

GUT FULLNESS OF THE DEPOSIT-FEEDING AMPHIPOD, *PONTOPOREIA HOYI*, IN SOUTHEASTERN LAKE MICHIGAN

Michael A. Quigley

U.S. Department of Commerce
National Oceanic and Atmospheric Administration
Great Lakes Environmental Research Laboratory
2205 Commonwealth
Ann Arbor, Michigan 48105-1593

ABSTRACT. *Pontoporeia hoyi* Smith, a deposit-feeding amphipod and a prominent member of the Great Lakes macrobenthic community, was collected at a 45-m-deep site in southeast Lake Michigan during October 1983 and March, May, June, August, and September 1984. Substantial numbers of animals with empty or partially-full guts indicated that *P. hoyi* feeds intermittently, unlike other continuous-feeding amphipods which routinely maintain uniformly full guts among all members of a population. The incidence of animals with empty, partially-full, and full guts also varied significantly with animal size and sampling date and implied that aspects of the amphipod's life history, and seasonality, were primarily responsible for changes in feeding rates. Overall, *P. hoyi* gut fullness was greatest in spring and, secondarily, in autumn, reflecting an opportunistic feeding strategy that exploited newly-deposited detritus generated from spring and autumn phytoplankton blooms. This strategy, in association with *P. hoyi*'s known capacity to store energy as lipids may largely explain *P. hoyi*'s exclusive and widespread distribution in profundal areas of the upper Great Lakes, compared to other amphipods.

ADDITIONAL INDEX WORDS: Benthos, detritus, feeding, sediment.

INTRODUCTION

Pontoporeia hoyi Smith, a deposit-feeding amphipod, is a prominent member of the macrobenthic community throughout the upper Great Lakes (Cook and Johnson 1974). In certain portions of Lake Michigan, *P. hoyi* densities may reach 23,000 individuals m⁻² (Powers *et al.* 1967) although mean densities of 7,000 m⁻² are more common (Nalepa *et al.* 1985).

P. hoyi generally inhabits the upper 2-cm layer of sediments and mixes particles in an eddy-diffusive manner while feeding and burrowing (Robbins *et al.* 1979). High densities, combined with its restriction to a thin surface layer, produce conditions in which *P. hoyi* affects sediment geochemistry through interaction with sediment particles and through metabolic activities (Gardner *et al.* 1981, Quigley and Robbins 1984).

Pontoporeia hoyi also forms an important food for Great Lakes fish. Primary predators include alewives (*Alosa pseudoharengus*, Wilson), smelt (*Osmerus mordax*, Mitchell), and deepwater

sculpin (*Myoxocephalus thompsoni*, Linnaeus) (Morsell and Nordin 1968, Anderson and Smith 1971, Wojcik *et al.* 1986). Secondarily, *P. hoyi* directly supports a variety of commercial and sport fishes, namely salmonids and coregonids (Ward 1896, Van Oosten and Deason 1938, Wells and Beeton 1963). The widespread predation on *P. hoyi* by Great Lakes fishes coupled with the amphipod's high lipid content (a mean of 38% of AFDW in southern Lake Michigan populations (Gardner *et al.* 1985) has prompted much work directed at determining the amphipod's role in the bioconcentration of hydrophilic organic contaminants. For example, up to 50% of the body burden of benzo(a)pyrene accumulated in *P. hoyi* has been attributed to its contact with sediments (Landrum *et al.* 1983). To date, the actual pathways or processes through which such PAH bioconcentration occurs have not been described. However, given *P. hoyi*'s deposit-feeding habits and its intimate association with sediment particles, a certain portion of contaminant uptake can be expected to occur via

the gut with particle feeding selectivity and feeding rate mediating uptake rates.

Despite *P. hoyi*'s widespread abundance in the Great Lakes, little is known about the amphipod's feeding habits. Substrate-feeding studies have shown that *P. hoyi* prefers fine, bacteria-rich sediments over coarse or sterile ones (Marzolf 1965). The amphipod also selects substrates of fine surficial material over a mixture of surficial and coarser material. Feeding activity of *P. hoyi* also varies with season. In Subarctic *P. affinis* (= *P. hoyi*) populations of Great Slave Lake, 20–100% of all animals had measurable solid material in their guts throughout spring and summer (Moore 1979). During autumn and winter, however, only 5–40% of all animals had material in their gut, implying that most individuals fed infrequently, or not at all, over this interval. The objective of this study was to examine the incidence and amount of gut contents in Lake Michigan *P. hoyi* populations to make inferences about the amphipod's feeding patterns relative to size and season. Detailed understanding of the amphipod's feeding habits is essential in designing and conducting subsequent experiments aimed at estimating overall sediment throughput rates of Lake Michigan *P. hoyi* populations. Quantification of such sediment processing rates is needed to complement larger models of energy and contaminant flow through benthic macroinvertebrate communities.

METHODS

P. hoyi were collected with a Ponar grab at a 45-m-deep site located 9.5 km west-southwest of the mouth of the Grand River, in southeastern Lake Michigan (43° 2' 0" N, 86° 21' 52" W). Sediments at the site consisted of a sandy silt with a 3–5 cm well-oxygenated surface layer.

Gut Fullness

The gut fullness of *P. hoyi* collected during the months of October 1983, and March, May, June, August and September 1984 was examined. Following collection, animals were anesthetized in an alcohol/chloroform solution to prevent loss of gut contents during preservation (Swift and Fedorenko 1973). One hour later, *P. hoyi* were preserved in 10% formalin. Prior to measurement, amphipods were cleared overnight in lactophenol solution at 60°C. This treatment allowed full observation of the alimentary tract and measurement of gut contents length (mm), location of gut contents (fore, mid, and

hindgut), and degree of gut fullness (full, partially-full, and empty). Gut contents length was later divided by total body length to produce a quotient that represented a percent gut fullness value (normalized to total body length). All measurements were made by tracing total body length (rostrum to telson) and gut contents length on paper using a camera lucida attachment on a dissecting microscope. Tracings were then measured to the nearest 0.1 mm with a map wheel measuring device.

Data Analysis

The amphipods with empty, partially-full, and full guts collected on each sampling date were assigned to mm size classes (e.g., the 2-mm size class included all animals having a length ≥ 2.0 and < 3.0 mm). A linear model that used weighted least-squares to obtain minimum chi-square estimates (Ray 1982) was used to test for differences in the incidence of the three gut fullness states among size classes and sampling dates. The model also allowed for identification of significant interaction between the two classification variables (size class and date).

RESULTS

The incidence of empty, partially-full, and full guts among *P. hoyi* collected on each of the sampling dates are shown in Figure 1. Substantial numbers of animals with empty and partially-full guts appeared throughout size classes and dates. Over the sampling period, most *P. hoyi* had at least some gut contents while a small portion of the population had empty guts. Calculation of mean percent gut fullness of animals collected on each of the six sampling dates (Fig. 2) revealed highest values (59%) in March and lowest (36%) in August.

Results of the two-way chi-square analysis demonstrated significant ($P < 0.05$) differences in numbers of empty, partially-full, and full guts among both mm size class and sampling date, with significant interaction existing between the two factors. Overall, the incidence (%) of animals with gut contents was highest among smaller (2–6 mm) size classes (Fig. 3). This size range also showed similar seasonal trends in gut contents incidence—a high percentage of individuals with gut contents in March that declined through May/June and subsequently increased in August/September. In larger size classes (7–9 mm) highest incidence of *P. hoyi* with gut contents in May declined through June/August.

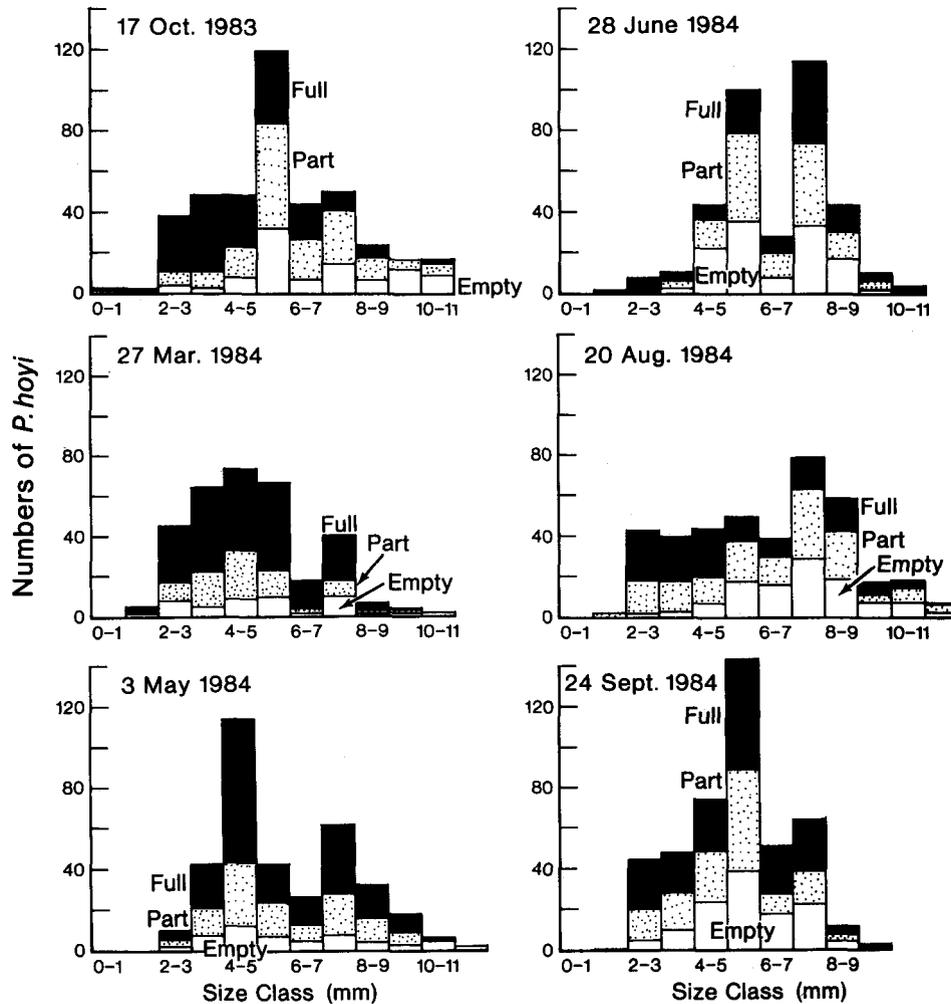


FIG. 1. Numbers of *P. hoyi* with empty (white), partially-full (stippled), and full (black) guts in each (2-10 mm) size classes on each of the six (October 1983 - September 1984) sampling dates.

Percent gut fullness (Fig. 4) tended to decline with increasing mm size class. Percent gut fullness of smaller (2-4 mm) size classes generally declined from March through June with subsequent increases in August/September. In the 5-8 mm size classes, percent gut fullness declined from March through August, followed by a slight increase in September. Percent gut fullness in the two largest (9 and 10 mm) size classes peaked in May and June respectively, followed by declines in August/September.

DISCUSSION

The marked incidence of Lake Michigan *P. hoyi* with empty and partially-full guts noted during the

October 1983 through September 1984 sampling interval implies that *P. hoyi*'s feeding is distinctly different from a continuous feeding mode described for a number of amphipod species (*Hyalella azteca*, Hargrave 1970; *Gammarus pulex*, Welton *et al.* 1983, Willoughby 1983; *Gammarus pseudolimnaeus*, Marchant and Hynes 1981; and *Pontogammarus robustoides*, Kititsyna 1975). In general, these species maintained constantly full guts and led investigators to conclude that continuous feeding is usually associated with the maintenance of uniformly full guts throughout a population. Most recently, this continuous feeding mode has been characterized and modeled as a "plug flow reactor" process common to both

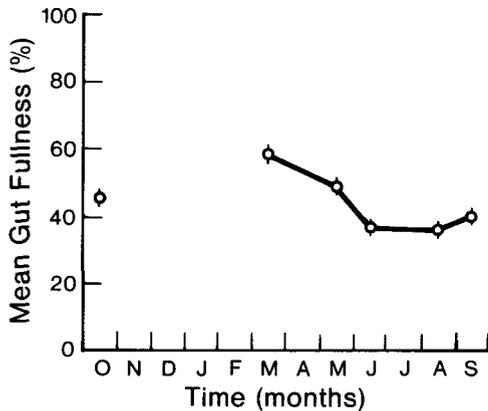


FIG. 2. Mean percent gut fullness (\pm SE) of *P. hoyi* in all (2-10 mm) size classes on each of the six (October 1983 - September 1984) sampling dates.

conveyor-belt feeding polychaetes and continuous-feeding amphipod (*Corophium*) species (Penry and Jumars 1987). Plug flow reactor processes were described as a continuous, orderly flow of material through a normally tubular reaction vessel (gut). Moreover, continuous feeders may depend upon sustained ingestion of food to maintain a steady throughput of gut material, since laboratory studies have demonstrated that when animals were deprived of food, subsequent gut clearance rates declined significantly with at least some material retained indefinitely in the hind gut (Hargrave 1972, Moore 1975, Monk 1977).

Intermittent feeding and a corresponding incidence of empty or partially-full guts has been described for three intertidal amphipod species (*Marinogammarus obtusatus* and *M. pirloti*, Martin 1964 and 1966; and *Gammarus palustris*, Gable and Croker 1977). All three species fed only during submerged (high tide) periods. *G. palustris* fed for short and irregular periods, during submersion, on saltmarsh detritus aufwuchs. In *M. obtusatus* 76-85% of all individuals had full guts following submersion, with this percentage declining to 56% 4 hours later. Percentages of *M. pirloti* with full guts following submersion were similar to *M. obtusatus* but the decline in numbers of animals with full guts was highly dependent on the type of habitat occupied during the exposure (receded tide) period. Overall, as period of exposure increased, numbers of individuals with empty or partially-full guts increased for both species.

Empty and partially-full guts among Lake Mich-

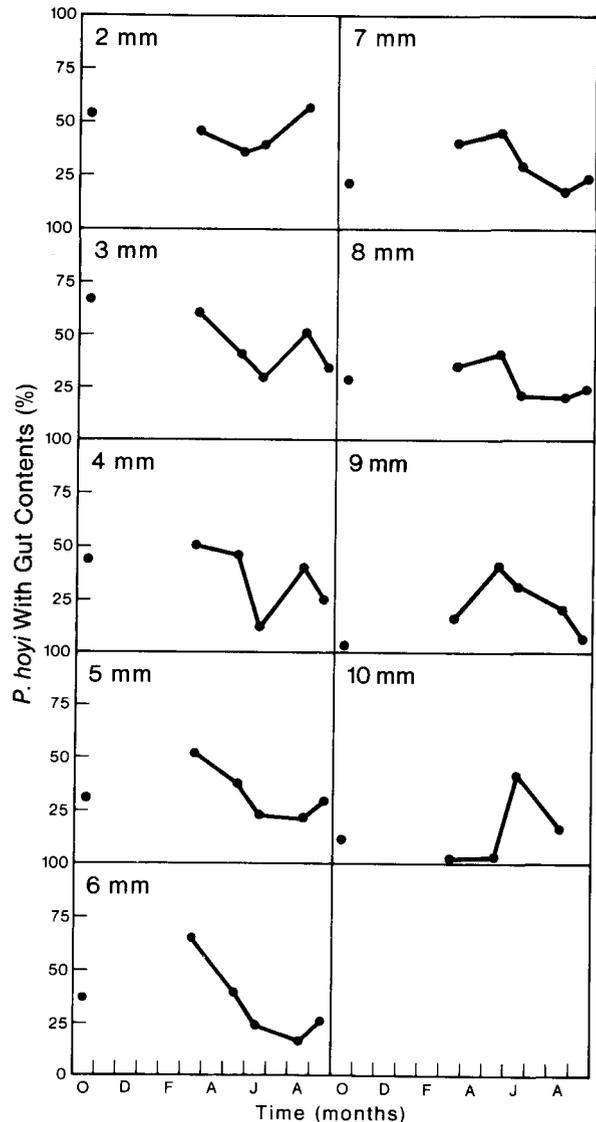


FIG. 3. Percentages of *P. hoyi* with gut contents in each (2-10 mm) size class on each of the six (October 1983 - September 1984) sampling dates.

igan *P. hoyi* imply that the amphipod feeds intermittently. At a 12-14 m deep site in Great Slave Lake, both mean gut contents volume and percentages of *P. hoyi* with gut contents rapidly declined from summer (June-August) to winter months, then increased from mid-winter (January) through spring (Moore 1979). Percent gut fullness data of the study could not be directly compared with Lake Michigan data since Moore expressed gut volume in mm³ rather than percent gut fullness and only presented data for 3-5 and 6-8 mm-sized ani-

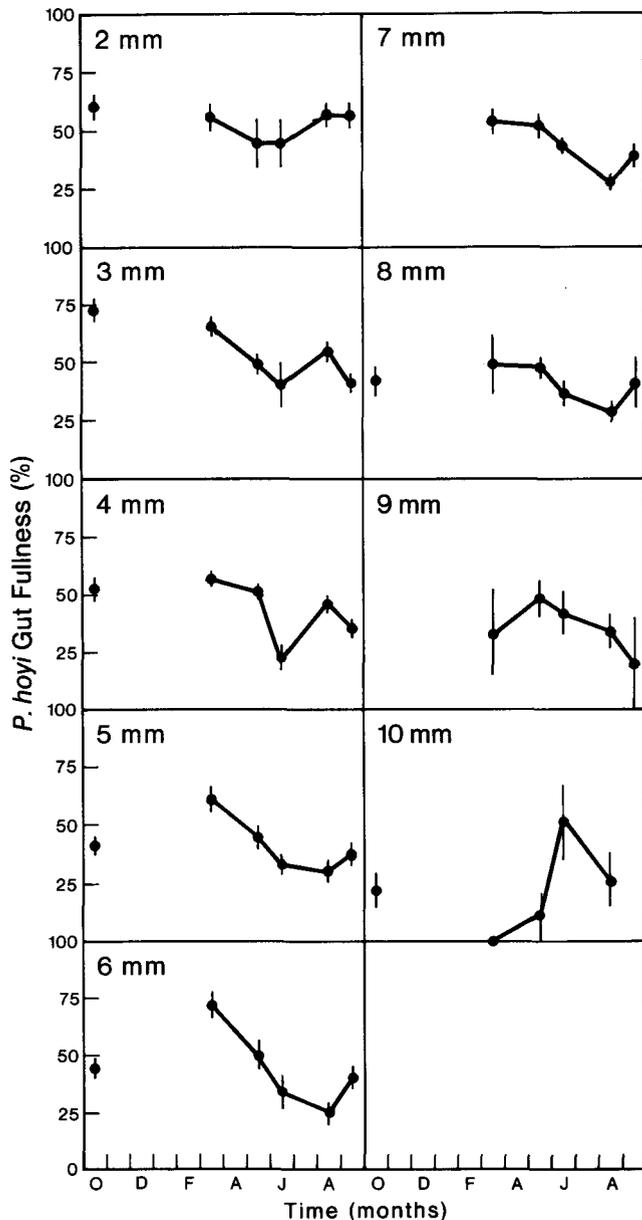


FIG. 4. Mean percent gut fullness (\pm SE) of *P. hoyi* in each (2–10 mm) size class on each of the six (October 1983 – September 1984) sampling dates.

mals. Results on percent animals with gut contents, however, could be compared with percentages of *P. hoyi* with full and partially-full guts noted in the present study (Fig. 5). In Lake Michigan, during a July–September interval, roughly 30% of the population consisted of animals with empty guts, while Great Slave Lake populations had few individuals with empty guts during this

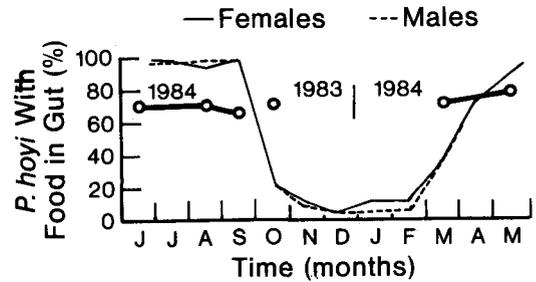


FIG. 5. Percentages of *P. hoyi* with food in gut plotted against collection date. Open dots/thick line represent Lake Michigan data (present study) and thinner solid and dashed lines show Great Slave Lake *P. hoyi* data (Moore 1979).

period. In October, Great Slave Lake samples showed a steep decline in animals with gut contents to 20% while 80% of all animals had empty guts. By contrast, Lake Michigan populations still contained 70% individuals with gut contents. Because sampling in Lake Michigan could not be conducted over winter months, it is not known if any declines in percent animals with gut contents occurred or if such a decline was similar to that of Great Slave Lake. However, since 70% of the animals had gut contents in March, in Lake Michigan, any possible decline from October to March must be of shorter duration than declines noted in Great Slave Lake. In March, 60% of Great Slave Lake individuals had empty guts compared with 30% for Lake Michigan. From March to May, Great Slave Lake percentages of *P. hoyi* with gut contents increased to nearly 100% while Lake Michigan populations showed only a small increase. Overall, since the Great Slave Lake data combined numbers of animals with full and partially-full guts within a more general category of animals with gut contents, no further breakdown or comparison is possible. Conceivably, Great Slave Lake *P. hoyi* populations might feed continuously and maintain generally full guts from May through September. Thereafter, an increasing percentage of animals may halt feeding altogether through autumn and winter, thus accounting for the decrease in percent animals with gut contents. By contrast, a substantial percentage of Lake Michigan *P. hoyi* had empty or partially-full guts over the October 1983 to September 1984 sampling interval and these results are characteristic of an intermittent feeding mode previously outlined in intertidal amphipods.

In Lake Ontario's eastern basin, seasonal Ponar-

collected samples of *P. hoyi* contained up to 69% individuals with empty or partially-full guts. Mean percent gut fullness was 48% and results indicated that Lake Ontario *P. hoyi* did not feed continuously (Dermott and Corning 1987). In general, smaller (≤ 6 mm) animals had higher percent gut fullness and peaks in gut fullness for all animals occurred in late spring/early summer (May-June) with a subsequent peak in early autumn.

P. hoyi's intermittent feeding mode is unusual compared to a more common continuous feeding pattern reported for deposit-feeding amphipods. Undoubtedly, *P. hoyi*'s intermittent feeding constitutes a response to a number of biotic and abiotic factors, and these factors warrant consideration.

Temperature and Light

Moore (1979) used multiple regression analysis to identify factors influencing feeding of *P. hoyi* in Great Slave Lake. Both gut contents volume and percentages of feeding animals (those with gut contents) were closely and positively correlated with temperature and photoperiod. Temperature accounted for 78% of the variation in gut contents volume and 66% of the variation of percent animals with gut contents. When light (photoperiod) was added to the regression equation, an additional 21% variation in gut contents volume and 28% of percent animals with gut contents was explained. In contrast to shallower (1.5–40 m) sampling sites in Great Slave Lake, where temperature ranged from 0–13°C, the present study's 45-m-deep site was located below the Lake Michigan thermocline and exhibited a much narrower (4.1–7.8°C; Table 1) temperature range. In Lake Michigan, where light extinction coefficients range from 0.20 to 0.23, only 0.12 to 0.03% of incoming light should reach bottom (45 m) (Scavia *et al.* 1986). This amounts to maximum summer light intensities of 0.6 to 2.4 $\mu\text{Ein m}^{-2} \text{sec}^{-1}$ that are insufficient to support any benthic algal growth (G. Fahnenstiel, Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, MI, personnel communication). Additionally, the 510–530 nm wavelength of this light corresponds to a green color that can be perceived by *P. affinis* and *P. femorata* (Donner 1971). While light may penetrate to the 45-m-deep sediment surface in winter, the spring stratification of Lake Michigan is accompanied by the development of a 1–2 m thick nepheloid layer of suspended particles over sediments at this

depth. Water transparency is zero in this layer which persists into late autumn (December) (Chambers and Eadie 1981).

Overall, the sediment environment at the 45-m Lake Michigan study site is one characterized by minor temperature fluctuation with little, or more often, no light reaching the sediment surface during the year. Compared to temperature and light regimes in Great Slave Lake, variation in these two factors at the 45-m Lake Michigan site is small and implies that other factors may be more important in seasonally affecting *P. hoyi* feeding activity at this site.

Reduced Feeding Associated with the Onset of Reproduction

While small changes in temperature or light at the study site may not be sufficient to bring about gross changes in feeding rates, these two factors may indirectly affect overall feeding of *P. hoyi* populations by triggering reproductive maturation and breeding among older animals. Change in amount of daylight (Seegerstrale 1970) and temperature variation (Wiederholm 1973) have both been linked with the onset of reproductive maturity in *P. affinis*. In Great Slave Lake, Moore (1979) noted a halt in feeding associated with *P. hoyi* reproductive maturation, and Johnson and Brinkhurst (1971) attributed cessation of feeding to the incidence of dead and emaciated post-reproductive animals that comprised the largest *P. hoyi* size classes in Lake Ontario. In the present study, the incidence of animals with empty or partially-full guts was most prevalent among the largest (8–10 mm) size classes (Figs. 1 and 3). Such reduced feeding activity may be associated with the onset of reproductive maturity expected among largest animals. Mature male *P. hoyi* were not apparent in samples, and given their short and largely pelagic 10 day life span (Green 1971), their absence was not surprising. At a 42-m site in southeast Lake Michigan, male *P. hoyi* were absent from April and July–November monthly Ponar samples and constituted only 0.6–2.5% of the population in May–July samples (Winnell and White 1984). Adult male *P. affinis* of the Baltic did not feed, possessed mandibles that were reduced in size, and had invariably empty guts (Seegerstrale 1937).

In the present study, the lactophenol clearing process used to expose gut contents also prevented definitive identification of mature female animals because it also cleared typically white opaque

TABLE 1. Numbers of *P. hoyi* collected by Ponar grab on each of the six (October 1983–September 1984) sampling dates. Bottom water temperature (°C) at time of collection is shown at right.

COLLECTION DATE	NUMBERS OF <i>P. HOYI</i>	NUMBERS m ⁻²	BOTTOM WATER TEMPERATURE (°C)
17 OCTOBER 1983	414	8,571	5.8
27 MARCH 1984	327	6,770	4.1
3 MAY 1984	353	7,309	4.3
28 JUNE 1984	414	8,571	5.0
20 AUGUST 1984	380	7,868	6.1
24 SEPTEMBER 1984	441	9,130	7.8

masses in the thoracic midsection that indicated maturation of ovaries and subsequent egg development. In more recent laboratory studies, mature females rarely fed and had almost uniformly empty guts. They apparently rely on stored lipids (primarily triglycerides) to support energy requirements during the remaining time of egg development. In summary, the onset of reproductive maturity among *P. hoyi* is marked by a permanent shutdown of feeding activity, and thus reproductively-mature animals are not important in the population's overall sediment processing activities.

Apart from reduced feeding upon the approach of reproduction, seasonal trends in gut fullness may be further confounded by peak influxes of recently-released young in spring (April) and autumn (October) (Lubner 1979). Moreover, *P. hoyi* populations in deeper (≥ 42 m) areas of southeastern Lake Michigan exhibit extensive winter reproduction and a subsequent release of young from May through July (Winnell and White 1984). Thereafter, significant declines in mean body length and biomass during October and November corresponded to release of young and the death of post-reproductive adults following a summer reproductive period. Such seasonal changes in *P. hoyi* size-frequency are similar to trends of the present study. These trends are, in turn, reflected in gut fullness results.

Reduced Feeding Associated With Molting

Aside from feeding stoppage linked with reproductive maturity, changes in amphipod feeding have been associated with other events in amphipod life history, namely, instances of molting. Temporary suspension of feeding and clearance of the gut in preparation for molting has been documented in the continuous feeder—*Gammarus pulex* (Wil-

loughby and Earnshaw 1982). In *Pontogammarus robustoides* (Kititsyna 1975) animals had only partially-full guts prior to molting rather than full guts routinely noted in this continuous deposit-feeder. Greze (1968) also noted a sharp reduction in feeding during molting of three Black Sea amphipod species. In the isopod, *Idotea baltica*, a halt in food consumption during molting was associated with the shedding of the fore- and hindgut during ecdysis (Strong and Daborn 1980). Shedding of the gut lining is also an expected part of amphipod molting and should result in relatively brief stoppage of feeding since empty or partially-full guts have been rarely noted among populations of continuous-feeding amphipod populations (see earlier portion of Discussion).

In recent laboratory observations of *P. hoyi* obtained at the present study site, individuals that molted within a 10-day period seldom fed and rarely egested fecal pellets. While some of the incidence of empty and partially-full guts noted in Lake Michigan *P. hoyi* may be associated with molting, the frequency and duration of molts are probably not sufficient to account for the large overall incidence of empty and partially-full guts. At present, the exact number of molts occurring throughout life is not known. However, Segerstrale's (1937) studies of antennal flagellum segment development indicate that *P. affinis* undergoes at least 6–8 molts. If *P. hoyi* molts in a similar pattern, molts over its 2–3 year lifespan (in deeper water, Alley 1968) would be extremely rare and these events would account for little of the overall incidence of empty and partially-full guts.

Food Availability

Large-scale temperature and light regimes have an indirect but profound effect on the Lake Michigan sediment environment. Temperature and light,

together with nutrient concentration, largely determine algal production in the water column, and the subsequent quantity and quality of detritus deposited on sediments through time. Noticeable increases in *P. hoyi* feeding in spring and autumn may reflect exploitation of large amounts of detritus reaching sediments during these periods following spring and autumn phytoplankton blooms (Rousar 1973, Bartone and Schelske 1982, Fahnenstiel and Scavia 1987, Scavia and Fahnenstiel 1987). Additionally, lipid accumulation in *P. hoyi* during spring has been linked with an influx of detritus generated by the Lake Michigan spring phytoplankton bloom (Gardner *et al.* 1985).

In the Baltic Sea, where the seasonal linkage between phytoplankton production and *P. affinis* and *P. femorata* production has been well-studied (Cedarwall 1977, Elmgren 1978, Sarvala 1986), both species had high growth rates in spring with little additional growth during the rest of the year. Overall, food availability was limited and was temporarily relieved only after the spring phytoplankton bloom (Hill and Elmgren 1987). In Lake Ontario, highest instantaneous *P. hoyi* growth rates occurred in spring (Johnson and Brinkhurst 1971) and may, in part, result from greater food availability derived from spring peaks in phytoplankton productivity (Munawar and Munawar 1982). While seasonal instantaneous *P. hoyi* growth rates in Lake Michigan are not known, increased growth during spring can be expected to accompany observed spring lipid accumulation (Gardner *et al.* 1985) as well as increased *P. hoyi* feeding noted in the present study. At other times of the year, when phytoplankton production and settling rates are lower and the quality and quantity of detrital input to sediment is correspondingly reduced (Scavia and Fahnenstiel 1987), food availability may be limited and feeding and growth may be likewise reduced. During these times, the capacity of *P. hoyi* to store energy in lipids may play a crucial role in fulfilling metabolic needs during food-limited periods. This energy storage capability is apparently large as recent experiments have indicated that *P. hoyi* can survive total food deprivation for up to 6 months (Gauvin 1987). As previously noted, adult *P. hoyi* do not feed and instead appear to sustain reproductive activities with energy stored in lipids. Thus, lipid storage probably represents a mechanism allowing *P. hoyi* to fully exploit food resources when they are temporarily available, and to survive during other

periods when food is limited or when feeding is not possible.

Additionally, seasonal links between feeding and growth have been noted for *P. affinis* populations of Lake Erken (Johnson 1987). Abundances of diatom species identified in the amphipod's gut reflected seasonal floral changes in the overlying water. Maximum *P. affinis* growth was highest in September and coincided with a Bacillariophyceae bloom that subsequently provided a highly nutritional source of particulate matter (Johnson 1985). Likewise, gut analysis of *P. hoyi* in Great Slave Lake (Moore 1977) indicated that individuals fed largely on planktonic algal forms rather than benthic ones. Although algae constituted only 0.1–1.5% of the gut contents, algal cells in the gut frequently had ruptured chloroplasts and could be nutritionally important.

The opportunistic, intermittent feeding strategy of *P. hoyi* is unusual compared to a more common continuous feeding strategy of other amphipod species such as *Hyaella* or *Gammarus*. Instead of relying on a constant throughput of material, *P. hoyi* feeds intermittently on, presumably, rich food sources. Although such food is only temporarily available, it is rapidly assimilated and its energy stored as lipids for subsequent use during growth or reproduction. In summary, lipid storage affords *P. hoyi* the option of feeding intermittently, and this overall feeding and energy storage strategy may explain *P. hoyi*'s exclusive and widespread distribution of profundal areas of the upper Great Lakes, compared to other amphipod species. Finally, because *P. hoyi* feeds intermittently rather than continuously, future efforts to estimate overall sediment throughput rate must account for both the frequency of feeding and the amount of time required for passage of an ingested ration through the gut.

ACKNOWLEDGMENTS

I wish to thank the crew of the R/V *Shenehon* for their assistance during sample collection. I also thank Ragnar Elmgren, Wayne Gardner, Angela Hamilton, Lynn Herche, Tom Nalepa, Peter Landrum, and Henry Vanderploeg for their valuable comments and suggestions on the manuscript. James Lubner, G. Richard Marzolf and an anonymous referee also provided valuable advice during the review of the manuscript for publication. GLERL Contribution No. 489.

REFERENCES

- Alley, W. P. 1968. *The ecology of the burrowing amphipod Pontoporeia affinis in Lake Michigan*. Spec. Rept. No. 36, University of Michigan Great Lakes Research Division, Ann Arbor, Michigan.
- Anderson, E. D., and Smith, L. L. Jr. 1971. *A synoptic study of food habits of 30 fish species from western Lake Superior*. Univ. Minn. Agric. Exp. Stn. Techn. Bull. no. 279.
- Bartone, C. R., and Schelske, C. L. 1982. Lake wide seasonal changes in limnological conditions in Lake Michigan in 1976. *J. Great Lakes Res.* 8:413-427.
- Cedarwall, H. 1977. Annual macrofauna production of a soft bottom in the Northern Baltic proper. In *Biology of Benthic Organisms*, B. F. Keegan, P. O'Ceidigh, and P. J. S. Boaden, pp. 155-164. 11th Europ. Symp. Mar. Biol. Oxford: Pergamon Press.
- Chambers, R. L., and Eadie, B. J. 1981. Nepheloid and suspended particulate matter in south-eastern Lake Michigan. *Sedimentology* 28:439-447.
- Cook, D. G., and Johnson, M. G. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. *J. Fish. Res. Board Can.* 31:763-782.
- Dermott, R., and Corning, K. 1987. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. Great Lakes Fisheries Res. Branch, Can. Dept. Fisheries and Oceans, P.O. Box 5050, Burlington, Ont., Can. L7S 4A6.
- Donner, K. O. 1971. On vision in *Pontoporeia affinis* and *P. femorata* (Crustacea, Amphipoda). *Soc. Sci. Fenn. Comment. Biol.* 41:1-17.
- Elmgren, R. 1978. Structure and dynamics of Baltic benthos communities with particular reference to the relationship between the macro- and meiofauna. *Kieler Meeresforsch. Sonderh.* 4:1-22.
- Fahnenstiel, G. L., and Scavia, D. 1987. Dynamics of Lake Michigan phytoplankton: primary production and growth. *Can. J. Fish. Aquat. Sci.* 44:499-508.
- Gable, M. F., and Croker, R. A. 1977. The salt marsh amphipod *Gammarus palustris* Bousfield 1969 at the northern limit of its distribution. I. Ecology and Life Cycle. *Est. Coast. Mar. Sci.* 5:123-134.
- Gardner, W. S., Nalepa, T. F., Quigley, M. A., and Malczyk, J. M. 1981. Release of phosphorus by certain benthic invertebrates. *Can. J. Fish. Aquat. Sci.* 38:978-981.
- _____, Nalepa, T. F., Frez, W. A., Cichocki, E. A., and Landrum, P. F. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. *Can. J. Fish. Aquat. Sci.* 42:1827-1832.
- Gauvin, J. F. 1987. The effects of food influx on nutrient release rates and energy reserves of the Great Lakes amphipod *Pontoporeia hoyi*. M.S. thesis, Eastern Michigan Univ., Ypsilanti, Michigan.
- Green, R. H. 1971. Lipid and caloric contents of the relict amphipod *Pontoporeia affinis* in Cayuga Lake, New York. *J. Fish. Res. Board Can.* 28:776-777.
- Greze, I. I. 1968. Feeding habits and food requirements of some amphipods in the Black Sea. *Mar. Biol.* 1:316-321.
- Hargrave, B. T. 1970. The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). *J. Anim. Ecol.* 39:427-437.
- _____. 1972. Prediction of egestion by the deposit-feeding amphipod *Hyalella azteca*. *Oikos* 23:116-124.
- Hill, C., and Elmgren, R. 1987. Vertical distribution in the sediment in the co-occurring benthic amphipods *Pontoporeia affinis* and *P. femorata*. *Oikos* 49:221-229.
- Johnson, M. G., and Brinkhurst, R. O. 1971. Production of benthic macroinvertebrates of the Bay of Quinte and Lake Ontario. *J. Fish. Res. Board Can.* 28:1699-1714.
- Johnson, R. K. 1985. Feeding efficiencies of *Chironomus plumosus* (L.) and *C. anthracinus* Zett. (Diptera: Chironomidae) in mesotrophic Lake Erken. *Freshwater Biol.* 15:605-612.
- _____. 1987. The life history, production and food habits of *Pontoporeia affinis* Lindstrom (Crustacea: Amphipoda) in mesotrophic Lake Erken. *Hydrobiologia* 144:277-283.
- Kititsyna, L. A. 1975. Feeding rates of *Pontogammarus robustoides* at different temperatures. *Hydrobiol. J.* 11:35-40.
- Landrum, P. F., Eadie, B. J., Faust, W. R., Morehead, N. R., and McCormick, M. J. 1983. Role of sediment in the bioaccumulation of benzo(A)pyrene by the amphipod *Pontoporeia hoyi*. In *Polynuclear Aromatic Hydrocarbons: Eighth International Symposium on Mechanisms, Methods and Metabolism*, eds. M. W. Cooke and A. J. Dennis, pp. 799-812. Columbus, Ohio: Battelle Press.
- Lubner, J. F. 1979. Population dynamics and production of the relict amphipod *Pontoporeia hoyi* at several Lake Michigan stations. Ph.D. thesis, Univ. Wisconsin, Milwaukee, Wisconsin.
- Marchant, R., and Hynes, H. B. N. 1981. Field estimates of feeding rate for *Gammarus pseudolimnaeus* (Crustacea: Amphipoda) in the Credit River, Ontario. *Freshwater Biol.* 11:27-36.
- Martin, A. L. 1964. The alimentary canal of *Marinogammarus obtusatus* (Crustacea, Amphipoda). *J. Zool.* 143:525-544.
- _____. 1966. Feeding and digestion in two intertidal gammarids: *Marinogammarus obtusatus* and *M. pirloti*. *J. Zool.* 148:515-525.
- Marzolf, G. R. 1965. Substrate relations of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. *Ecology* 46:579-591.
- Monk, D. C. 1977. The digestion of cellulose and other dietary components, and pH of the gut in the amphipod *Gammarus pulex* L. *J. Anim. Ecol.* 44:719-729.

- Moore, J. W. 1975. The role of algae in the diet of *Asellus aquaticus* L. and *Gammarus pulex* (L.) *Freshwater Biol.* 7:431-440.
- _____. 1977. The importance of algae in the diet of *Gammarus lacustris* and *Pontoporeia affinis*. *Can. J. Zool.* 55:637-641.
- _____. 1979. Ecology of a subarctic population of *Pontoporeia affinis* Lindstrom (Amphipoda). *Crustaceana* 36:267-276.
- Morsell, J. W., and Norden, C. R. 1968. Food habits of the alewife *Alosa pseudoharengus* (Wilson) in Lake Michigan. In *Proceedings 11th Conference on Great Lakes Research*, pp. 96-102. Internat. Assoc. Great Lakes Res.
- Munawar, M., and Munawar, I. F. 1982. Phycological studies in Lakes Ontario, Erie, Huron and Superior. *Can. J. Bot.* 60:1837-1858.
- Nalepa, T. F., Quigley, M. A., Childs, K., Gauvin, J. M., Heatlie, T. S., Parker, M., and Vanover, L. 1985. *The macrobenthos of southern Lake Michigan*. NOAA Data Report ERL GLERL-28, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.
- Penry, D. L., and Jumars, P. A. 1987. Modeling animal guts as chemical reactors. *Amer. Naturalist* 129:69-96.
- Powers, C. F., Robertson, A., Czaika, S. A., and Alley, W. P. 1967. Lake Michigan biological data, 1964-1966. In *Studies on the environment and eutrophication of Lake Michigan*, pp. 179-227. Univ. of Michigan Great Lakes Research Div. Spec. Rep. 30. Ann Arbor, Michigan.
- Quigley, M. A., and Robbins, J. A. 1984. Silica regeneration processes in nearshore southern Lake Michigan. *J. Great Lakes Res.* 10:383-392.
- Ray, A. A. 1982. *SAS User's Guide: Statistics*. Cary, N.C., SAS Institute Inc.
- Robbins, J. A., McCall, P. L., Fisher, J. B., and Krezoski, J. R. 1979. Effects of deposit-feeding on migration of ¹³⁷Cs in lake sediments. *Earth Planet. Sci. Lett.* 42:277-287.
- Rousar, D. C. 1973. Seasonal and spatial changes in primary production and nutrients in Lake Michigan water. *Air Soil Poll.* 2:497-514.
- Sarvala, J. 1986. Interannual variation of growth and recruitment in *Pontoporeia affinis* (Lindstrom) (Crustacea: Amphipoda) in relation to abundance fluctuations. *J. Exp. Mar. Biol. Ecol.* 101:41-59.
- Scavia, D., Fahnenstiel, G. L., Evans, M. S., Jude, D. J., and Lehman, J. T. 1986. Influence of salmonid predation and weather on long-term water quality trends in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 43:435-443.
- _____, and Fahnenstiel, G. L. 1987. Dynamics of Lake Michigan phytoplankton: mechanisms controlling epilimnetic communities. *J. Great Lakes Res.* 13:103-120.
- Segerstrale, S. G. 1937. Studien uber die Bodentierwelt in sudfinnlandischen Kustengewassern III. Zur morphologie und biologie des amphipoden *Pontoporeia affinis*, nebst einer revision der *Pontoporeia*-systematik. *Commentat. Biol.* 7(1).
- _____. 1970. Light control of the reproductive cycle of *Pontoporeia affinis* Lindstrom (Crustacea, Amphipoda). *J. Exp. Mar. Biol. Ecol.* 5:272-275.
- Strong, K. W., and Daborn, G. R. 1980. The influence of moulting on the ingestion rate of an isopod crustacean. *Oikos* 34:159-162.
- Swift, M. C., and Fedorenko, A. Y. 1973. A rapid method for the analysis of the crop contents of *Chaoborus* larvae. *Limnol. Oceanogr.* 18:795-797.
- Van Oosten, J., and Deason, H. J. 1938. The food of the lake trout (*Cristivomer namaycush namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. *Trans. Amer. Fish. Soc.* 67:155-177.
- Ward, H. H. 1896. A biological examination of Lake Michigan in the Traverse Bay region. *Bull. Mich. Fish. Comm* No. 6, Lansing, Michigan.
- Wells, L., and Beeton, A. M. 1963. Food of the bloater *Coregonus hoyi* in Lake Michigan. *Trans. Am. Fish. Soc.* 92:245-255.
- Welton, J. S., Ladle, M., Bass, J. A. B., and John, I. R. 1983. Estimation of gut throughput time in *Gammarus pulex* under laboratory and field conditions with a note on the feeding of young in the brood pouch. *Oikos* 41:133-138.
- Wiederholm, T. 1973. On the life cycle of *Pontoporeia affinis* (Crustacea, Amphipoda) in Lake Malaren. *Zoon.* 1:147-151.
- Willoughby, L. G. 1983. Feeding behaviour of *Gammarus pulex* (L.) (Amphipoda) on *Nitella*. *Crustaceana* 44:245-250.
- _____, and Earnshaw, R. 1982. Gut passage times in *Gammarus pulex* (Crustacea, Amphipoda) and aspects of summer feeding in a stony stream. *Hydrobiologia* 97:105-117.
- Winnell, M. H., and White, D. S. 1984. Ecology of shallow and deepwater populations of *Pontoporeia hoyi* (Smith) Amphipoda in Lake Michigan. *Freshwat. Invert. Biol.* 3:118-138.
- Wojcik, J. A., Evans, M. S., and Jude, D. J. 1986. Food of deepwater sculpin, *Myoxocephalus thompsoni*, from southeastern Lake Michigan. *J. Great Lakes Res.* 12:225-231.