J. N. Am. Benthol. Soc., 1988, 7(2):100-108

Abundance and growth of three species of aquatic insects exposed to surface-release hydropower flows

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Abstract. Abundance and growth of *Ephemerella subvaria, E. invaria,* and *Isoperla signata* nymphs were examined at five riffle sites near a surface-release hydroelectric power plant on the Sturgeon River in northern Michigan. Abundance ($51/m^2$) and growth of *E. invaria* nymphs were similar at sites above and below the plant. Growth of *I. signata* nymphs was similar at all sites, but nymphs were 6× more abundant ($46/m^2$ vs. $7/m^2$) below the power plant. *Ephemerella subvaria* nymphs grew more slowly, but were 4× more abundant ($136/m^2$ vs. $33/m^2$), below the power plant. Growth rates of *E. subvaria* increased as distance below the plant increased, but at 10 km below the power plant growth rates were still lower than those above the plant. The presence of macrophytes and the release of seston from the reservoir resulted in high densities of invertebrates immediately below the power plant. Releases of warm reservoir surface waters by the power plant in autumn suppressed the growth rates of *E. subvaria* nymphs near the plant, but apparently had no observable effect on growth rates of the other species examined.

Key words: Ephemerella subvaria, Ephemerella invaria, Isoperla signata, stream regulation, growth rate, temperature, hydropower, surface release, emergence, Michigan.

The operation of hydroelectric power stations often imposes unnatural environmental conditions on the downstream environment. Altered water temperature patterns and modified flow regimes associated with hydroelectric facilities can have profound effects on downstream benthos. Changes in benthos community structure, standing crop, and drift have been attributed to the operation of hydroelectric facilities (Brusven et al. 1974, Fisher and LaVoy 1972, Gislason 1985, Kraft and Mundahl 1984, Lehmkuhl 1972, Pearson et al. 1968, Radford and Hartland-Rowe 1971, Trotzky and Gregory 1974).

Despite present knowledge of the effects of hydropower stations on benthos communities, little is known concerning the influences such facilities may have on life cycle phenomena of individual species (Cushman 1985, Ward 1976). Water temperature and current velocity, which change rapidly and frequently in streams below hydroelectric facilities (Brusven et al. 1974, Kraft and Mundahl 1984, Pearson et al. 1968, Pfitzer 1954, Trotzky and Gregory 1974), are known to affect development, hatching, growth, emergence, and fecundity of aquatic insects (Corkum 1978, Fahy 1973, Heiman and Knight 1975, Kondratieff and Voshell 1981, Nebeker 1971, Perry et al. 1986, Rodgers 1983, Sweeney 1978, Sweeney and Vannote 1978, 1981, Sweeney et al. 1986b). It is likely that these factors associated with hydropower flows may influence life histories of aquatic invertebrates downstream from hydroelectric power stations.

We have reported previously (Kraft and Mundahl 1984) that flows from a surface-release hydroelectric power plant in the Upper Peninsula of Michigan reduced insect community diversity downstream, but had no adverse effects on total number of taxa, total density, or standing crop biomass during any season. In the present study we examined the influence of power plant operations on the abundance and life histories of two congeneric mayflies, *Ephemerella subvaria* McDunnough and *Ephemerella invaria* (Walker) (Ephemeroptera:Ephemerellidae), and a stonefly, *Isoperla signata* (Banks) (Plecoptera:Perlodidae). The nymphs of these species are collector-gatherers with similar diets consisting of detritus and diatoms (Shapas and

Hilsenhoff 1976), and were among the most abundant insects present above and below the power plant.

Methods

Study area

The study was conducted on the Sturgeon River, Houghton and Baraga Counties, Michigan (46°40'N, 88°40'W; Fig. 1). The river flows through a forested, 1890-km^2 watershed, and is impounded by Prickett Dam and Hydrostation, a hydroelectric peaking facility that normally operates for 4–18 hr/day Monday through Friday, ceasing operation at night and on weekends. River flows downstream average 18.0 and 0.4 m^3/s when the power plant is and is not operating, respectively. All water used for power generation is drawn from the surface of Prickett Reservoir (surface area = 327 ha, mean depth = 5.6 m).

Five collecting sites (A–E) were established in riffles along the river (Fig. 1): site A, 6 km upstream from the reservoir, and sites B–E at increasing distances (200 m, 1 km, 2 km, 10 km, respectively) downstream from the hydrostation. Stream width varied from 15 to 40 m at the collecting sites, but substrata (boulders, cobble, pebbles) and illumination were generally similar. Aquatic bryophytes (*Fontinalis dalecarlica* and *F. hypnoides*) were present at sites B and C only. Complete site descriptions can be found in Kraft and Mundahl (1984).

Collections and analyses

The study was conducted from May 1979 through May 1980. Invertebrates were collected by kick sampling (three samples per site and date, each approximately 2700 cm^2; Coleman and Hynes 1970, Hynes 1961) with a D-frame aquatic net (0.5-mm mesh), and preserved in the field in 80% ethanol. Samples were collected monthly from May to October 1979 and in May 1980 at sites A, B, and E, and from December 1979 to March 1980 at sites B–E. A thick ice cover prevented sampling at site A from December to March; sites B–E remained ice-free throughout this period as a result of changing water flows associated with power generation. No samples were collected in November or April because of high water. Current velocity was measured within 2 cm of the substratum at each site and date with a Weather Measure pygmy current meter (Model 583). Because access to sites C and D was limited to periods when the hydrostation was not operating, no measurements of current velocities during power generation are available for these two sites. Water temperature was monitored by pre-calibrated Peabody-Ryan thermographs (Models F and J) at sites A, B, and E from June to October 1979 (single 7-d period each month), and at sites B–E from December 1979 to March 1980 (continuous monitoring).

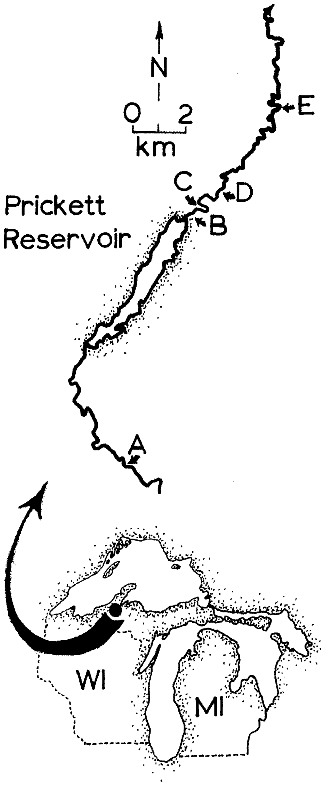

FIG. 1. Location of sampling sites (A–E) on the Sturgeon River near Prickett Reservoir. Inset map shows location of study area in Michigan's Upper Peninsula.

Nymphs of *E. subvaria*, *E. invaria*, and *I. signata* were sorted from each sample and counted. Head widths (widest point) were measured to the nearest 0.033 mm with an ocular micrometer on a dissecting microscope. Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1981) were used to compare size distributions of nymphs between sites on a given date. Emer-

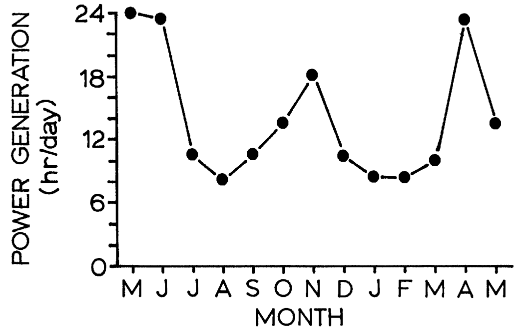

FIG. 2. Mean daily duration of Prickett Hydrostation operation per month during the study period, May 1979-May 1980.

gence periods of the three species were inferred from changes in nymphal densities.

Results

Physical environmental conditions

Precipitation during the study period was above normal, and resulted in an increase in the average daily operation of Prickett Hydrostation. Power generation during the study ranged from 24 hr/d in May 1979 to 8.1 hr/d in August (Fig. 2). Power generation during much of the study period averaged 4 hr/d longer than during years of more normal precipitation (Upper Peninsula Power Company records).

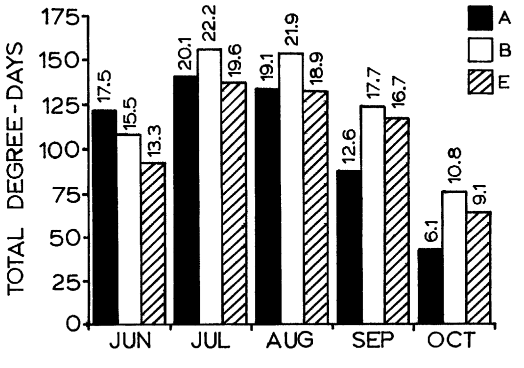

FIG. 3. Total degree-days (°C) accumulated during simultaneous, monthly 7-d periods at sites A, B, and E in the Sturgeon River, June-October 1979. Values above bars show mean water temperatures during the 7-d periods.

Release of reservoir surface water by Prickett Hydrostation delayed spring warming, raised summer water temperatures, and delayed autumn cooling at the downstream sites (Fig. 3). Water temperature from July to October averaged 2-5°C higher at downstream site B than at upstream site A. July and August water temperatures were similar at sites A and E, but during September and October temperatures at site E averaged 3-4°C higher than at site A (Fig. 3). Water temperatures at site A fluctuated 1.0-3.0°C during a 24-hr period throughout summer and autumn; fluctuations at sites B and E during continuous power generation (0.8-3.0°C) were similar to those at site A, but were greater on days with no generation (1.0-5.3°C) and intermittent generation (0.7-4.7°C). The daily temperature range at site B averaged 1.9°C less than at site E during power generation. Winter water temperatures at sites B-E ranged from −1 to +3°C, with daily temperature changes of <1°C. See Kraft and Mundahl (1984) for a more detailed description of the influence of Prickett Hydrostation on Sturgeon River water temperatures.

When the hydrostation was not operating, mean bottom current velocities at the downstream sites (site B—0.381 m/s, C—0.225 m/s, D—0.415 m/s, E—0.478 m/s) were similar to that (0.421 m/s) at upstream site A. Mean bottom current velocity nearly doubled at site B (0.751 m/s) during power generation, but did not change (0.476 m/s) at site E.

Nymphal hatching

Newly hatched (head widths <0.5 mm) mayfly nymphs began appearing in collections in mid-summer. *Ephemerella subvaria* nymphs were first observed at downstream sites B and E on 14 July, and at upstream site A on 5 August. *Ephemerella invaria* nymphs were first collected at sites A, B, and E on 8 September. Small (head widths = 0.5 mm) *I. signata* nymphs were first found in low numbers at sites A and E on 5 August, and at site B on 8 September.

Nymphal densities and growth

Nymphs of *E. subvaria*, *E. invaria*, and *I. signata* achieved maximum densities at sites A, B, and E in September and October (Fig. 4). Maximum

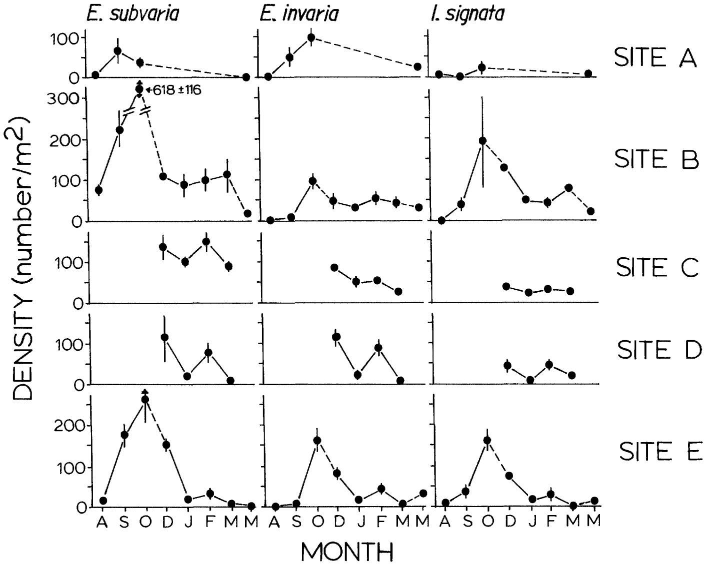

FIG. 4. Mean densities (±1 SE, $n = 3$) of *Ephemerella subvaria, Ephemerella invaria,* and *Isoperla signata* nymphs at five sampling sites (A-E) on the Sturgeon River, August 1979-May 1980.

densities of *E. invaria* were similar at these sites, whereas those of *E. subvaria* and *I. signata* were 3-8× higher below the hydrostation at sites B and E than above. Winter densities for each species ranged generally from 25-100 individuals/m².

Nymphs of the three species had high growth rates in late summer and autumn (August-October), and reduced rates during winter (December-March; Fig. 5). *Ephemerella subvaria* and *E. invaria* displayed higher rates again in spring (March-May) preceding emergence. Growth rates of *E. invaria* and *I. signata* were generally similar at all sites, as there were seldom any size differences among nymphs of these species collected from different study sites during a given month (Fig. 5). However, growth rates of *E. subvaria* nymphs often differed greatly among sites, resulting in significant size differences (Fig. 5). *Ephemerella subvaria* nymphs were larger in September and October at upstream site A than at sites B and E downstream from the hydrostation. In addition, nymphs at site E were significantly larger than those at site B immediately below the hydrostation. Significant nymphal size differences persisted among the downstream sites throughout the winter, with nymphal size increasing with increasing distance from the hydrostation (Table 1).

Emergence

Of the three species, *E. subvaria* emerged the earliest, apparently from late April through early May. No *E. subvaria* nymphs were collected above or below the hydrostation on 17 May 1979, or at sites A or E on 21 and 25 May 1980. However, emergence appeared to be delayed slightly in 1980 at site B immediately below the hydrostation, as large nymphs were still collected in low numbers at this site in late May (Figs. 4, 5).

Emergence of *I. signata* apparently occurred from early to late May. No *I. signata* nymphs were collected from any site in mid-May 1979, but they were present in low numbers at all sites sampled in late May 1980 (Fig. 4).

Ephemerella invaria emergence appeared to occur from late May to early June. In 1979, *E. invaria* nymphs were present at the collection sites on 2 June, but not on 30 June. In late May 1980, nymphs remained abundant at all collection sites (Fig. 4).

Discussion

Although many factors can influence the abundance of aquatic insects in running waters (see review by Hynes 1970), the increased den-

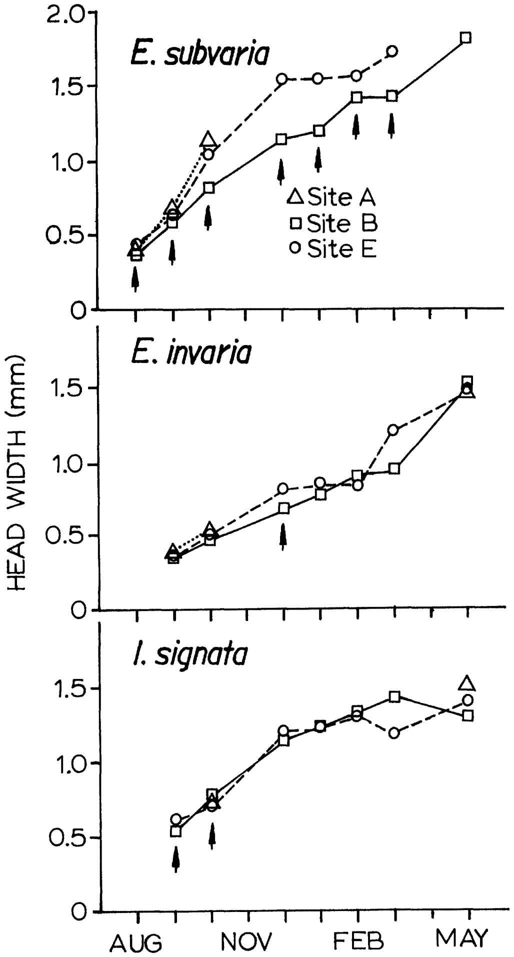

FIG. 5. Mean head widths of *Ephemerella subvaria*, *Ephemerella invaria*, and *Isoperla signata* nymphs at three sampling sites (A, B, and E) on the Sturgeon River, August 1979–May 1980. Arrows indicate months when significant ($p < 0.05$) differences in mean nymph size occurred among sampling sites (Kolmogorov-Smirnov tests). Small sample sizes for *E. invaria* and *I. signata* in March inhibited detection of size differences.

sities of *E. subvaria* and *I. signata* observed immediately below the hydrostation (site B) probably resulted from the presence of macrophytes and increased food availability. These species are collector-gatherers (Shapas and Hilsenhoff 1976), and their densities near the power plant are probably indicative of the large amounts of seston and detritus that settled into the substrata or were trapped on bryophytes. Large patches of aquatic bryophytes were present in the Sturgeon River near the hydrostation. Aquatic bryophytes often harbor such high densities of invertebrates that their numbers spill over into non-vegetated areas (Minckley 1963). Ephemerellid mayflies are known to make extensive use of bryophytes for attachment and refuge (Glime and Clemons 1972, Percival and Whitehead 1929), and *E. subvaria* nymphs were found in their greatest abundance below the hydrostation in and near bryophyte patches. In addition, macroinvertebrate densities are often correlated directly with standing crop and productivity of periphyton and seston, as well as with detritus volume, in both natural and regulated rivers (Egglishaw 1964, Hawkins 1986, Perry et al. 1986). Although no measurements of food quantity were made in the present study, releases of reservoir surface water for power generation apparently contained a heavy seston load which supported a large population of filter-feeders (e.g., the caddisflies *Hydropsyche* sp. and *Cheumatopsyche* sp., and the chironomid *Rheotanytarsus* sp.; Mundahl 1980) near the hydrostation.

Populations of *E. subvaria* and *I. signata* were also high at site E, 10 km downstream from the power plant. However, no aquatic bryophytes were present at this site, and the site was too far below the reservoir to receive any significant seston loading (e.g., Maciolek and Tunzi 1968, Mackay and Waters 1986). Small tributaries entering the Sturgeon River upstream from site E may have added allochthonous materials to the river, and these may have helped support greater numbers of insects at site E. Site E also was slightly wider and had a more open canopy than other sites. As a result, primary productivity may have been higher at this site, and been able to support greater densities of collector-gatherers (Hawkins 1986).

The intermittent operation of Prickett Hydrostation had no apparent effect on growth of either *E. invaria* or *I. signata* in the Sturgeon River. The growth of *E. subvaria*, however, was depressed below the power plant, and adult emergence seemed to be delayed. Two factors associated with impoundment and power generation may have been responsible for the observed effects: elevated water temperatures resulting from release of reservoir surface waters for power generation, and high current velocities during power generation.

TABLE 1. Mean (±1 SE) head widths of *Ephemerella subvaria* nymphs collected from four sites below Prickett Hydrostation, December 1979–March 1980. Numbers below values are sample sizes. Within each row, values followed by a common letter are not significantly different from one another.

	Site			
Month	B	C	D	E
December	1.13 (0.02) d 50	1.33 (0.02) c 50	1.45 (0.01) b 50	1.54 (0.02) a 50
January	1.20 (0.03) c 50	1.39 (0.02) b 79	1.53 (0.03) a 16	1.55 (0.02) a 17
February	1.42 (0.02) b 50	1.46 (0.02) b 66	1.61 (0.01) a 60	1.59 (0.02) a 28
March	1.43 (0.02) b 50	1.56 (0.02) b 50	1.69 (0.02) ab 3	1.71 (0.04) a 7

Elevated water temperature in late summer and autumn is the factor most likely responsible for depressing growth rates of *E. subvaria* nymphs downstream from Prickett Hydrostation. Temperature has been identified in laboratory and field studies as an important regulator of mayfly growth (Corkum 1978, Kondratieff and Voshell 1981, Sweeney 1978, Sweeney and Vannote 1978, 1981). Release of warm surface water from Prickett Reservoir for power generation in summer produced average temperatures in the downstream reach 2°C higher than in upstream areas. Temperature increases of this magnitude may reduce significantly the embryonic development time of *E. subvaria* (Sweeney and Vannote 1981), hence the collection of nymphs below the power plant 2–3 wk earlier than from the upstream site. After hatching, water temperatures 1–3°C above normal can depress significantly the growth rate of *E. subvaria* (Sweeney and Vannote 1978, 1981). In the Sturgeon River, delayed cooling of the reservoir in autumn produced water temperatures that were warmest near the hydrostation (site B, 4–5°C warmer than site A), and nymphs in this area exhibited the slowest growth rates. Temperatures gradually became cooler with increasing distance from the power plant (site E, 3–4°C warmer than site A), and *E. subvaria* growth rates improved. Nymphal growth rates were most rapid above the reservoir where temperatures were coolest.

Although elevated summer and autumn water temperatures were probably the factors most responsible for reducing the growth rate of *E. subvaria* below Prickett Hydrostation, other factors also may have played some role. For example, high current velocities are believed to suppress insect growth rates, as increased physiological demands for position maintenance result in less energy being channeled into growth (Hynes 1970, Kovalak 1978a). Slower growth rates of *E. subvaria* have been attributed to faster current speeds in a Michigan river (Kovalak 1978a), and in the present study the average size of *E. subvaria* nymphs at the collection sites was inversely correlated with current speeds during power generation (e.g., October $r^2 = 0.97$). Even though few *E. subvaria* nymphs occupy the exposed surfaces of rocks during the daytime (Kohler 1983, Kovalak 1978b) when current speeds below the hydrostation were the greatest, current speeds may have been high enough to modify flow patterns around or under substratum particles and affect the growth of *E. subvaria* nymphs in these microhabitats. Although poor food quality can significantly reduce growth rates of aquatic insects (e.g., Anderson and Cummins 1979, Sweeney et al. 1986b, Ward and Cummins 1979), it is unlikely that it limited the growth of *E. subvaria* nymphs below Prickett Hydrostation. The nutritional quality (total assimilable energy) of seston and detritus in rivers below impoundments can be much poorer than that in free-flowing systems (Voshell and Parker 1985), but collector-gatherers may be able to compensate for reduced food quality and exhibit normal growth rates (Cummins and Klug 1979, Kondratieff and Voshell 1981). No measurements were made of food quality in the Sturgeon River, but Hawkins (1986) found little evidence that implicated food as the cause for observed differences among study sites in the growth rates of six species of ephemerellid mayflies.

Why did operation of Prickett Hydrostation affect the growth rates of *E. subvaria* nymphs, but not those of the other two species examined? Not all species respond equally to environmental changes; a species' response is dependent upon its environmental optima, as well as the timing of the change during the species' life cycle (Hawkins 1986, Sweeney and Vannote 1978, Vannote and Sweeney 1980). Even congeneric species occurring together in the same habitat may respond in opposite ways to the same environmental alteration (Sweeney and Vannote 1978, 1981). Apparently, increased water temperatures in the Sturgeon River were above the growth optimum for *E. subvaria*, but within the optimum range for *E. invaria* and *I. signata*. It is likely that some species had their growth rates enhanced by the warmer waters, the increased temperature bringing them closer to their optimum for growth. In addition, eggs of *E. invaria* and *I. signata* hatched out 3–7 wk after those of *E. subvaria*. Differences in developmental stages among the species during their exposure to the increased summer and autumn temperatures may have contributed to the different responses.

What influence will altered growth rates of *E. subvaria* nymphs below the hydrostation have on their population? Previous investigators have reported that human activities (e.g., reservoir construction, power plant operation) that slightly modify the normal temperature regimes of lotic systems may produce subtle but significant changes in life histories of mayflies or other aquatic organisms (Kondratieff and Voshell 1981, Langford 1975, Obrdlik et al. 1979), and potentially eliminate some species from a system. Temperature-induced changes in mayfly growth rates may lead to reduced adult size and fecundity (Sweeney 1978, Sweeney and Vannote 1978, 1981), and may ultimately serve to limit a species' distribution both locally and over a wide geographic area (Kondratieff and Voshell 1981, Sweeney and Vannote 1978, Vannote and Sweeney 1980). In addition, Sweeney et al. (1986a) reported considerable genetic variability among *E. subvaria* populations above and below reservoirs in the Delaware River system, and hypothesized that reduced gene flow between populations resulted from factors (e.g., temperature) that affected the timing and duration of adult emergence below the reservoirs. Reduced gene flow between populations may lead eventually to lower genetic diversity (especially in populations immediately downstream from reservoirs), and reduced ability of the population to cope with natural or human-induced environmental changes (Ferguson 1980, Gillespie and Guttman 1988).

In conclusion, surface-release hydroelectric power plants can affect the growth rates of aquatic insects downstream by modifying the normal water temperature regime, and possibly by subjecting organisms to high current velocities. Even subtle changes in environmental conditions may have significant effects on growth rates of some species. Abundance of these forms appears to be more closely tied to food and habitat availability.

Acknowledgements

We thank the employees of Upper Peninsula Power Company for their cooperation during this study, J. Rocker for assisting with collections, and M. Moore, R. J. Mackay, B. W. Sweeney, and two anonymous reviewers for their helpful comments on an earlier version of the manuscript. This research was supported in part by a grant from the Office of Water Research and Technology to K. J. Kraft.

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Received: 14 December 1987
Accepted: 25 May 1988