

COMPARATIVE ECOLOGY OF *PONTOPOREIA HOYI* POPULATIONS IN SOUTHERN LAKE MICHIGAN: THE PROFUNDAL REGION VERSUS THE SLOPE AND SHELF REGIONS

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ABSTRACT. *This study investigates Pontoporeia hoyi ecology in the profundal region (approximated by a 97-m station) of southern Lake Michigan and compares these results with previous investigations conducted in the slope and shelf regions of the lake. Pontoporeia typically attains its maximum abundance in the slope region, suggesting that this region of the lake is the most favorable for amphipod growth and survival. Profundal and slope P. hoyi exhibited little seasonal variation in mean size while shelf-region populations exhibited strong seasonal variation in mean size. Deepwater sculpins, a major predator on profundal populations of P. hoyi, selectively consumed the largest amphipods: mean size consumed was 6-7 mm. The relative sparsity of larger (> 5 mm) P. hoyi in the profundal, slope, and shelf-regions of the lake may arise from intense size-selective fish predation on this size class of amphipods. Gut content studies revealed that profundal P. hoyi populations feed intermittently. Such feeding behavior was subtly different from that previously observed for slope P. hoyi populations: profundal populations feed more continuously but less intensively than slope populations. Regional differences in feeding behavior may be related to differences in food regime and to predation avoidance strategies. Pontoporeia hoyi apparently is capable of inhabiting a broad range of depth regimes by modifying its physiology (reproductive cycles, generation time) and behavior (feeding, motility) to adjust to spatial variations in temperature, food level, and predation.*

INDEX WORDS: *Benthos, amphipods, crustaceans, Lake Michigan, predation, sculpin.*

INTRODUCTION

Pontoporeia hoyi Smith (Crustacea, Amphipoda) is a major component of Great Lakes macrobenthic communities (Cook and Johnson 1974, Mozley and Howmiller 1977). In southeastern Lake Michigan, it occurs in approximately 70% of all benthic samples, averages more than 2,000/m² in abundance, and comprises nearly 30% of all

macrozoobenthos on a numerical basis (Winnell and White 1984). *Pontoporeia hoyi* accounts for approximately 65% of the macrobenthic community on a biomass basis and 70% on a calorific basis (Nalepa and Quigley 1981). *Pontoporeia hoyi* is broadly distributed in Great Lakes waters with its range extending from shallow (5-10 m) inshore to profundal (> 100 m) offshore waters (Mozley and Howmiller 1977). The taxonomy of nearctic *Pontoporeia* remains under investigation. It is possible that *P. hoyi* is represented by more than one

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species and/or subspecies (Mozley and Howmiller 1977).

Pontoporeia hoyi plays an integral role in the trophodynamics of the Lake Michigan ecosystem. These amphipods may assimilate up to 30% of the total bioavailable organic matter settling into the offshore hypolimnion (Gardner *et al.* 1985) based on summer inputs (Eadie *et al.* 1984). Moreover, these amphipods are an important component in the diet of a large number of fish including yellow perch (*Perca flavescens*), rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), slimy sculpin (*Cottus cognatus*), spottail shiner (*Notropis hudsonius*), deepwater sculpin (*Myoxocephalus thompsoni*), and lake trout (*Salvelinus namaycush*) (Wells and Beeton 1963, Morsell and Norden 1968, Scott and Crossman 1973, Wojcik *et al.* 1986). Because *P. hoyi* contains moderately high concentrations of PCB and DDT (Evans *et al.* 1982, Borgmann and Whittle 1983), these amphipods may represent an important pathway by which organic contaminants are recycled from sedimentary sinks and biomagnified by the fish community (Jensen *et al.* 1982, Breck and Bartell 1988).

The purpose of this paper is to examine several aspects of the ecology of *Pontoporeia hoyi* populations in the profundal zone of southern Lake Michigan. Such aspects include abundance, size-frequency distribution, feeding behavior (gut fullness and contents), and sculpin predation. The particular location where sampling occurred was especially relevant because it has been the site of several investigations over the years, including studies on contaminant body burdens in mysids, *P. hoyi*, plankton, and deep-water sculpins (Evans *et al.* 1982); zooplankton population dynamics (Evans and Jude 1986, Scavia *et al.* 1986, Evans 1988); water clarity (Scavia *et al.* 1986); and deep-water sculpin feeding habits (Wojcik *et al.* 1986).

MATERIALS AND METHODS

Pontoporeia hoyi and deepwater sculpins were collected as part of an EPA-funded study investigating factors affecting contaminant body burdens in the Lake Michigan ecosystem. All collections were made at a 97-m station located approximately 20 km offshore of Grand Haven (Evans and Jude 1986). Sampling dates were 12 May, 13 June, 18 July, 18 August, 16 September, and 8 October 1986, and 15 May, 24 June, 14 July, and 12 August 1987.

Benthic samples were collected during all cruises except May 1986. Four PONAR (Wildco No. 1725; mouth dimensions 23 cm × 23 cm) grabs were collected on each sampling date, with all collections made during daylight hours. Immediately upon recovery, sediment type was noted and the sample washed through an elutriation device equipped with a 0.5 mm sieve (Mozley and Howmiller 1977). All benthos retained were placed in a 1-pt (470-mL) Mason jar along with approximately 200 mL of lake water. Tonic water or club soda was added to relax the animals (to prevent regurgitation). After several minutes, a sugar-formalin solution was added as a preservative.

Sculpins were collected on all sampling dates with a semi-balloon nylon otter trawl equipped with a 4.9 m headrope and a 5.8 footrope. The body and cod end of the net were composed of 1.6 cm-bar mesh. All collections were made during daylight hours (except May 1986). The net was towed for 5 to 10 minutes along the lake floor. After the trawl was retrieved, approximately 20 sculpins were randomly selected and immediately preserved in 10% formaldehyde solution.

Surface-water temperature was measured during each cruise by means of a thermometer immersed in a bucket of freshly-collected lake water. A mechanical bathythermograph was used to obtain a temperature-depth profile.

In the laboratory, all *P. hoyi* in the samples were removed and counted. The *P. hoyi* sample was then subdivided in a Folsom plankton splitter as many times as necessary to obtain a subsample of approximately 40 animals. The resulting subsample was examined to determine the size-frequency distribution and feeding condition of amphipods during each collection date. Individuals from only one replicate were examined for each sampling date in 1986 (for a total of $n = 36-64$ per sampling date), but individuals from all four replicate samples were examined for each sampling date in 1987 (for a total of $n = 116-157$ per sampling date). Specimens were cleared in a lactophenol solution to allow for full observation of the alimentary tract. Each individual was placed on a microscope slide and total body length (rostrum to telson) and gut contents traced on to a sheet of paper using a camera lucida attached to a Wild M8 Stereo Microscope. Gut content length was later divided by total body length to estimate percent gut fullness (normalized to total body length). Tracings were converted to length using

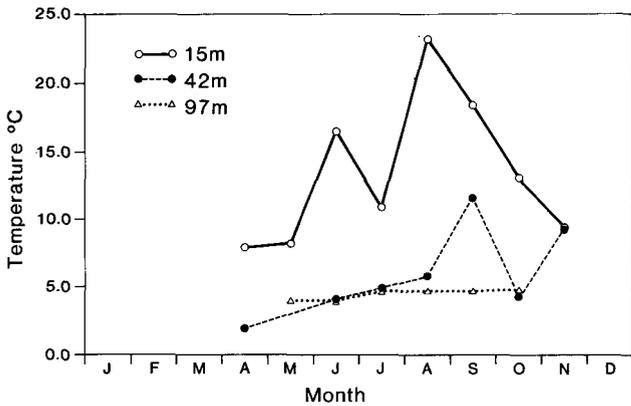


FIG. 1. Mean seasonal bottom-water temperature in the profundal (97 m) region over 1986–1987. Also shown are the mean bottom-water temperatures in the slope (42 m), and shelf (15 m) regions sampled by Winnell and White (1984) over 1981–1982.

the digitizing procedure described in Quigley and Lang (1989).

To obtain qualitative estimates of *Pontoporeia hoyi* food habits, the gut contents of 10 individuals from each sample date in 1986 were examined. The entire gut of each individual was dissected onto a microscope slide, a few drops of lactophenol added as a mounting medium, and then the slide examined under a Leitz compound microscope at a magnification of 400X. Food items (excluding sediment) were enumerated and the approximate percent volume (of the total food volume) estimated.

Subsamples of 5–6 sculpins collected in May (spring), July (summer), and in September (autumn) 1986 were examined to determine the size frequency distribution of *P. hoyi* consumed by deepwater sculpins. All amphipods were removed from each sculpin stomach and counted. Total body length of each amphipod then was determined using the camera-lucida digitizer procedure.

RESULTS

Bottom-water temperature at the 97-m station varied little over the May-October period, ranging from 4.0°C to 4.7°C (Fig. 1): June, July, and August 1986 and 1987 temperatures are averaged to facilitate later comparisons (see Discussion) with *P. hoyi* ecology in other depth regions of the lake. Similarly, seasonal variations in gross sediment type were not pronounced. Sediments were silty-clay with small amounts of fine sand. The

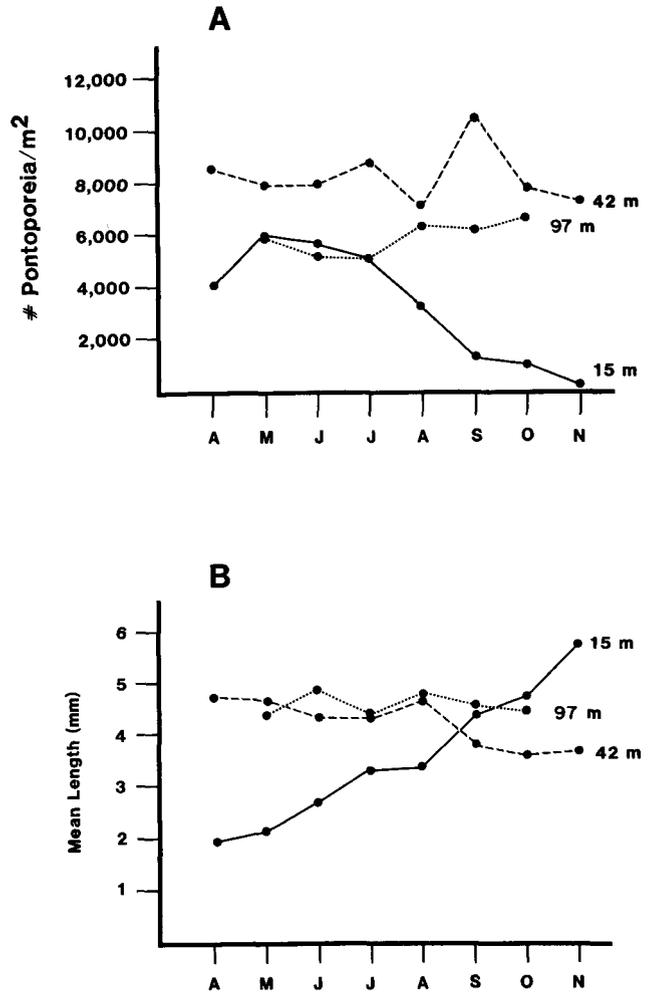


FIG. 2. Mean seasonal A) abundance and B) length of *Pontoporeia hoyi* inhabiting the profundal (97 m), slope (42 m), and shelf (15 m) regions of Lake Michigan. Data for the slope and shelf regions are from Winnell and White (1984).

surface-layer was a rich, chocolate-brown ooze approximately 2–3 cm thick. This layer was underlaid by a layer of paler brown sediment. Occasionally, there was a reddish-brown hardpan layer a few cm below the sediment surface.

Pontoporeia hoyi exhibited little seasonal variation in total abundance or in size frequency distribution (Fig. 2) at the 97-m (profundal region) station. Lowest densities were observed in early to mid-summer: densities appeared to increase in late summer/early autumn. Size-frequency distribution patterns were unimodal with monthly mean length ranging from 4.4 to 5.2 mm (Fig. 3). Very small immatures (< 3 mm) were relatively rare during all

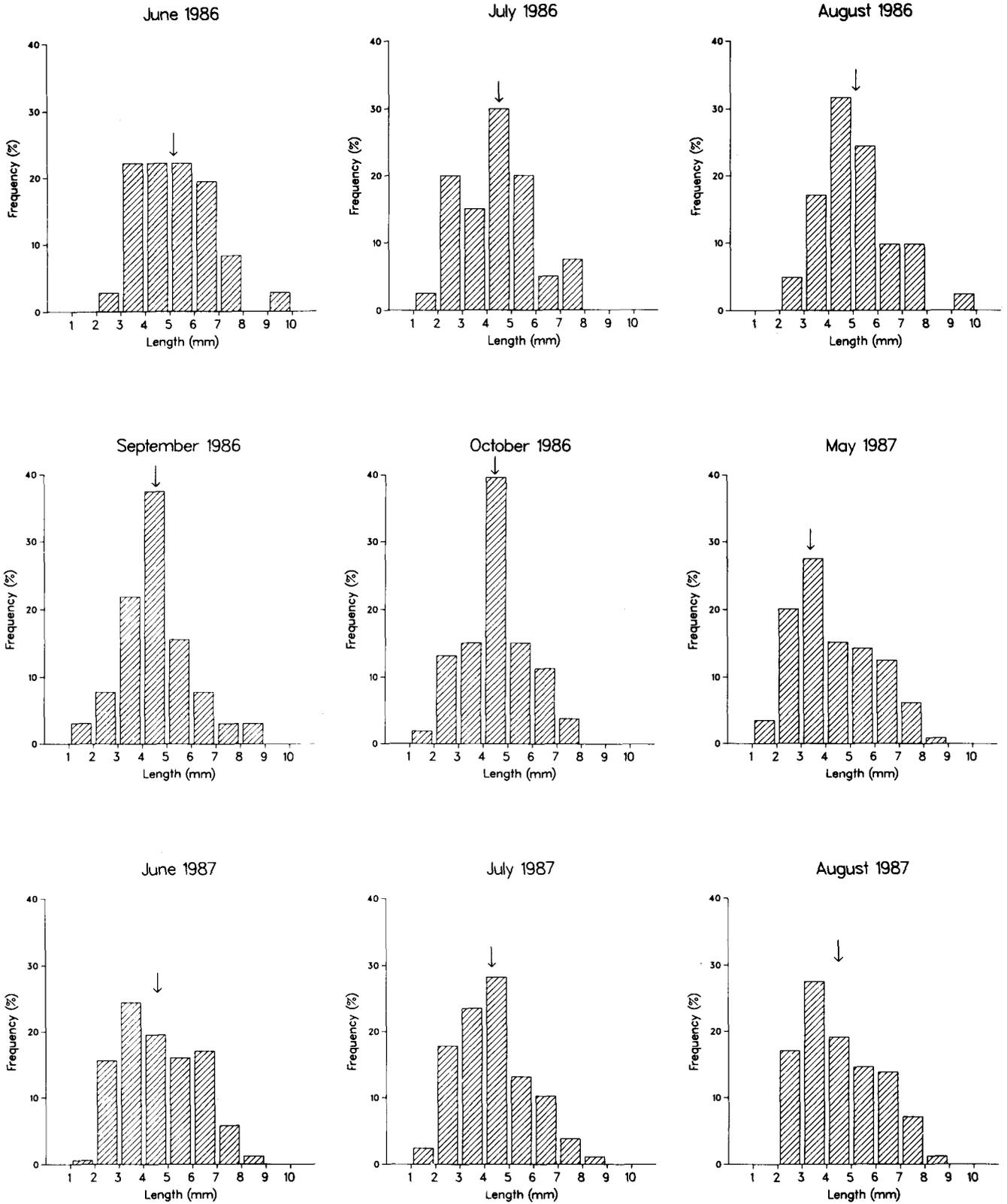


FIG. 3. Size-frequency distribution, by month, of *Pontoporeia hoyi* inhabiting the 97-m depth region in southeastern Lake Michigan, June 1986–August 1987. Arrows indicate mean values.

collection periods as were very large (> 8 mm) animals.

The mean length of sculpins examined for *P. hoyi* predation investigations was 132.0 mm (s.d. = 11.3 mm) in May, 116.2 mm (s.d. = 18.5 mm) in July, and 125.2 mm (s.d. = 6.6 mm) in September. Sculpins tended to consume larger *Pontoporeia* (Fig. 4). The mean size *P. hoyi* consumed in May, July, and September were 6.54 mm (s.d. = 1.09 mm), 7.97 mm (s.s. = 0.76 mm), and 6.82 mm (s.d. = 0.68 mm), respectively, or approximately 2–3 mm larger than the mean size of *P. hoyi* collected directly from the sediments (Fig. 3). Very large (> 9 mm) *P. hoyi*, which were only rarely collected in the PONAR grabs, were commonly observed in sculpin stomachs. *Pontoporeia* appeared to become increasingly vulnerable to sculpin predation after they reached a length of 5 mm. Although adults were extremely rare (< 1%) in the PONAR collections, males were, on occasion, relatively abundant in sculpin stomachs. Adult males accounted for 7.6% of the consumed *P. hoyi* in September and 46.2% in July; no males were observed in sculpin stomachs in May. Adult males ranged in length from 6 mm to over 10 mm. The mean length was 8.23 mm (s.d. = 1.50 mm) in July and 8.75 mm (s.d. = 1.87 mm) in September. Adult females were not observed in sculpin stomachs. This absence could be due to the fact that adult females were rarely consumed by sculpins and/or to the difficulty in distinguishing partially-digested females from juveniles.

Very few *Pontoporeia hoyi* had full guts during any of the collection periods while empty guts were common (Fig. 5). Mean percent gut fullness averaged 41%. Seasonal patterns in percent gut fullness were not strongly evident. The percent frequency-percent gut fullness distribution was, with the exception of June 1986, bimodal. One mode was associated with animals with empty to slightly full (< 30%) guts while the second mode was associated with animals with moderately full (50–80% approximately) guts.

The bimodal pattern in gut fullness appeared to be associated with all size categories of *P. hoyi* (Fig. 6). Feeding patterns appeared to vary with amphipod size. As amphipod increased in size, the percent of animals with empty guts also increased, i.e., the mean percent of 2–4 mm (n = 116), 4–6 mm (n = 141), 6–8 mm (n = 157), and 8–10 mm (n = 11) animals with empty guts was 15.2%, 12.2%, 28.9%, and 27.3%, respectively. The mean percent of 1–2 mm amphipods with empty guts was 30.8%.

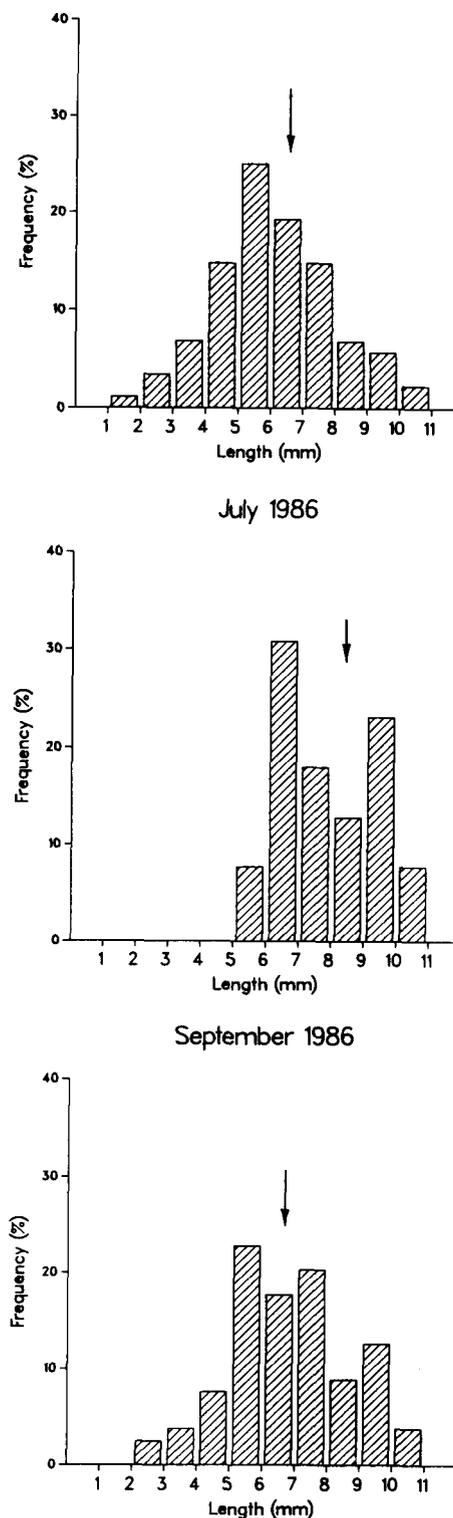


FIG. 4. Size-frequency distribution of *Pontoporeia hoyi* in deepwater sculpin stomachs. Sculpins were collected at a 97-m station in southeastern Lake Michigan in May, July, and September 1986. Arrows indicate mean values.

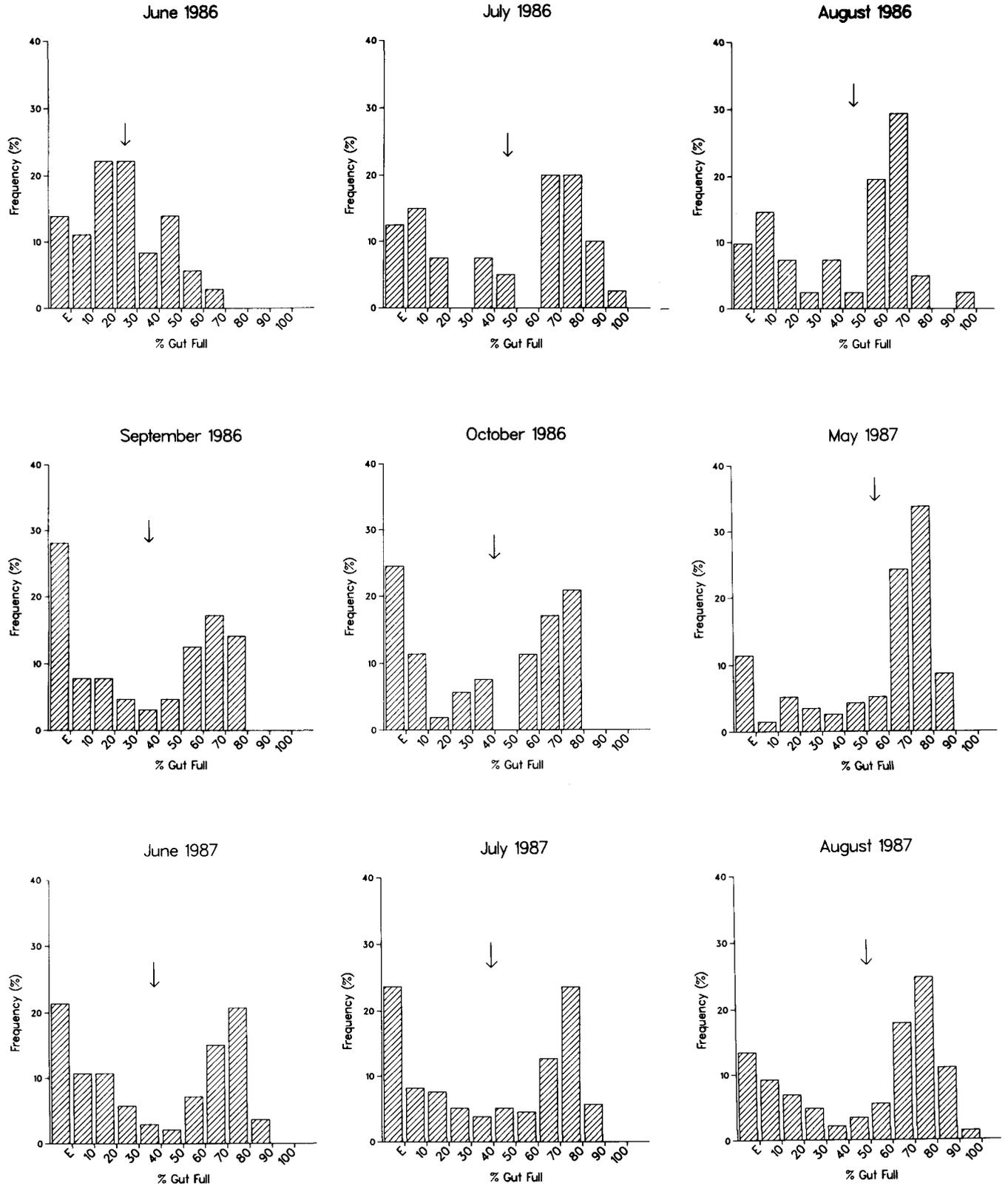


FIG. 5. Gut fullness-frequency distribution, by month, of *Pontoporeia hoyi* inhabiting the 97-m depth region in southeastern Lake Michigan, June 1986–August 1987. Arrows indicate mean values.

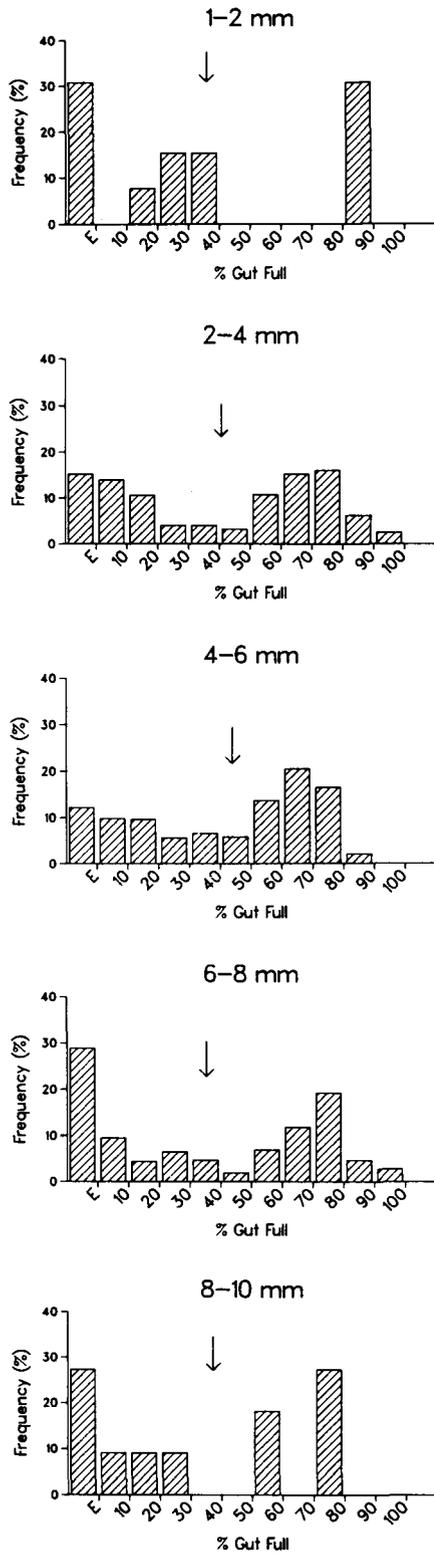


FIG. 6. Gut fullness-frequency distribution, by size, of *Pontoporeia hoyi* inhabiting the 97-m depth region in southeastern Lake Michigan, June 1986–August 1987. Arrows indicate mean values.

However, because only a very small number (13) of these animals were encountered, this estimate is not precise. Mean gut fullness increased from 36.6% in 1–2 mm animals to 40.7% in 2–4 mm and 43.6% in 4–6 mm animals and then decreased in 6–8 mm (35.7%) and 8–10 mm (38.5%) *P. hoyi*. However, differences in mean gut fullness were less variable among size categories when estimates were based only on animals with food in their guts. Mean values for the five size categories ranging from 1–2 mm to 8–10 mm were 53.5%, 55.4%, 50.4%, 49.9%, and 46.3%, respectively.

Pontoporeia hoyi consumed large amounts of silt and other sediment: such material comprised approximately 99% of gut contents. *Cyclotella* fragments were the most frequently identified biological remains, being present in most amphipods examined from most months. *Melosira* fragments also were commonly observed in most months. Pollen, structures resembling fungal spores, and yeast aggregates also were commonly observed. *Dinobyron* lorica, *Ceratium*, *Peridinium*, and green algae fragments were observed in August collections. Insect fragments, chitin fragments, dead rotifers, and amoeboid tests were observed on some occasions.

DISCUSSION

Abundance patterns of *P. hoyi* with respect to depth have been studied on several occasions in Lake Michigan. The most detailed study was conducted by Alley (1968) over 1964–1967. During this time period, *P. hoyi* attained its maximum abundance between the 25-m and 60-m depth contours (Fig. 31 in Alley 1968; this study, Fig. 7). Macrobenthos, including *P. hoyi*, increased in abundance between the mid 1960s and the early 1980s (Nalepa 1987). However, the general features of *P. hoyi* abundance with respect to depth have continued. Thus, Winnell and White (1984) observed greater *P. hoyi* abundances at their 15-m station than at their 42-m station: their study was conducted primarily in 1981 in a region offshore of Bridgman, Michigan. Winnell and White's estimate of mean *P. hoyi* abundance at their 42-m station was similar to that determined by Quigley (1988) at a 45-m station offshore of Grand Haven, Michigan: Quigley's collections were made in 1983 and 1984. Lubner (1979) investigated *P. hoyi* populations dynamics over 1975–1977 at 65-, 90-, and 115-m stations offshore of Milwaukee, Wisconsin: amphipod abundances decreased with increasing depth as

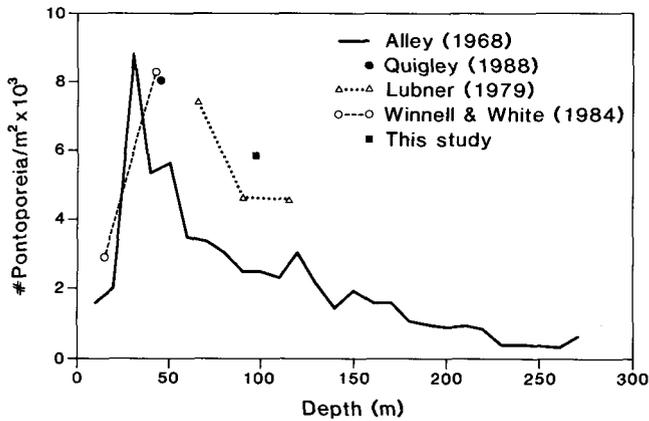


FIG. 7. Mean abundance of *Pontoporeia hoyi* with depth in southern Lake Michigan as reported by various investigators.

also observed by Alley (1968). Our abundance estimates, based on 1986–1987 collections made at a 97-m station offshore of Grand Haven, are lower than those Winnell, White, and Quigley made at their 42- and 45-m stations in the early 1980s but higher than those observed by Lubner at his 65-, 90-, and 115-m stations. Thus, while *P. hoyi* continues to follow a similar abundance-depth distribution pattern as observed by Alley (1968), the pattern has been slightly modified as *P. hoyi* increased in abundance, especially in the deeper regions of the lake. Increases in abundance may be due to a reduction in fish predation pressure and/or an increase in lake productivity (Nalepa 1987).

Intermediate depths appear to represent the optimum environment for *P. hoyi* in lakes with a well-oxygenated hypolimnion (Dadswell 1974, Mozley and Howmiller 1977). The reasons for this remain open to investigation. In the following paragraphs, we explore this issue by examining various aspects of *P. hoyi* ecology in different depth regions of Lake Michigan. We compare our data (Figs. 1 and 2) collected at a 97-m station with Winnell and White's (1984) collected at 15- and 42-m stations in southeastern Lake Michigan. Data collected by Winnell and White (1984) are used as a basis of comparison because their study was relatively recent and was conducted in a similar region of Lake Michigan as our investigations. Data collected from these three stations will be considered as being generally representative of the shelf, slope, and profundal regions of Lake Michigan. Eadie *et al.* (1984) have defined these depth regions as < 25 m, 25–80 m, and > 80 m, respectively.

Pontoporeia hoyi Population Dynamics

Pontoporeia hoyi life cycle characteristics vary with respect to water-column depth (Winnell and White 1984). In the warmer, more productive shelf region, *P. hoyi* has a 1-year life cycle. Adults reproduce in winter with females carrying developing eggs until spring. Juveniles grow rapidly through spring and summer, reaching adulthood by winter (Winnell and White 1984). Shelf populations of *P. hoyi* exhibit strong seasonal variations in size and abundance (Fig. 2), reflecting the 1-year life cycle in this region of the lake.

In the slope region, *P. hoyi* has a 2-year life cycle. Adults reproduce in winter and summer. Males die shortly after mating while females carry the developing eggs until spring (winter reproduction) or late summer (summer reproduction). In the colder, less-productive profundal region, *P. hoyi* requires 2.5 to 3 years to complete its life cycle (Lubner 1979, Winnell and White 1984, Siegrid 1985). Slope and profundal *P. hoyi* exhibit little seasonal variation in size and abundance (Fig. 2), reflecting the 2- to 3-year life cycle and the two annual breeding periods in the deeper regions of the lake. *Pontoporeia* inhabiting the profundal region (Fig. 2) attained a May–October average abundance of 5,842/m² or 70% that (8,290/m²) of the slope and 262% that (2,898/m²) of the shelf region.

Although *P. hoyi* is able to complete its life cycle in 1 year in the shelf region, this region is not favorable for *P. hoyi* survivorship during all months of the year. From spring to early summer, *P. hoyi* abundances are relatively high and similar to that observed in the profundal region although lower than in the slope region (Fig. 2). However, abundances decline rapidly through late summer and autumn indicating a reduction in environmental quality of the shelf region for *P. hoyi* survivorship. A number of factors could contribute to this decline including increased thermal stress (possibly affecting an offshore migration of amphipods), fish predation, and food limitations (Mozley and Howmiller 1977, Lubner 1979). These factors also may be of some importance in affecting *P. hoyi* ecology in the slope and profundal regions.

Temperature and *Pontoporeia hoyi*

Temperature has been implicated as a major factor affecting the distribution of *P. hoyi*, especially in the shelf region (Mozley and Howmiller 1977). Winnell and White (1984) did not report bottom-

water temperatures at the time of their various collections: temperatures for these sampling periods and locations are shown in Figure 1 (Evans, unpublished data). More detailed information on the seasonal, vertical, and spatial aspects of lake temperatures in this region of the lake are illustrated in Evans *et al.* (1985).

Shelf bottom-water temperatures vary markedly with season (Fig. 1), increasing from spring lows of less than 4°C in some years (Evans *et al.* 1985) to highs of 23–24°C by July–August. Decreases in *P. hoyi* abundances in the shelf region coincide with the summer maximum in lake temperatures, possibly suggesting that amphipods are thermally stressed during this period. This hypothesis is partially supported by experimental studies which determined that *P. hoyi* experiences significant mortality when exposed to temperatures as low as 10–12°C (Smith 1972). Based on these studies, *P. hoyi* inhabiting the shelf region should begin experiencing thermal stress as early as mid to late spring. Upwellings, which result in a rapid lowering of water temperature (e.g., as in July of Fig. 1), also may thermally stress shelf populations of *P. hoyi*. Bottom-water temperatures decrease in late summer and autumn (Fig. 1). However, despite this cooling trend, *P. hoyi* continues to decline in abundance (Fig. 2). Other factors, in addition to high temperature, must be important in affecting *P. hoyi* abundances at this time.

Bottom-water temperatures are less variable in the slope than shelf region (Fig. 1). Temperatures gradually increase through summer to reach an autumn maximum. Upwellings, downwellings, and internal waves can affect rapid changes in thermal regime (e.g., as in October of Fig. 1), although such events are not as pronounced as in the shelf region. Bottom-water temperatures are lowest and least variable in the profundal region (Fig. 1), ranging from 4–5°C in spring-autumn 1986 and spring-summer 1987. These relatively low temperatures may be an important factor affecting the greater longevity of *P. hoyi* in the profundal than slope region. There is no evidence that *P. hoyi* are thermally stressed by the water temperatures typical of the slope and profundal regions.

Fish Predation and *Pontoporeia hoyi*

Fish predation has been implicated as a potentially important factor affecting *P. hoyi* populations (Mozley and Howmiller 1977, Nalepa 1987). Although little research has been conducted in this

matter with respect to *P. hoyi*, numerous studies have been conducted using other macrobenthic organisms. It is highly likely that the same factors affecting the predation risk of these macrobenthic organisms affect *P. hoyi*.

One of the first studies investigating factors affecting macroinvertebrate vulnerability to fish predation was conducted by Ware (1973). The amphipod *Hyaella* was one of the prey organisms studied. Amphipod activity, exposure, density, and size were the major determinants of prey risk. Moreover, physical factors such as temperature were important, directly affecting amphipod activity. During the cold winter months, much of the *Hyaella* population was buried in the sediments and thus not readily detected by fish predators. As temperatures increased, an increasing proportion of the *Hyaella* population was exposed at the sediment-water interface. Moreover, *Hyaella* activity decreased at temperatures greater than 10°C, possibly suggesting that the amphipod was thermally stressed and less capable of escaping predators at higher temperatures. Amphipod size also was important in affecting predation risk; *Hyaella* smaller than 3 mm in length were relatively immune to fish predation. Overall, *Hyaella* predation risk varied seasonally, being greatest in spring when immatures matured into adults and in autumn as the spring cohort increased in size. Predation risk decreased through late autumn and winter as water temperatures declined and an increasingly large proportion of the *Hyaella* population became buried in the sediments.

Similarly, water temperature, amphipod activity, and body size must be important factors affecting the vulnerability of *P. hoyi* to fish predation. In the shelf region, fish predation pressures must increase through late spring and summer with increasing water temperatures and amphipod activity. This thermally-induced increase in predation pressure may contribute to the mid summer to early autumn decline in *P. hoyi* abundances in the shelf region. In contrast, temperature must play a smaller role in affecting the vulnerability of *P. hoyi* to fish predation in the slope and profundal environments: seasonal variations in temperature are relatively small in these two regions.

Size also must be an important factor affecting the vulnerability of *P. hoyi* to predation as observed by Ware (1973) for *Hyaella*. In the profundal region, small (< 4 mm) *P. hoyi* were relatively immune to sculpin predation while larger animals were increasingly vulnerable to such pre-

dation (Fig. 4). Larger (> 8 mm) *P. hoyi*, which were a relatively minor component of the profundal amphipod assemblage, were common components of the sculpin diet. Predation pressures on *P. hoyi* in the slope and shelf regions must remain relatively constant with season because *P. hoyi* inhabiting these regions of the lake exhibit little seasonal variation in size (Fig. 2). In the shelf region, predation pressures must vary seasonally with seasonal variations in *P. hoyi* length, i.e., predation pressures must increase during summer and autumn as shelf *P. hoyi* attain lengths of 3 mm greater.

Another factor affecting the vulnerability of amphipods to predation is the distribution and abundance of fish predators. The shelf region serves as an important spawning and nursery area for many species of fish. From late spring to early autumn, there is a dense congregation of young-of-the-year smelt, alewife, spottail shiners, slimy sculpins, and yellow perch and adult yellow perch, slimy sculpins, and spottail shiners in this region (Wells 1968). As larval spottail shiners, yellow perch, and smelt increase in size through late spring, they switch from a planktonic to a more strongly benthic diet (Scott and Crossman 1973). Thus, predation pressures on the amphipod community must intensify at this time, possibly contributing to the strong midsummer decline in amphipod abundance (Fig. 2). With autumn cooling and the offshore migration of fish such as the alewife, smelt, and yellow perch (Wells 1968), predation pressures on the amphipod community must decline.

Size-selective fish predation also must be an important factor modifying *P. hoyi* populations in the slope region. However, because the slope region is not a major spawning and nursery area, predation pressures on amphipods probably are less intense than in the shelf region. Major benthic predators in the slope region include smelt, alewife, and bloater (Wells 1968). These fish are planktivorous as larvae, but consume increasingly larger proportions of benthic prey with increasing age and size (Wells and Beeton 1963, Morsell and Norden 1968, Scott and Crossman 1973). Bloaters maintain a relatively constant presence in the slope region: smelt and alewife migrate inshore to spawn in spring but rapidly return to the slope region after spawning (Wells 1968). In contrast to the shelf region, there must be relatively small seasonal variations in predation pressure on *P. hoyi* in the slope region.

Benthic predators are less abundant in the profundal than slope region (Wells 1968). This may account for the fact that the mean size of *P. hoyi* appears to be somewhat smaller in the slope than profundal region (Lubner 1979; this study, Fig. 2). The major benthic predators in the profundal region are the deepwater sculpin and bloater (Wells 1968). These fish maintain a relatively constant seasonal presence in the profundal region. Thus, seasonal variations in predation pressure on *P. hoyi* are relatively small.

Predation Avoidance Strategies and *Pontoporeia hoyi*

Several studies have determined that benthic organisms employ various strategies to avoid predation. Burrowing is one important strategy. Large-bodied chironomids, by burrowing deeply in the sediments, are less vulnerable to fish predation than smaller, more surface-dwelling chironomids (Hershey 1985). There is some evidence that *P. hoyi* may employ a similar strategy. Small (1–3 mm) *P. hoyi* were relatively sparse in our collections (Fig. 3) and in those of Winnell and White (1984). This relative absence of small animals in grab collections has been noted by other researchers (Johnson and Brinkhurst 1971, Dermott and Corning 1988). It appears to be related to the fact that young *P. hoyi* reside on or slightly above the sediment surface and are displaced by the pressure wave of the descending grab sampler (Krezoski *et al.* 1978, Nalepa *et al.* 1988). In contrast, larger/older animals more commonly reside within (rather than on) the sediments (Krezoski *et al.* 1978) and thus are more effectively captured by bottom grabs. This shift from an epibenthic existence when small to a burrowing existence when large may be a strategy enabling *P. hoyi* to minimize fish predation.

Benthic organisms with poor escape capabilities also may avoid predation by becoming quiescent (Sih 1982). Motility clearly is an important factor affecting the vulnerability of *Hyaella* to predation (Ware 1973). It also is an important factor affecting *P. hoyi* vulnerability. We observed that adult male *P. hoyi* were especially vulnerable to sculpin predation. These short-lived (days) males are highly motile (Marzolf 1965a, Segerstrale 1971).

Fish predation avoidance strategies based on immotility are not without a cost, i.e., immotility may result in reduced feeding rates (Sih 1982). This reduction in feeding rate may be affected by food

regime. When food supplies are constant, benthic prey reduce their feeding time at a patch in the presence of a fish predator (Dixon and Baker 1987). In contrast, when food supplies are more ephemeral, feeding behavior is less strongly affected by the presence of a fish predator (Dixon and Baker 1987). Moreover, a prey should be more likely to expose itself to a given degree of predation risk when food-limited than when well-fed (Sih 1982). Similarly, *P. hoyi* feeding strategies may vary as a function on the temporal and spatial distribution of food resources and predators. This is discussed below.

Resource Utilization and *Pontoporeia hoyi*

Historically, *P. hoyi* has been considered to be a detritivore, ingesting large amounts of sediment and relying primarily upon bacterial assimilation for its energy supply (Marzolf 1965b). The results of our gut content studies appear to confirm this hypothesis: detrital material predominated, with algae accounting for the next largest fraction in the *P. hoyi* gut. However, more recent studies involving comparisons of gut composition with sedimentary composition and/or of fore and hind-gut comparisons suggest that *P. hoyi* is highly selective in its feeding, ingesting and assimilating some phytoplankton species more efficiently than others (Moore 1977, 1979; Johnson 1987). Moreover, *P. hoyi* may be capable of some predatory feeding. *Pontoporeia femorata*, a related European species, has been shown capable of locating and crushing 220–250 μm mollusc larvae (Elmgren *et al.* 1986). Thus, the presence of occasional animal remains in *P. hoyi* guts may be due to ingestion of detrital remains and/or predation. Like the epibenthic mysid *Mysis relicta* (Grossnickle 1982), *P. hoyi* may be an opportunistic feeder altering its feeding strategies as a function of its food regime.

Pontoporeia hoyi feeds intermittently in some environments. In the slope and profundal regions of Lake Michigan, *P. hoyi* can be divided into two groups on the basis of percent gut fullness (Quigley 1988; Fig. 5, this study). One group (or mode) is associated with non-feeding animals, i.e., animals with empty to relatively empty guts. The second group (or mode) is associated with actively-feeding *P. hoyi*, i.e., animals with large amounts of material in their guts. However, despite some similarities, *P. hoyi* feeding patterns in the profundal region are subtly different from those in the slope region (Quigley 1988; this study, Fig. 5). First,

amphipod feeding behavior is less seasonal in the profundal than the slope region (Quigley 1988; this study, Fig. 5). Such differences in seasonality between the two depth regions may reflect a more seasonally-variable food supply in the slope than shelf region. Second, a larger proportion of slope than profundal *P. hoyi* had empty guts (average value = 30% and 18%, respectively). This suggests that slope *P. hoyi* feed less frequently than profundal populations. Third, although profundal *P. hoyi* populations more commonly had food in their guts than slope populations, the gut was not as full. Gut fullness for profundal populations peaked around 50–80%: less than 1% of the animals had full guts (Figs. 5, 6). In contrast, slope populations commonly had full guts with the percentage of animals with full guts often exceeding that of animals with empty guts (Quigley 1988). However, despite these regional differences in the percentages of animals with empty versus full guts, the mean gut fullness of slope and profundal *P. hoyi* populations was similar, i.e., a mean of approximately 41% over the May–October period (Quigley 1988, this study). This implies that slope and profundal *P. hoyi* populations have, on average, similar ingestion rates but employ different feeding strategies. Profundal populations appear to feed more continuously but less intensively than slope *P. hoyi* populations.

Differences in *P. hoyi* feeding strategies in the slope and profundal regions of Lake Michigan may be related to differences in resources and to predation avoidance strategies. Food supplies probably are richer in the slope region than in the profundal region where much of the organic matter is decomposed before reaching the profundal lake floor. Food patches may be more ephemeral in the slope region as organic matter is transported offshore with episodic events such as upwellings and downwellings. Thus, *P. hoyi* inhabiting the slope region may be more likely to find ephemeral, food-rich micropatches than amphipods inhabiting the profundal region. Consequently, slope *P. hoyi* may be relatively selective in their feeding, delaying ingestion until a rich patch of organic matter is found: at that time, *P. hoyi* pack their guts with such material. In contrast, profundal *P. hoyi* are less likely to encounter such food-rich patches. Because profundal-region microenvironments are less nutritious (and possibly smaller) than slope microenvironments, profundal *P. hoyi* may be less likely to fill their guts before moving onto a new area of the lake floor. Moreover, because profun-

dal populations are less likely than slope populations to be satiated in their feeding, profundal populations may spend a greater proportion of their time in feeding.

Some support for this hypothesis of food richness affecting feeding behavior is obtained by comparing *P. hoyi* feeding behavior in Lake Ontario, a mesotrophic lake, and in Great Slave Lake, a highly-oligotrophic, subarctic lake. In nutritionally-poor Great Slave Lake, only 10% of the *P. hoyi* collected between May and September had empty guts (Moore 1979) versus 18% of profundal and 30% of slope Lake Michigan *P. hoyi* populations. In mesotrophic Lake Ontario, 32% of the medium-size (4–6 mm) *P. hoyi* inhabiting a 70-m station had empty guts: this percentage increased to 41% at a 35-m station (Dermott and Corning 1988). Lake Ontario *P. hoyi* which had ingested material, had fed well: 29% of the 35-m and 31% of the 70-m amphipods had full guts. Overall, these results suggest that *P. hoyi* feeding strategies are strongly affected by food levels in their environment. As food levels increase, *P. hoyi* spend proportionately less time in feeding but feed more intensively when food is encountered.

Egestion, in addition to ingestion, behavior must vary as a function of food level. *Pontoporeia hoyi* inhabiting food-rich environments typically have full rather than partially-full guts (Quigley 1988, Dermott and Corning 1988). This suggests that once the gut is filled, food is retained for some period of time before egestion occurs. In contrast, profundal Lake Michigan *P. hoyi*, which feed more continuously, may have more continuous egestion rates.

Feeding behavior of *P. hoyi* may also be affected by predation avoidance strategies. Because *P. hoyi* is a macrobenthic organism with relatively weak swimming capabilities (unlike *M. relicta*), its strategies for avoiding predation must be based on minimizing detection by predators rather than escaping predation once detected, i.e., by burrowing within the sediments and/or becoming immotile. Immotility strategies must vary as a function of predation pressures with animals being least quiescent in low-predation environments (Sih 1982, Dixon and Baker 1987). Moreover, such predation-avoidance strategies may affect feeding behavior as observed by Dixon and Baker (1987) for larval dragonflies.

Gut content studies of slope and profundal populations lend some support to this hypothesis of feeding rate (and motility) varying as a function of

predation pressures. A greater percentage of *P. hoyi* inhabiting the food-rich slope region had empty guts (approximately 30%) than animals inhabiting the food-poor profundal region (18%). These regional differences in empty guts cannot be entirely related to the greater satiation of *P. hoyi* in the slope region. Other factors, such as predation avoidance, must be involved. There are several arguments for this hypothesis. First, there is no reason to assume that food resources along the slope are sufficiently rich as to allow for satiation. Second, if satiation were the major factor affecting gut fullness, *P. hoyi* inhabiting productive environments should have relatively low and not high incidences of empty guts. Finally, there is no obvious physiological benefit gained by reduced feeding. Rather, there is a major cost in reduced feeding, i.e., a prolongation in development time and a consequent delay in reproduction with its attendant risks in increased predatory mortality. A more likely hypothesis is that a nonfeeding mode (empty guts) is associated with predation-avoidance strategies based on immotility. Thus, in the slope region where benthic-feeding fish are numerous and food resources abundant but variable, *P. hoyi* may minimize predation by spending significant periods of time in a nonfeeding mode. In contrast, because fish predators are less abundant in the profundal region, *P. hoyi* may spend smaller proportions of time avoiding predators by remaining quiescent. Moreover, because food resources are less rich in the profundal than the slope region, *P. hoyi* may need to spend longer periods of time in feeding. Thus, a small fraction of *P. hoyi* in low-productivity, low-predation environments have empty guts. Amphipods that have fed have ingested proportionately less material than those in more productive environments. Immotility as a predation-avoidance strategy may also account for the fact that larger, and hence more vulnerable, *P. hoyi* appeared to have a greater percent of empty guts (Quigley 1988, this study, Fig. 6), i.e., these animals spend proportionately less time in feeding than smaller, less vulnerable *P. hoyi*.

If feeding strategies vary as a function of food level, then *P. hoyi* inhabiting the shelf region may become increasingly vulnerable to fish predation during summer for four reasons. These include: the summer increase in *P. hoyi* size; an increase in amphipod activity and/or exposure with increasing water temperatures; and a switch in larval fish (smelt, yellow perch, and spottail shiners) feeding from the plankton to the benthos. Finally, changes

in *P. hoyi* foraging strategies may be important, i.e., as food levels decline through summer, *P. hoyi* may shift its feeding behavior from a more intermittent (and quiescent) strategy as observed in the slope region to a more continuous (and active) strategy as observed in the profundal region. This increased feeding activity may enhance the vulnerability of *P. hoyi* to fish predation and ultimately affect the strong summer decline in amphipod abundances (Fig. 2.). Thus, while moderately warm water and rich food-regimes in the shelf region allow *P. hoyi* to complete its life cycle in 1 year, this is not without a cost. High water temperatures, reduced food levels, and increased fish predation may be important factors contributing to a precipitous decline in *P. hoyi* abundance through mid summer to late autumn.

SUMMARY

Pontoporeia hoyi exhibits many important regional differences in its ecology. Not only does *P. hoyi* adapt to the specifics of its environment by altering its life cycle characteristics (developmental times, reproductive periods), but also its feeding behavior. This adaptability has allowed this glacial relict to become widespread in North America, inhabiting a variety of lakes and, within large lakes, depth regions (Ricker 1959, Segerstrale 1976).

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