Effect of Temperature on Feeding and Survival of *Mysis relicta*

Lars Gösta Rudstam*, Amy Lee Hetherington, and Ali Martonius Mohammadian

Cornell University Biological Field Station
Department of Natural Resources
Cornell University
900 Shackelton Point Road
Bridgeport, New York 13030

ABSTRACT. During their diel vertical migration, *Mysis relicta* can experience temperatures from 4°C to about 15°C. High temperatures may limit the ascent due to direct effects on survival or through decreased feeding rates. *Mysis relicta* survival (over 8 hours) was high up to 17°C (93%) and decreased with an increase in temperature over 18°C to 0% at 26°C. Feeding rates on newly hatched nauplii of *Artemia salina* were measured in 4-hour experiments at temperatures between 4 and 20°C. Feeding rates for 13 to 16 mm mysids were highest at 12°C and decreased at both higher and lower temperatures to 40% of peak feeding rates at 18 to 20°C and to 75% of peak feeding rates at 4°C. Smaller mysids (average length 10.5 mm) had peak feeding rates at 14°C. These results are consistent with field observations. Mysids seldom occur in temperatures above 15°C and smaller mysids are often found higher in the water column than larger animals. Consumption rates at both higher and lower temperatures were higher relative to peak consumption than assumed in a published bioenergetics model for *Mysis* (Rudstam 1989).

INDEX WORDS: *Mysis relicta*, consumption, mortality, temperature.

INTRODUCTION

*Mysis relicta*, the opossum shrimp, is a 15 to 20 mm animal common throughout the Northern Hemisphere (Lasenby *et al.* 1986). It is an omnivore that feeds on zooplankton, phytoplankton, and detritus (Grossnickle 1982) and is an important prey for planktivorous and young piscivorous fish (Larkin 1948, Rand *et al.* 1995). Predation by *Mysis* on zooplankton has resulted in dramatic and persistent changes in the zooplankton communities after the animals were introduced in lakes and reservoirs (Lasenby *et al.* 1986, Langeland *et al.* 1991, Martinez and Bergersen 1991). Mysids spend the day on the bottom or in deep water and ascend at dusk to the metalimnion and lower epilimnion to feed on zooplankton and/or algae when mortality risk from visually feeding predators is minimized (Ricker 1959, Beeton and Bowers 1982). The extent of the diel migration determines the overlap between mysids and their prey as well as the overlap between mysids and their predators (Shulze and Brooks 1987, Lehman *et al.* 1990). Understanding the factors controlling these migrations is therefore crucial for predicting both the predatory impacts of mysids on zooplankton and their availability as prey for fish.

Mysid ascent is reported to be limited by light as low as 10^{-2} to 10^{-4} lux (Teraguchi *et al.* 1975, Rudstam *et al.* 1989) and temperature above 16 to 20°C (Ricker 1959, Beeton and Bowers 1982). But the direct effects of temperature and light on mysid physiology and feeding rates are very different. High light levels are not harmful (DeGreave and Reynolds 1975) and feeding rates can be higher in dim light than in total darkness (Ramcharan and Sprules 1986). On the other hand, even moderate low temperatures can be lethal to cold adapted animals like *Mysis relicta*. Smith (1970) stated that the animals were adversely affected by temperatures above 10°C and DeGreave and Reynolds (1975) found increased mortality at temperatures above 13°C and an upper incipient lethal temperature of 22°C for *Mysis relicta*. These results were based on long term survival (several days) under small temperature increments (1 to 5°C per day). This is a much slower increase than would be experienced by mysids during their diel vertical migration. Temperature also affects feeding rates of animals. In—
Increased temperatures generally increase consumption rates up to an optimum temperature; further increase in temperature leads to a decrease in consumption. This is common in fish (Coutant 1977, Magnuson et al. 1979) and has been observed for several mysid species (Kuhlman 1984, Toda et al. 1987, Chipps 1998). Thus the occupied temperature can directly affect mortality and feeding rates of mysids whereas higher light levels indirectly affect mysid mortality by increased predation risk.

Although a number of authors have studied mysid feeding rates in the laboratory (Cooper and Goldman 1980, Folt et al. 1982, Mohammadian et al. 1997, Gorokhova and Hansson 1998), most studies were done at one temperature and little is known about the effect of temperature on feeding rate. In a bioenergetic model for mysids, Rudstam (1989) suggested that consumption rates of *Mysis relicta* peaked at 10°C then declined dramatically at temperatures above 12°C and ceased at 16°C. Only two experimental studies of the effect of temperature on feeding rate of *Mysis relicta* are known. Cooper and Goldman (1982) observed higher feeding rates of mysids at 5 than at 10°C and 15°C when using *Diaptomus* as prey but no effect of temperature with *Epishura* as prey. Chipps (1998) conducted long-term feeding rate experiments on *Mysis relicta* acclimated at 4, 10, 15, and 18°C and found highest feeding rates at 10°C (using *Daphnia* as prey).

In this paper experimental results on mysid survival at various temperatures and on the effect of temperature on 4-hour feeding rates are presented. These results are compared with the consumption curve suggested by Rudstam’s (1989) bioenergetic model for *Mysis relicta*.

**MATERIALS AND METHODS**

Live specimens of *Mysis relicta* were collected with a large plankton net (1 m diameter opening, mesh size = 500 µm) from Cayuga Lake, New York in early May and mid-June and from Lake Ontario in mid-July, 1996. The mysids were maintained in the laboratory at 10°C for the temperature tolerance experiments and at 4°C for the feeding rate experiments for several days to weeks prior to the experiments. Only apparently healthy individuals were used. The animals were transferred to the experimental aquaria with a spoon to minimize direct handling. Mysids were not fed for 12 hours prior to each feeding rate experiment.

Thermal tolerance experiments were performed on three occasions in a 10°C cold room. Lighting was provided by a 25 W red light, as *Mysis relicta* is insensitive to the red region of the visible spectrum (Beeton 1959). Twenty 3.6-L aquaria held one mysid each and were fitted with an 8″ automatic 50 W aquarium heater and an air stone. Mysids were held at 10°C prior to the experiment and transferred directly into the experimental chambers without prior acclimation. Five aquaria were maintained at each experimental temperature (10, 14, 18, and 22°C for the first run, 10, 15, 20, and 25°C for the second and third runs of experiments). Temperature and the state of the mysids were noted every 15 minutes during the first 2 hours and every hour thereafter for a total of 8 hours. The heaters maintained temperatures at the preset value ± 1°C for temperatures below 15°C and ± 2°C for temperatures 18°C and above. Experimental temperatures are calculated as the average of the temperature measurements during the 8-hour period in each individual aquarium. After the 8-hour period, the length of each mysid was measured from the tip of the rostrum to the tip of the telson.

Feeding rate experiments were also conducted in the cold room using the 3.6-L aquaria equipped with aquarium heaters. Brine shrimp nauplii (*Artemia salina*) were used as prey. Brine shrimp eggs were hatched at 25°C and nauplii separated from the cultures after 36 to 48 hours with the use of a dissecting microscope. The average size of these brine shrimp nauplii was 0.54 mm (SD = 0.10). Preliminary experiments indicated that about half of 200 brine shrimp would be consumed by one mysid in 4 hours. Prior to the experiments, *Artemia* were kept in the cold room at 4°C for 12 hours. Experiments were performed in the 4°C cold room where the mysids were kept. Mysids were transferred directly to the experimental temperature from a 4°C holding tank. Three runs of these experiments were performed with four replicates at each of 4, 8, 12, and 16°C. In addition, four replicates were conducted at 18°C during the first run and four replicates at 20°C in each of the two subsequent runs. Experiments were started in the afternoon. Four control aquaria without mysids were run for each of 4, 8, 12, 16, and 20°C to compare the natural mortality of the prey in the experimental chambers. *Artemia* mortality in these controls was below 2.5% at all temperatures and was therefore considered negligible.

The second set of feeding experiments was designed to test for differences in the response of small and large animals to temperature. Three runs
of 20 experiments were conducted at 10, 12, 14, 16, and 18°C. Four aquaria were kept at each temperature in each of the three runs, with two aquaria containing a large mysid (> 14 mm) and two containing a small mysid (< 13.5 mm). Thus, the total number of replicates per temperature class and mysid size class was 6 and the total number of experiments in the second set was 60. Two hundred brine shrimp were again added to each chamber.

Temperature and physical appearance of the mysids were noted every 15 minutes during the first 2 hours and every hour thereafter for a total of 4 hours. At the end of each experiment, all mysids were measured and the remaining brine shrimp frozen and counted within 24 hours. There was no mortality of mysids during these experiments.

Statistical analyses were performed on the number of brine shrimp nauplii consumed in 4 hours with standard ANOVA and Tukey’s pair-wise comparison (Systat, Wilkinson 1990). The first set of experiments was classified by temperature with mysid length as a co-variate. The second set of experiments was classified by both temperature and mysid size (small/large).

The total dry mass of prey ingested was calculated by using a value of 0.002 mg (measured length of 0.54 mm, Barata et al. 1996) for Artemia nauplii dry weight. Dry weight of the mysids was calculated from a length to dry weight regression for Lake Ontario mysids (Johannsson 1995). These values for 4-hour feeding rates were multiplied by 6 to get maximum 24-hour consumption rates to compare with the model presented by Rudstam (1989). The equation in Rudstam (1989) is for wet weight but it was derived from dry weight data presented by Cooper and Goldman (1980). To minimize errors associated with dry/wet weight conversions, Cooper and Goldman’s data were reanalyzed in dry weight to obtain the equation:

\[ C = 0.026 W^{-0.32} \]  

where C is consumption in g dwt/g dwt/day, W is mysid weight in g dry wt (from log-log linear regression: \( \ln(C) = -3.64 - 0.32 \ln(W), r^2 = 0.64, N = 11 \)). This equation is for maximum consumption at 10°C.

RESULTS

Temperature Tolerance Experiment

*Mysis relicta* showed strong signs of stress at temperatures over 22°C. These animals were lethargic and remained relatively motionless close to the bottom. In comparison, animals at temperatures of 21°C and below swam everywhere in the aquaria. Only 2 out of 30 mysids died after 8 hours at temperatures below 17°C. Mortality over 8 hours increased at higher temperatures to 40% at 18°C and 19°C, 60% at 21°C, and 80% at 23°C (Fig.1). At 25°C, all mysids died within 30 minutes of being introduced to the experimental chamber. There was no mortality within the first hour at temperatures at or below 17°C. The mysids used in these experiments ranged from 11 to 16 mm in length (average 13.4 mm, SD 1.1 mm, range 11 to 16mm, N = 60). There was no difference in length among temperature groups (\( F_{7.52} = 0.60, P = 0.76 \)), and no difference in length of surviving and dead mysids (\( F_{1.13} = 1.03, P = 0.33 \), temperatures 18 and 20°C).

Feeding Rates

Mysids fed aggressively on brine shrimp nauplii. As the live brine shrimp dispersed throughout the water, the mysids in all chambers moved in rapid, jerking motions to intercept them. After the brine shrimp nauplii had been present in the chambers for 20 minutes, a more continuous and passive method of feeding was observed. Mysids sometimes swam upside down near the surface of the water feeding on nauplii.

In both sets of feeding rate experiments, each run of 20 experiments (four replicates at five tempera-

![FIG. 1. Proportion of mysids surviving for 8 hours as a function of temperature. The number of replicates is indicated. All mysids died within 30 minutes at temperatures over 25°C. Survival is plotted against mean temperature observed during the experiment, not the target temperatures (see methods).](image-url)
tures) was first treated as a block in the ANOVA analysis. Because there was no significant block effect in either set of experiments (P > 0.05), the block variable was removed in subsequent analysis.

In the first set of experiments feeding rates at 4, 8, 12, 16, 18, and 20°C were investigated using sixty mysids with an average length of 13.4 mm (SD 1.0 mm, range 11 to 15.5 mm, N = 60). Temperature, but not mysid size, significantly affected feeding rate (single factor ANOVA with size treated as a co-variate). Peak feeding rates occurred at 12°C where the mysids consumed a mean of 120 brine shrimp in 4 hours (Table 1, Fig. 2). This represented 60% of the brine shrimp introduced to the experimental chamber. Feeding rate at 12°C was significantly higher than at 16, 18, and 20°C but not significantly higher than feeding rates at 4 and 8°C (Table 1, Tukey HSD pair-wise comparison with an experiment-wise error rate of 0.05, Wilkinson 1990).

The second set of feeding experiments investigated feeding rates at 10, 12, 14, 16, and 18°C using two size classes of mysids: larger mysids with an average length of 15.9 mm (SD 0.82 mm, range 14 to 18 mm, N = 30) and smaller animals with an average length of 10.6 mm (SD 1.55 mm, range 8 to 13.5 mm, N = 30). Temperature, mysid size, and their interaction term significantly affected feeding rate (two-factor ANOVA). Peak feeding rates of larger mysids occurred at 12°C and of smaller mysids at 14°C (Fig. 3). Larger mysids had significantly higher feeding rates at 12°C than smaller mysids and the opposite was true at 14, 16, and 18°C. Feeding rates of small mysids were significantly higher at 14 and 16°C compared to 10, 12, and 18°C whereas feeding rates of larger mysids were significantly higher at 12°C compared to 14, 16, and 18°C. Feeding rates of larger mysids at

### TABLE 1. ANOVA table for comparison of feeding rates at 4, 8, 12, 16, 18, and 20°C (13.4 mm, average length mysids). The model explained 74.5% of the variance in feeding rates (temperature explained 74%). Mysid length was treated as a co-variate and was not significant in this experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum-of-squares</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>F ratio</th>
<th>P level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>49,784</td>
<td>5</td>
<td>9,957</td>
<td>30.3</td>
<td>0.0001</td>
</tr>
<tr>
<td>Mysid length</td>
<td>54.8</td>
<td>1</td>
<td>54.8</td>
<td>0.167</td>
<td>0.684</td>
</tr>
<tr>
<td>Error</td>
<td>17,405</td>
<td>53</td>
<td>328</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results of Tukey HSD pair-wise comparison with an experiment-wise error rate of 0.05. Homogenous groups have the same super script.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Mean no. of brine shrimps consumed in 4 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>102 a,c</td>
</tr>
<tr>
<td>8</td>
<td>111 a,c</td>
</tr>
<tr>
<td>12</td>
<td>119 a</td>
</tr>
<tr>
<td>16</td>
<td>92 c</td>
</tr>
<tr>
<td>18</td>
<td>44 b</td>
</tr>
<tr>
<td>20</td>
<td>34 b</td>
</tr>
</tbody>
</table>

FIG. 2. Feeding rates of *Mysis relicta* measured as the number of brine shrimp nauplii consumed in four hours as a function of experimental temperature. Average size of the mysids was 13.4 mm. Each point represents results for one animal. Mean consumption at each temperature are joined with lines.
Effect of Temperature on Feeding and Survival of Mysis relicta

10°C were not significantly different from 12 or 14°C (Table 2, Tukey HSD pair-wise comparison with an experimental-wise error rate of 0.05). There was no difference in feeding rates between the larger mysids in the second set of experiments and the mysids in the first set of experiments (average length 13.4 mm).

Feeding rates were about twice those predicted by Rudstam’s (1989) bioenergetics model at the optimum temperature. The difference was larger at both high and low temperatures indicating that the shape of the temperature response of mysid consumption is not well described by that model (Fig. 4).

DISCUSSION

These experiments were conducted through June and July in a cold room set at 10°C (for temperature tolerance) and 4°C (for feeding rates). The animals were then introduced to the experimental chambers without previous acclimation to the experimental temperature. In the field, mysids can experience changes in temperature from 4°C to 15°C in as short a time as 10 minutes during their vertical ascent (Rudstam pers. obs.). The experimental protocol will therefore better mimic field conditions encountered by the animals over a diel cycle than experiments in which the animals are allowed to slowly acclimate to the experimental temperatures over a period of days to weeks. Relatively large aquaria (3.6 L) with one mysid each were used, which should minimize the effect of container size on mysid feeding rates and eliminate interference.

FIG. 3. Feeding rates for two size classes of Mysis relicta measured as the number of brine shrimp nauplii consumed in four hours as a function of experimental temperature. Average size of the mysids were 15.9 mm (large animals) and 10.6 mm (small animals). Each point represents results for one mysid. Mean consumption at each temperature are joined with lines (solid for large mysids and dashed for small mysids).

TABLE 2. ANOVA table for comparison of feeding rates between large (15.9 mm) and small (10.6 mm) Mysis relicta at different temperatures (10, 12, 14, 16, and 18°C). Temperature and mysid length explain 78.2% of the variance in feeding rates. The interaction is also significant. Feeding rates peak at 14°C for small mysids and 12°C for large mysids.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum-of-squares</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>F ratio</th>
<th>P level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>13,894</td>
<td>4</td>
<td>3,474</td>
<td>23.8</td>
<td>0.0001</td>
</tr>
<tr>
<td>Mysid size</td>
<td>821</td>
<td>1</td>
<td>821</td>
<td>5.6</td>
<td>0.021</td>
</tr>
<tr>
<td>Temp*Mysid size</td>
<td>11,419</td>
<td>4</td>
<td>2,855</td>
<td>19.6</td>
<td>0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>7,275</td>
<td>50</td>
<td>145</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results of Tukey HSD pair-wise comparison with an experiment-wise error rate of 0.05. Homogenous groups have the same super script.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Mysid size</th>
<th>Mean no. of brine shrimps consumed in 4 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Small</td>
<td>90 c,d</td>
</tr>
<tr>
<td></td>
<td>Large</td>
<td>111 a,b,c</td>
</tr>
<tr>
<td>12</td>
<td>91 c,d</td>
<td>122 a</td>
</tr>
<tr>
<td>14</td>
<td>121 a</td>
<td>97 b,c,d</td>
</tr>
<tr>
<td>16</td>
<td>115 a,b</td>
<td>81 d</td>
</tr>
<tr>
<td>18</td>
<td>82 d</td>
<td>52 e</td>
</tr>
</tbody>
</table>
between mysids. Cooper and Goldman (1982) found that mysid feeding rates increased with container size between 1 and 3 L but not between 3 and 17.7 L whereas Gorokhova and Hansson (1998) did not find significant container size effects on feeding rates for volumes between 1 and 8 L. *Artemia* were used as prey because they are easy to produce and readily eaten by mysids. The size of these crustaceans is similar to the size of crustaceans (*Dicyclops* and *Bosmina*) commonly consumed by mysids in Lake Ontario (Johannsson *et al.* 1994). Gorokhova and Hansson (1998) did not observe any differences in biomass consumed by *Mysis mixta* when fed *Artemia* nauplii compared to small *Daphnia magna*. The mysids depleted their prey from 200 *Artemia* per aquaria to about 100 per aquaria during the experiment. This probably had a minimal effect on feeding rate. Feeding rates calculated from preliminary experiments with an initial density of 100 *Artemia* per aquaria were only 1 to 25% lower than feeding rates with 200 *Artemia* indicating that predation rates are not markedly affected by a prey depletion from 200 to 100 *Artemia* per aquaria. Using a starvation period likely increased feeding rates compared to non-starved individuals (Gorokhova and Hansson 1998). However, mysids are likely feeding at lower rates on the bottom during the day than in the water column at night (Rudstam *et al.* 1989), and hence the experimental protocol is more realistic than feeding mysids prior to the experiments. All experiments were started in the afternoon and may be affected by diel rhythms in feeding behavior. However, Gorokhova (1998) found no diel pattern in feeding rates of *Mysis mixta* in similar experiments at 10°C. Finally, mysids from two populations, Cayuga Lake (for temperature tolerance experiments and preliminary feeding rate experiments) and Lake Ontario (the two sets of feeding experiments reported here) were used. These two populations experience similar temperatures throughout the year and both have an 18 to 24 month generation time (Johannsson 1995, Rudstam pers. obs.). Large differences in feeding rate were not observed between the preliminary trials (using Cayuga Lake mysids) and the results reported here (using Lake Ontario mysids).

The results on survival of *Mysis relicta* at different temperatures are similar to those reported by Smith (1970) and DeGreave and Reynolds (1975). They reported increased mortality at temperatures above 10 to 13°C and an incipient upper lethal level of 22°C from experiments in which temperatures in the aquaria were increased by 1°C to 5°C per day. Short-term survival at 18°C was 80% with a steep increase in mortality at higher temperatures. Mysids tolerated temperatures up to 17°C with an 8 hour exposure time and two out of five survived 8 hours at 21°C. Thus, both previous studies and these results indicate that short-term mortality is low up to 17°C and direct mortality should not limit mysid vertical distribution unless temperatures are above 18°C.

Feeding rates of *Mysis relicta* peaked at an intermediate temperature of 12 to 14°C. A dome shaped relationship of feeding rate to temperature has been hypothesized for *Mysis relicta* by Rudstam (1989) and observed by Chipp (1998) for *Mysis relicta* and by Kuhlman (1984) and Toda *et al.* (1987) for *Neomysis*. This type of relationship is common for fish (Hewett and Johnson 1992). Chipp (1998) used *Daphnia pulex* as prey and observed maximum feeding rates over a period of 5 days for mysids acclimated to the experimental temperatures. He observed slightly higher feeding rates at 10 than at 15°C but only about 50% of peak feeding rates at 18°C. These results are similar to those reported here and show an optimum temperature for consumption between 10 and 15°C. These results indicate that the decline in feeding rates at low temperatures is relatively small compared to the decline at high temperatures. Cooper and Goldman (1982) also observed minimal differences among feeding rates at 5, 10, and 15°C. Mysids need primarily to avoid high temperatures to maximize feeding rates during their diel vertical migration cycle. Avoiding low temperatures is less important.

Peak daily feeding rates calculated by expanding the 4-hour rates to 24 hours are higher than assumed in the bioenergetic model of Rudstam (1989, based on experiments by Cooper and Goldman 1980, Fig. 4). Part of this difference can be due to the expansion of the short-term feeding rates to 24h (Cooper and Goldman 1982, Gorokhova and Hansson 1998). However, when 200 brine shrimp nauplii were left for 8 hours with mysids in pilot experiments, almost twice the number were consumed than during 4 hours indicating continued high consumption rates at least over an 8 hour period (similar to the time the animals spend in the water column during the summer nights). Cooper and Goldman (1980) expanded 12 h feeding rate experiments to rates per 24 h. Predation rates are also affected by prey type (Cooper and Goldman 1982) and *Artemia* is likely an easier prey for mysids to catch than the larger copepods used by Cooper and Goldman (1980).
Effect of Temperature on Feeding and Survival of *Mysis relicta* of Hewett and Johnson (1992), the relationship for maximum consumption rates reflects the limitation of food intake due to the temperature dependence of digestion and growth processes and are generally measured with animals acclimated to the experimental temperature and fed *ad libitum* over several days. Results of such experiments for cold water fish like coregonids and gadoids (Binkowski and Rudstam 1994, Hansson *et al.* 1996) show stronger effects of low temperatures similar to Chipps’ (1998) observations for mysids. The results in this study are not directly comparable to the traditional bioenergetics model. However, it is possible that the results from this work are more appropriate than the bioenergetics model for understanding the effect of temperature on mysid feeding rates when they perform diel vertical migrations. Mysids moving up into the water column at night have spent the day in 4°C water and are not acclimated to higher temperatures. Gut evacuation rates will be slowed by low temperature for all mysids during the day. The 1-day time step used in the bioenergetic model of Rudstam (1989) and others may not be sufficiently small for analysis of the effect of temperature on feeding rates of a diel vertically migrating animal like *Mysis relicta*. It should be noted that Gorokhova (1998) recently showed that the bioenergetics model is appropriate for calculating consumption given observed growth at 10°C (the application of the model used by Rudstam *et al.* 1992 and Johansson *et al.* 1994), but the model has not been tested at other temperatures or with diel temperature cycles.

Declines of physiological rates at high temperatures and larger declines at low temperatures than predicted from standard equations for the effect of temperature on enzyme kinetics (first-order temperature effects) can be considered second-order temperature effects (Yurista 1999). For invertebrates that can be classified as cold stenothermal, the range of first-order effects is narrow and about 10°C. However, some glacial relicts appear to show first-order temperature effects over a larger temperature range. For example, there is no indication of second-order effects on *Limnocalanus* respiration from 0 to 15°C (Roff 1973). *Mysis relicta* may exhibit a similar large range of first-order temperature effects as little decline in feeding rates from 15 to 4°C can be seen. A wider range for first-order effects would be especially beneficial for a vertically migration species like *Mysis relicta*.

Feeding rates of smaller mysids peaked at a higher temperature (at 14°C) than feeding rates of these experiments and those of Chipps (1998) show considerably higher feeding rates at higher temperatures than assumed in the bioenergetic model (Fig. 4, Rudstam 1989). Although the peak feeding rate in the bioenergetic model (10°C) and in these experiments for larger animals (12°C) are similar, the bioenergetics model does not give a good representation of the temperature dependence of feeding rate. Mysids feed at rates of about 50% of their peak feeding rates at 18°C whereas the bioenergetics model predict feeding rates to be zero at temperatures above 16°C. At lower temperatures, the experiments and the results of Chipps (1998) differ. Higher feeding rates were observed at 4°C compared to the model whereas Chipps’ (1998) observed lower feeding rates compared to the model at that temperature. It is possible that the difference between Chipps’ (1998) results and those reported here is due to differences in experimental design. Chipps (1998) fed his mysids maximum rations for 5 days. In this study, feeding rates were observed during 4 hours using animals starved for 12 hours prior to the experiments. Chipps’ (1998) results are consistent with observation of faster gut evacuation rates of mysids at 10°C than at 4°C. In the bioenergetics modeling approach of Hewett and Johnson (1992), the relationship for maximum consumption rates reflects the limitation of food intake due to the temperature dependence of digestion and growth processes and are generally measured with animals acclimated to the experimental temperature and fed *ad libitum* over several days. Results of such experiments for cold water fish like coregonids and gadoids (Binkowski and Rudstam 1994, Hansson *et al.* 1996) show stronger effects of low temperatures similar to Chipps’ (1998) observations for mysids. The results in this study are not directly comparable to the traditional bioenergetics model. However, it is possible that the results from this work are more appropriate than the bioenergetics model for understanding the effect of temperature on mysid feeding rates when they perform diel vertical migrations. Mysids moving up into the water column at night have spent the day in 4°C water and are not acclimated to higher temperatures. Gut evacuation rates will be slowed by low temperature for all mysids during the day. The 1-day time step used in the bioenergetic model of Rudstam (1989) and others may not be sufficiently small for analysis of the effect of temperature on feeding rates of a diel vertically migrating animal like *Mysis relicta*. It should be noted that Gorokhova (1998) recently showed that the bioenergetics model is appropriate for calculating consumption given observed growth at 10°C (the application of the model used by Rudstam *et al.* 1992 and Johansson *et al.* 1994), but the model has not been tested at other temperatures or with diel temperature cycles.

Declines of physiological rates at high temperatures and larger declines at low temperatures than predicted from standard equations for the effect of temperature on enzyme kinetics (first-order temperature effects) can be considered second-order temperature effects (Yurista 1999). For invertebrates that can be classified as cold stenothermal, the range of first-order effects is narrow and about 10°C. However, some glacial relicts appear to show first-order temperature effects over a larger temperature range. For example, there is no indication of second-order effects on *Limnocalanus* respiration from 0 to 15°C (Roff 1973). *Mysis relicta* may exhibit a similar large range of first-order temperature effects as little decline in feeding rates from 15 to 4°C can be seen. A wider range for first-order effects would be especially beneficial for a vertically migration species like *Mysis relicta*.

Feeding rates of smaller mysids peaked at a higher temperature (at 14°C) than feeding rates of
larger individuals (at 12°C). This is consistent with observations that smaller mysids are higher in the water column than larger ones in the field (Grossnickle and Morgan 1979, Rudstam et al. 1989). Higher optimum temperature for feeding by younger individuals is common for fish (Hewett and Johnson 1992) but has not previously been reported for mysids. Thus, a deeper distribution of large compared to small mysids can be related to differences in optimum feeding temperatures in addition to the more common explanation of higher predation risk for larger individuals in the upper waters of lakes (Rudstam et al. 1989). These mechanisms are inter-related as increased predation risk in the upper water column may be the driving force for adaptation towards higher feeding rates of large mysids in cold temperatures.

ACKNOWLEDGMENTS

We thank Steve Chipps, Peder Yurista, Gary Sprules, and an anonymous reviewer for helpful comments on the manuscript. This paper is a result of research funded by the National Oceanic and Atmospheric Administration award # NA46RG0090 to the Research Foundation of State University of New York for New York Sea Grant. The US Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. Additional support was given by a summer internship from the Cornell Biological Field Station to ALH. This is contribution no 182 of the Cornell Biological Field Station.

REFERENCES


Chipps, S. R. 1998. Temperature-dependent consump-


Submitted: 4 March 1998
Accepted: 15 February 1999
Editorial handling: W. Gary Sprules