ln I_0 - \ln I_z$$

the 1% light transmission depth range recorded in Riley Lake, 3.7-4.1 m, corresponds to a critical light intensity depth for 50 lux of 5.9-6.5 m, precisely the level observed by Brynildson to mark the transition in distribution between small and large *D. pulex*. We believe that the relative positions of the thermocline with respect to the oxygen minimum barrier and the critical light intensity ceiling in Peter and in Paul Lake can account for the different responses to predation in the two lakes.

In Paul Lake, the lack of electivity for *D. rosea* is to be expected due to the animal's small size, while the apparent lack of electivity for *D. pulex* is a result of the relationship between oxygen, temperature, and light transmission. The euphotic zone consistently lies above the thermocline (Fig. 7). Rainbow trout that must

remain at the thermocline because of summer temperatures are in a zone in which they cannot effectively see their prey. Eggers (1977) suggested that if light intensity is low, reactive distance will not vary with prey size. Vinyard and O'Brien (1975) demonstrated that predation under low light intensity is nearly independent of prey size. Thus, vertical migration effectively separates the prey from the predator in Paul Lake both by an oxygen barrier and by a lack of contrast.

In the experimental lake, however, the euphotic zone penetrated the thermocline (Fig. 7). Heisey and Porter (1977) predicted that a highly visible species like *D. pulex* would, upon shift of the anoxic zone toward the surface, quickly lose its deep-water refuge and be subjected to intensive predation pressure. But in Peter Lake, the anoxic zone was shifted further from the surface, resulting in increased hypolimnetic oxygen concentrations. However, because of the relationship of light and oxygen in the euphotic zone, the depth of light penetration also was shifted toward greater depths. Hence, any advantage accrued to *D. pulex* by oxygenation of these deeper, darker waters was lost because they were also made more transparent, so that a visual predator could perceive *D. pulex* with enhanced contrast. Size-selective predation was intensive as a result, and only differences in the relative abilities of prey and predator to withstand low oxygen concentrations separated a narrow refuge from the zone of predation.

We have seen that the mean size of *D. pulex* declined to 1.2 mm before its near elimination; this is the apparent minimum size for reproduction of that species. Galbraith (1967) concluded that size at first reproduction is more significant than overall size in determining the effects of predation on coexisting zooplankton species. A shift in minimum size at sexual maturity concomitant with increasing fish predation has been reported by Wells (1970), Warshaw (1972), and Archibald (1975). The dynamics of *D. pulex* are best understood in Peter Lake in terms of intense size-selective predation:

both its large size and its dependence on a relatively large size for reproduction made *D. pulex* particularly vulnerable. But in the absence of intensive size-selective predation, as in Paul Lake, *D. pulex* remained dominant.

When *D. pulex* abundances declined in the experimental lake, *D. rosea* came to dominance. *Daphnia rosea* can reproduce at a smaller size and, because it is smaller, is less vulnerable to vertebrate predation. The mean size of *D. rosea*, however, had remained at least 0.9 mm, suggesting a size strategy that would minimize invertebrate predation (Dodson 1970, 1972, 1974). Johnson (1954) reported that *Chaoborus* was present in both Peter and Paul Lakes. Von Ende (1979) reported that *Chaoborus flavicans* and *Chaoborus punctipennis* are still present in both lakes. These species both migrate vertically. Consequently, we suggest that the lower mean size of *D. rosea* represents a response to invertebrate predation by *Chaoborus*, whereas the upper mean size was held in check by competition with *D. pulex*.

Smaller species, like *D. rosea*, that invade a system once the dominant species is reduced by predation are subject to selective pressure for reproduction at a size just below the lower range of predatory interest (Sprules 1972). A puzzling aspect of the response of *D. rosea* is that it increased in mean size to 1.4 mm, which should subject it to strong vertebrate predation. Galbraith (1967) observed that 96% of the zooplankton consumed by rainbow trout were >1.3 mm. In Peter Lake before experimentation, 99% of the daphnids larger than 1.3 mm were *D. pulex*. However, in the uppermost sediment with enough daphnid remains for statistical analysis, 76% of the daphnids >1.3 mm long were *D. rosea*. How could *D. rosea* succeed?

We initially assumed that reactive distance and electivity respond only to changes in prey body size and light intensity. Prey visibility, however, is also a function of pigmentation. Zaret (1972) observed two morphs of *Ceriodaphnia cornuta* coexisting in the same lake de-

spite no discernible differences in behavior or size. The observable difference between the morphs was that of relative reduction in eye pigmentation by that morph least susceptible to predation. Confer et al. (1978) have determined that these reported differences in mean eye pigmentation would result in decreases of reactive distance by 1.9–5.5 cm, enough to reduce predation intensity significantly. An experimental test of prey selectivity, in which *D. pulex* was grown under low oxygen conditions to increase pigmentation by hemoglobin production, confirmed that contrast increases prey accessibility but does not alter the predator's preference (Vineyard and O'Brien 1975). Confer and Blades (1975) similarly found a difference in reactive distance to hemoglobin-pigmented and to translucent *Daphnia magna* of similar size; eye pigmentation diameters did not differ significantly. Zaret and Kerfoot (1975), however, reported a significant decrease in eye pigmentation diameter of *Bosmina longirostris* during daylight hours, which they attributed to selective predation. O'Brien et al. (1979) have reported a greater reactive distance to hemoglobin-pigmented *D. pulex* than to transparent *Daphnia middendorffiana* of similar size.

We could estimate prey body sizes from recovered postabdominal claws. The same plankton samples from which the claw length–body length regressions had been determined were used to determine relative eye pigmentation diameters. Figure 8 shows the relationship between pigmented eye diameter and body length for the two species. *Daphnia rosea* has a smaller eye : body ratio than *D. pulex*. The regression is $Y = 0.0017 + 0.0504X$ with an $r^2 = 0.91$ for *D. rosea* and $Y = 0.0341 + 0.0358X$ with an $r^2 = 0.86$ for *D. pulex*. An eye diameter of 0.073 mm corresponds to a body length of 1.4 mm for *D. rosea*, of 1.05 mm for *D. pulex*. For equivalent eye diameters, *D. rosea* can be nearly 40% larger.

Assuming a maximum visual acuity of $2'$ of arc for planktivorous fish (Blaxter 1970: used by Confer et al. 1978 to ana-

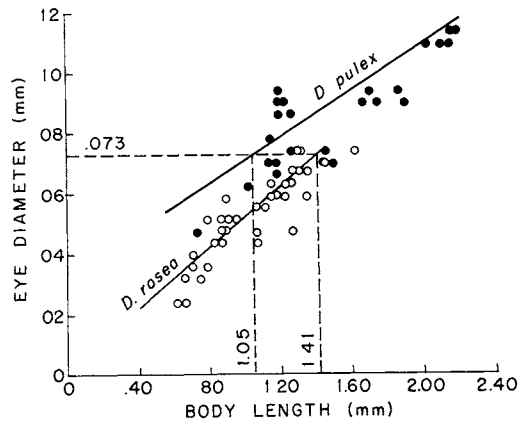


Fig. 8. Relationship between eye diameter and body length for *Daphnia pulex* and *Daphnia rosea*.

lyze the response of reactive distance to pigmented eye diameters), we calculated differences in reactive distance for the two prey species over a prey size range of 1.0–1.4 mm. Specifically, for a body length of 1.0 mm, the reactive distance to the eye diameter of *D. rosea* is 8.9 cm compared to 12.2 cm for that of *D. pulex*. For a body length of 1.4 mm, it is 12.4 cm for *D. rosea* and 14.8 cm for *D. pulex*. Although the implied causal relationship between eye diameter and size change in *D. rosea* is speculative, the computed reactive distances are significantly different for the two species. If the visual acuity of rainbow trout is substantially less than the estimated maximum, then these calculated reactive distances will be overestimated. However, small differences in reactive distance are accentuated when expanded to estimate the volume searched, increasing approximately as the square of reactive distance when a cylindrical field is searched (Eggers 1977) and as the cube of reactive distance in a spherical field (Werner and Hall 1974).

We tentatively conclude that the intermediate success of *D. rosea* in Peter Lake was due both to its ability to reproduce at a smaller size than *D. pulex* and to its reduced vulnerability to predation at comparable sizes, related to its reduced contrast. Differences in hemoglo-

bin may also have played a role in determining selective predation. Because of its initial small size, *D. rosea* in Peter-Paul Lake should not have had to migrate vertically to the same depths as *D. pulex*. Zaret and Suffern (1976) presented evidence that *Daphnia galeata mendotae*, which came to dominance in Fuller Pond after the elimination of *D. pulex* by an introduced planktivore, exhibited the same strong migration pattern as *D. pulex*. Zaret and Suffern concluded that this new behavioral adaptation was in response to a significant increase in predation pressure. *Daphnia rosea* in Peter Lake after the manipulation may similarly have had to begin vertical migration.

Intense size-selective predation often leads to a replacement of *Daphnia* spp. by *Bosmina* spp. (Brooks and Dodson 1965; Galbraith 1967; Brynildson and Kempinger 1973). Kerfoot (1974) observed a reciprocal relationship between the abundance of large *Daphnia* and of *Bosmina*. It would be interesting to know whether this response by *Bosmina* is due to a release of competitive pressure or to a decline in invertebrate predation pressure brought about by increased predation by trout on *Chaoborus* as *Daphnia* availability declines. The same mechanisms that facilitated trout predation on *Daphnia* would presumably increase predation pressure on large invertebrate predators.

Northcote et al. (1978) observed a decrease in the size of *Daphnia* and an increase in that of *Bosmina* after fish were introduced to a previously fishless lake. They attributed the increase in size of *Bosmina* to the elimination of *Chaoborus*, whose second and third instars prey directly on *Bosmina*. However, the rapid elimination of *Chaoborus* from these fishless lakes was facilitated by the relatively minor vertical migration of *Chaoborus americanus*, a species restricted to fishless lakes. In Peter and Paul Lakes, *C. americanus* is absent; fish predation on *C. flavicans* and *C. punctipennis*, species that do migrate, would be less effective. Hence, the relaxation of predation pressure on *Bosmina* in Peter

and Paul Lakes would be of smaller magnitude and presumably take a longer time.

As an addendum to our discussion, since our cores were taken in 1978 the effects of the liming manipulation on light transmission and oxygen concentration have continued. However, Peter Lake is now undergoing a further species change that represents reversion toward its original condition. Largemouth bass were stocked in very low densities ($10 \cdot \text{ha}^{-1}$) for 1 year (1975) and have replaced rainbow trout; fyke netting and minnow trapping in 1979 indicate that natural reproduction is occurring. Furthermore *D. pulex* is once again abundant in Peter Lake and exhibits vertical migration. Apparently *D. pulex* is relatively less susceptible to predation by largemouth bass. Its diel migration puts it in the hypolimnion during daylight hours where, although it is visible, there are now no planktivorous predators to exploit this visibility. Bass are generally less efficient planktivores than rainbow trout (Werner 1977), and, unlike rainbow trout that stay at the thermocline or in the hypolimnion during summer, even planktivorous juvenile bass are epilimnetic summer residents.

We have provided documentation of the effects of predation by an introduced planktivore, over a long time, in response to experimentally manipulated changes in light transmission and oxygen stratification. By verifying the sensitivity of the sediment record to the results of known manipulations, we have presented evidence of a technique equivalent to long term experiments.

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