



Life History Characteristics, Abundance, and Distribution of *Mysis diluviana* in the South Arm of Rainy Lake, Minnesota and Ontario

Natural Resource Report NPS/VOYA/NRR—2020/2069



ON THE COVER

Mysis diluviana (opossum shrimp)

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Life History Characteristics, Abundance, and Distribution of *Mysis diluviana* in the South Arm of Rainy Lake, Minnesota and Ontario

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Abstract

Information on the abundance, distribution, and life history characteristics of *Mysis diluviana* in the South Arm of Rainy Lake, Minnesota and Ontario, was obtained through a combination of daylight and night sampling with vertical net tows. From 1998 through 2002, daylight sampling was done bi-weekly at eight fixed stations from May through September. In 1998 and 2000, daylight versus night comparisons of *Mysis* catches in vertical tows were made from June through September at three of the fixed stations. Additionally, sampling was done along 21 line transects arranged cross-contour, with sample sites stratified by 10-m depth zones. *Mysis* abundance and biomass varied from year to year and increased with depth. Mean densities of adults and juveniles determined from daylight samples ranged from 13.3 to 41.3/m² for adults and from 184.6 to 453.5/m² for juveniles. The mean late summer biomass ranged from 110.62 to 218.40 mg/m². Comparable daylight and night samples showed that *Mysis* were concentrated on or near the bottom during the day and migrated vertically at night. The night migrations into the epilimnion, particularly of the smaller juveniles, exposed them to temperatures >20°C. Reproduction, brood size, and growth of *Mysis* in Rainy Lake generally followed life history patterns reported for the species from other temperate zone lakes. Size frequency distributions showed that *Mysis* in Rainy Lake have a 1-year life cycle, with the influx of juveniles occurring in early summer. Summer growth rates of juvenile *Mysis* (1.7–2.5 mm/month) exceeded values reported for both oligotrophic lakes (<1 mm/month) and mesotrophic lakes (1–1.5 mm/month). Correlation analyses suggested that juvenile growth was negatively affected by abundance of juvenile and adult *Mysis* and by higher summer temperatures in the epilimnion. Negative correlations between *Mysis* abundance and predatory Rainbow Smelt and Cisco were consistent with other field observations.

Acknowledgments

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All hard copy and computer data files for this study are stored in the Voyageurs National Park archives.

Introduction

The opossum shrimp *Mysis diluviana* (formerly *M. relicta* [Audzijonyte and Vainola 2005]) is a freshwater macroinvertebrate found in glaciated areas of North America and Europe (Balcer et al. 1984). It is an omnivore that feeds on zooplankton, phytoplankton, and detritus (Grossnickle 1982) and is an important prey for many fish species (Evans and Loftus 1987, McDonald et al. 1990, Johannson et al. 1994). *M. diluviana* was the predominant prey of Rainbow Smelt (*Osmerus mordax*) that colonized the upper Rainy Lake watershed following human introduction (Franzin et al. 1994) and first appeared in Rainy Lake in 1990 (Kallemeyn 2019). *Mysis* also comprised a significant portion of the diet of Cisco (*Coregonus artedii*), and Walleye (*Sander vitreus*) and Sauger (*Sander canadensis*) in Rainy Lake (Kallemeyn 2019).

There is extensive literature from studies of *Mysis diluviana* in lakes where it occurs naturally (Carpenter et al. 1974, Beeton and Bowers 1982, Grossnickle 1982, Nero and Sprules 1986, Beeton and Gannon 1991, Johannson 1992, Johannson et al. 1994, Almond et al. 1996, Pothoven et al. 2000, Gal et al. 2006, and Rudstam and Johannson 2009), and in water bodies where it has been introduced (Morgan 1980, Lasenby et al. 1986, Lasenby 1991, Nesler and Bergersen 1991). Data from these and other studies show *Mysis* life history patterns are highly variable among lakes (Morgan 1980, Lasenby 1991).

Prior to the Rainbow Smelt invasion and the assessment of its food habits, little was known about the *Mysis* population in Rainy Lake. The objectives of this study were (1) to gather information on relative abundance, depth distribution, and reproduction, brood size, and growth of *Mysis diluviana* in the South Arm of Rainy Lake, and (2) to compare these findings with previously published information for other *Mysis* populations. This baseline data may then be used to evaluate the complex food web interactions between *Mysis*, fish, and zooplankton.

Study Area

Rainy Lake is located on the United States-Canada border, has a total area of 92,110 ha, and is composed of three geographically distinct basins (Figure 1). The North Arm (34,590 ha) and Redgut Bay (8,320 ha) are in Ontario, while the South Arm is divided between Ontario (27,300 ha) and Minnesota (21,900 ha). About 14,738 ha, or 67%, of the Minnesota portion is located within Voyageurs National Park. The South Arm is the deepest of the three basins, having maximum and mean depths of 49 m and 11 m, respectively. The lake is irregular in shape and has a shoreline of 1,495 km with about 1,600 islands. Sampling for this study included both Minnesota and Ontario portions of the South Arm.

Rainy Lake was classified as oligotrophic to mesotrophic based on mean chlorophyll trophic-state indices from 2001 through 2003 (Christensen et al. 2004). The South Arm is dimictic, although in some years there may only be a gradual temperature decrease rather than a defined thermocline. Average mid-August epilimnion thicknesses and temperatures usually range from 11 to 13 m and 18°C to 23°C, respectively, and average late summer hypolimnion temperatures have ranged from about 8°C to 12°C since 1983 (Kallemeyn et al. 2003). Hypolimnetic dissolved oxygen

concentrations exceed 5 mg/L throughout the summer (Kallemeyn et al. 2003). Light penetration is regulated more by stain or color associated with organic materials than by algal productivity

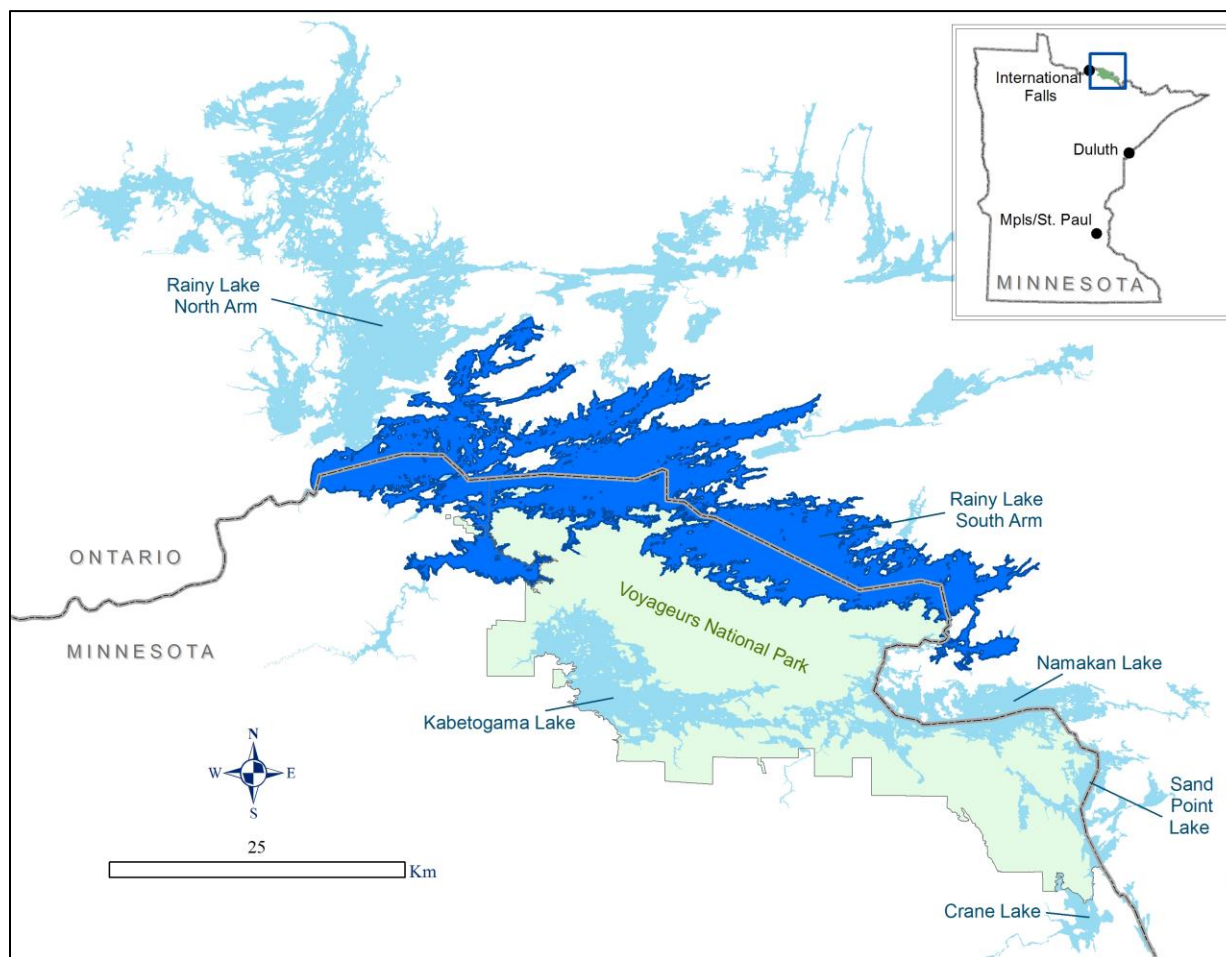


Figure 1. Rainy Lake and Namakan Reservoir, Minnesota and Ontario.

(Kepner and Stottlemeyer 1988, Payne 1991). Water transparency, as determined from Secchi disk readings, averages about 2.5 m, and incident light is rapidly reduced, falling to about 1% at depths of 4 m and 0.06% at 8 m. Mean specific conductance was 49 $\mu\text{S}/\text{cm}$ at 25°C, and mean pH 7.2 from 2001 through 2003 (Christensen et al. 2004).

Water levels on Rainy Lake are controlled by a hydroelectric dam that was built in 1909 and is regulated by the International Joint Commission (IJC) through the Water Levels Committee of the International Rainy-Lake of the Woods Watershed Board. Regulation of lake levels is based on “rule curves”, which are bands of lake elevations, within which the water levels are to be maintained during normal operations throughout the year. In 2000, the IJC revised the rule curves to reduce the adverse ecological affects associated with the 1970 rule curves. The 2000 rule curve did not change the annual fluctuation of 1.05 m but did call for a slightly wider band during the spring refill period and a modest drawdown in late summer and fall.

Rainy Lake supports coolwater recreational fisheries, with Walleye and Northern Pike (*Esox lucius*) being the principal harvested species. Other important species in the fishery are Sauger, Smallmouth Bass (*Micropterus dolomieu*), and Black Crappie (*Pomoxis nigromaculatus*). Yellow Perch (*Perca flavescens*), Spottail Shiner (*Notropis hudsonius*), and several other Cyprinid species are the primary prey species (Kallemeyn et al. 2003). The most common coldwater species are Lake Whitefish (*Coregonus clupeaformis*), Cisco, and Burbot (*Lota lota*). Rainbow Smelt first appeared in Rainy Lake in 1990.

Methods

Field Sampling

Exploratory sampling for *Mysis diluviana* (hereafter *Mysis*) was conducted in 1997 at six stations at biweekly intervals from May to September in the South Arm. Vertical tows with a 0.3-m diameter collapsing plankton net (153 μ m mesh) at five-meter depth intervals were conducted from the surface to the bottom during daylight hours. Comparable daylight and night samples at three stations showed *Mysis* were concentrated on or near the bottom during the day and migrated vertically at night. This sampling suggested the 0.3-m diameter net was not suitable for monitoring and assessing *Mysis* abundance because the number of *Mysis* collected was small and variable. The exploratory sampling also demonstrated that any extensive sampling throughout the South Arm would have to be done during daylight because night navigation was hazardous due to the basin's size and many islands and rock reefs.

Annual and Spatial Patterns

Mysis relative abundance in the South Arm of Rainy Lake was monitored from 1998 to 2002 at eight locations (Table 1). Distance between stations and depths ranged from 2.4 to 8 km and 26 to 46 m, respectively (Table 1, Figure 2). *Mysis* were collected by vertical tows from the lake bottom to the surface with a 1.0-m diameter net with a 3-meter-long cone constructed of 243- μ m mesh (Grossnickle and Morgan 1979, Nero and Davies 1982). The net was lowered to the bottom using a hand-operated winch and 3.2-mm aircraft cable. The cable was allowed to go slack for about 20 to 30 seconds, after which the net was raised at a rate of about 0.3 m/second. Two replicate samples (total vertical lifts) were collected during daylight hours at the fixed stations biweekly from late May through September. Samples were preserved in 70% ethanol until they could be analyzed in the laboratory.

Table 1. Locations of the fixed *Mysis diluviana* monitoring stations in the South Arm of Rainy Lake, Minnesota-Ontario, 1998–2002. Coordinates (NAD83; UTM Zone 15) for the fixed monitoring stations were generated by digitizing maps of Rainy Lake. ** Indicates sites used in the daylight-night comparisons.

Station	Location	UTM E	UTM N	Depth, m
1	1 mile east of Dryweed Island**	495283	5385287	31–35
2	0.5 miles north of Steamboat Island**	497946	5385220	32–35
3	0.25 miles north of Buoy 10**	500515	5385236	31–35
4	0.75 miles south of Fox Island	502536	5384586	23–27
5	0.5 miles south of Pater Noster Island	508929	5381352	28–30
6	0.5 miles south of Anchor Island	512727	5379918	30–35
7	0.5 miles north of Minnitaki Island	519364	5376208	45–48
8	0.75 miles north of Smith Island	524400	5376986	25–26

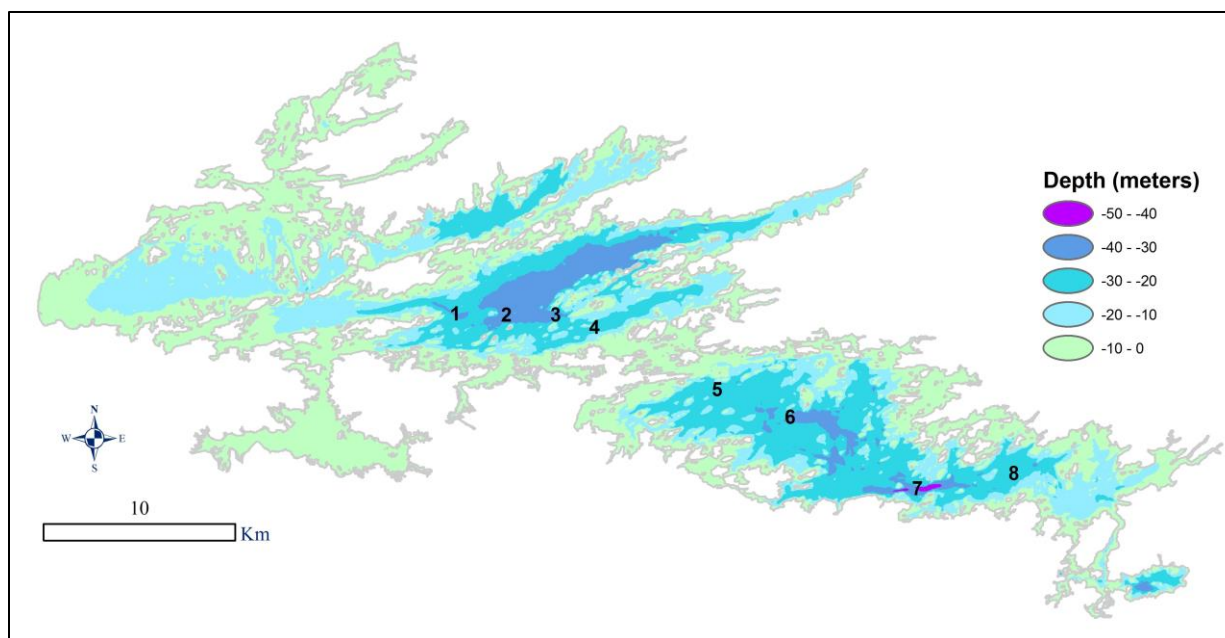


Figure 2. Map of the South Arm of Rainy Lake showing the 10 m contour lines and the eight *Mysis* monitoring stations. Stations 1, 2, and 3 were used in day-night comparison.

Daylight-Night Comparisons

In 1998 and 2000, daylight versus night comparisons of *Mysis* catches in vertical tows were made once-a-month from June through September at three of the fixed stations that could be safely accessed in the dark (Figure 2). Depths at the stations ranged from 31 to 34 m. Because moonlight can inhibit ascent of *Mysis* at night (Bowers and Grossnickle 1978), each month sampling was done on the day of the new moon when there was a minimal amount of light. In a few instances, high winds delayed sampling 1–2 days. Daylight samples were collected during mid-day while night samples were collected at least one hour after sunset. In addition to two total vertical lifts, two replicate tows were made from 10 and 20 m in 1998 to evaluate the vertical distribution of *Mysis*. All samples were collected using the same net and procedure that was used for monitoring at the fixed stations.

A systematic transect-station method was used to assess the areal and depth distribution of *Mysis* in the South Arm in Rainy Lake. Transects that ran cross-contour (S to N) were established that provided equal coverage across the west-east axis of the South Arm. Sampling along the transects was done in late July and early August from 1999 to 2002. All sampling was conducted during daylight. Sampling sites were stratified by 10 m depth zones, with samples taken at two separate sites from each depth zone represented on each transect. The <10-m and 10- to 19.9-m depth zones were available on all 21 transects, the 20- to 29.9-m zone on 15 transects, the 30- to 39.9-m zone on four transects, and the >40-m zone on one transect. All samples were collected using the same net and procedure used at the fixed stations.

Laboratory Analyses

All *Mysis* collected were counted and antennal lengths were determined for up to 50 juveniles and 50 adults at each fixed station on each sampling occasion. All *Mysis* were also counted from the samples collected along the 21 transects, but antennal length measurements were only taken from up to 25 juveniles and adults from those samples. Sample counts were converted to the number per square meter ($\#/m^2$) based on the cross-sectional area of the net (0.7854 m^2). No correction for filtering efficiency was made.

Antennal scale lengths were measured with an ocular micrometer. Total length (the length from the tip of the rostrum to the tip of the telson) was determined from a regression between antennal scale length and total length (Grossnickle and Beeton 1979). The relationship was determined to be $\text{Log}_{10}\text{TL (mm)} = 0.8508 + 1.0199 (\text{Log}_{10}\text{ANT})$, $df\ 1,115$; $F = 15231.97$; $P = 0.00$; $r^2 = 0.9925$, where TL is total length and ANT is antennal length. Sex was determined for adults collected at the eight fixed stations from 1998 through 2000 by examining the structure of the fourth pleopod, which bifurcates in males (Balcer et al. 1984). Egg and embryo counts were made in 1998 and 2002 to estimate brood size.

In 1999, a length-weight relationship was determined for *Mysis* measuring 3 to 23 mm in length. Mean dry weights were determined by placing 10 preserved animals from 1-mm size classes in pre-weighed aluminum dishes and drying them at 105°C for 24 hours. An initial weight was determined and *Mysis* were then dried for another 24 hours to ensure the organisms had reached a constant weight. Except for the 22-mm ($n = 3$) and 23-mm ($n = 1$) size classes, weights were obtained from at least two groups of 10 individuals from each 1-mm interval.

Data Analyses

Annual and spatial patterns

Total, juvenile, and adult *Mysis* densities from 1998 to 2002 were not chronologically independent. Thus, *Mysis* densities among the fixed stations were first $\log_{10}$ transformed to normalize the residuals and then compared through time and among stations using repeated-measures analysis of variance (ANOVA). When significant differences among treatments were detected, Tukey's LSD was used to separate differences among stations and years. Statistical significance was determined at $\alpha = 0.05$.

Daylight-night comparisons

A linear mixed effect model (Kutner et al. 2004) of $\log_{10}$ transformed adult and juvenile abundance was used to test for time-of-day effects on catch rates. The models contained random effects for sample year and sample date nested within year to account for correlations among samples taken on the same date. Sample station was included as a fixed effect in the model, as was time-of-day. The contrast of the two levels of time-of-day was used to test for differences in catch rate between day and night samples taken on the same date. Kolmogorov-Smirnov two-sample tests were used to determine if there were significant differences in length distributions of juvenile and adult *Mysis* collected from the 1998 daylight and night total vertical lifts at each station ($n = 3$) and in each month ($n = 4$). This resulted in 12 tests for both juveniles and adults. *Mysis* densities in the 10- m and 20-m tows were determined for comparison with the results from the total vertical lifts and to assess the depth distribution of the *Mysis*, particularly at night.

Depth transect collections

Data from the transect surveys, besides providing information on areal and depth distributions of *Mysis*, were used to estimate biomass. Yearly mean *Mysis* densities were calculated for each 10-m depth strata at the stations sampled on the transects from 1999 to 2002. Lengths from all juvenile and adult *Mysis* measured from the stations in each 10-meter depth strata >20 m were pooled to develop length frequency distributions for each age group. The proportion of *Mysis* measured in each 1-mm interval was then multiplied by the mean number of *Mysis* from that age group for that strata to obtain the overall size frequency distribution for that strata. The estimated number of *Mysis* in each 1-mm interval was then multiplied by the mean dry weight for that length provided by the length-weight relationship. Summing the products from each 1-mm interval provided estimates of the average biomass dry weight of juvenile and adult *Mysis* per square meter for each depth strata. A weighted average biomass value for the portion of the South Arm greater than 20 m deep was calculated by multiplying the combined juvenile and adult biomass for the 20- to 29-m, 30- to 39-m, and 40-m+ strata by the acreage encompassed in each depth zone. The products from the three depth zones were then summed, and that value was divided by the total area of the basin more than 20 m deep to obtain the weighted dry weight average biomass/m².

Growth and fecundity

Seasonal growth patterns of juvenile and adult *Mysis* were determined by combining the length frequency distributions from the fixed stations on each sampling date. To determine summer growth rates, mean lengths of juveniles and adults from each sampling period at each fixed station were plotted against day of the year, and the slope of the regression line was used to determine average daily growth. Differences in mean lengths were tested using analysis of variance (ANOVA) with Tukey's LSD used to separate differences among years. To estimate winter growth rates, the mean values of juveniles in the last fall sample were subtracted from the mean values of the adults in the first May sampling period in the following spring. This value was then divided by the number of days between the two sampling dates.

The number of eggs and embryos per female in 1998 and 2002 were compared using analysis of covariance (ANCOVA) because brood sizes have been found to vary with female length (Morgan 1980, Beeton and Gannon 1991, Johannsson 1995, Pothoven et al. 2000).

Environmental Correlations

Pearson correlation coefficients were used to assess possible relationships among juvenile and adult *Mysis* density and growth with water temperatures, reservoir discharge, and relative abundance of Rainbow Smelt, Cisco, Walleye, and Sauger. *Mysis* densities used in the correlations were the yearly mean values based on the catches from all eight fixed stations. Growth values used were the growth rates and estimates of total lengths on 1 October calculated with the regressions determined from mean lengths and day of the year.

Water temperature data were obtained from the Voyageurs National Park long-term monitoring program. Sampling was done bi-weekly from late May through September at a *Mysis* fixed station where the depth was 34 m. Measurements of water temperature and dissolved oxygen concentration were taken throughout the water profile at one-meter intervals using a portable field instrument. The

temperature data were used to determine the summer (late May through September) mean temperatures of the surface to 10 m and the >20 m depth zones. Mean reservoir discharge data (m^3/sec) for May through September were obtained from the Water Survey of Canada for the Rainy Lake at Fort Francis station.

Data on relative abundance of Rainbow Smelt, Cisco, Walleye, and Sauger were obtained from a small-mesh gill-netting program designed primarily to obtain an index of abundance for Rainbow Smelt (Kallemeyn 2019). From 1996 through 2002, 61-meter-long, multifilament nylon nets consisting of two 30.5×1.8 m panels with bar mesh sizes of 9.5 and 12.7 mm were fished in three areas in the South Arm in August and September. A total of 18 overnight bottom gill net sets were made each month at depths between 10 and 30 m.

All variables were $\log_{10}(x+1)$ transformed prior to analysis. Due to low sample size ($n = 5$ years), correlations were deemed biologically meaningful when $r > 0.70$.

Results

Abundance at Fixed Stations

Total *Mysis* densities, of which juveniles typically comprised 80% to 90%, varied significantly among years and stations (ANOVA, $F=5.00$; $df=28,262$; $P<0.0001$) (Figure 3). Juvenile densities also varied significantly among years and stations (ANOVA, $F=4.71$; $df=28,262$; $P<0.0001$) as did adult densities (ANOVA, $F=8.95$; $df=28,271$; $P<0.0001$).

In 1998, total and juvenile densities were higher at stations 1, 2, 3, 4, and 7 compared to stations 5, 6, and 8 ($P<0.05$). In 1999, total and juvenile densities decreased at six of the eight stations, resulting in all but stations 7 and 8 having an average density of $<200/\text{m}^2$. After 1999, total and juvenile densities generally increased so that by 2002 averages at all eight stations were $>200/\text{m}^2$ and Stations 7 and 8 had average densities $>600/\text{m}^2$. Similar patterns were evident for adults, though their numbers were much lower.

Total and juvenile *Mysis* densities at individual stations fluctuated across years, except at station 7 where density was similar across years ($P>0.05$) (Figure 3). Densities at stations 1, 2, and 3 were significantly higher in 1998 than in all subsequent years ($P<0.05$). Total and juvenile *Mysis* density at station 4 was highest in 1998, 2001, and 2002, and lower in 1999 and 2000 ($P<0.05$). Total and juvenile *Mysis* densities at stations 5 and 6 gradually increased through time. Densities at station 5 were significantly lower from 1998 through 2000 than in 2001 and 2002 ($P<0.05$). Total and juvenile *Mysis* densities at station 6 were significantly lower in 1998 and 1999 than in the following three years ($P<0.05$). There were no significant differences in the latter three years. Total and juvenile *Mysis* densities at station 8 were significantly lower in 1998 than in the following four years ($P<0.05$). The 1999 and 2000 densities, which were similar, were significantly lower than the 2002 densities ($P<0.05$), but not those from 2001.

With the exception of Station 2, densities of adult *Mysis* at individual stations also fluctuated across years (Figure 3). At Station 1, the 1998 and 2002 adult densities were significantly higher than the 2000 and 2001 densities ($P<0.05$). Adult densities at Station 3 were significantly higher in 1998 than in the following years ($P<0.05$). Adult densities at Station 3 were also higher in 2002 than in 1999 and 2001 ($P<0.05$). At station 4, adult densities were significantly higher in 2002 than in 1998, 1999, and 2000, while 2001 densities were also higher than in 1999 and 2000 ($P<0.05$). Adult densities at stations 5, 6, 7, and 8 all increased from 1998 to 2002. At all four stations, adult densities in 2001 and 2002 were higher than in the three previous years ($P<0.05$). With the exception of station 5, there were no significant differences between the 2001 and 2002 adult densities. The 1998 adult densities at Stations 6 and 8 were also lower than in 1999 and 2000, while at Station 6 adult density in 1999 was lower than in 2000 ($P<0.05$).

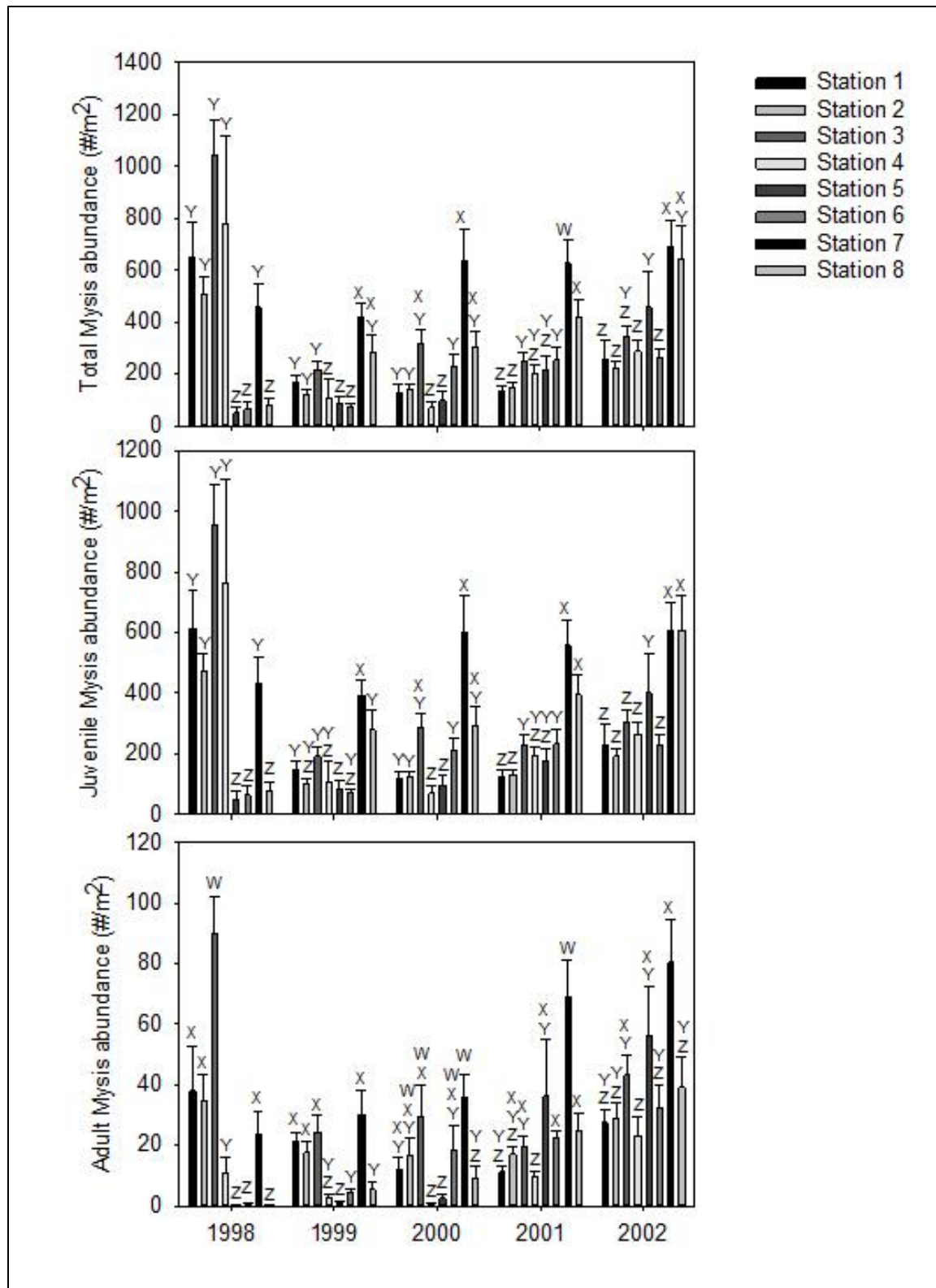


Figure 3. Mean densities $\pm$ 1 SE (#/m²) of *Mysis diluviana* at eight fixed stations in the South Arm of Rainy Lake, Minnesota and Ontario, May through September 1998–2002. Within years abundance at stations with common letters were not significantly different.

Table 2. Juvenile and adult *Mysis diluviana* densities (#/m²) in daylight (D) and night (N) vertical tows from depths of 10, 20, and >30 m at three stations in the South Arm of Rainy Lake, Minnesota and Ontario, June through September, 1998 and 2000.

Month	Depth (m)	Dryweed (#1) Juvenile		Dryweed (#1) Adult		Steamboat (#2) Juvenile		Steamboat (#2) Adult		Buoy 10 (#3) Juvenile		Buoy 10 (#3) Adult	
		D	N	D	N	D	N	D	N	D	N	D	N
June 1998	0–10	0.0	4.5	0.0	0.0	0.0	59.2	0.0	5.7	0.0	640.4	0.0	1.9
	0–20	26.7	12.7	0.0	1.3	49.7	126.7	0.0	3.2	100.6	543.0	0.0	9.6
	>30	697.1	153.4	31.8	3.2	781.8	319.6	83.4	13.4	374.3	595.9	100.6	8.3
June 2000	>30	92.9	100.6	24.2	46.5	63.7	105.7	6.4	12.1	368.6	234.3	22.3	12.7
July 1998	0–10	0.0	398.5	0.0	8.3	0.0	175.7	0.0	1.9	0.0	5.1	0.0	0.0
	0–20	0.0	860.1	0.0	17.2	0.0	921.8	0.0	31.8	0.0	89.8	0.0	7.0
	>30	282.0	994.4	8.9	34.4	520.1	927.6	10.2	54.1	638.5	137.5	81.5	41.4
July 2000	>30	33.7	90.4	3.8	37.6	96.8	70.0	8.9	15.3	173.2	87.8	26.7	1.9
August 1998	0–10	0.0	0.0	0.0	0.6	0.0	259.7	0.0	1.3	0.0	199.9	0.0	0.6
	0–20	0.0	45.8	0.0	0.6	0.0	636.0	0.0	3.8	0.0	474.9	0.0	9.6
	>30	315.1	255.3	15.9	39.5	513.8	942.8	28.7	70.7	416.4	692.6	85.9	48.4
1 August 2000	>30	127.3	170.6	10.8	17.8	95.5	184.6	7.6	43.9	375.0	259.7	27.4	28.6
29 August 2000	>30	117.8	170.6	13.4	17.8	140.7	77.0	14.0	5.7	161.7	202.4	18.5	11.5
September 1998	0–10	0.0	3.2	0.0	0.0	0.0	29.3	0.0	0.6	0.0	10.8	0.0	0.0
	0–20	0.0	42.6	0.0	0.6	0.0	100.6	0.0	0.6	0.0	68.1	0.0	2.6
	>30	753.1	138.8	8.9	3.2	259.7	304.9	5.1	14.0	907.2	135.6	35.6	10.8
September 2000	>30	83.4	33.1	10.2	3.8	32.5	35.0	1.9	1.3	183.4	73.8	2.6	1.3

juveniles occurred eight times during the day and seven times at night. For adult *Mysis*, the highest densities occurred seven times during the day and five times at night in 1998 and eight and seven times during the two periods, respectively, in 2000. Mean lengths of juvenile and adult *Mysis* in night samples exceeded the lengths in daylight samples in most instances in 1998. However, results from the Kolmogorov-Smirnov two-sample test showed that the differences were only significant in three instances for juveniles and two for adults.

The 10- and 20-m tows and >30-m vertical tows in 1998 demonstrated that there were differences in the depth distribution of *Mysis* during the two time periods. *Mysis* captured during daylight were restricted to the >30-m tows, except in June when juvenile *Mysis* were caught in the 20-m tows at all three stations (Table 2). Juveniles and adults were collected in both the 10- and 20-m tows as well as the >30-m tows at night. Densities of juveniles were variable, being greatest in the >30-m tows in six cases, in the 20-m tows in five cases, and in one instance in the 10-m tow. Adult densities, which were typically $<1/\text{m}^2$, were largest in the >30-m tows in 10 of the 12 night sampling periods.

Areal and Depth Distributions

Mysis samples collected from each of the 10-m depth intervals on the 21 transects showed that *Mysis* primarily occurred at depths greater than 20 m during daylight hours. Significant relationships existed between densities and depth in all four years the transect sampling occurred ($P<0.05$) (Figure 4). *Mysis* occurred infrequently and usually at densities of $<1/\text{m}^2$ in the <10-m and 10- to 19.9-m depth zones, which comprise 65.2% and 16.7 % of the South Arm's total area, respectively. An exception occurred in 2002 when *Mysis* occurred at 16 of the 21 stations in the 10- to 19.9-m depth zone. Juveniles comprised 96.2% of the *Mysis* captured in the two shallower depth zones.

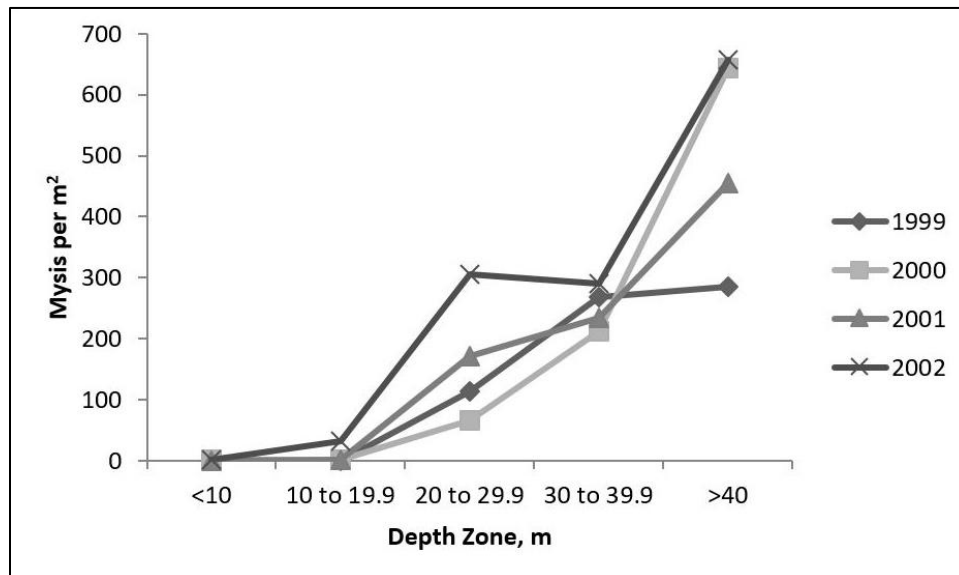


Figure 4. Mean *Mysis diluviana* densities versus depth on Rainy Lake transects, 1999–2002.

Dry weight biomass calculations were made using weights estimated from the regression: $\text{Log}_{10} \text{ Dry Weight (milligrams)} = -2.6653 + 2.6314 (\text{log}_{10} \text{ total length, mm})$ ($F=1425.8629$; $df=1,49$; $P=0.00$;

$r^2=0.97$). Biomass, like abundance, varied from year to year and increased with depth (Table 3). Biomass of juveniles exceeded that of adults in all but two instances. The exceptions occurred in 2001 (>40 m) and in 2002 (30 to 39.9 m), when adults comprised 19% and 13% of the population, respectively. Although average biomass in the >40-m depth zone was consistently greater than in the 20- to 29.9-m and 30- to 39.9-m depth zones, its influence on the overall weighted average biomass estimates was limited due it only covering 17.4 ha, or 0.2%, of the portion of the South Arm >20 m deep. Because the 20- to 29.9-m and 30- to 39.9-m depth zones covered 6,953.4 ha (14.4%) and 1,734.2 ha (3.6%), respectively, their mean biomasses had a larger influence on the overall weighted average values, which ranged from 110.62 mg/m² in 2000 to 218.40 mg/m² in 2002 (Table 3).

Table 3. Dry weight biomass (mg/m²) of *Mysis diluviana* in the South Arm of Rainy Lake, Minnesota and Ontario, 1999–2002.

Year	Age	Depth Zones (m)			Weighted Average
		20–29.9	30–39.9	40+	
1999	Juveniles	126.28	232.78	319.49	–
	Adults	20.38	102.20	86.68	–
	Total	146.66	334.98	406.17	184.70
2000	Juveniles	65.26	206.84	574.94	–
	Adults	4.89	59.35	202.46	–
	Total	70.15	266.19	777.40	110.62
2001	Juveniles	96.61	129.45	184.08	–
	Adults	24.00	122.77	333.09	–
	Total	120.61	252.22	517.17	147.62
2002	Juveniles	151.49	125.97	231.98	–
	Adults	57.22	129.66	143.81	–
	Total	208.70	255.63	375.79	218.40

Length-Frequency Distributions and Growth

Two cohorts were distinguishable throughout the summer each year based on length-frequency histograms (Figure 5). The first group consisted of juveniles that were recruited to the population in the spring, while the second group was composed of adults produced the previous year. In May, when sampling started, mean total lengths of juveniles ranged from 3.7 to 4.8 mm, while mean total lengths of the adults ranged from 16.5 to 17.5 mm (Table 4). Growth of the two cohorts could be followed because their length distributions never overlapped and no additional cohorts entered the population during the summer. While mean lengths of juveniles in 1998, 1999, and 2001 were not significantly different, mean lengths in 2000 were significantly greater and 2002 mean lengths were significantly less than in the other four years. Significant differences were also evident in the mean

total lengths of the adults, the exceptions being the similar small mean lengths in 1998 and 2002 and the intermediate lengths in 1999 and 2001. Daily summer growth rates ranged from 0.0583 to 0.0819 mm/day for juveniles and 0.0077 to 0.0196 mm/day for adults (Table 4). Winter growth rates for juveniles were 0.013 mm/day for the winter of 2000–2001, 0.015 mm/day for 1999–2000, and 0.019 mm/day for the winters of 1998–1999 and 2001–2002.

Table 4. The mean lengths (mm) and estimated summer growth rates (mm/day) and length (mm) on 1 October of juvenile and adult *Mysis diluviana* in the South Arm of Rainy Lake, Minnesota and Ontario, May–October, 1998–2002.

Date	Juvenile					Adult				
	1998	1999	2000	2001	2002	1998	1999	2000	2001	2002
25–31 May	4.26	3.97	4.75	4.79	3.70	16.75	17.08	17.53	17.26	16.53
7–14 June	5.39	4.84	5.67	5.57	3.71	16.61	17.12	17.81	17.84	15.95
22–27 June	6.74	5.82	7.92	6.78	5.48	16.67	17.75	18.77	17.73	16.43
6–11 July	8.34	7.44	9.72	7.68	6.66	16.86	17.53	19.17	17.87	16.61
20–25 July	8.66	8.62	10.80	8.43	7.91	16.76	18.08	19.30	18.00	16.80
1–11 Aug	9.50	9.88	11.30	9.36	8.61	16.58	18.37	18.98	18.25	17.17
16–23 Aug	10.52	11.05	11.72	10.60	9.28	17.46	18.61	18.62	18.45	17.08
29 Aug–7 Sept	10.75	12.17	12.59	10.85	10.01	17.22	19.04	19.10	18.46	17.46
13–20 Sept	11.44	13.03	13.21	11.64	10.75	17.30	19.18	19.03	18.60	17.22
26 Sept–3 Oct	12.31	13.78	14.15	12.22	11.77	17.73	19.41	19.54	18.74	17.26
Growth rate	0.0583	0.0819	0.0721	0.0590	0.0660	0.0077	0.0196	0.0113	0.0105	0.0097
Est. length 1 Oct	12.20	13.98	14.51	12.37	11.74	17.45	19.40	19.47	18.77	17.45

Reproductive Characteristics

Females dominated the adult *Mysis* collections at the fixed stations throughout the summers of 1998 through 2000. The proportion of females in the 10 sampling periods ranged from 84% to 99% (mean = 90%) in 1998 and from 92% to 99% in 1999 (mean = 96%). In 2000, 99% of the 1,735 adults examined were females.

Females with broods were only present in May and early June. The mean length of female *Mysis* with broods in 1998 (15.23 mm, SD = 4.29) was significantly larger than in 2002 (13.88 mm, SD = 4.00). Brood size in both years increased significantly with female length (Figure 6). The regressions were $\text{Log}_{10} \text{Mysis eggs} = 1.9967 (\text{Log}_{10} \text{female total length}) - 1.2801$ for 1998 ($\text{df} = 1,174$; $F = 36.2714$; $P = 0.0000$) and $\text{Log}_{10} \text{Mysis eggs} = 1.1266 (\text{Log}_{10} \text{female total length}) - 0.2461$ for 2002 ($\text{df} = 1,112$; $F = 8.2554$; $P = 0.0049$). However, there was no significant difference (ANCOVA) between the regressions from the two years.

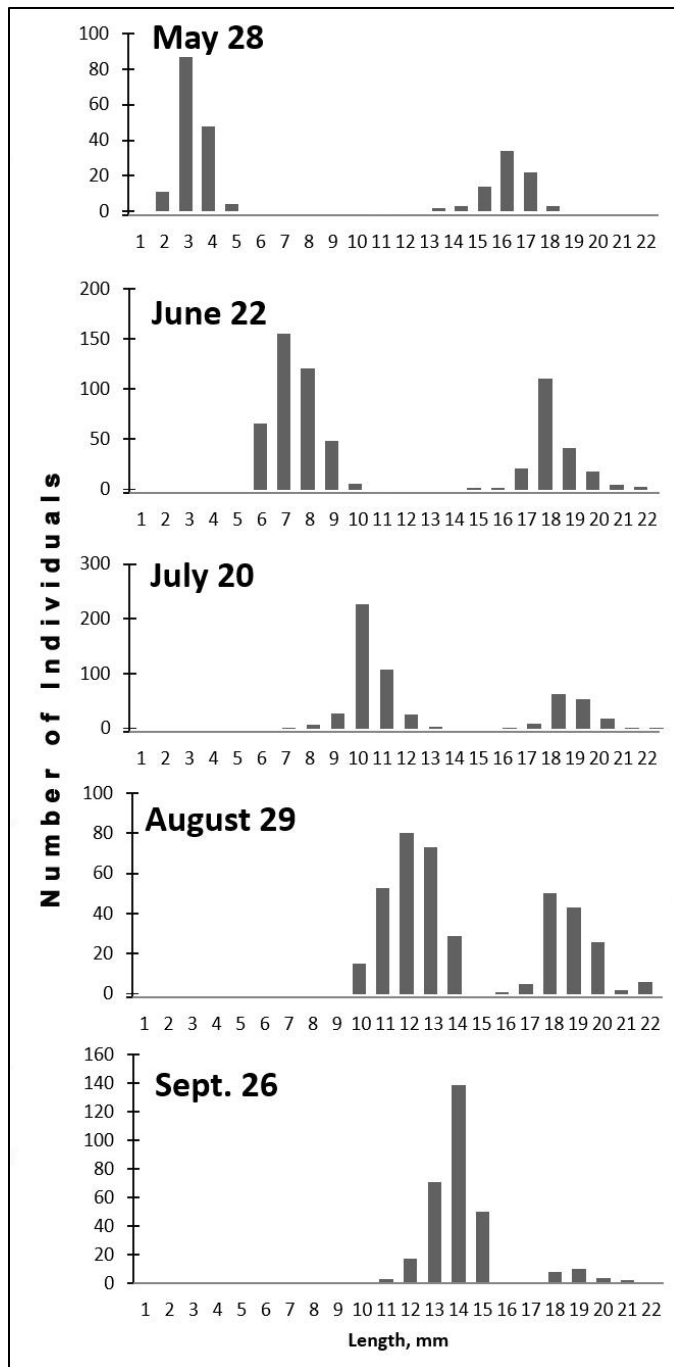


Figure 5. Seasonal length frequency distributions of *Mysis diluviana* in the South Arm of Rainy Lake, Minnesota and Ontario, 2000. Note different y-axis values for each month.

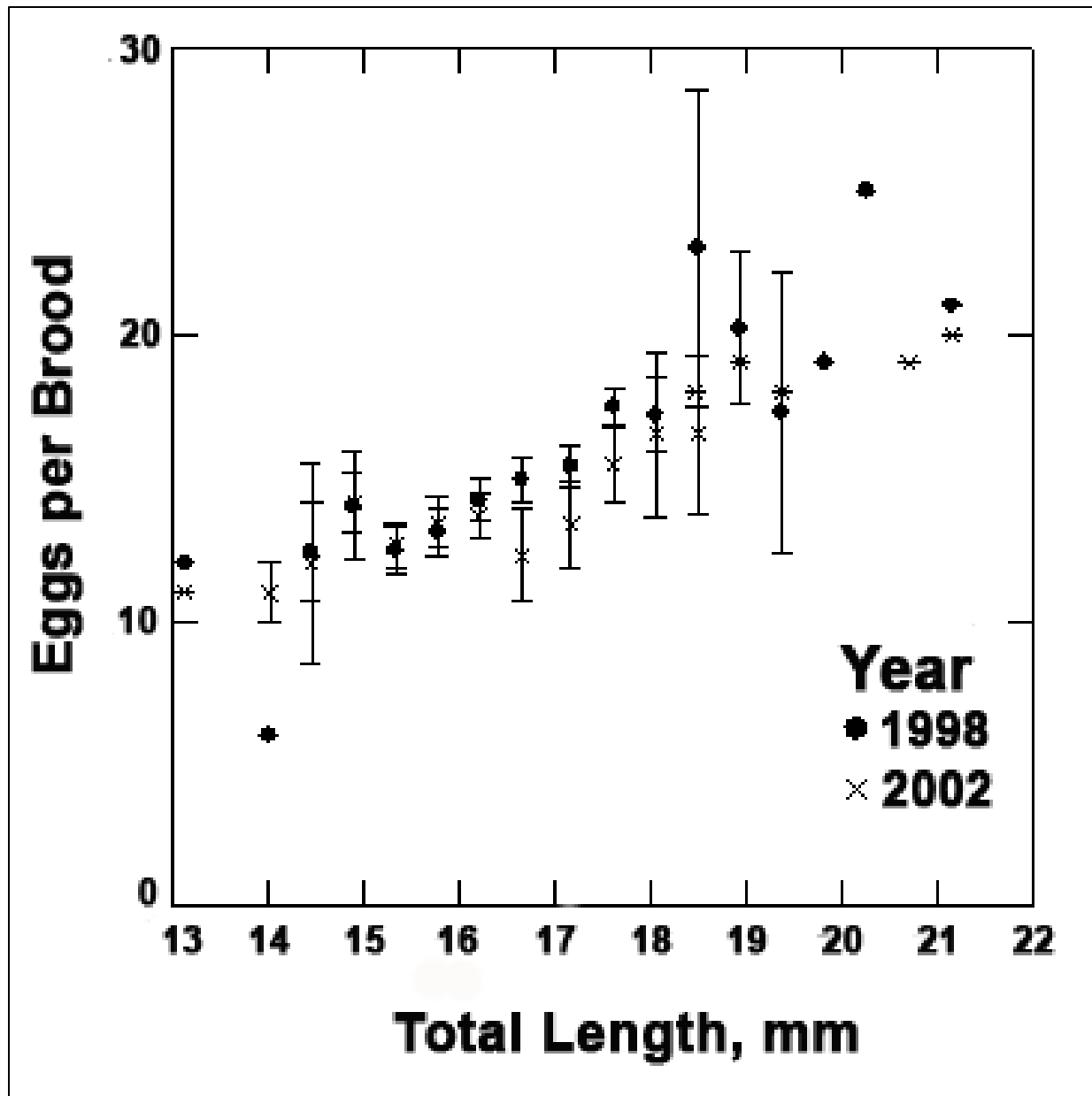


Figure 6. Relationship between total length of gravid female *Mysis diluviana* and eggs per brood in Rainy Lake, Minnesota and Ontario, 1998 (n=176) and 2002 (n=114). Mean $\pm$ 1 SE.

Correlation Analysis

Based on r-values that exceeded 0.70, abundance of juvenile and adult *Mysis* (which were positively correlated) were negatively correlated with juvenile growth rates and estimated lengths on 1 October (Table 5). However, for adults the r-value did not exceed 0.70 when compared with the juvenile growth rates. Adult *Mysis* abundance was negatively correlated with relative abundances of Rainbow Smelt and Cisco, while juvenile abundance was negatively correlated with relative abundance of Cisco. Juvenile growth rates and estimated lengths on 1 October were negatively correlated with mean summer temperatures (range 16.8°C–18.3°C) in the surface to 10-m depth zone.

Table 5. Correlation coefficients for relationships between *Mysis diluviana* abundance and juvenile growth rates, and estimated length on 1 October and various abiotic variables and abundance of four potential fish predators (catch per unit effort, CPUE) in the South Arm of Rainy Lake, Minnesota and Ontario, 1998–2002.

Variable	Juvenile (No/m ²)	Adult (No/m ²)	Juvenile growth rate (mm/day)	Juvenile length on 1 Oct (mm)
Log ₁₀ juvenile No/m ²	–	–	–	–
Log ₁₀ adult No/m ²	0.75^a	–	–	–
Log ₁₀ juvenile growth rate	–0.81^a	–0.67	–	–
Log ₁₀ juvenile length, 1 Oct	–0.80^a	–0.92^a	0.64	–
Log ₁₀ mean temperature, May–Sep, surface–10m	0.58	0.44	–0.82^a	–0.71^a
Log ₁₀ mean temperature, May–Sep, depth >20 m	0.18	–0.30	–0.35	0.34
Log ₁₀ mean discharge	–0.68	0.06	0.32	0.20
Log ₁₀ rainbow smelt CPUE	–0.29	–0.84^a	0.38	0.62
Log ₁₀ cisco CPUE	–0.71^a	–0.85^a	0.57	0.61
Log ₁₀ walleye CPUE	0.61	0.54	–0.17	–0.68
Log ₁₀ sauger CPUE	–0.34	0.01	0.50	0.37

^a Correlation >0.70, also shown in bold text.

Discussion

Information on the abundance, distribution, and life history characteristics of *Mysis* in the South Arm of Rainy Lake was obtained through a combination of daylight and night sampling with vertical net tows. Although night tows, which are generally considered preferable (Beeton and Bowers 1982, Nero and Davies 1982), were essential for describing the vertical migration of *Mysis* in Rainy Lake, there were no significant differences in *Mysis* densities between night and daylight total vertical lifts. Thus, net avoidance, which Grossnickle and Morgan (1979) suggested reduced daylight *Mysis* catches in the clearer waters of Lake Michigan, did not appear to be an issue in the heavily stained waters of Rainy Lake. Boscarino et al. (2009) concluded that light and temperature were sufficient for predicting *Mysis* vertical distribution across seasons in Lake Ontario.

Comparison of Rainy Lake's *Mysis* density and biomass estimates to those from other lakes is complicated by the temporal and spatial variation the organisms exhibit and the variety of sampling methods used by different investigators. While nighttime vertical tows have been commonly used to assess *Mysis* abundance, the mouth size and shape and the mesh sizes of the nets used have been highly variable. Because of these complicating factors, estimates from the literature must be viewed with caution (Lasenby 1991).

Mysis densities fluctuated both temporally and spatially. Density estimates varied among daylight-night comparisons, fixed stations, and transect sampling. The magnitude of interannual variation we observed was similar to that observed in multi-year studies in Lake Ontario and Lake Michigan (Johannsson 1992, Pothoven et al. 2000).

Comparisons based on night vertical net tows show that the *Mysis* densities in Rainy Lake in 1998 were greater than *Mysis* densities determined from night vertical net tows in four of the five Great Lakes (Table 6). This was true for *Mysis* densities from both more comparable shallower, nearshore stations and deeper, offshore stations, which usually have higher densities (Johannsson 1992, Pothoven et al. 2000). However, densities from night samples at the same stations in Rainy Lake in 2000 were similar to those reported from the Great Lakes. Reported mean *Mysis* densities from five lakes with maximum depths less than 100 m overlapped the ranges from both the day and night densities in Rainy Lake (Table 6). Average *Mysis* densities in Rainy Lake were similar to the 91–595/m² densities Nero and Schindler (1983) reported as being typical in Precambrian Shield Lakes.

Spatially, *Mysis* abundance in Rainy Lake increased with depth during the day, as has been frequently observed in large, deeper lakes like the Great Lakes (Carpenter et al. 1974, Johannsson 1992, Jensen et al. 2009). The relationship between depth and abundance observed in the transect samples, however, did not always hold for the fixed stations. While Station 7, the deepest station (46 m), consistently had the highest *Mysis* densities, the relatively shallow (26 m) Station 8 had the second highest densities from 1999 to 2002. Pothoven et al. (2004) suggested that patchy spatial distribution may be a defining characteristic of *Mysis* regardless of the scale of the observation area.

Table 6. Comparison of mean densities (#/m²) of *Mysis diluviana* determined with vertical net hauls in Rainy Lake and other North American lakes. N = samples collected at night, D = samples collected during day light.

Years	Season	Lake	Location	Depth (m)	Mesh size (µm)	Mean Density (#/m ²)	Reference
1998	June–Sept (N)	Rainy	S. Arm 3 stations	30–35	243	406–662	This study
2000	June–Sept (N)	Rainy	S. Arm 3 stations	30–35	243	113–182	This study
1998–2002	May–Sept (D)	Rainy	S. Arm 8 stations	28–45	243	182–459	This study
1999–2002	July–Aug (D)	Rainy	Transects	20–29	243	66–306	This study
1999–2002	July–Aug (D)	Rainy	Transects	30–39	243	213–291	This study
1999–2002	July–Aug (D)	Rainy	Transects	>40	243	286–656	This study
1995,96,98	May–Sept (N)	Michigan	Muskegon	40	1000	41–168	Pothoven et al. 2000
1995,96,98	May–Sept (N)	Michigan	Muskegon	113	1000	210–373	Pothoven et al. 2000
1976	Apr,May,July (N)	Michigan	Milwaukee	115	570	256–553	Grossnickle and Morgan 1979
1971	Mar,Aug,Nov (N,D)	Ontario	Lakewide(33 stat.)	<25–225	505	72–113	Carpenter et al. 1974
1984–1987	Apr–Oct (N)	Ontario	Stat. 41	125	250 cod end	271–602	Johannsson 1992
1971	May,July,Oct (N,D)	Superior	Lakewide(33 stat.)	<25–275	505	145–162	Carpenter et al. 1974
2005	Aug, Oct (N)	Superior	Lakewide(17 stat.)	100–300	64 cod end	190	Jensen et al. 2009
1971	Apr–Nov (N,D)	Huron	Lakewide(33 stat.)	<25–225	505	3–83	Carpenter et al. 1974
2007–2008	April, Aug (N)	Huron	Lakewide(10 stat.)	40–136	250	16–59	Mida 2010
1981–82	July–Oct (N)	George	Lakewide (8 stat.)	30–54	220	0–254	Siegfried 1987
1979	June–Sept (N)	Lake 239	8 stations	5.9–29.9	210	41–176	Nero and Davies 1982
1982–83	May–Aug (N)	Gull	North station	45	150	602	Nero and Sprules 1986
1982–83	May–Aug (D)	Bob	Central station	64	150	284	Nero and Sprules 1986
1975,2012	Summer (N)	Champlain	Fixed station	100	250	82 (2012) –712 (1975)	Ball et al. 2015

In addition to the physical environment, other factors they suggested that could contribute to the patchiness might be abundance of zooplankton prey and fish predators. Determining how or if these factors contribute to spatial variation in *Mysis* abundance in Rainy Lake would require more detailed complementary studies.

Mysis biomass in Rainy Lake, like abundance, varied from year to year and increased with depth (see Table 3). The weighted averages, which were based on the late July and early August transect surveys, presumably represent a summer peak like that recorded in 2000 in Lake Michigan by Pothoven et al. (2004). Rainy Lake's maximum summer biomass of 218 mg dry weight/m² was similar to Lake Michigan's mean annual biomass in 2001 (216 mg/m²) and 2009 (202 mg/m²) (Pothoven et al. 2010). *Mysis* biomass at depths between 30 and 40 m in Rainy Lake were approximately three-to-four times higher than the 80 mg dry weight/m² mean mysid biomass recorded at a 35-m site in Lake Ontario (Shea and Makarewicz 1989). However, the mean mysid biomass of 680 mg/m² at a 100-m site in Lake Ontario was higher than all the estimates from Rainy Lake, except in 2000 for depths >40 m (777 mg/m²). Mean *Mysis* biomass in White Partridge Lake, a Canadian Shield lake with mean and maximum depths and water chemistry similar to Rainy Lake, was 348 mg dry weight/m² (Langeland et al. 1991).

Reproduction, brood size, and growth of *Mysis* in Rainy Lake generally followed the life history patterns reported in other temperate zone lakes (Beeton and Gannon 1991). The reproduction pattern in Rainy Lake appears to be similar to that described by Berrill (1969) for *Mysis* in Stony Lake, Ontario. Females in that lake laid their eggs into their brood pouches in mid-December. The female then carried her 10–20 embryos through the winter until the developing young hatched in early to mid-May. In Rainy Lake, the number of embryos per female also ranged from 10 to 20, but the hatching did not occur until later in May and early June. Brood size, as has been commonly observed, was related to the size of the female (Beeton and Gannon 1991).

The summer growth rates of juvenile *Mysis* in Rainy Lake (range 0.0583 to 0.0819 mm/day, or 1.7 to 2.5 mm/month) exceeded the values reported by Beeton and Gannon (1991) for both oligotrophic lakes (<1 mm/month) and mesotrophic lakes (1 to 1.5 mm/month). Rainy Lake's mean hypolimnion water temperatures in early August ranged from 10.9°C to 15.5°C. Thus, temperatures were within the 10°C to 15°C dome-shaped range that has been identified as being optimum for consumption (Chipps 1998, Rudstam et al. 1999). Winter growth rates of juveniles in Rainy Lake, which ranged from 0.013 to 0.019 mm/day, were slightly faster than in Lake Ontario (0.012 mm/day) and similar to those in Lake Michigan (0.018 and 0.02 mm/day) (Johannsson 1992, Pothoven et al. 2000). Slower winter growth has been attributed to size-selective predation against larger instars or food limitation (Johannsson 1992), or reduced food consumption and food availability at colder water temperatures (Chipps 1998, Rudstam et al. 1999).

Summer growth rates of adult *Mysis* from 1998 to 2002 ranged from 0.008 to 0.020 mm/day. The growth rate of mysids in Lake Ontario during their second summer was 0.029 mm/day (Johannsson 1992), and in Lake Michigan 0.026 and 0.041 mm/day at offshore and nearshore stations, respectively (Pothoven et al. 2000).

Berrill and Lasenby (1983) predicted that mysids living in waters of at least 8°C during their first summer of life, as do *Mysis* in Rainy Lake, will complete their life cycle or time to maturity in one year. Size frequency and growth analyses showed that all Rainy Lake juveniles in May and June were large enough by fall to produce a new cohort the following spring. Although the adult cohort, which included some *Mysis* >20 mm long was still evident at the end of September, it is unknown if they survived long enough to release a second brood. In contrast, in an introduced *Mysis* population in Lake Tahoe, California-Nevada, only 40% of the females and 75% of males bred their first year (Morgan 1981). After the release of the juveniles, the Lake Tahoe population continued to grow and ultimately produced a second cohort. Males completely died out by February and the females disappeared 2 to 3 months after releasing their broods by May (Morgan 1980).

Comparable daylight and night samples showed that *Mysis*, which were concentrated on or near the bottom during the day, migrated vertically at night. The night vertical migrations, particularly of the smaller juveniles, into the 0–10-m depth zone of Rainy Lake from late July into early September of 1998 exposed them to temperatures that ranged from 19.3°C to 22.5°C. Mean August epilimnion temperatures in Rainy Lake in 1999–2002 consistently exceeded 20°C (Kallemeyn et al. 2003). *Mysids* were also found in the 0–10-m depth zone at night in another Canadian Shield lake, where temperatures in July and August exceeded 20°C (Langeland et al. (1991). Other investigators have also found juveniles higher in the water column than adults (Beeton 1960, Grossnickle and Morgan 1979, Rudstam et al. 1989).

Thus, juvenile *Mysis* in Rainy Lake routinely encountered temperatures greater than 16°C–18°C; temperatures at which mortality rates reportedly increase (DeGraeve and Reynolds 1975, Rudstam et al. 1989, Rudstam et al. 1999, Boscarino et al. 2007). It is uncertain how applicable those temperatures are to the distribution of smaller *Mysis* since most of the studies tested the responses of *Mysis* >10–12 mm long. Juvenile *Mysis* in Rainy Lake did not reach those lengths until mid to late August except in 2000. Boscarino et al. (2009) speculated that the difference in the vertical distribution of juvenile and adult *Mysis* might be because smaller *Mysis* have higher light and temperature tolerances than larger *Mysis*. Another suggested explanation was that smaller *Mysis* can venture higher into the water column to feed on zooplankton because they are at less risk of predation than larger *Mysis* (Beeton and Bowers 1982, Rudstam et al. 1989).

Whether the movement of *Mysis* into the epilimnion is affecting Rainy Lake's zooplankton community is unknown. Numerous studies have shown that predation by mysids may depress or alter zooplankton abundance and size structure, particularly in oligotrophic waters (Lasenby et al. 1986, Nero and Sprules 1986, Almond et al. 1996, Chipps and Bennett 2000). Higher temperatures in the epilimnion during summer stratification have commonly been thought to provide refuge for epilimnetic cladocerans (Morgan et al. 1981, Reiman and Falter 1981). However, that was not the case in White Partridge Lake, Ontario where epilimnion temperatures exceeding 20°C failed to provide an effective safety zone for epilimnetic cladocerans (Langeland et al. 1991).

Although relatively rapid growth rates were observed, negative r -values >0.70 resulting from the correlation between *Mysis* juvenile growth rate and estimated length on 1 October and mean summer temperatures in the surface to 10-m depth zone suggests growth may be compromised by their diel

vertical migrations. Peak feeding rates of, and presumably growth for *Mysis* occur at temperatures well below those they might encounter in Rainy Lake's epilimnion. Feeding rates for 13 to 16 mm and 10.5 mm *Mysis* were highest at 12°C and 14°C and were only 40% of the peak rates of larger *Mysis* at 18°C to 20°C. (Rudstam et al. 1999).

Juvenile growth rate and their estimated length on 1 October were also negatively correlated with adult and juvenile *Mysis* abundance, which were positively correlated with one another. A limited dataset with only five years of observations precludes stating with any certainty that this was a density dependent effect. However, Johannsson et al. (2011) observed that *Mysis* mortality rates in Lake Ontario were dependent on cohort density, and they suggested that competition for food limited abundance. However, first year growth was not altered.

Negative relationships between *Mysis* abundance and Rainbow Smelt and Cisco abundance were consistent with other field observations. *Mysis* have been identified as an important constituent of the smelt diet in glacial lakes (Evans and Loftus 1987) and was the dominant food item in Rainbow Smelt stomachs in Rainy Lake (Kallemeyn et al 2019). In one instance Rainbow Smelt predation kept mysid densities at a low level (Siegfried 1987), and in a Finnish lake such predation contributed to the collapse of the *Mysis* population (Horppila et al. 2003). *Mysis* were also an important item in the Cisco diet, occurring in 15% of 138 Cisco stomachs collected from Rainy Lake (Kallemeyn 2019). Cisco predation also occurred on *Mysis* in the Great Lakes and lakes in northern Saskatchewan (Dryer and Beil 1964, Koshinsky 1965). Although the correlation analysis did not suggest a relationship between *Mysis* and Walleye and Sauger abundance, *Mysis* were a dominant food item of smaller (<200 mm) Walleye and Sauger captured in the smelt netting program. From 1998 through 2002, *Mysis* were found in 79% of 846 Walleye/Sauger stomachs that contained food and comprised 63% of the total number of organisms found in the stomachs. Other fish species known to prey on *Mysis* in Rainy Lake include Yellow Perch, Trout Perch (*Percopsis omiscomaycus*), Burbot, Slimy Sculpin (*Cottus cognatus*), and Lake Whitefish (Kallemeyn 2019).

Conclusions

This five-year study characterized the *Mysis* population of the South Arm of Rainy Lake and provides data that can be used to evaluate future changes in that population and in the organisms with which they interact. Abundance and life history characteristics generally were similar to those observed for other *Mysis* populations. Although summer water temperatures in Rainy Lake are relatively warm compared to those in the Great Lakes and other lakes where *Mysis* have been intensively studied, they do not appear to be limiting the population. More detailed investigations and experimental studies are needed to gain a more thorough understanding of *Mysis* in Rainy Lake, particularly its trophic position and role in the food web.

To conduct such investigations and to address the spatial and temporal variation in abundance observed in this study may require other sampling methods in addition to vertical net hauls. Alternative sampling methods that have been used to estimate *Mysis* densities include optical plankton counters, laser optical plankton counters, and acoustics (Gal et al. 1999, Gal et al. 2006, Jensen et al. 2009). We attempted exploratory acoustic sampling at night in Rainy Lake in 1996, but it was unsuccessful due to an inability to differentiate *Mysis* from *Chaoborus*, which also are abundant and migrate vertically in the dark (Kallemeyn et al. 2003).

Integrated monitoring of *Mysis*, zooplankton, fish abundance and diet, and the physical environment are needed to assess the effects of stressors like climate change and invasive species on *Mysis*. Responses of boreal lakes such as Rainy Lake to climate change have been predicted to involve complex interactions between the effects of climate on temperature, hydrology, lake catchments, and in-lake processes (McKnight et al. 1996, Schindler et al. 1996, Stefan et al. 1996, McGinn 2002). *Mysis* in Rainy Lake appear to be particularly susceptible to thermal habitat reductions, given that only 17.7% of the South Arm is more than 20 m deep and provides *Mysis* habitat. Potential *Mysis* habitat is even more limited in the North Arm, where only 1,840 ha or 5.3% of the basin is more than 20 m deep (personal communication with Darryl McLeod, Ontario Ministry of Natural Resources). Paleolimnological analyses suggests that thermocline depth has increased substantially in some boreal lakes due to increased wind strength related to climate change (Saros et al. 2012). Any degree of warming that decreases the cold-water habitat could have a significant adverse effect not only on *Mysis* but also on cold-water fish species such as Cisco and Lake Whitefish.

At the time our study was conducted, the concern relative to invasive species in Rainy Lake was focused on Rainbow Smelt. In 2006, those concerns switched to the predatory cladoceran *Bythotrephes longimanus* that had recently invaded Rainy Lake and other lakes in Voyageurs National Park. While concerns regarding this zooplankter have primarily focused on its ability to alter species richness and composition of crustacean zooplankton (Yan et al. 2002, Strecker et al. 2006), mysids have also been found to be affected (Johannson et al. 2011). A study of zooplankton samples collected from Rainy Lake and other lakes in Voyageurs National Park pre- and post-*B. longimanus* invasion determined that cladoceran and cyclopoids had undergone serious population declines, and microcrustacean biomass was reduced 40%–60% (Kerfoot et al. 2016). Because our study was conducted prior to the *B. longimanus* invasion, conceivably the results might be used in a

similar pre- and post-invasion assessment to determine whether the Rainy Lake *Mysis* population has also been affected by the invasion.

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