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OCCURRENCE OF A RESTING STAGE IN CYCLOPOID AND HARPACTICOID COPEPODS IN NEARSHORE LAKE MICHIGAN

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ABSTRACT. Temporal and spatial differences in the abundance of dormant harpacticoid and cyclopoid copepods in a nearshore area of southeastern Lake Michigan are described. Core samples were taken at three depths (11, 17, and 23 m) at monthly intervals from May to November 1976–79. All dormant harpacticoids were Canthocamptus robertcokeri *or* Canthocamptus staphylinoides, *and all dormant cyclopoids were stage IV copepodids, likely* Diacyclops thomasi. *The percentage of* Canthocamptus *and copepodids IV found in the resting state declined dramatically with increased sampling depth. Dormant* Canthocamptus *were most abundant in late summer/fall in each of the four sampling years. During this period, usually over 50% of all* Canthocamptus *were found in the dormant condition. Dormant cyclopoids were most abundant between June and September, but exact seasonal patterns varied from year to year. Factors initiating the dormant condition are not clear, but water temperatures and day length may be important environmental cues. Some of the spatial and year-to-year differences in the proportion of dormant individuals appeared related to variations in the amount of surface detritus. This is the first report of a resting stage in the life cycle of cyclopoids in the Great Lakes.*
ADDITIONAL INDEX WORDS: Benthos, detritus, core, sediment, dormant copepods, cysts, detritus.

INTRODUCTION

The occurrence of a dormant phase in the life cycle of freshwater copepods was first reported by Birge and Juday (1908). Since then, a number of investigators in North America and Europe have found a resting stage in the life cycles of both cyclopoids and harpacticoids (Moore 1939; Deevey 1941; Cole 1953; Fryer and Smyly 1954; Elgmork 1955, 1959, 1962; Smyly 1961; Szlauer 1963; George 1973). In cyclopoids, a dormant stage is quite common; Elgmork (1967) listed 18 species that have some form of resting stage. However, in harpacticoids, a resting stage has been reported only for a few species of the genus *Canthocamptus*.

In the Great Lakes, reports of dormant copepods are generally lacking, probably because most investigators have used screens with meshes too large to retain benthic copepods (Nalepa and Robertson 1981a). Only one previous study in the Great Lakes has reported finding copepods in a resting stage and all individuals were *Canthocamptus* (Evans and Stewart 1977).

In this paper, the temporal and spatial distribution of dormant cyclopoids and harpacticoids in a nearshore area of Lake Michigan is described.

METHODS

Benthic samples were taken at nine stations in southeastern Lake Michigan near the mouth of the Grand River (Fig. 1). Five stations were located at 11 m, two at 17 m, and two at 23 m. All nine stations were sampled in 1976, but only four were sampled in 1977 (Stations 4, 7, 10, and 11) and two in 1978 and 1979 (Stations 4 and 7). Samples were generally taken on a monthly basis from May to November each year. Four replicate cores were taken at each station on each date by divers using SCUBA. A clear, acrylic tube 23 or 30 cm long and 5 cm in diameter was forced into the sediment (penetration 7–12 cm) and then stopped at both ends.

The samples were preserved in formalin containing rose bengal stain and then washed through a

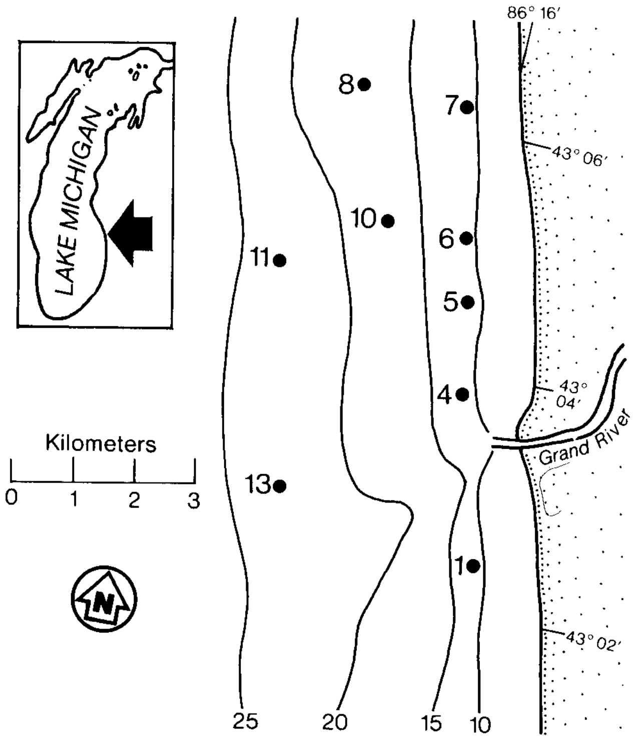

FIG. 1. Location of sampling stations in southeastern Lake Michigan. Depth contours in meters.

series of screens having mesh openings down to 45 μm. All organisms retained were counted and identified to the lowest practical taxonomic level. Further details on sampling and counting procedures are given by Nalepa and Quigley (1980, 1981, 1983).

Bottom temperatures were recorded at Stations 4, 7, 10, and 11 each time samples were taken. Also, the amount of surface detritus in each replicate core was measured to the nearest millimeter.

RESULTS

Benthic Environment

Sediments in the study area consisted of fine to coarse sand overlaid by a patchy layer of fine detritus. Detrital amounts were generally greatest in the spring, and then decreased throughout summer until little or no detritus was observed in fall (see Fig. 2 in Nalepa and Quigley 1983). The exception to this seasonal pattern was in 1978 when a local patch of detritus was present at Station 4 throughout the summer. In general, the amount of detritus tended to decrease with increasing sampling depth. Also, more detritus was usually present at the station nearest the river mouth (Station 4) than at the station farthest away (Station 7).

Harpacticoida

All harpacticoids found in the resting stage were adult *Canthocamptus robertcokeri* or *Canthocamptus staphylinoides*. Although two other harpacticoids, *Bryocamptus* cf. *vejdovskyi* and *Bryocamptus nivalis*, were commonly found in the sediments, dormant individuals of these two species were not found. Dormant *Canthocamptus* occurred in cysts that resembled those described by Moore (1939) and Fryer and Smyly (1954). The dorsally flexed animal was usually visible through the cyst wall, but often the cyst was covered with adhering substrate particles, making the animal impossible to discern (Figs. 2a, b).

In both *C. robertcokeri* and *C. staphylinoides*, a slightly greater percentage of females than males were found in cysts at each of the three depths; also, greater percentages of encysted individuals were found at 11 m and 17 m than at 23 m (Table 1).

C. robertcokeri was more abundant and widely distributed than *C. staphylinoides*, accounting for 73% of the total number of *Canthocamptus*. Seasonal and annual fluctuations in the abundance of both active and encysted *Canthocamptus* (both species combined) are given in Figure 3. The abundance of active *Canthocamptus* was usually greatest in spring/early summer and then declined. The exceptions were the midsummer peaks of *C. robertcokeri* at Stations 4 and 7 in 1978 and at Station 4 in 1979. The spring/early summer peak of active *Canthocamptus* tended to occur earlier at the two deeper stations, Stations 10 and 11; abundances at these two stations were often greatest on the first sampling date in May.

In contrast, the number of encysted *Canthocamptus* was low in spring and increased to a maximum in late summer/fall. This seasonal pattern occurred consistently in each of the four sampling years at each of the stations. After the late summer peak, the number of cysts either declined or remained high until the end of the sampling period in late fall. During the late summer/fall peak, at least 50% of adult *Canthocamptus* were found in cysts at a given station in every year except 1977 (Fig. 3).

Cyclopoida

All cyclopoids found in a dormant condition were stage IV copepodids. These copepodids were not identified to species during routine sample processing, but later examination of about 30 representative individuals indicated that all were *Diacyclops thomasi* (= *Cyclops bicuspidatus thomasi*). The dominant cyclopoids in the study area are this species and *Acanthocyclops vernalis* (= *Cyclops vernalis*) (Nalepa and Quigley 1983). While a resting stage in the life cycle of *D. thomasi* has been found previously (Birge and Juday 1908, Moore 1939, Cole 1953), there are no reports of a resting stage in *A. vernalis*. Coker (1933) did find a state of arrested development in *A. vernalis*, but the copepodids remained active. Stage IV copepodids found in the active state therefore include individuals of both *D. thomasi* and *A. vernalis*, while copepodids found in the dormant state are likely all *D. thomasi*.

Dormant copepodids typically had their first antennae aligned next to the body and their legs drawn forward. The urosome was bent ventrally, with the angle of the bend varying from 45° to just less than 180° (relative to the axis of the body). Most individuals were covered with a crusty material consisting of cemented substrate particles (Fig. 2c).

The number of dormant copepodids decreased greatly with increased sampling depth. Although this coincided with a general decline in the number of active copepodids, the percentage found in the resting stage also declined; overall, the percentage of dormant copepodids at 11, 17, and 23 m was 27.9%, 8.7%, and 0%, respectively (Table 1). Dormant copepodids were found at 17 m in 1976 but not in 1977, while no dormant copepodids were found at 23 m in either 1976 or 1977.

Since *D. thomasi* copepodids become dormant while *A. vernalis* copepodids likely do not, the observed decline in the number and proportion of dormant individuals with increased depth would have occurred if numbers of *D. thomasi* decreased with depth relative to numbers of *A. vernalis*. However, the relative proportion of adult *D. thomasi* actually increased with increased depth; the mean ratios of adult *D. thomasi* to adult *A. vernalis* at 11, 17, and 23 m were 0.9, 4.5, and 8.5, respectively. Assuming that the number of stage IV copepodids of each species occurred in proportion to the number of adults, then the decline in dormant copepodids with increased sampling depth was unrelated to changes in species composition.

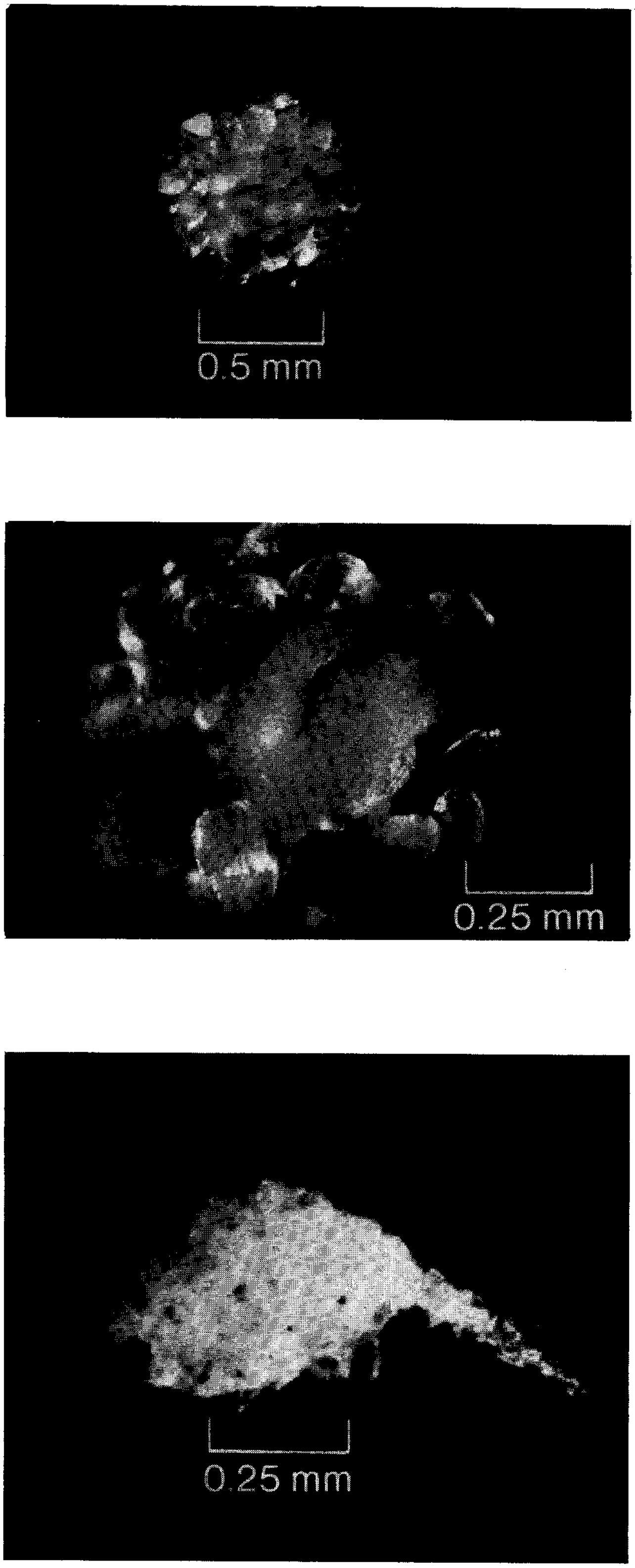

FIG. 2. (a) **Canthocamptus** *cyst with adhering substrate particles (sand grains); (b)* **Canthocamptus** *cyst with substrate particles removed showing dorsally-flexed animal; (c) stage IV copepodid in dormant condition.*

A consistent seasonal pattern in the number of dormant copepodids was not apparent at any of the stations (Fig. 4). At Station 4, peak numbers of dormant copepodids were found in spring/early summer (1976, 1977) or in midsummer (1978, 1979). The peak in 1979 was due solely to an extremely large number of individuals (236 active, 241 dormant) in just one of the replicate cores. At Station 7, peak numbers were found in either spring (1979) or midsummer (1976); often a distinct peak did not even occur (1977, 1978). The percentage found in the resting stage at these two stations was generally greatest between June and September, but again, a consistent pattern between years was not evident (Fig. 4). At the two deeper stations, dormant copepodids were found only at Station 10 in 1976, with peak numbers occurring in late spring/early summer.

In each of the 4 years, a greater proportion of dormant copepodids were found at Station 4 than at Station 7 (Fig. 4). For the entire sampling period, 37% of all stage IV copepodids at Station 4 were dormant compared to only 8% at Station 7. In contrast, the proportion of *Canthocamptus* found in cysts at Stations 4 and 7 were 21% and 33% respectively. Again, as with depth differences, the differences between Stations 4 and 7 were apparently unrelated to changes in the relative proportion of *D. thomasi* and *A. vernalis*. The mean proportion of adult *D. thomasi* to adult *A. vernalis* at Stations 4 and 7 were 0.5 and 1.1, respectively.

Since *D. thomasi* is considered primarily a planktonic form, the significance of finding dormant individuals in the sediments must be considered relative to the number of active individuals in the water column as well as in the sediments. In 1977, plankton samples were collected each time sediment cores were taken (Nalepa and Quigley, in preparation). The mean number of active stage IV copepodids in the water column was calculated on an areal basis and added to the number found in the sediments. Again, assuming that all dormant IV copepodids were *D. thomasi* and that the relative proportion of *D. thomasi* and *A. vernalis* occurring as active IV copepodids was the same as the proportion occurring as adults, the percentage of dormant IV copepodids relative to all IV copepodids (of *D. thomasi*) found in both the water column and sediments in 1977 was 30% at Station 4 and 11% at Station 7. As noted earlier, no dormant IV copepodids were found at Stations 10 and 11 in 1977.

DISCUSSION

Laboratory experiments have implicated several environmental factors in initiating and terminating the resting stage in copepods. These include temperature (Smyly 1962, Fryer and Smyly 1954, Wierzbicka 1962), oxygen concentrations (Deevey 1941, Wierzbicka 1962), photoperiod (Einsle 1964), or photoperiod modified by temperature (Watson and Smallman 1971, George 1973). Yet attempts to correlate the incidence of the resting stage to conditions in the field have been largely unsuccessful (Elgmork 1967). In this study, temporal and spatial differences in the number of dormant individuals are likewise difficult to interpret in terms of environmental variables.

With regard to seasonal patterns, the greatest number of dormant individuals were found during summer; the number of encysted *Canthocamptus* consistently increased throughout summer to reach a peak in late summer/early fall, while dormant cyclopoids were mainly found between June and September. Since water temperatures in the study area increased throughout the summer to reach a maximum in late summer (see Table 1 in Nalepa and Quigley 1983), the occurrence of the resting stage may certainly be related to warmer water temperatures. Under laboratory conditions, warmer water temperatures have induced the resting stage in both *Canthocamptus* (Lauterborn and Wolf 1909, Donner 1928) and cyclopoids (Wierzbicka 1962). However, although others have also found a summer resting stage in both *Canthocamptus* and *D. thomasi* (Birge and Juday 1908, Moore 1939, Cole 1953), the relationship between the dormant condition and water temperature is not clear. For instance, Moore (1939) found that the number of *Canthocamptus* cysts declined from early summer to fall overturn even at deeper depths where temperatures remained low and unchanged. Also, Birge and Juday (1908) found that *D. thomasi* entered the resting stage in late spring when water temperatures were low and emerged before temperatures declined in the fall.

The occurrence of a summer resting stage may also be a response to the longer periods of daylight at this time. Increased periods of light exposure have induced the dormant condition in *C. vicinus* under laboratory conditions (Einsle 1964). Although light penetration was not measured in our study area, visibility at the bottom was generally 2–4 m throughout the sampling period.

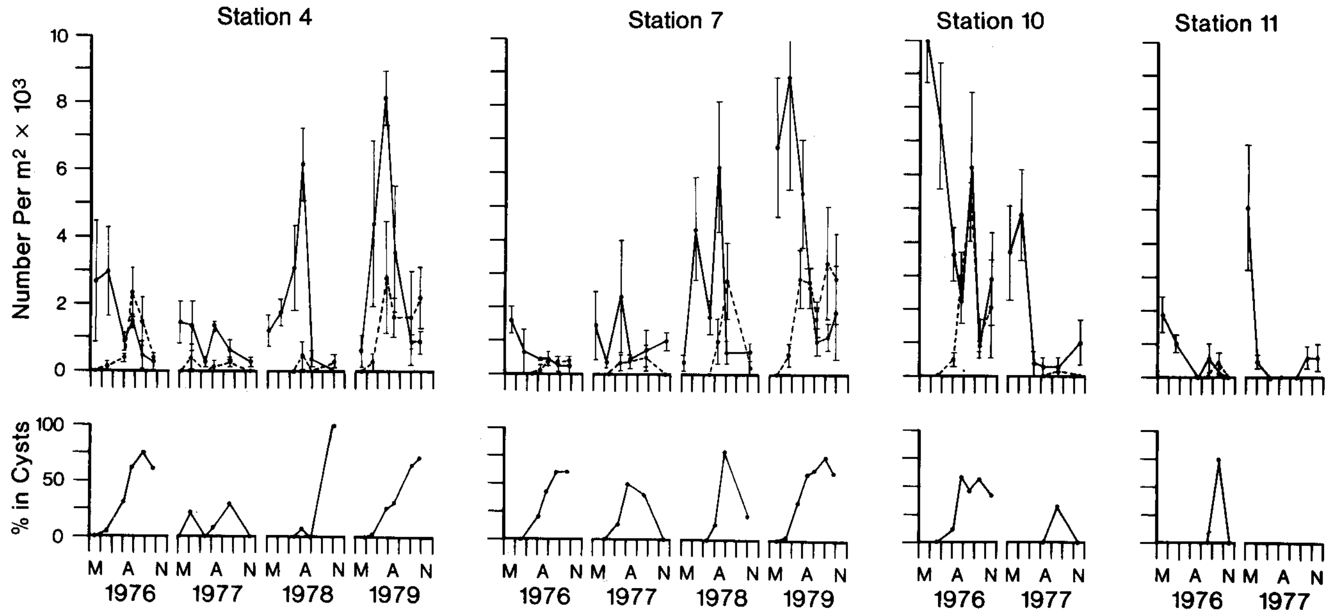

FIG. 3. Upper: Mean density (± SE) of total Canthocamptus *on each sampling date at Stations 4, 7, 10, and 11. Solid line = active* Canthocamptus; *dashed line = encysted* Canthocamptus. *Densities at the stations sampled only in 1976 (Stations 1, 5, 6, 8, and 13) are not shown, but are generally comparable to the stations of similar depth that are shown. Lower: Percentage of total number of* Canthocamptus *found in cysts on each sampling date at the four stations.*

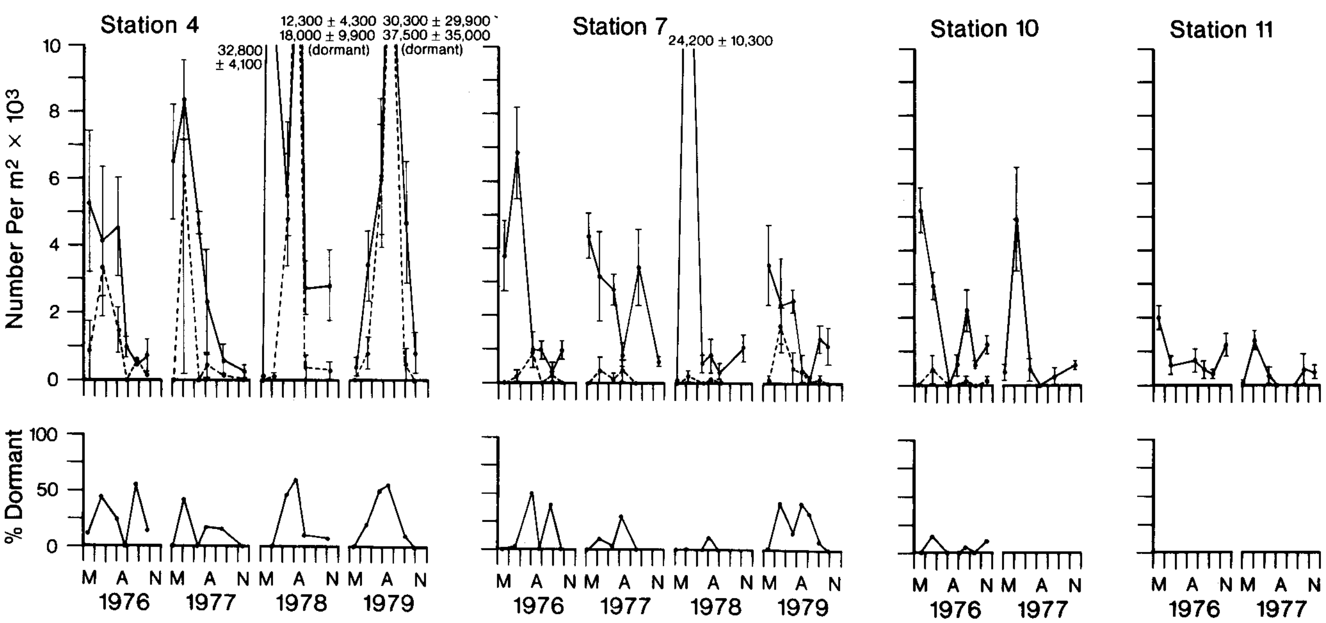

FIG. 4. Upper: Mean density (± SE) of stage IV copepodids on each sampling date at Stations 4, 7, 10, and 11. Solid line = active copepodids; dashed line = dormant copepodids. Densities at the stations sampled only in 1976 (Stations 1, 5, 6, 8, and 13) are not shown, but are generally comparable to the stations of similar depth that are shown. Lower: Percentage of total number of stage IV copepodids found in the dormant condition.

TABLE 1. Percentage of **Canthocamptus robertcokeri, Canthocamptus staphylinoides,** *and stage IV copepodids found dormant at 11, 17, and 23 m. These percentages include all individuals from all stations that were sampled in the 4-year period. Total number (both dormant and active) in parentheses. The chi-square test was used to determine if dormancy was independent of sampling depth (* = reject at 5%, *** = reject at 0.1% level).*

Organism	Depth (m) 11	17	23	Chi-Square
C. robertcokeri, female	25.2 (508)	41.4 (507)	2.6 (78)	***
C. robertcokeri, male	22.2 (311)	32.1 (196)	4.1 (49)	***
C. staphylinoides, female	36.0 (322)	27.2 (92)	15.0 (20)	*
C. staphylinoides, male	32.8 (128)	15.9 (44)	11.1 (9)	*
Stage IV copepodids	27.9 (2793)	8.7 (229)	0.0 (95)	***

Without experimental work, the exact role of temperature and photoperiod in initiating and terminating the resting stage cannot be determined, but likely both factors were important. Watson and Smallman (1971) and George (1973) have found that photoperiod and temperature interact in initiating the dormant condition in cyclopoids. It is unlikely that oxygen conditions were a relevant factor in our study area since near-bottom oxygen levels were at saturation throughout the sampling period (Nalepa and Quigley, unpubl. data, Great Lakes Environmental Research Laboratory) and aerobic conditions in the sediments extended down to about 5 cm (Nalepa and Robertson 1981b).

Many of the spatial and year-to-year differences in the proportion of dormant individuals might be related to variations in the amount of surface detritus. This material had a higher organic carbon content than the sandy substrate (Nalepa and Robertson 1981b) and more dormant copepods are generally found in rich, organic sediments. For instance, a direct correlation was found between the amount of sediment organic carbon and the number of dormant *C. vicinus* (George 1973), and more dormant *M. leukarti* were found in areas where ooze accumulated than in similar areas with hard bottoms (Monakov 1959). At 11 m depth, Moore (1939) found 10 times more *Canthocamptus* cysts at a site with a muck bottom than at a site with a sand bottom. While these studies seem to indicate an active selection of resting site, some cyclopoids have been found to omit the resting stage altogether if a suitable substrate is not available (Wierzbicka 1962). Thus, variations in substrate may not only affect spatial distributions of dormant copepods, but may also affect temporal changes by influencing whether or not the copepod will even enter the resting stage. At our study site, consistently greater amounts of detritus were found at Station 4 compared to Station 7, likely a result of the former station being located much nearer the mouth of the Grand River. In turn, consistently greater proportions of stage IV copepodids were found in the dormant condition at Station 4. Proportions of dormant *Canthocamptus* at the two stations were similar, however, and may indicate that dormancy in cyclopoids is more influenced by substrate than dormancy in harpacticoids. The decrease in the proportion of both dormant cyclopoids and *Canthocamptus* with increased depth coincided with a general decrease in the amount of detritus, but this decrease may also have been related to the lower water temperatures found at the deeper depths. On an annual basis, less detritus was found in the study area in 1977 than in any other year (see Fig. 2 in Nalepa and Quigley 1983). In turn, the overall proportion of IV copepodids and *Canthocamptus* found in the resting stage in 1977 was the lowest in the 4 years of sampling. Correlation analysis (Kendall's Tau) did not indicate any relation between numbers of dormant individuals and detrital amounts when each core was treated as an individual replicate (grouped by station and season). Considering the ephemeral nature of these detrital deposits, what may be more important than the amount of detritus on any given sampling date is the presence or absence of detritus over an extended period.

This is the first report of a dormant stage in the life cycle of cyclopoids in the Great Lakes. Evans and Stewart (1977) sampled in a nearshore area of Lake Michigan just 125 km south of our study site and, although they found dormant *Canthocamptus*, they did not find any dormant cyclopoids. Perhaps *D. thomasi* is more likely to become dormant in areas near river mouths. At any rate, how widespread this phenomenon is in the Great Lakes remains unclear. Both Watson (1976) and Heberger and Reynolds (1977) interpreted a midsummer decline in the number of copepodids of *D. thomasi* in Lake Erie as a period of arrested development in the sediments. A similar seasonal pattern has not been observed in Lake Ontario, Georgian Bay, or Lake Superior although *D. thomasi* is the dominant cyclopoid in all these areas (N. Watson, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, B2Y 4A2 pers. comm.; Selgeby 1975). The midsummer decline in Lake Erie was attributed to a decrease in oxygen levels, causing the copepodids to enter the dormant state as a result of these unfavorable conditions (Heberger and Reynolds 1977). However, at our Lake Michigan site, dormant individuals were present even though oxygen levels did not decrease.

Regardless of causes or factors influencing the resting stage, the discovery of dormant cyclopoids in Lake Michigan indicates that future studies of the life cycle or production of cyclopoids in nearshore areas of the Great Lakes must consider the possibility of a summer dormant period in the sediments.

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