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Effect of Environment on Reproduction and Growth of *Mysis relicta*[1]

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Abstract.—Published and unpublished data were examined to determine whether the time to first reproduction, brood size, and growth rate of *Mysis relicta* are related to environmental conditions. Time to first reproduction ranged from 1 year in eutrophic lakes to 4 years in an ultraoligotrophic lake. Mysids in nutrient-rich lakes may have 45 eggs per brood, whereas those in less productive lakes had 10–12 eggs per brood. Growth rates ranged from 1.0 to 1.5 mm/month in productive lakes to only 0.2 mm/month in ultraoligotrophic Lake Tahoe. Some differences in reproduction and growth rate consistent with the above observations occurred between areas of Lakes Tahoe and Michigan that differed in trophic conditions.

The opossum shrimp *Mysis relicta* is important in the food web of glacial and alpine lakes of northern Europe, Asia, and North America. Its habits and life history must be considered in evaluating its role in the ecology of lakes or in assessing feasibility of introductions. During the day at least part of a population is benthic, and at night mysids migrate extensively into the water column to become part of the plankton (Beeton and Bowers 1982). Mysids are omnivorous, filter-feeding on phytoplankton, zooplankton, and detritus, and attacking individual prey including macrozooplankton and macrobenthos up to its own size (Parker 1980; Lasenby and Fürst 1981; Grossnickle 1982). Because of its mobility and omnivory, *M. relicta* fits into more than one type of food web and, as a consequence, a large population of mysids can enhance the movement and distribution of nutrients and toxic substances within an aquatic ecosystem.

The relatively large size of mysids, up to 30 mm in some freshwater lakes, and their availability in the water column or on the bottom make them desirable fish food, especially for fishes such as lake trout *Salvelinus namaycush*, salmon, coregonids, and other fishes of the hypolimnion. Fisheries biologists recognized the importance of *M. relicta* as food, and they introduced populations in many lakes in North America and Europe (Lasenby et al. 1986).

A sound knowledge of the environmental requirements and the life history of *M. relicta* is essential to predict the possible success of introductions. Because mysids occur in deep, glaciated lakes of the northern temperate zone, the common misconception has been that *M. relicta* requires deep, cold, well-oxygenated water. Actually, *M. relicta* is the most eurytopic of the group of organisms called glacial relicts (Dadswell 1974). Populations of *M. relicta* occur in clear or turbid water, where temperatures range from near 0 to 21°C, and where dissolved oxygen concentrations range from 2 mg/L to saturation. It is sensitive to light (Beeton 1959) and, as a consequence, it occurs in deep water in clear lakes and at shallower depths in turbid lakes (Dadswell 1974).

Mysid patterns of reproduction and growth in various water bodies are basically similar, but there is a considerable range in brood size and they appear to vary chronologically—that is, the time to first reproduction and growth rate may vary greatly among populations in different lakes or even within a lake (Morgan 1980). The purpose of this study was to examine published and unpublished data to determine whether the above differences in life history are related to different environmental conditions—that is, whether they are genotypic or phenotypic.

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Sources of Data

Most of the data used in this study are from the literature or are available in unpublished dissertations. The sampling methods and other information about the 1954 Lake Michigan data were presented in Beeton (1960). Mysids were collected in the cod end of a fishing trawl off of Laughing Fish Point, Lake Superior, at a depth of 45 m in 1954 (A.M.B., unpublished). Several thousand mysids were collected, mostly large specimens because of the large mesh. Growth rate of *M. relicta* was calculated by plotting the mode of total length for size-groups against collection date, with the method of Morgan and Beeton (1978). In addition, growth rate per month was calculated for several mysids collected from Lake Michigan by rearing them in the laboratory under conditions similar to the field from June 29 through September 1955 (A.M.B., unpublished). Lake Michigan water was held at a temperature of approximately 5°C. Light was usually on a 12 h:12 h light:dark cycle at 10.8 lux intensity. Laboratory mysids fed on naturally occurring plankton and occasionally on dead mysids.

New analyses of published and unpublished data that were prepared for this paper are identified as "present study."

Results and Discussion

Observations on *M. relicta* reproduction in various water bodies indicate considerable variation in the timing of reproduction and the number of broods per year. Holmquist (1959) reported that eggs of mysids in Lake Ivosjon, Sweden, were released into the brood pouch during November and December and young left the pouch in spring (March through May). A similar pattern was observed by Juday and Birge (1927) in Green Lake, Wisconsin, where about 50–75% of females were gravid in November and almost all young had emerged by May. The breeding season extended from October through May, with some broods carried into June, in Cayuga Lake, New York (Brownell 1970). McWilliam (1970) sampled a deep-water station (260 m) and a shallower station (150 m) in Lake Michigan and found that reproduction occurred all year, with the major activity from October through November to mid-June, and the lowest reproduction in summer. McWilliam's data on molts and maturation of ovaries led her to conclude that females produced two broods annually. She also suggested that reproduction periods occur more frequently in shallow than in deep water. Morgan and Beeton (1978) reported peaks in juvenile abundance for Lake Michigan (109–121 m depth range) in March, July, and November. Carpenter et al. (1974) found two breeding populations in Lake Huron. A summer breeding population gave rise to a winter breeding one, which in turn produced the summer breeders.

There is consensus that reproduction occurs during the colder months, but there is disagreement on the extent of summer reproduction and the number of broods per year. Some of this disagreement can be resolved by recognizing that reproductive cycles may differ significantly between deep- and shallow-water populations in the same lake. Furthermore, several cohorts may exist in a population, and they will be releasing young at different times. For example, a cohort may produce two groups of young, one when the females are 12 months old and another at 16 months, resulting in a complex population structure, such as that observed in Lake Michigan where six cohorts were represented in the population during the year (Morgan and Beeton 1978).

Some of this variation in reproductive patterns may be caused by variations in trophic conditions within lakes (especially large ones) and between lakes. For example, Holmquist (1959) examined mysid populations from various lakes and concluded that the food supply influenced the time and period of breeding, especially in some large lakes.

Two aspects of reproduction that appear to be related to lake typology and consequently to food supply are the time to first reproduction and the brood size (Table 1). The time to first reproduction—actually, the average time between release from the brood pouch and female reproduction—ranged from 1 to 4 years. The 1-year time was for mysids from eutrophic and mesotrophic lakes, including Lake Michigan. Although Lake Michigan is considered a mesooligotrophic lake, it tends to be more productive and therefore more mesotrophic near shore (Holland and Beeton 1972). The population upon which the reproduction estimates were based came from this zone. Mysids require 2 years of growth before their first reproduction in oligotrophic lakes and 4 years in ultraoligotrophic Lake Tahoe. Mysids from somewhat more productive lakes, such as Huron and Ontario, are positioned between the mesotrophic and clearly oligotrophic lakes, such as Superior, in their time to first reproduction.

Brood size also appears to be related to lake

TABLE 1.—Growth rates and aspects of *Mysis relicta* reproduction in various types of lakes.[a]

Lake	Type	Time to first reproduction (years)	Average number of eggs per brood	Growth rate (mm/month)	Reference
Tahoe	Ultraoligotrophic	4	10.7	0.2[b]	Morgan (1980)
Char	Oligotrophic (Arctic)	2	12	0.6[b]	Lasenby and Langford (1972)
Superior	Oligotrophic	2	10.3[c]	0.7[b]	Carpenter et al. (1974)
Great Slave	Oligotrophic	2		0.8	Larkin (1948)
Huron	Oligotrophic	1.5		0.9[b]	Carpenter et al. (1974)
Emerald Bay (Tahoe)	Oligotrophic	1–2	13.9	1.3	Morgan (1980)
Michigan	Mesooligotrophic	1	19.2[d] 23.0[b]	1.0	McWilliam (1970); Morgan and Beeton (1978)
Ontario	Oligomesotrophic	1.5		0.7	Carpenter et al. (1974)
Cayuga	Mesotrophic	1	16.0	1.0–1.5	Brownell (1970)
Dratzigsee	Mesotrophic (?)	1	10–40	1.0	Samter and Weltner (1904)
Ivosjon	Mesotrophic (?)	1	40–45	>1.0[b]	Holmquist (1959)
Stony	Eutrophic	1	10–14	>1.0[b]	Lasenby and Langford (1972)

[a]Some data on time of first reproduction and numbers of eggs are from Table 5 of Morgan (1980).
[b]Growth rates for the present study calculated from data in cited reference.
[c]Data from Beeton (unpublished).
[d]Data from McWilliam 1970.

typology (Table 1). Although data are available for few lakes, and eggs and young are frequently lost when adults are captured by net, it appears that mysids in the less productive lakes have 10–12 eggs per brood, whereas mysids in the more productive lakes may have up to 45 eggs per brood. The reason for the small brood size in Stony Lake, Ontario, is unknown, but a mysid population in a eutrophic lake may be under stresses (e.g., low hypolimnetic dissolved oxygen concentrations or high interspecific competition in the more productive waters) that would result in less energy for egg production.

Most investigators who have collected data on *M. relicta* brood size observed that size of brood was related to size of female. McWilliam (1970) found a highly significant correlation between brood size and length of female on all sampling dates. In contrast, Brownell (1970) stated that there was no relationship between brood size and size of females in Cayuga Lake, New York. In general, however, it appears that the number of eggs produced by marine as well as freshwater mysids is directly dependent on size of female (Tattersall and Tattersall 1951).

The correlation between brood size and size of female appears to be a function of lake productivity (Figure 1). Among the populations studied, mysids of the mesotrophic Dratzigsee produced the most eggs per female at all sizes, whereas mysids in Lake Superior generally produced the least eggs per female for a given size. The three data sets for Lake Michigan mysids collected at three depths showed differences that may reflect lower nutrients and food in deeper waters. The data for 1954 were for mysids collected at 72 m, and their egg production was closest to that observed in productive Dratzigsee. Data for mysids collected in 1967 at 80 and 150 m showed decidedly lower egg production per female. The thermal cycle and extremes were similar at 72, 80, and 150 m (Carr et al. 1973). This lower production at 150 m probably reflects the lower productivity of

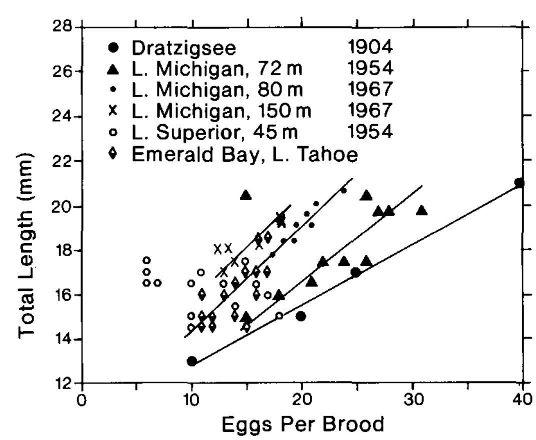

FIGURE 1.—Relationship between total length of gravid female *Mysis relicta* and eggs per brood. (Data from following sources: Dratzigsee, Samter and Weltner 1904; Lake Michigan 1954, Beeton 1960, present study; Lake Michigan 1967, McWilliam 1970; Emerald Bay, Morgan 1980; Lake Superior, unpublished data and present study.) Regression lines are approximate; data for Emerald Bay (Lake Tahoe) and Lake Michigan (80 m) are represented by the same line.

a deep-water population, but the 13 years between sampling and data analysis make firm conclusions difficult. Data for Lake Superior showed no positive trend between length of female and number of eggs (Figure 1). It is possible that eggs were lost from brood pouches of larger females as a result of sampling with a fish trawl, although the smaller females exhibited no apparent loss of eggs. These data do suggest that Lake Superior mysids have fewer eggs.

Reported growth rates of *M. relicta* tend to be based on calculations from field data (i.e., on total length at various collection dates). Such rates have been verified in a few instances in the laboratory, where mysids were reared by Holmquist (1959) and in our study. We documented a growth rate of 1 mm/month for Lake Michigan mysids, which agrees closely with calculations from field data (Morgan and Beeton 1978). Some authors have not calculated growth rates even though they had the data needed to do so. For example, Carpenter et al. (1974) stated that for Lake Huron the peaks in abundance shifted seasonally so that "the peak at 10 mm in April appeared to represent the same group as that of 15 mm in October, and that at 4 mm in April the same as that at 10 mm in October." This is a growth rate of 1 mm/month. Curiously, they concluded that the young enter the population at 3 mm in spring and are 10–12 mm next spring and 15 mm by summer. At a growth rate of 1 mm/month, the young emerging in spring should be 15 mm by the following spring. These data perhaps suggest a growth rate of less than 1 mm/month over winter, when all food sources for mysids are probably reduced.

The growth rate is greater than 1 mm/month for more productive waters (Table 1). It is approximately 1 mm/month for mesooligotrophic to oligotrophic lakes and less than 1 mm/month in oligotrophic lakes. It decreases from 0.9 mm/month in Lake Huron to only 0.2 mm/month in ultraoligotrophic Lake Tahoe. Growth rate curves are available only for a few lakes; nevertheless, these show the slow growth in an arctic lake such as Char, compared with that in a productive lake such as Stony (Figure 2). Growth rates for *M. relicta* from shallow (72 m) and deep (115 m) sampling locations in Lake Michigan suggest that the overall growth rate is greatest at the shallow depth (Figure 2).

The possible differences in one lake are shown by comparing the data on time to first reproduction, size of brood, and growth rates for mysids in

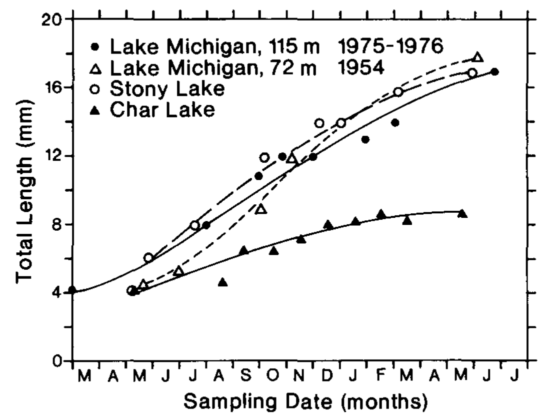

FIGURE 2.—Estimated growth rate of *Mysis relicta* in several lakes. (Lake Michigan 1954, present study; Lake Michigan 1975–1976, Morgan and Beeton 1978; Char and Stony lakes, Lasenby and Langford 1972.)

Lake Tahoe proper and in Emerald Bay (Table 1). Emerald Bay, although part of Lake Tahoe, is semiisolated (Morgan 1980). Lake Tahoe is different from all the lakes, as well as from Emerald Bay, in the lengthy time to first reproduction and the slow growth rate of mysids. Emerald Bay is similar to the mesooligotrophic lakes, and the trend in eggs per brood with increasing size is similar to the 80-m samples from Lake Michigan (Figure 1).

It seems reasonable to assume that the general patterns observed in the reproduction of *M. relicta* are a genotypic expression. If the populations are genetically similar, the fact that differences occur among lakes in times of first reproduction, size of broods, and growth rates, and that these differences can be related to lake typology, suggests these are broad phenotypic responses to environmental conditions.

The introduction of *M. relicta* as a food source for target fish species has had mixed results in North America and Europe (Lasenby et al. 1986). Viable populations have become established in some lakes but not in others. In those lakes with viable populations, the effects on target species vary from positive in some instances to negative in some others. Positive effects include increased growth rates of target species, whereas negative effects include no or only minor increases in fish growth rates and adverse alterations of zooplankton community structure. In most instances, follow-up monitoring investigations have been insufficient to determine the effects of mysid introductions on biological community structure and fisheries resources (Li and Moyle 1981). Our investigation indicates that environmental conditions, especially as they influence trophic status, are important to the expression of *M. relicta* life history characteristics, which may influence the success or failure of introductions. We do not believe mysid introductions should be accepted as a fishery management technique for widespread application. Rather, any contemplated mysid introductions should proceed cautiously with potential environmental impacts carefully considered, and the introductions should be based on a comprehensive evaluation of each situation (Li and Moyle 1981). Moreover, lakes where *M. relicta* has already been introduced should receive periodic evaluation so that information can be gathered about the long-term effects of these introductions.

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