

Temperature-dependent consumption and gut-residence time in the opossum shrimp *Mysis relicta*

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Abstract. Maximum daily consumption was estimated for *Mysis relicta* fed *ad libitum* rations of *Daphnia pulex* at 4, 10, 15 and 18°C. Gut-residence time was also evaluated for *M. relicta* fed cladoceran prey at 4, 10 and 15°C. Mean daily consumption (g dry weight of *Daphnia* g⁻¹ dry weight of *Mysis* day⁻¹) ranged from 6% at 4°C to 12% at 10°C. At 18°C, *Mysis* feeding rate declined to 9% day⁻¹. Mean, weight-adjusted consumption rates exhibited a 'dome-shaped' response in relation to water temperature. Consumption rate was highest at 10°C and lowest at 4°C. Estimated Q_{10} was more sensitive from 4 to 10°C ($Q_{10} = 3$) than from 10 to 15°C ($Q_{10} = 1.2$). Gut-residence time for *Mysis* was inversely related to water temperature, implying that evacuation rate increases linearly with water temperature. Feeding and gut-evacuation rates become disassociated at water temperatures >10°C. As water temperature increased above 10°C, relative evacuation rate increased, whereas feeding rate declined. It is postulated that at higher water temperatures, disassociated feeding and gut-evacuation rates reduce the scope for growth of vertically migrating *Mysis* and impose a physiological constraint that isolates *Mysis* from warm, epilimnetic water during thermal stratification.

Introduction

The opossum shrimp *Mysis relicta* is an important zooplankton predator in lakes and reservoirs throughout North America and Scandinavia (Lasenby *et al.*, 1986; Rudstam, 1989). As an omnivore (Grossnickle, 1982), *Mysis* play an important role in aquatic food webs and can significantly alter zooplankton assemblages in non-native habitats (Richards *et al.*, 1975; Rieman and Falter, 1981; Lasenby *et al.*, 1986). Recent applications of a *Mysis* bioenergetic model (Rudstam, 1989; Johannsson *et al.*, 1994; Chipps, 1997) underlie the need to assess *in situ* feeding rates of mysids accurately. However, information concerning effects of water temperature on *Mysis* feeding and gut evacuation rate remains scarce (Rudstam, 1989; but see Murtaugh, 1984; Toda *et al.*, 1987). As a result, the temperature-dependent feeding rate for mysids has been approximated in bioenergetic models (Rudstam, 1989). Because output from these models can be sensitive to error in temperature-dependent functions (Bartell *et al.*, 1986), accurate quantification of *Mysis* feeding rate is needed to parameterize the model appropriately (Ney, 1993).

Knowledge of maximum daily ration can be useful for predicting optimal foraging temperatures (Binkowski and Rudstam, 1994) and estimating seasonal prey demand (Brandt *et al.*, 1992). Understanding the influence of water temperature on feeding and gut evacuation rates can facilitate knowledge of *Mysis* growth and distribution in the natural environment. For example, the nocturnal, vertical distribution of *M. relicta* is limited primarily by light intensity (Teraguchi *et al.*, 1975),

since *Mysis* generally avoid light levels above 10^{-4} lux (Rudstam *et al.*, 1989). However, the extent of the vertical, night-time distribution of mysids can also be limited by water temperature, particularly on dark, summer nights when lakes are thermally stratified (Beeton and Bowers, 1982; Lehman *et al.*, 1990). In general, adult mysids rarely migrate into strata where the water temperature exceeds 17°C (Rieman and Falter, 1981; Beeton and Bowers, 1982; Lehman *et al.*, 1990).

In this study, feeding rates were determined for *M.relicta* fed *ad libitum* rations of *Daphnia pulex* at water temperatures of 4, 10, 15 or 18°C. In a separate series of experiments, gut-residence time was assessed for *M.relicta* fed crustacean zooplankton at water temperatures of 4, 10 or 15°C. The objectives were to (i) evaluate temperature and allometric relationships associated with *Mysis* feeding and (ii) examine interrelationships between feeding and gut-evacuation rates across a range of water temperatures. Relationships between feeding and gut evacuation rates are summarized, and the physiological constraint imposed by water temperature on the vertical distribution of *M.relicta* is discussed.

Method

Two experiments were conducted to examine the effects of water temperature on feeding rates and gut-residence time in *M.relicta*. Mysids were collected from Lake Pend Oreille, Idaho, on 13 September 1996 with a vertical tow net (0.5 m diameter \times 2 m; 1 mm mesh), transported live to the laboratory, and transferred to 5 l jars filled with dechlorinated, pathogen-free well water. Rearing containers were maintained in a temperature-controlled water bath (2 \times 0.5 m trough) at 8°C for 2–4 weeks. The trough was covered to provide a dark environment (Smith, 1970; DeGraeve and Reynolds, 1975). As a food source, zooplankton were collected from Lake Pend Oreille and a local pond, and frozen in filtered lake water. Zooplankton were thawed and fed (pipetted) to mysids every 2–4 days.

To avoid effects of thermal stress, water temperatures were increased or reduced in the rearing trough at rates of 1–1.5°C day⁻¹ (DeGraeve and Reynolds, 1975; Binkowski and Rudstam, 1994). Mysids were maintained at experimental temperatures for 1–2 days prior to initiating experiments (Smith, 1970; Elliott, 1981). Experiments 1 (feeding rates) and 2 (gut-residence time) were conducted using the same experimental design, although dates and methodologies differed.

Feeding rates

Feeding experiments were initiated by pipetting individual mysids into 800 ml glass jars filled with 500 ml of dechlorinated water. Twelve mysids were used as replicates in each feeding experiment and a different group of mysids was used in each trial ($N = 48$). Mysids were starved for 3–4 days prior to beginning a feeding trial. Experiments were conducted for 5 days at water temperatures of 4, 10, 15 or 18°C.

Mysids were fed *ad libitum* rations of thawed *D.pulex*. The mean weight of *D.pulex* was estimated from length–dry weight regressions (Dumont *et al.*, 1975).

Based on a random sample, 40 *D.pulex* were measured to the nearest 0.0175 mm and individual dry weight (μg) estimated as:

$$\text{Dry weight} = 5.29L^{2.7} \quad (1)$$

where L is *Daphnia* length in millimeters. The mean dry weight of *Daphnia* used in the experiments was 0.026 mg (SE = 0.0011).

Mysids [0.001–0.01 g dry weight (wt)] were fed 0.0011–0.0017 g dry wt *Daphnia* day⁻¹. Mysids were reared in the dark and visually inspected once a day, at which time all uneaten *D.pulex*, along with mysid fecal pellets, were pipetted from jars. Uneaten *D.pulex* were enumerated and preserved in 4% formalin. At the end of each 5 day feeding experiment, individual mysids were pipetted from jars, blotted dry and weighed wet to the nearest 0.0001 g. Individual dry weights were obtained by drying mysids to a constant weight in a drying oven at 60°C. Mean daily consumption (g dry wt day⁻¹) was calculated for each mysid by averaging the biomass of consumed prey across all 5 days. Because *Mysis* consumption varies as an allometric function of weight, allometric dependency was removed by dividing absolute consumption by mysid dry weight (W) to the power of 0.41 (L.Rudstam, Cornell Biological Field Station, personal communication; Hewett and Kraft, 1993; this study). Using weight-adjusted consumption data, mean daily consumption (g day⁻¹ $W^{-0.41}$) was estimated at each water temperature. These data were used to calculate Q_{10} values associated with temperature-dependent feeding rates. Q_{10} values were calculated as:

$$Q_{10} = (k_2/k_1)^{(10/t_2 - t_1)} \quad (2)$$

where k_2 is the consumption rate at temperature t_2 and k_1 is the consumption rate at temperature t_1 .

Gut-residence time

Experiment 2 was initiated similarly to experiment 1 with the following exceptions: (i) individual mysids ($n = 21$) were pipetted into 21, 800 ml jars filled with 300 ml of dechlorinated water; (ii) mysids were starved 1–2 days prior to beginning experiments.

To quantify gut-residence time, an approach similar to that of Murtaugh (1984) was used. Naturally occurring, red *Diaptomus* copepods were used as food markers for observations of gut clearance in mysids. Gut-residence time was quantified at water temperatures of 4, 10 or 15°C and a new group of mysids used for each trial. For all trials combined, the dry weight of individual mysids ranged from 0.001 to 0.010 g. A variety of mysid body sizes were included in each experiment to examine relationships among water temperature, body size, ingestion rate and gut-residence time.

Mysids were fed 3–5 bright red *Diaptomus ashlandi*. After sinking to the bottom of the jars, thawed copepods were quickly attacked and consumed by most mysids. Mysids were incubated in the dark during each experiment, but

were visually checked every 30–45 min to verify stomach contents. Once a substantial amount of red *Diaptomus* remains could be identified in the stomach, any remaining *Diaptomus* were removed and mysids were immediately fed three *Simocephalus veretulus*, obtained from pure laboratory cultures. This cladoceran was used because of its relatively large size (mean dry wet wt = 0.030 mg, SE = 0.0024) and characteristic yellow–brown coloration, which could be easily distinguished in the gut once consumed by mysids. Consumed *Simocephalus* were replaced at 30–45 min intervals.

Gut-residence time for each mysid was calculated as the time interval between the first appearance of *Diaptomus* or *Simocephalus* material in the stomach and its first appearance in fecal pellets (Murtaugh, 1984). Fecal pellets were pipetted from jars and visually inspected under a dissecting scope to verify the predominant color of egested material. Experiments were ended when most mysids had produced light brown fecal pellets corresponding to *Simocephalus* remains (usually < 6 h). Individual mysids were then removed from jars, blotted dry and weighed wet to the nearest 0.0001 g. Dry weights of mysids were obtained by drying individuals to a constant weight at 60°C. Ingestion rates for *Simocephalus* were calculated as the total number of *Simocephalus* consumed divided by the time interval representing first offering of *Simocephalus* and the end of the experimental trial. Gut residence times were compared across water temperatures using analysis of variance (Statistical Analysis Systems Institute Inc., 1987).

Results

Feeding rates

Mean, specific consumption rate (g dry wt prey g⁻¹ dry wt *Mysis* day⁻¹) ranged from 6% at 4°C to 12% body weight at 10°C (Table I). On average, individual *Mysis* consumed between 11 and 23 *Daphnia* day⁻¹ at water temperatures ranging from 4 to 18°C.

Specific consumption rate varied similarly with *Mysis* mass across the range of water temperatures examined (covariance analysis, homogeneity of slopes, $P = 0.1$; Figure 1). Maximum consumption (C_{max} ; g g⁻¹ day⁻¹) at 10°C was described by the log–log least squares regression equation:

$$C_{max} = 0.005W^{-0.59} \quad (3)$$

Table I. Mean mass and daily consumption (1 SE) for *M. relicta* fed *ad libitum* rations of *Daphnia* at 4, 10, 15 and 18°C

Water temperature (°C)	Mean <i>Mysis</i> mass (g dry wt)	<i>n</i>	Mean daily consumption (mg dry wt)	Mean specific consumption (g g ⁻¹ day ⁻¹)
4	0.0005 (0.0009)	12	0.30 (0.05)	0.062 (0.008)
10	0.0005 (0.0006)	11	0.65 (0.03)	0.120 (0.008)
15	0.0004 (0.0005)	8	0.50 (0.06)	0.119 (0.015)
18	0.0006 (0.001)	6	0.40 (0.05)	0.090 (0.029)

Consumption and gut-residence time in *Mysis relicta*

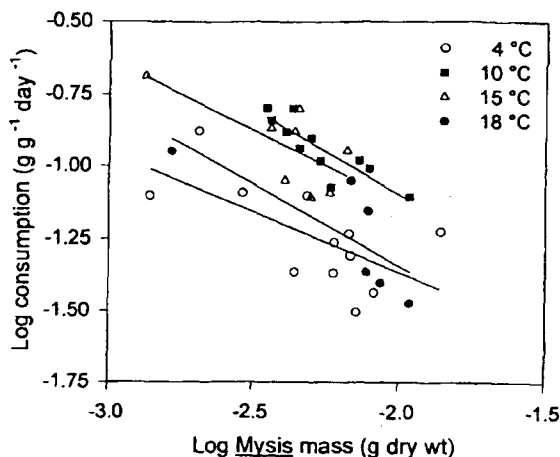


Fig. 1. Allometric relationships between maximum daily consumption and body mass for *M. relicta* fed *ad libitum* rations of *D. pulex* at 4, 10, 15 and 18°C.

where W is *Mysis* dry mass in g ($r^2 = 0.75$, $n = 11$). Estimates of maximum daily consumption at 10°C ($0.12 \text{ g g}^{-1} \text{ day}^{-1}$; Table I) were similar to those reported by Cooper and Goldman (1980). In wet weight form, intercept (0.05) and exponent (-0.414) values were similar to those reported by Rudstam (1989) for estimates of maximum daily consumption.

Mean, weight-standardized consumption rate increased from 0.0026 at 4°C to $0.0053 \text{ g day}^{-1} W^{-0.41}$ at 10°C, then declined to 0.003 at 18°C (Figure 2). Q_{10} sensitivity was higher in the range of 4–10°C ($Q_{10} = 3$) than from 10 to 15°C ($Q_{10} = 1.2$). Weight-standardized, daily consumption differed significantly across water temperatures (analysis of variance, $P < 0.0001$, d.f. = 3), and was lower at 4 and 18°C than at 10°C (Figure 2). Mortality of *Mysis* during the 5 day feeding experiment increased with water temperature. Final mortality ranged from 0% at 4°C to 50% at 18°C (Table I).

Gut-residence time

Initial quantification of *Diaptomus* passage times was met with mixed success. Although red *Diaptomus* remains could be easily observed in the stomach once consumed, definitive observation in initially egested fecal pellets was more difficult. Mixing of red *Diaptomus* remains with material already present in the guts of many mysids made differentiation of initially egested fecal material difficult. In contrast, yellow-brown material associated with *Simocephalus* remains could be tracked through the gut and easily differentiated from previously egested red (or dark) fecal material. Hence, results are presented based on *Simocephalus* prey, since gut-residence times associated with this prey type were more reliably quantified.

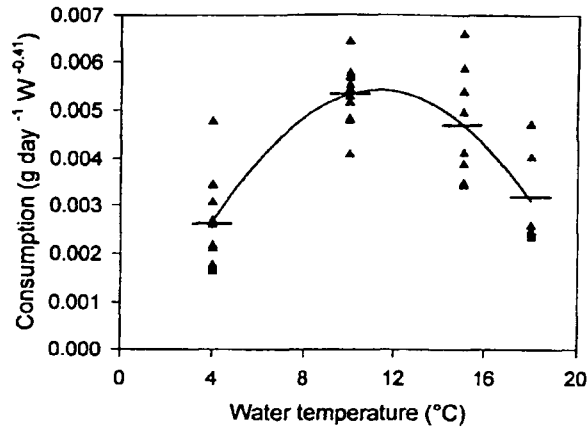


Fig. 2. Weight-standardized, daily consumption for *M. relicta* fed *ad libitum* rations of *D. pulex* at 4, 10, 15 and 18°C. Horizontal bars represent mean values. The solid line was fitted to a polynomial regression where consumption (C) was estimated as a function of water temperature (T) using the equation: $C = -0.00119 + 0.001169T - 0.0000517T^2$ ($r^2 = 0.64$).

Positive correlations were observed between absolute consumption rate (no. *Simocephalus* h⁻¹) and body weight (g wet wt) for *Mysis* incubated at 4 ($r = 0.65$, $P = 0.002$, $n = 19$), 10 ($r = 0.49$, $P = 0.04$, $n = 18$) and 15°C ($r = 0.49$, $P = 0.08$, $n = 13$). Gut-residence time, however, was not significantly correlated with *Mysis* mass at 4 ($r = -0.28$, $P = 0.23$, $n = 19$), 10 ($r = 0.15$, $P = 0.57$, $n = 15$) or 15°C ($r = 0.07$, $P = 0.80$, $n = 13$). Similarly, gut residence time, although generally inversely related to ingestion rate at 4, 10 and 15°C ($r = -0.31, -0.22, 0.3$), was not significantly correlated to consumption (correlation analysis, $P = 0.18, 0.41, 0.26$).

Water temperature had a significant effect on mean gut-residence time (analysis of variance; $P < 0.0001$, d.f. = 2; Figure 3). At 4°C, mean gut-residence time for *Simocephalus* prey was 4.6 h compared to 3.1 h at 10°C and 2.0 h at 15°C. For the range of *Mysis* sizes used, gut-residence time (GRT) can be estimated as a function of water temperature using the equation:

$$\text{GRT} = 10.367T^{-0.580} \quad (4)$$

where T is water temperature (°C) and 10.367 and -0.580 are regression coefficients.

Discussion

Water temperature had a significant effect on *Mysis* feeding rate and gut-residence time. Feeding rate exhibited a dome-shaped response in relation to water temperature and was higher at 10–15°C than at 4 and 18°C. In fish, temperature-dependent consumption is typically characterized by a dome-shaped response similar to that observed here for *M. relicta* (Kitchell *et al.*, 1977; Binkowski and Rudstam,

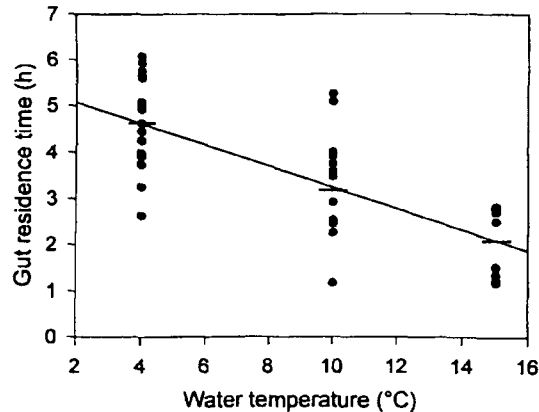


Fig. 3. Relationship between gut-residence time and water temperature for *M. relicta* fed *Simonecephalus veretulus* at 4, 10 and 15°C.

1994; Hayward and Arnold, 1996). Other studies report similar findings in that feeding and growth rate of mysids can be negatively affected at high water temperatures (Cooper and Goldman, 1982; Toda *et al.*, 1984, 1987).

In the natural environment, *Mysis* can experience a wide range of daily temperatures (4–20°C) due to extensive diel vertical migrations. In this study, the Q_{10} value from 4 to 10°C ($Q_{10} = 3$) was within the range (2.6–3.9) reported for feeding rates by *Neomysis intermedia* (Toda *et al.*, 1987). However, recent evidence from feeding studies that mimicked the natural daily thermal regime experienced by *Mysis* indicate a Q_{10} value closer to 2 (L.G. Rudstam, A.L. Hetherington and A.M. Mohammadian, unpublished data). By acclimating *Mysis* to constant temperatures, Q_{10} sensitivity from 4 to 10°C may vary from that exhibited by vertically migrating mysids in the natural environment.

The mortality rate of mysids increased with increasing water temperature. DeGraeve and Reynolds (1975) reported similar findings and suggested that the mortality rate of *M. relicta* increases linearly from 15 to 25°C. Despite increased mortality, however, *Mysis* continued to feed at 18°C. As a result, the upper thermal maxima in the *Mysis* bioenergetic model should be extended beyond 16°C, since this value represents cessation of *Mysis* feeding (see Rudstam, 1989).

Gut-residence time for *M. relicta* was inversely related to water temperature, suggesting that absolute gut evacuation rate increases with increasing water temperature. Studies describing effects of water temperature on gut-residence time in mysids are scarce. For many aquatic invertebrates, gut-residence time decreases with increasing water temperature (Fedorenko, 1975; Welton *et al.*, 1983; Murtaugh, 1984). Murtaugh (1984) observed variable gut-residence time (1.1 to >11 h) for *N. intermedia* fed *Daphnia* at 10°C. He concluded that gut-residence time depends on feeding activity and relative stomach fullness, which may invalidate attempts to estimate mysid feeding rates using gastric evacuation models (Elliott and Persson, 1978; Murtaugh, 1984).

Gut-residence times observed in this study were less variable (SE range 0.215–0.287) than those reported for *N.intermedia* fed *Daphnia* at 10°C (SE = 0.563; Murtaugh, 1984). Acclimation conditions and starvation periods differed between this study and that of Murtaugh (1984), and may help explain differences in variation. In this study, for example, *Mysis* were fed natural *Diaptomus* prey prior to initiating experiments and were acclimated to laboratory conditions for 2–4 weeks prior to experiments. In contrast, *N.intermedia* were fed diaptomid copepods collected from a saline lake and were used in experiments within 24 h after capture (Murtaugh, 1984). Factors such as relative stomach fullness (Murtaugh, 1984) and starvation period (Windell, 1967; Persson, 1979) are known to affect gut-residence time and can contribute to variability in these estimates. Variation in gut-residence time may also be related to interspecific differences between *N.intermedia* and *M.relicta*. *Neomysis intermedia* is tolerant to a wider range of water temperatures (0–30°C; Toda *et al.*, 1987), whereas *M.relicta* typically avoid water temperatures >17°C (Beeton, 1960; Smith, 1970). Food quality can also affect feeding and gut-residence time of aquatic animals (Brett and Higgs, 1970; Persson, 1979). In this case, qualitative differences between *Simocephalus* and *Daphnia* prey may contribute to variability associated with gut-residence time in mysids.

Feeding and gut evacuation rates are important components affecting the scope for growth of aquatic animals (Brett and Higgs, 1970). Although feeding rates of mysids declined as water temperature increased above 10°C, gut evacuation rate (mass or number of *Simocephalus* egested h⁻¹) continued to increase (Figure 4).

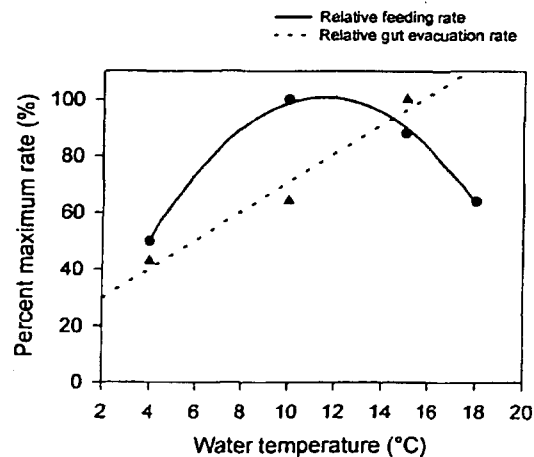


Fig. 4. Relationship between relative feeding and gut evacuation rate with increasing water temperature. Rates are expressed as a percent of the maximum observed rate and demonstrate the dissociation between feeding and evacuation rate at water temperatures >10°C. Solid circles represent feeding rate, whereas triangles represent relative gut evacuation rate.

At temperatures from 4 to 10°C, the feeding rate is likely limited by temperature-dependent processes associated with digestion and growth (Brett and Higgs, 1970; Berrill and Lasenby, 1983). However, at higher temperatures, disassociation between feeding and the gut evacuation rate suggest that mechanisms other than the digestion rate limit the feeding rate of *Mysis*. One explanation may be that, at higher temperatures, increased metabolic demand, coupled to activity costs associated with capturing and handling prey, combine to suppress feeding rates of *Mysis*. In sockeye salmon *Oncorhynchus nerka*, for example, appetite and conversion efficiencies were significantly reduced at water temperatures from 20 to 24°C (Brett and Higgs, 1970). Hence, at higher temperatures, the capacity to consume and digest food was not accompanied by growth since metabolism, maintenance ration and excretion all combined to suppress growth rate (Brett and Higgs, 1970).

For *Mysis*, reduced appetite and increased metabolic rate at higher water temperatures lead to disassociated feeding and gut evacuation rates that likely reduce scope for growth. As a result, foraging in water temperatures of >15°C for extended periods of time may be energetically costly for *Mysis*, regardless of prey density. Disassociation of these rates represents a physiological constraint that limits the summer vertical distribution of *Mysis*. In addition, thermal stress associated with higher water temperatures (>18°C) can lead to appreciable mortality of *Mysis* and contribute to behavioral avoidance of epilimnetic strata.

Acknowledgements

This paper benefitted from discussions with Elena Gorokhova, Lars Rudstam, David Bennett, Ora Johannsson, James Congelton and an anonymous reviewer provided helpful comments that improved the manuscript. I thank C. Michael Falter and Christine Moffitt for use of laboratory equipment. Michelle Bouchard and Catherine O'Brien provided much technical assistance with the study. This work was supported, in part, by a University of Idaho research assistantship provided to the author.

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Received on July 20, 1997; accepted on August 11, 1998