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Population Dynamics of *Mysis relicta* in Southeastern Lake Michigan, 1995–1998

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ABSTRACT. *The abundance and life history characteristics of* Mysis relicta *were evaluated at an offshore (110-m) and a nearshore (40 to 45-m) station during 1995, 1996, and 1998. Data were collected to monitor mysids relative to ongoing ecological changes in Lake Michigan and as a comparison to studies from the 1970s and 1980s. Mean densities of* M. relicta *during May through September each year were higher offshore (210/m^2 to 373/m^2) compared to nearshore (41/m^2 to 168/m^2). Growth rates ranged between 0.026 to 0.041 mm/day and did not differ between stations or with age. Juvenile mysids (< 10 mm) dominated the population, and accounted for 30 to 90% of the catch. The size distribution of* M. relicta *suggested that reproduction occurred year-round with the most consistent influxes of juveniles in the spring (April through June) each year; winter (February and March) and summer (July through September) influxes of juveniles did not occur consistently each year. Mean length of females with broods differed between nearshore (14 mm) and offshore (16 mm). Brood size and the proportion of females with broods did not differ between stations. Abundance estimates were equal or higher and life history characteristics were similar to reported data from the 1970s and 1980s. However, ongoing declines in the benthic macroinvertebrate* Diporeia *may result in higher fish predation pressure on* M. relicta *in the near future.*

INDEX WORDS: Mysis relicta*, population dynamics, zooplankton, Lake Michigan.*

INTRODUCTION

The opossum shrimp *Mysis relicta* is a large zooplankter common in the hypolimnetic waters of Lake Michigan. *Mysis relicta* plays a key role in the transfer of energy between phytoplankton and fish production, and between the benthic and pelagic food webs. During the day mysids inhabit low light areas near the lake bottom, feeding on detritus and benthic invertebrates (Lasenby and Langford 1973, Parker 1980). At night, mysids migrate upward into the water column as far as the metalimnion (Beeton 1960, Lehman *et al.* 1990), where they feed on zooplankton and phytoplankton (Lasenby and Langford 1973, Bowers and Grossnickle 1978, Grossnickle 1979). Mysids in turn provide a major food re-

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source for several deepwater fish species in Lake Michigan, including rainbow smelt (*Osmerus mordax*), bloater (*Coregonus hoyi*), alewife (*Alosa pseudoharengus*), and deepwater sculpin (*Myoxocephalus thompsoni*) (Crowder *et al.* 1981, Crowder and Crawford 1984, Kraft and Kitchell 1986).

The ecology of Lake Michigan has changed dramatically since *M. relicta* were studied extensively during the 1970s and 1980s. Invasions by zebra mussels (*Dreissena polymorpha*) (Marsden *et al.* 1993) and the spiny water flea (*Bythotrephes cederstroemi*) (Evans 1988) may change food web linkages and affect *M. relicta* growth and production (Beeton and Gannon 1991). Bloater replaced alewife as the dominate planktivorous fish during the 1980s (Jude and Tesar 1985), a change which may have increased predation on *M. relicta* (Crowder and Crawford 1984, McDonald *et al.* 1990, Rand *et al.* 1995). Major declines in the benthic macroinvertebrate *Diporeia* observed in the early 1990s (Nalepa *et al.* 1998) may result in increased fish predation pressure on *M. relicta* (McDonald *et al.* 1990, Shea and Makarewicz 1989).

Abundance and life history characteristics of mysids from this 1990s study in southeastern Lake Michigan are compared to published data from southern Lake Michigan in the 1970s and 1980s to evaluate how mysids have responded to recent ecological changes. These data will also provide a baseline to evaluate the potential indirect effects of *Diporeia* declines on *M. relicta* populations in Lake Michigan, because *Diporeia* only began to decline during fall 1998 at the sampling stations located off Muskegon, Michigan (T. Nalepa, Great Lakes Environmental Research Laboratory, Ann Arbor, MI, personal communication).

METHODS

Mysids were collected from southeastern Lake Michigan from a 110-m station (hereafter referred to as offshore), and from a 40 to 45-m station (hereafter referred to as nearshore), during 1995, 1996, and 1998. The nearshore and offshore stations were located about 10- and 20-km off Muskegon, Michigan, respectively. Collections were scheduled monthly at each station, but some sample periods were missed because of adverse weather. Sampling was done May to September during 1995, April to December during 1996, and March to October during 1998. Sampling was generally done during the new moon period, and began at least 1-h after sunset.

Two to three replicate samples were collected with a 1-m diameter plankton net (1,000-µm mesh) towed vertically from 2 to 3 m above the bottom to the surface at speeds of 0.3 to 0.5 m/s. Although net efficiency was not measured, it was assumed to be 100% because of the large mesh size. Mysids were anesthetized with carbonated water, and preserved in 10% sugar-buffered formalin.

In the laboratory all mysids were counted, and body length, sex, and eggs per female were recorded for 100 randomly selected individuals in 1995 and for all individuals in 1996 and 1998. Mean density for each year was calculated for samples collected May through September for annual comparisons. Body length was measured from the tip of rostrum to the tip of the telson. To determine size structure and growth, length frequency distribution plots were constructed by combining all replicates for each respective station and date (Figs. 1–3). The lengths from the most populated size

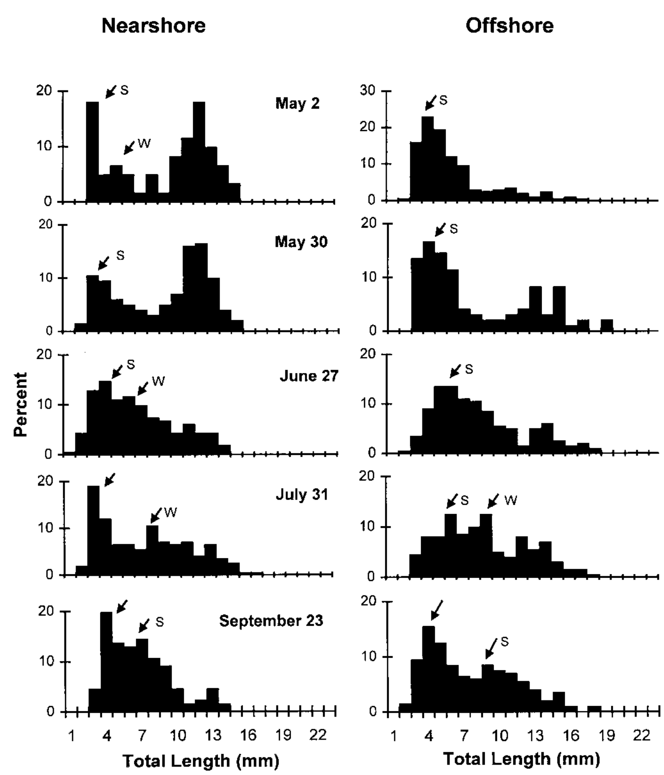

***FIG. 1.** Seasonal size distribution of* **Mysis relicta** *caught with a 1,000-µm net at a nearshore and offshore station in southeast Lake Michigan during 1995. Arrows labeled S and W indicate spring and winter juvenile cohorts respectively used for growth analysis; unlabeled arrows indicate summer cohorts which were not used for growth analysis.*

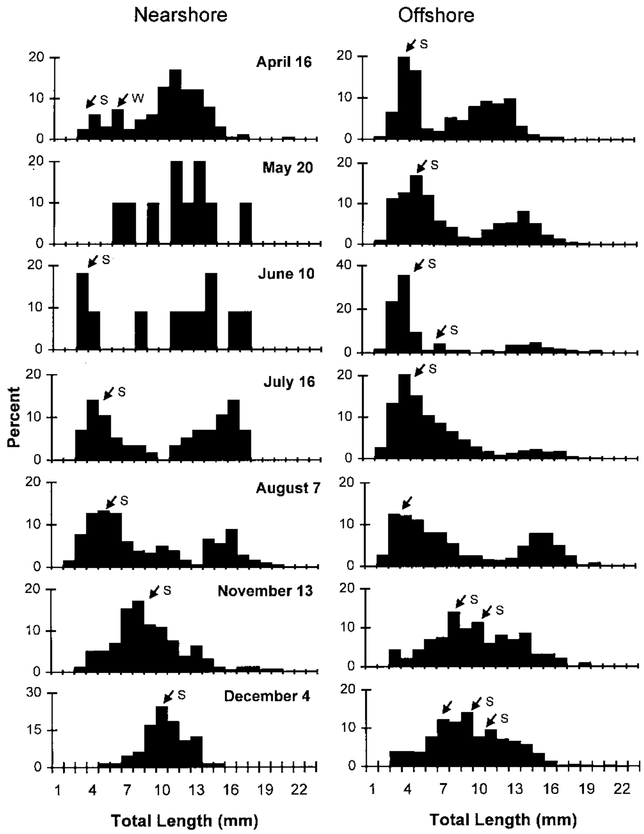

FIG. 2. Seasonal size distribution of* Mysis relicta *caught with a 1,000-μm net at a nearshore and offshore station in southeast Lake Michigan during 1996. Arrows labeled S and W indicate spring and winter juvenile cohorts respectively used for growth analysis; unlabeled arrows indicate summer cohorts which were not used for growth analysis.

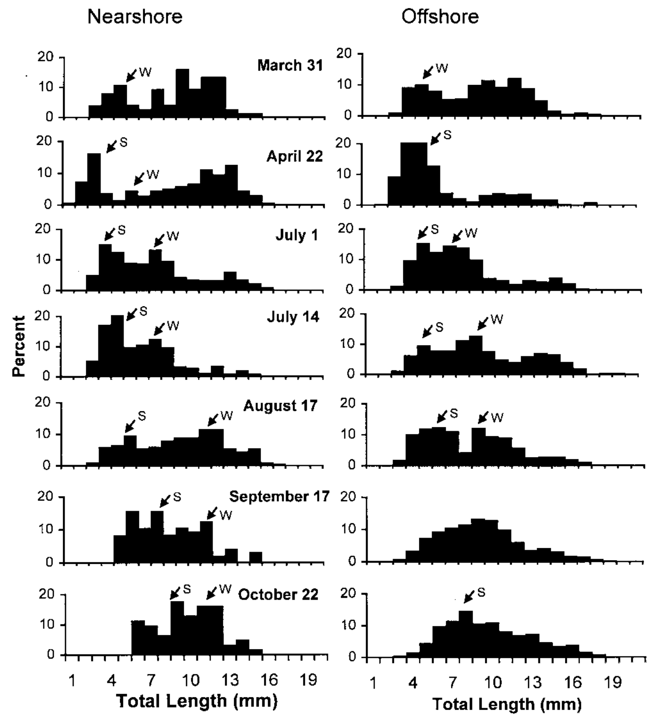

FIG. 3. Seasonal size distribution of* Mysis relicta *caught with a 1,000-μm net at a nearshore and offshore station in southeast Lake Michigan during 1998. Arrows labeled S and W indicate spring and winter juvenile cohorts respectively used for growth analysis; unlabeled arrows indicate summer cohorts which were not used for growth analysis.

classes of a cohort (mode and two adjacent size classes) were averaged to calculate mean cohort length (Johannsson 1992). To determine daily growth rates, mean cohort length was plotted against Julian day, and a regression was used to determine average daily growth. Growth rates were compared between stations using a t-test (Zar 1974).

Sex was determined by examining the structure of the fourth pleopod, which bifurcates in males (Balcer *et al.* 1984). Sex was only determined for animals longer than 10-mm, because most smaller individuals were undistinguishable. Brood size for females larger than 10-mm was calculated as the number of eggs plus embryos present. The proportion of females with broods was compared among years and between depths using categorical analysis. The mean length of females with broods was compared between depths and across years using two-way ANOVA (SYSAT 8.0). The number of eggs plus embryos per female was compared between depths and among years using ANCOVA, because brood sizes may vary with female length (Johannsson 1995).

RESULTS

Abundance

Mean density of *M. relicta* for samples collected between May and September at the offshore station was 254/m^2, 210/m^2, and 373/ m^2 in 1995, 1996, and 1998, respectively. Maximum densities occurred in early May and late September in 1995; in late May, mid-July to early August, and early

TABLE 1. Mean density (no/m² ± 1 S.E.) of* Mysis relicta *at a nearshore (40- to 45-m) and an offshore (110-m) station on Lake Michigan during 1995, 1996, and 1998. Range given in parentheses if n < 3. n = number of vertical net tows taken for each sample.

Date	Nearshore	n	Offshore	n
1995				
2 May	39 (25–52)	2	342 (175–508)	2
30 May	167 (152–183)	2	61 (53–69)	2
27 June	104 (93–114)	2	232 (224–241)	2
31 July	194 (188–199)	2	281 (236–327)	2
23 September	84 (80–88)	2	354 (201–507)	2
1996				
16 April	70 ± 6	3	64 ± 11	3
20 May	6	2	227 ± 62	4
10 June	7 (5–9)	2	51 ± 12	4
16 July	36 (30–42)	2	333 ± 26	4
7 August	114 (111–118)	2	237 ± 19	3
13 November	100 (78–122)	2	118 (107–128)	2
4 December	41 (32–51)	2	225 (204–246)	2
1998				
31 March	95	1	354 ± 89	3
22 April	58 ± 7	3	178 ± 60	3
1 July	255 (246–265)	2	450 ± 17	3
14 July	228 (204–523)	2	394 ± 103	3
17 August	128 (120–136)	2	192 ± 14	3
17 September	61 (60–62)	2	458 ± 29	3
22 October	39 (34–44)	2	204 ± 15	3

December in 1996; and in late March, early to mid-July, and mid September in 1998 (Table 1). Maximum densities were usually associated with high catches of 3 to 5 mm juveniles (Figs. 1–3).

Mean densities of *M. relicta* at the nearshore station were 117/m², 41/m², and 168/m² in 1995, 1996, and 1998, respectively. Mysid densities nearshore were always lower compared to offshore except in late May 1995 and April 1996. Maximum densities occurred in late May and late July in 1995; in early August and mid November in 1996; and in July in 1998 (Table 1). Maximum densities of *M. relicta* nearshore were always associated with high catches of juveniles.

Population Structure

Juvenile mysids (< 10 mm) dominated the population, and accounted from 60 to 89% of the catch offshore and from 30 to 90% nearshore. The presence of 2- to 5-mm individuals throughout the year at both stations suggests some reproduction occurred year-round (Figs. 1–3). However, modes from the size distribution plots of *M. relicta* suggested that there were influxes of juveniles (3 to 5 mm) each spring (April through June) and in some cases in the late winter (February and March) or late summer (July through September).

During 1995, a spring influx of juveniles appeared in early May (3 to 4 mm) at both stations, and a late summer influx occurred nearshore in July (3 mm) and offshore in September (4 mm) (Fig. 1). The 5-mm individuals captured in early May at the nearshore station may represent recruitment from the late winter assuming growth rates of 1 mm/month (Reynolds and DeGraeve 1972). In late July, the 8- to 9-mm individuals may have corresponded to a late winter cohort at the offshore station, but this cohort was not evident in other 1995 offshore samples.

During 1996, there was a more protracted period of reproduction as indicated by the appearance of small individuals (Fig. 2). An early spring cohort was evident in April at the offshore station (4 mm), and may have occurred at the nearshore station, though it was far less evident at the nearshore station. A second spring influx appeared in early June nearshore (3 mm). At the offshore station, 3- to 4-mm juveniles were present June through August. A mode of 6-mm individuals at the nearshore station in April may have corresponded to a late winter cohort, but this cohort was not clearly evident in later samples. A mode at 13 mm in November and December at the nearshore station may have corresponded to the late winter cohort or the early spring cohort.

During 1998, the size distribution suggested that only two major influxes of juveniles occurred (Fig. 3). A winter cohort was evident at both stations, corresponding to 5-mm individuals caught in March. A spring influx of 3- to 4-mm individuals occurred at both stations in April. No late summer reproduction was evident during 1998.

In addition to juvenile mysids, there appeared to be 2 to 3 cohorts of mysids present from the previous year at the offshore station, mostly evident during the earliest samples each year (Figs. 1–3). At the nearshore station, only 1 distinct cohort from the previous year was evident each spring.

TABLE 2. Reproductive characteristics of* Mysis relicta *from a nearshore (40- to 45-m) and an offshore (110-m) station in southeast Lake Michigan in 1995, 1996, and 1998. Female lengths with common letters were not significantly different (Tukey's test). Brood size is reported as the adjusted mean (ANCOVA). Significant differences in brood size (ANCOVA) and percent females with broods (χ^2) between depths or among years are noted with an asterisk. A significance level of 0.05 was used for all tests.

		Female Length (mm) (mean ± 1 SE)	Brood size (mean ± 1 SE)	Females with broods (%)
Depth	Nearshore	14 ± 0.3^a	17 ± 1.2	8
	Offshore	16 ± 0.2^b	16 ± 0.8	7
Year	1995	14 ± 0.4^a	21 ± 1.5*	9*
	1996	16 ± 0.2^b	17 ± 1.2	10
	1998	15 ± 0.2^b	14 ± 1.0	5

Growth Rates

Growth rates were similar between nearshore and offshore and between juveniles and adults ($p > 0.05$). For juvenile mysids, growth rates offshore were 0.031 and 0.027 mm/day for the winter and spring cohorts, respectively. Nearshore, growth rates were 0.037 and 0.032 mm/day for the winter and spring cohorts, respectively. Growth rates of age-1 mysids were 0.026 and 0.041 mm/day at the offshore and nearshore stations, respectively. For winter growth, it was assumed that the modes at 7 and 9 mm in September 1995 at the nearshore and offshore stations, respectively corresponded to the 11 and 13 mm individuals caught the following April. Growth rates over the winter of 1995 were 0.018 and 0.02 mm/day offshore and nearshore, respectively.

Reproductive Characteristics

The sex ratio of mysids indicated a slightly higher percentage of females compared to males. The proportion of mysids over 10 mm that were females was 57% and 53% at the offshore and nearshore stations respectively. The mean length of female mysids with broods differed among years ($p < 0.001$), ranging from 14 ± 0.4 mm (1995) to 16 ± 0.2 mm (1996) (Table 2). Females with broods were larger offshore (16 ± 0.2 mm) compared to nearshore (14 ± 0.3 mm) ($p < 0.001$) (Table 2). The depth * year interaction was not significant ($p = 0.05$).

The proportion of females with broods differed among years ($\chi^2 = 18.6$, $p < 0.001$), ranging from 5% in 1998 to 10% in 1996, but did not differ between the nearshore (8%) and offshore (7%) stations for all years combined ($\chi^2 = 0.82$, $p = 0.36$) (Table 2). The proportion of females with broods was highest each year sometime in the spring between April and June, depending on the year, ranging between 13 and 37%. Following the maximum, the percentage of females with broods dropped, and then gradually increased through the summer to 7 to 14% by September to December. During 1996, over 10% of females had broods during May through November, reflecting the protracted influx of juveniles that occurred that year.

Brood size increased significantly with female length ($p < 0.0001$) ($y = 2.305\,x - 19.57$). Adjusted mean brood size (ANCOVA) differed among years ($p < 0.001$), ranging from 14 ± 1.0 (1998) to 21 ± 1.2 (1995) (Table 2). Brood size did not differ between depths ($p = 0.22$), ranging from 16 ± 1.2 offshore to 17 ± 0.8 nearshore.

DISCUSSION

Mysis relicta abundances were equal or higher during the mid- to late 1990s compared to historical values from the 1950s through the 1980s despite major changes in food web dynamics of Lake Michigan (Table 3). Since the 1970s, zebra mussels (Marsden *et al.* 1993) and *B. cederstroemi* (Evans 1988) have disrupted the pelagic food web in Lake Michigan and the fish community has changed with bloater replacing alewife as the dominant planktivorous fish (Jude and Tesar 1985). Because bloater feed more heavily on *M. relicta* than alewife, the

TABLE 3. Comparisons of* Mysis relicta *densities from various studies in Lake Michigan during 1954 through 1998 from offshore (> 70 m) and nearshore (30–50 m) stations. VT = vertical tow, C-B = Clarke Bumpus net; mesh sizes (mm) are given in parentheses.

Year	Season	Depth (m)	Location	Density (no./m²)	Gear	Reference
1954	June–Nov.	74	Grand Haven	349	C–B (366)	Beeton 1960[1]
1970	Aug–Sept	73	Saugatuck	154	Sled (656)	Reynolds and DeGraeve 1972
1971	May–July	73	Saugatuck	69	Sled (656)	Reynolds and DeGraeve 1972
1975–76	Aug–July	109–121	Milwaukee	188	Sled (570)	Morgan and Beeton 1978
1976	May–July	115	Milwaukee	317	Sled (570)	Grossnickle and Morgan 1979
1976	May–July	115	Milwaukee	288	VT (570)	Grossnickle and Morgan 1979
1977	Aug–Sept	80–110	Grand Haven	313	VT (243)	McDonald *et al.*1990
1985	Aug–Sept	80–110	Grand Haven	59	VT (243)	McDonald *et al.*1990
1985	June–Aug	100	Grand Haven	108	VT (300)	Lehman *et al.*1990
1986	June–Sept	100	Grand Haven	199	VT (130)	Lehman *et al.*1990
1987	June–Sept	100	Grand Haven	57	VT (130)	Lehman *et al.*1990
1988	May–Sept	100	Grand Haven	70	VT (130)	Lehman *et al.*1990
1989	May–Sept	100	Grand Haven	99	VT (130)	Lehman *et al.*1990
1995	May–Sept	113	Muskegon	254	VT (1000)	this study
1996	May–Sept	113	Muskegon	210	VT (1000)	this study
1998	May–Sept	113	Muskegon	373	VT (1000)	this study
1970	Aug–Sept	45	Saugatuck	2	Sled (656)	Reynolds and DeGraeve 1972
1971	May–July	45	Saugatuck	27	Sled (656)	Reynolds and DeGraeve 1972
1975–76	July–May	30–50	Milwaukee	466	VT (570)	Grossnickle and Morgan 1979
1977	Aug–Sept	40–45	Grand Haven	app. 100–200	VT (243)	McDonald *et al.*1990[2]
1984	Aug–Sept	40–45	Grand Haven	app. 100	VT (243)	McDonald *et al.*1990[2]
1985	Aug–Sept	40–45	Grand Haven	app. 150–125	VT (243)	McDonald *et al.*1990[2]
1995	May–Sept	40	Muskegon	117	VT (1000)	this study
1996	May–Sept	40	Muskegon	41	VT (1000)	this study
1998	May–Sept	45	Muskegon	168	VT (1000)	this study

[1]as calculated by Sell (1982)
[2] estimated from Figure 2

change in the fish community was predicted to place heavy consumptive demands on mysids relative to annual production (McDonald *et al.* 1990, Rand *et al.* 1995).

In comparison to historical mysid numbers in the southern basin of Lake Michigan, offshore densities of mysids in the 1990s were higher than during the 1980s and were similar to 1954 and the 1970s (Beeton 1960, Reynolds and DeGraeve 1972, Morgan and Beeton 1978, Grossnickle and Morgan 1979, Lehman *et al.* 1990, McDonald *et al.* 1990) (Table 3). Nearshore, mysid densities in the 1990s were within the range of densities found in the 1970s and 1980s (Reynolds and DeGraeve 1972, Grossnickle and Morgan 1979, McDonald *et al.* 1990) (Table 3). Comparisons of mysid densities across studies must take into account differences in gear type (Grossnickle and Morgan 1979), mesh size (Johannsson 1992), and proximity of stations. In this study a larger mesh size was used than previous studies, therefore the catches of smaller mysids may have been lower than in previous studies (Johannsson 1992). Also, the historical sampling stations are spread throughout the southern basin of Lake Michigan; Grand Haven is 20 km south of Muskegon and is the closest geographic historical station to the sampling station in this study. In spite of differences in gear types and sampling locations, data from the late 1990s suggest that mysid populations in southern Lake Michigan have remained relatively stable and have not decreased dramatically due to increased fish predation as predicted (McDonald *et al.* 1990, Rand *et al.* 1995).

Growth rates during the 1990s were similar to reported values from the 1970s. Growth rates during spring through late fall for juvenile and age-1 mysids were 0.027 to 0.041 mm/day, or about 1 mm/month. Winter growth rates were about 0.5

mm/month. During the 1970s, growth rates were just under 1-mm/month (Reynolds and DeGraeve 1972, Beeton and Gannon 1991). Low overwinter growth was noted in other studies (Beeton and Gannon 1991), and is probably related to reduced consumption and food availability at colder water temperatures (Chipps 1998, Rudstam *et al.* 1999) or to size selective fish predation (Johannsson 1992).

Reproductive characteristics of mysids were similar to those reported during the 1970s. Just over half the mysids were female at both depths in this study, and the mean length of females with broods was 14 mm and 16 mm at the nearshore and offshore stations, respectively. Seven to 8% of the females had broods, and the mean adjusted brood size was 17 and 16 at the nearshore and offshore stations, respectively. The proportion of females with broods generally peaked at 18 to 37% during the spring and again at 7 to 14% during the late summer into fall. During the 1970s, sex ratios were similar to the data in this study, and mean length of females with broods was 16 mm (Reynolds and DeGraeve 1972, Morgan and Beeton 1978). During 1970–71, about 6% of the females had broods, with peaks of 10 to 13% during spring and late summer (Reynolds and DeGraeve 1972). Brood size ranged between 12 and 23 during the 1970s (Reynolds and DeGraeve 1972, Beeton and Gannon 1991).

Growth rates and brood size did not differ between nearshore and offshore during the 1990s, but were reported to decrease with depth during the 1970s (Reynolds and DeGraeve 1972, Beeton and Gannon 1991). Mysid growth rates and brood size have been tied to lake productivity (Beeton and Gannon 1991). Offshore productivity has changed little since the 1980s (Fahnenstiel *et al.* 1998), but nearshore productivity is likely decreasing because of reduced nutrient loading and zebra mussel filtering activities because zebra mussels occur to depths of 65 m off Muskegon (G. Fahnenstiel, unpublished data). If nearshore productivity is decreasing, this may be a factor in the current similarity in growth rates and egg production between nearshore and offshore stations.

Population dynamics varied among years, suggesting multi-year studies are necessary to adequately characterize mysid populations. Differential movements of some size groups (Morgan and Threlkeld 1982) or migrations caused by water currents (Johannsson 1992) may also affect size structure and catch rates of mysids. Reproduction appeared to occur during much of the year at both depths based on size distributions and the presence of females with eggs throughout the year. However, the size distributions suggested consistent influxes of juveniles into the population during the spring each year. Winter and late summer influxes appeared with less consistency. Differences in population dynamics of mysids in Lake Michigan have been reported in other studies. Reynolds and Degraeve (1972) suggested that protracted breeding occurred offshore during April to October, whereas only 1 nearshore cohort appeared each year. In contrast, Morgan and Beeton (1978) observed maximum juvenile abundance in March, July, and November. Annual differences in food supply may affect the timing and duration of breeding (Beeton and Gannon 1991).

Although there were few temporal differences in the mysid population between the 1990s and historical data from the 1970s and 1980s, there were some spatial differences in the population between nearshore and offshore. Most notable was higher offshore densities compared to nearshore. Other studies have suggested several explanations for higher abundance offshore, including temperature tolerance (Shea and Makarewicz 1989), light sensitivity (Beeton 1960), and fish predation (McDonald *et al.* 1990, Lehman *et al.*1990). Mysid sensitivity to light and fish predation pressure probably resulted in the differences in abundance between nearshore and offshore sites rather than water temperature, because the hypolimnion provided a cold water refuge at the nearshore site during the summer. Predation likely limited mysid abundance nearshore because planktivorous fish densities are higher in nearshore areas (Brandt *et al.* 1991) and mysids may be more susceptible to predation at shallower depths (Lehman *et al.* 1990). Mysids at the nearshore station exhibited characteristics of a predation pressured community, including smaller overall length of females with broods and fewer cohorts of larger individuals compared to offshore (Johannsson 1995). In addition to higher fish predation nearshore, mysid sensitivity to light may have limited mysid numbers at the nearshore station (Beeton 1960, Morgan and Threlkeld 1982).

Although the mysid population appears stable relative to historical data, changes continue to occur in the Lake Michigan ecosystem. Recent declines of *Diporeia* may indirectly affect *M. relicta*. *Diporeia* numbers have declined from 3,000 to 8,000/m^2 in the 1980s to nearly zero at many sites in Lake

Michigan south of Muskegon (Nalepa *et al.* 1998, T. Nalepa, Great Lakes Environmental Research Laboratory, Ann Arbor, MI, personal communication). The decline of *Diporeia* is spreading northward, and had advanced as far as Muskegon by late fall 1998; *Diporeia*, along with *M. relicta*, are the two main diet items for two common deepwater fishes, bloater and deepwater sculpin (Crowder and Crawford 1984, Kraft and Kitchell 1986). Therefore, declines in *Diporeia* may place heavy predation pressures on *M. relicta* in the near future.

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