

Effects of Food Removal on Nutrient Release Rates and Lipid Content of Lake Michigan *Pontoporeia hoyi*¹

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Pontoporeia hoyi, the dominant benthic invertebrate in the upper Great Lakes, appears to be well adapted to environments with seasonal inputs of high-quality food such as those supplied by the spring diatom bloom. Ammonium and phosphate excretion rates and lipid content were examined in *P. hoyi* under the following conditions: (1) field animals sampled seasonally, (2) food-deprived animals in filtered lake water, and (3) control animals held in native sediments without new food inputs. Nutrient excretion rates for *P. hoyi* (0.5 to 2 nmole NH₄ (milligrams dry weight)⁻¹·h⁻¹ and 0 to 0.15 nmole PO₄ (milligrams dry weight)⁻¹·h⁻¹) were low relative to rates previously reported for other benthic and pelagic invertebrates and varied little among the three treatment groups. In contrast to the animals held in the laboratory without new food inputs, field-collected *P. hoyi* accumulated increased levels of lipids following the spring diatom bloom. However, after lipid levels in field animals peaked in May, they decreased during the rest of the season at rates similar to those of starved and control animals. *P. hoyi*'s low nutrient-excretion rates, and its ability to accumulate and store energy as lipids, for periods when food is not abundant, appear to be important factors allowing this animal to thrive in temperate lakes with spring diatom blooms.

Pontoporeia hoyi, principal invertébré benthique des Grands Lacs d'amont, semble bien adapté aux milieux qui reçoivent des apports saisonniers d'aliments de grande qualité, tel celui fourni par la prolifération printanière de diatomées. On a mesuré les taux d'excrétion des ions ammonium et phosphate et les teneurs lipidiques chez des spécimens : (1) recueillis chaque saison sur le terrain; (2) privés de nourriture dans de l'eau de lac filtrée; (3) témoins conservés dans les sédiments d'origine sans nouvel apport alimentaire. Les taux d'excrétion (0,5 à 2 nmoles NH₄·mg de poids sec⁻¹·h⁻¹ et 0 à 0,15 nmole PO₄·mg de poids sec⁻¹·h⁻¹) étaient faibles par rapport aux taux mesurés chez d'autres invertébrés pélagiques ou benthiques, et ont peu varié parmi les trois groupes étudiés. Contrairement aux animaux soumis au jeûne en laboratoire, les spécimens récoltés sur le terrain avaient accumulé des réserves de lipides après la prolifération des diatomées. Cependant, après avoir culminé en mai, les teneurs en lipides diminuaient durant le reste de la saison à un rythme semblable à celui des témoins et des spécimens soumis au jeûne. Le taux faible d'excrétion d'éléments nutritifs chez *P. hoyi*, ainsi que son aptitude à accumuler des réserves lipidiques pour les périodes de disette, semblent être des facteurs importants de la survie de cet animal en lacs tempérés sujets aux proliférations de diatomées.

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The amphipod, *Pontoporeia hoyi* (previously called *Pontoporeia affinis*), is an important benthic animal in the Great Lakes. It constitutes up to 88% of the zoobenthic biomass in the upper Great Lakes (Cook and Johnson 1974) and can reach densities of 34 000 individuals·m⁻² (Nalepa et al. 1985). *Pontoporeia hoyi* is eaten by a wide variety of fishes (Wells 1980) and may affect contaminant transfer dynamics in the lakes (Nalepa and Landrum 1988). Lipophilic toxins such as polychlorinated biphenyls and polycyclic aromatic hydrocarbons are bioaccumulated by *P. hoyi* to levels much greater than occur in surrounding sediments (Eadie et al. 1983; Landrum 1983; Evans et al. 1982). *Pontoporeia hoyi* also mineralizes nutrients in Great Lake sediments; excretion by *P. hoyi* appears to account for a significant fraction of total sediment-

water nitrogen flux at some sites in Lake Michigan (Gardner et al. 1987).

In contrast to most other known amphipods, *P. hoyi* feeds intermittently and appears to eat more frequently (as evidenced by gut fullness) in the spring than during other times of the year (Quigley 1988). *Pontoporeia hoyi* growth rates (Johnson and Brinkhurst 1971; Johnson 1988) and lipid levels (Gardner et al. 1985b; Landrum 1988) increase following spring phytoplankton blooms and then decrease during late summer and winter. Diatoms are the dominant phytoplankton component in Lake Michigan in the spring, when abundant silica is available, but decrease as the season progresses (Fahnenstiel and Scavia 1987). Sinking of large diatoms (e.g. *Melosira* spp.) is the major factor causing losses of phytoplankton from the epilimnion during the spring, whereas later in the season, zooplankton grazing removes most of the diatoms from the water (Scavia and Fahnenstiel 1987). Thus, large diatoms of high nutritional quality may be available to *P. hoyi* for a period in the spring,

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but not during the rest of the year when the nutritional quality of available particles may be lower (Gardner 1989a, 1989b).

We suspected that the availability of this high-quality food in the spring may allow *P. hoyi* to accumulate lipid reserves that, in turn, would support its metabolic needs during later months when nutrient inputs are low. For example, cold water arctic zooplankton, that experience sporadic food supplies and accumulate high lipid levels, can survive months without food (e.g. Lee and Barnes 1975). For this scenario to be feasible for *P. hoyi*, its metabolic rates would have to be sufficiently low to allow it to survive for long periods without depletion of critical reserves of energy and nutrients. Low temperatures may be essential for long survival time, as warm water pelagic invertebrates such as *Daphnia* (Holm and Shirpiro 1984) and the subtropical marine copepod *Eucalanus pileatus* (Gardner and Paffenhöfer 1982) can survive only for periods of days/weeks without food.

To gain insights into *P. hoyi*'s physiological and biochemical characteristics that allow it to thrive in oligotrophic, temperate environments such as the upper Great Lakes, we examined *P. hoyi*'s potential longevity and measured its ammonium and phosphate excretion rates and its lipid content under the following conditions: (1) field animals sampled seasonally, (2) group and individual food-deprived animals in filtered lake water, and (3) control animals held in native sediments (without new food inputs) for several months after collection.

Methods

Collection and Experimental Handling of *Pontoporeia*

Pontoporeia hoyi samples were collected in southeastern Lake Michigan at a site 9.5 km southwest of Grand Haven, Michigan, where the water depth is 45 m. This site had a mean *P. hoyi* density of about 6900 individuals·m⁻² (Nalepa 1987). Sediment samples containing *P. hoyi* were taken with a PONAR grab, placed in a cooler containing hypolimnetic water, packed in ice, and transported to the laboratory in Ann Arbor, Michigan. Animals were stored with sediments in the laboratory at 4°C until they were analyzed within 6 d of collection.

Samples were collected from the lake on April 23, May 7, May 22, July 8, August 20, November 26, and December 8, 1986. Animals for the long-term laboratory studies were collected on April 23, 1986. On April 29, the animals were divided into "control" (those incubated in native sediments) and "starved" groups. Each group consisted of approximately 250 animals placed in a 24 cm long × 15 cm × 15 cm glass aquarium (to give a density of 7000 animals·m⁻²) that was about three-fourths filled with cold (ca 4°C) lake water from the collection site. For the control group, freshly collected sediment from 0–4 cm depth at the same site was sieved through a 250-µm mesh size screen to remove invertebrates, so a known density of animals could be added. The sieved sediment was added to the aquarium to a depth of 3 cm. For the starved group, no sediments were placed in the aquarium and the lake water was first filtered through a Gelman AE glass fiber filter (1 µm retention) to remove particles and associated nutrients. The water surfaces of both aquaria were covered with a layer of plastic Saran Wrap to prevent animals from being trapped at the air–water surface but yet allow oxygen to diffuse into the water. The animals incubated as a group without added food may not have been completely starved because they likely received some nutrition from the remains of animals that died

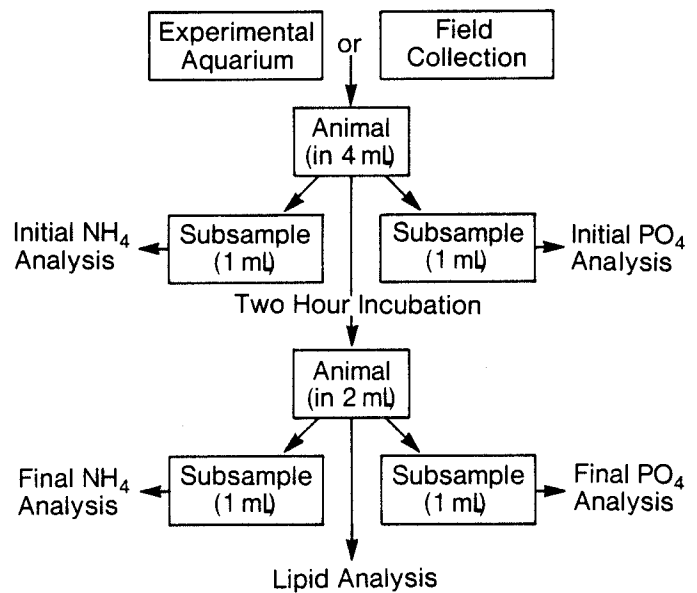


FIG. 1. Outline of incubation and nutrient sampling scheme for measuring nutrient excretion and lipid content on individual *Pontoporeia hoyi*.

during the experiments. For comparison, lipid concentrations were also determined on a second set of animals (sampled in December, 1986) that were incubated individually in scintillation vials, for up to 40 d, in oxygen-saturated filtered lake water over a substrate of ashed, coarse sand.

Analytical Measurements

Ammonium and phosphate excretion rates, dry weight, and lipid content were successively determined on the same animals (see schematic flow diagram, Fig. 1). Mean *P. hoyi* dry weights on the different sampling dates ranged from 1.2 to 2.2 mg·individual⁻¹ for field animals, 0.8 to 1.1 mg·individual⁻¹ for starved animals, and 0.9 to 1.3 mg·individual⁻¹ for control animals. Ammonium and phosphate release rates were determined after 2-h incubations at 4°C under dim light in low-nutrient media (double strength NOPN, Lehman 1980). Before incubations, individual animals were gently removed from sediments and placed in a beaker of filtered lake water to remove associated debris. Each of 5 to 10 animals from each group was placed separately into its own 5-ml polyethylene vial containing 4 ml of low-nutrient water. The water was then gently mixed and 2 ml were immediately drawn off with a clean plastic syringe for initial NH₄ and PO₄ measurements. The initial samples were stored in clean, capped vials until the end of incubations. The animals were incubated in the remaining 2.0 ml of water for 2.0 h to allow accumulation of nutrients for excretion-rate measurements. After incubation, the contents of each vial were gently stirred and most of the incubation water was removed for final nutrient measurements. Ammonium was measured with a micro-fluorometric technique (Gardner 1978) and phosphate with a discrete-injection autoanalyzer method (Gardner and Malczyk 1983).

Immediately following incubations, the animals from the excretion experiments were placed in individual tared glass tubes and dried at 55°C for 4 d in preparation for lipid analysis. Lipid content was determined on each animal with a micro-gravimetric procedure (Gardner et al. 1985a). Occasional outlying data points for any group of animals were rejected by the

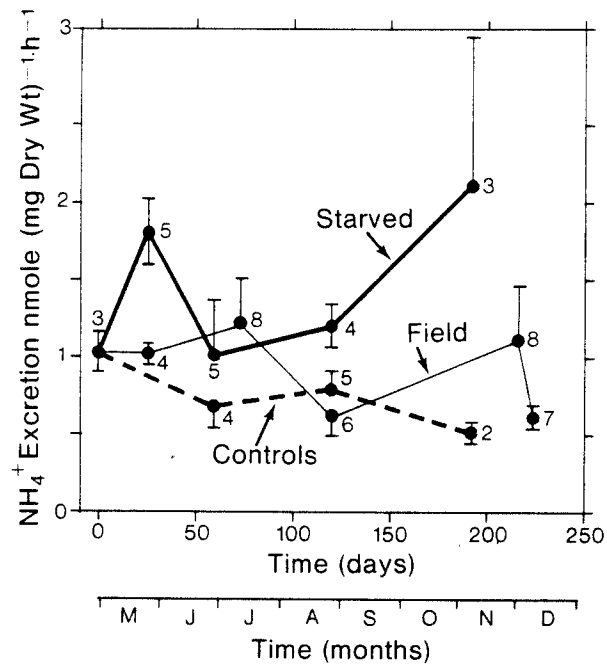


FIG. 2. Ammonium release rates of experimental and field *Pontoporeia hoyi* collected at various times in 1986. The numbers adjacent to the data points indicate the number of animals analyzed to obtain the mean. Range bars are SE.

Q test (Skoog and West 1963) and were not used in calculations of means.

Results

Ammonium Release

Except for the last measurements on starved animals on Day 191, mean *P. hoyi* ammonium release rates ranged between 0.5 and 1.8 nmole (milligrams dry weight)⁻¹·h⁻¹ (Fig. 2). When the data sets for field-collected animals were combined, the ammonium excretion rates correlated significantly ($P=0.02$) to the dry weights of the animals ($r = -0.374$, $n=38$) but this relationship accounted for only a small portion (14%) of the total variance in excretion rates. Although ammonium excretion rates were remarkably consistent throughout the experiment (Fig. 2), the rates were lower than ash free dry weight (AFDW) specific excretion rate values previously reported for *P. hoyi* in Lake Michigan at either 4°C (3–5 nmole (milligrams ash free dry weight)⁻¹·h⁻¹) or 11°C (6 nmole (milligrams ash free dry weight)⁻¹·h⁻¹) (Gardner et al. 1987). A small part (10–20%) of the apparent discrepancy between the two studies at 4°C was caused by the use of dry weight versus AFDW. The remaining differences may have been partially caused by a variation in the delay between sampling and excretion measurements (see discussion below). Both data sets indicated that excretion rates for *P. hoyi* at 4–11°C tend to be comparable or lower than those for other Lake Michigan macroinvertebrates held at higher temperatures (4.5 and 7.8 nmole NH₄ (milligrams dry weight)⁻¹·h⁻¹ for chironomids and 9.2 and 4.8 nmole NH₄ (milligrams dry weight)⁻¹·h⁻¹ for tubificids at 12° and 22°C, respectively Gardner et al. 1983). The excretion rates at 4°C overlapped with rates for oligochaetes (1–4 nmole NH₄ (milligrams AFDW)⁻¹·h⁻¹) held at the same temperature (Gardner et al. 1987) and were within a range of rates observed for a variety of benthic species in Danish coastal waters (0.3 to

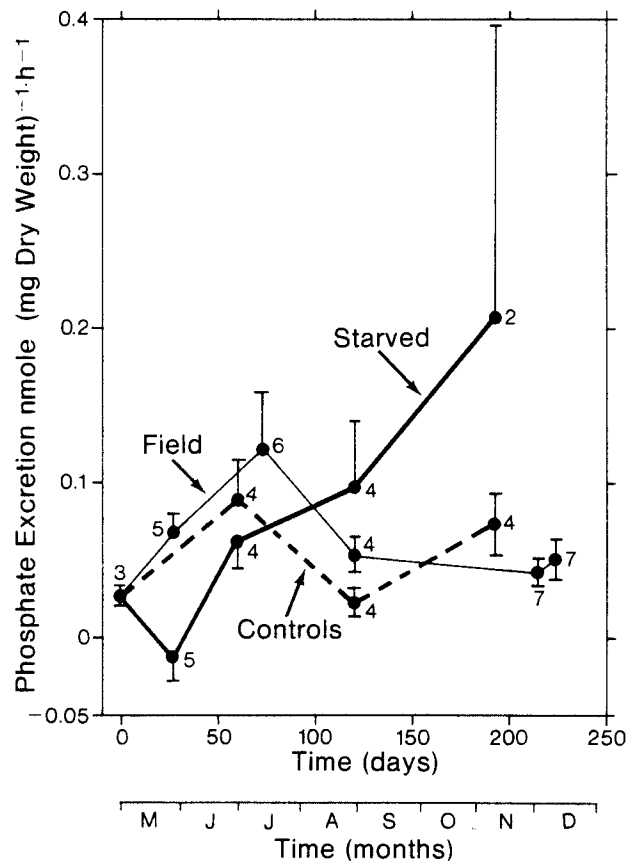


FIG. 3. Phosphorus release rates of experimental and field *Pontoporeia hoyi* collected at various times in 1986. The numbers adjacent to the data points indicate the number of animals analyzed to obtain the mean. Range bars are SE.

3.0 nmole NH₄ (milligrams dry weight)⁻¹·h⁻¹ (= averaged results from a variety of measurements taken over the temperature range of 3.5 to 13.6°C; Blackburn and Henriksen 1983), based on an assumed wet weight:dry weight ratio of 10). Excretion rates for all of these benthic invertebrates were much lower than those reported for warm water pelagic invertebrates (e.g. 35 to 82 nmole NH₄ (milligrams dry weight)⁻¹·h⁻¹ for *Daphnia* spp. at temperatures of 20–25°C; Lehman 1980; Vanderploeg et al. 1986).

Phosphorus Release

Phosphorus release rates among the different groups were less than 0.15 nmole PO₄ (milligrams dry weight)⁻¹·h⁻¹ throughout most of the experiment (Fig. 3) and resembled previous results for *P. hoyi* from Lake Michigan (0.08–0.11 nmole P (mg AFDW)⁻¹·h⁻¹; Nalepa et al. 1983). Phosphorus release rates were not significantly correlated with dry weights ($r = -0.231$ ($n=32$) for field-sampled animals). As was true for ammonium, phosphorus excretion rates by *P. hoyi* were low relative to those of other benthic invertebrates in Lake Michigan (0.12 to 0.81 nmole PO₄ (milligrams dry weight)⁻¹·h⁻¹ for *Stylodrilus*, tubificids and chironomids incubated at 5 and 20°C; Gardner et al. 1981; Nalepa et al. 1983). They were also on the low end of the range reported for various benthic invertebrates from Danish coastal sediments (0.06 to 0.7 nmole PO₄ (milligrams dry weight)⁻¹·h⁻¹; Blackburn and Henriksen 1983) and much lower than rates reported for *Daphnia pulex* held at 20°C (5.0 to 7.4 nmole PO₄ (milligrams dry weight)⁻¹·h⁻¹; Lehman 1980).

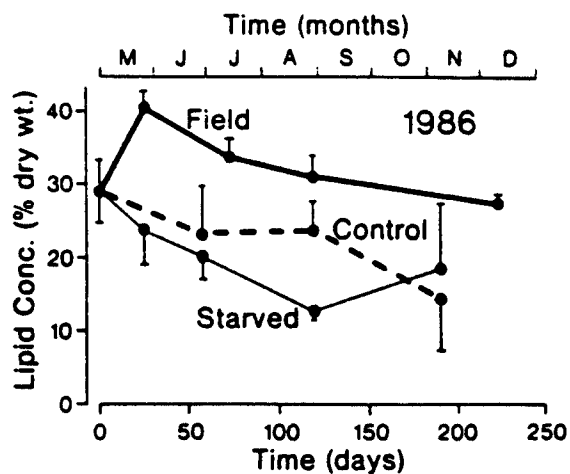


FIG. 4. Lipid content of experimental and field *Pontoporeia hoyi* collected at various times in 1986. Range bars are SE.

Weight specific phosphorus release rates for the field animals peaked at about $0.12 \text{ nmole PO}_4 \text{ (milligrams dry weight)}^{-1} \cdot \text{h}^{-1}$ in early July, a period when lipid content of the same animals was already decreasing (Fig. 4). Ammonium release rates also appeared to peak at this time (Fig. 2) but the peak was not as pronounced as that for phosphorus. Although the magnitude of phosphorus release appeared to be low, phosphorus release-rate patterns for the control animals were similar to those of the field animals except for a possible second peak on day 191 (Fig. 3). In contrast, the starved animals showed a minimum in phosphorus release rates (not significantly different from zero) at the end of May but then the rate progressively increased up to ca $0.2 \text{ nmole PO}_4 \text{ (milligrams dry weight)}^{-1} \cdot \text{h}^{-1}$ by the middle of November (Fig. 3).

Lipid Content

In agreement with previous *P. hoyi* results in southeastern Lake Michigan (Gardner et al. 1985b; Landrum 1988), the percent lipid content of field-collected animals increased sharply between April 29 and May 25 and then decreased gradually through the rest of the year (Fig. 4). This trend was not explained by animal size, as the lipid contents was not significantly correlated with animal dry weight ($r=0.0361$ ($n=30$) for field-collected animals). In contrast to the seasonal trends observed for field animals, the weight-specific lipid content of the starved animals decreased to about 12% of dry weight through the first 120 d of the experiment, but then they appeared to increase during the last interval. The control animals showed trends in lipid content intermediate between those of field and starved animals. They did not exhibit the high lipid increases observed for the field animals, but showed lower rates of lipid losses than did the starved animals (Fig. 4).

Discussion

The relatively low ammonium and phosphorus excretion rates for *Pontoporeia hoyi*, that we observed at approximately in situ temperatures, could suggest a comparatively low metabolic rate that may help explain *P. hoyi*'s ability to survive long periods without food. The similarity in ammonium excretion rates between field and starved animals, and the small degree of change in rates at various intervals after food removal (Fig. 2) suggest that ammonium excretion in these benthic animals may

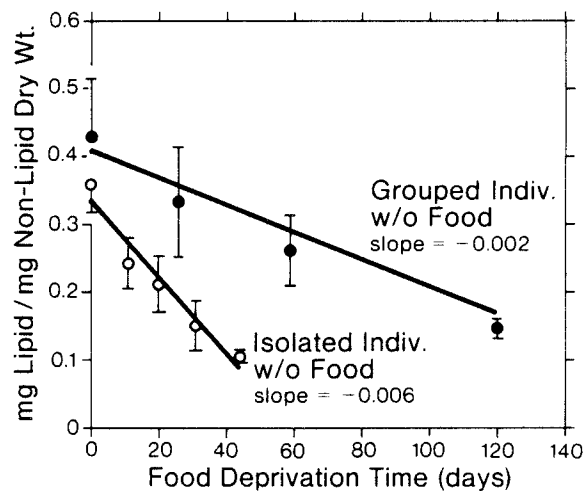


FIG. 5. Comparison of decreases in lipid content, relative to nonlipid dry weight, in grouped and individual *Pontoporeia hoyi* with time after removal of food. The grouped animals were sampled in April 1986 whereas the individual animals were sampled in December 1986. Range bars are SE.

be primarily endogenous and not substantially affected by the quality and/or quantity of food supply. The expected increase in food ingestion following the spring diatom bloom did not appear to cause our measured ammonium excretion rates to increase greatly. Ingested organic nitrogen may have been primarily assimilated into biomass during this "rapid growth" period (Johnson and Brinkhurst 1971; Johnson 1988). It is also possible that a portion of the mineralized nitrogen and phosphorus may not have been released from *P. hoyi* by direct excretion. If the mineralized nutrients were incorporated into fecal material, they would not have been measured as soluble compounds. *Pontoporeia hoyi* fecal pellets are enclosed tightly in a peritrophic membrane that is resistant to abrasion or chemical breakdown (M. Quigley, unpubl. data). The low magnitude of measured rates may also have been caused partially by the delay (up to 6 d) between sampling and the time of excretion-rate measurements. Although the animals were held in their native sediments, they may have stripped out fresh food inputs (e.g. settling diatoms) quite rapidly after samples were removed from the lake.

Alternatively, excretion rates may have been low because the animals obtained their energy from nutrients or body constituents that were low in nitrogen and phosphorus relative to carbon (e.g. carbohydrates or storage-lipids; Mayzaud and Conover 1988; Quigley et al. 1989). The decrease in lipid content relative to dry weight in the various groups of animals likely reflects the loss of triglycerides, as this lipid class is the primary energy-storage lipid in *P. hoyi* (Gardner 1985b). Comparing the ratio of respiration to ammonium excretion by *P. hoyi* (i.e. O:N ratios; Mayzaud and Conover 1988) also suggests that this animal uses more lipid than protein or carbohydrate for metabolic processes (Quigley et al. 1989).

"Weight-specific" decreases in lipid content may not reflect the full effects of starvation on the animal because simultaneous losses of other tissue components may be proportional to that of total lipids, especially after nonessential lipids are depleted. The "weight-specific lipid content" therefore may not change as dramatically during starvation as would absolute lipid content or "total weight loss" of the animals. Likewise, in the data presented above, excretion rates are based on dry weights of

the animals and do not accurately reflect changes in "absolute excretion rates" per animal during starvation. We could not obtain initial dry weights or lipid contents on the same animals that were examined during the experiment, but we were able to normalize the lipid data on starved animals to some extent by examining the "early" changes relative to lipid-free dry weight rather than to total dry weight (e.g. Fig. 5). The apparent increase in weight-specific lipid content observed after 191 d of starvation (Fig. 4) may actually reflect selective catabolism of nonlipid materials over that of essential lipids under conditions of severe starvation. The progressive increase in phosphorus release rates in the starved animals after the minimum at about 30 d may have been due in part to the catabolism of phospholipids (for energy) as triglycerides became depleted.

As indicated by the long starvation period (Fig. 2-4), grouped *P. hoyi* were able to survive in the laboratory for several months without an added food supply. Animals remaining in the starved group after the last measurements lived for up to 217 d after the experiment began. The ability of *P. hoyi* to survive this extended period in the absence of added food can likely be attributed both to the animal's low-temperature habitat and to their ability to store energy as lipids, particularly as energy-storing triglycerides. However, the "group-starved" *P. hoyi* were not necessarily completely deprived of food, as surviving animals likely obtained some nutrition from the residues of other animals that died during the experiment. This possibility was indicated by a comparison of lipid depletion rates in the grouped animals (2 µg lipid (milligrams nonlipid dry weight)⁻¹·d⁻¹) to those of animals starved individually for 40 d as a part of another experiment (6 µg lipid (milligrams nonlipid dry weight)⁻¹·d⁻¹) (Fig. 5). We made a rough estimate of the potential survival time of the latter animals based on their total available lipid and on their observed lipid-depletion rate. Assuming that storage lipids would no longer be available to the animals for energy after total lipids were decreased to about 5% of nonlipid dry weight, this calculation suggests that available lipid reserves would be adequate to support *P. hoyi* for about 50 d in the total absence of food. In addition, the animals may also obtain energy during starvation from other biochemical classes in their tissues such as proteins, as has been observed for some zooplankton (Mayzaud 1976).

The ability to accumulate lipids and live for extended periods without food may provide *P. hoyi* an advantage for survival in an ecosystem with variable food inputs (Griffiths 1977) such as the hypolimnion of Lake Michigan (Scavia and Fahnenstiel 1987; Gardner 1989a). Our data agree with the hypothesis that this organism is physiologically equipped to survive in oligotrophic, temperate lakes with seasonal inputs of diatoms. In conjunction with the spring diatom bloom, *P. hoyi* appears to grow rapidly (Johnson and Brinkhurst 1971; Johnson 1988) and accumulates energy in the form of lipids (Fig. 4), yet, it exhibits only low rates of nutrient release (Fig. 2 and 3). These characteristics reflect *P. hoyi*'s role as an efficient energy-transfer link between phytoplankton and small fish in temperate lakes where adequate silica levels support springtime blooms of large diatoms (Gardner 1989b).

Like *P. hoyi*, *Mysis relicta* and chironomids (Gardner et al. 1985b) as well as some hypolimnetic zooplankton (H. Vanderploeg and coworkers, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan, unpubl. data) in Lake Michigan have high and seasonally-variable lipid levels that may in part reflect their strategies for survival in a low-food environment. On the other hand, *Stylodrilus heringianus*, an oligo-

chaete that lives in close proximity to *P. hoyi*, does not exhibit high or variable lipid levels (Gardner et al. 1985b). A feasible explanation for this inconsistency is that *S. heringianus* obtains its nutrition from microflora associated with particles below the sediment surface (McCall and Tevesz 1982). This feeding strategy may provide the oligochaete with a food supply that is more stable over the season than the relatively high-quality food, in the form of spring diatoms, that is seasonally available to *P. hoyi*.

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