

ASTA AUDZIJONYTĖ (VILNIUS UNIVERSITY, LITHUANIA)
2001 03 23

EFFECTS OF TEMPERATURE ON BIOENERGETICS OF MYSIDS

A few remarks on the essay:

This essay is only the first my attempt to analyze numerous data about mysids bioenergetics and evaluate it in the light of DEB assumptions. The aim of the essay was to study several papers, which did not seem to correspond to DEB. Therefore, I could not avoid the detailed analysis, which might be difficult to read if you are not familiar with the discussed papers. You may skip the experimental details (notes about the study) and read assumptions and conclusions of each paper.

INTRODUCTION

Mysis relicta spp. is the glacial relict crustacean group inhabiting fresh waters of Northern Hemisphere and along with *M. mixta* also the Baltic Sea. The factors limiting distribution of these crustaceans were discussed widely, pointing first, the post-glacial history and available routes for colonization of lakes and secondly, prevailing environmental conditions and ecological niche of mysids. These mysids have traditionally been considered a relict organism, able to survive only in cold, well-oxygenated water. The eutrophication of lakes at the southern border of *M. relicta* spp. distribution is assumed to be the main reason, driving these species to extinction. On the other hand, *M. relicta* spp. were introduced to many Scandinavian and N. American lakes to provide food basis for fish. The results of introductions were, however, controversial. In many cases mysids turned out to be severe competitor with fish for zooplankton and were able to extirpate some zooplankton species. There was a great reduction in fish catches, leading even to courts against introductions. At that time it was realized that mysids might play a key-role in food webs, which enhanced quantitative approach and development of bioenergetic models. A vast amount of studies was carried aiming to evaluate predatory effects of mysids, competition with fish and their energy budgets. In this essay I will analyze several studies on mysids bioenergetics - the results and conclusions will be opposed to Dynamic Energy Budgets (Koojiman 2000) assumptions.

Assumptions and conclusions:

1. "...mysid is the most metabolically efficient in cold temperatures, regardless of food supply..." (p. 156), at lower temperatures mysids accumulate lipids at costs of lower growth rate (Chess & Stanford 1999) – these lipids were then assumed to increase reproduction capacity at low temperatures.
2. At higher temperatures feeding rate (dome-shaped response) decreases, but gut evacuation rate (power function – almost linear response) increases and this disassociation might define temperature tolerance ranges of mysids. Gut residence time was not correlated to consumption rates. (Chippis 1998)
3. The bioenergetic model for *Mysis* growth and consumption – very different responses of consumption (dome-shaped) and respiration (exponential) to temperature (see Fig.2) (Rudstam, 1989). Application of the model to particular population requires precise estimation of the temperatures as the energy conversion efficiency becomes very sensitive to the temperature.

DEB assumptions:

1. "If each reaction was depended in a different way on temperature, cells would have a hard time coordinating the different processes at fluctuating temperatures" (To describe rates of processes within an acceptable range of temperatures, the same Arrhenius relationship can be applied) – DEB, p. 54
2. Gut residence time depends on the body volume and ingestion rate – it decreases for increasing ingestion rate and is minimal at scaled feeding response $f=1$ – DEB, p. 80-82, 240.
3. It is assumed in DEB, that the most important parameters describing energy budget of organism are maximum specific ingestion rate, maximum volume, kappa and some others (?). In the range of temperatures, organism is adapted for, these parameters should change in a concordant manner and hence the total organism investment in growth and reproduction should depend only on available food and remain constant among populations.

The possible implications of the first set of assumptions:

First of all it is clear that there is much of inter-population variability in the annual temperature, mysids endure. *Mysis relicta* spp. have wide adaptation abilities, being classified as stenothermal as well as eurythermal organism, indicating the upper temperature limits from 14 to 22 C (Samter & Welter 1904, Ekman 1920, Gordeev 1951, Ricker 1953, Holmquist 1959, Bowers & Grossnickle 1978, Morgan 1978, etc....). The more appropriate measure should probably be the preferred temperature or the temperature that the populations encounter for the longest periods and here three groups can be distinguished

- a) The arctic or very deep, oligotrophic lakes' populations, where mysids most of the time stay at 3-5 C (Arctic lakes – Char, Greenland costs), also 7 C in Paajarvi (Hakala 1978), S. Volos (Suschenia 1986).
- b) The population of temperate lakes, experiencing daily fluctuations in temperature during the vertical migrations (mainly from 4-5 to 17-18C or even more).
- c) Populations of shallow lakes, which are well mixed in summer time and thus in summer temperature is constantly about 18 C (Dadswell 1974, Furst 1972, Kinsten 1986-1994, pers. comm., Håkan Turesson, pers. comm.).

In addition to inter-population variability, the analyzed group comprises several species. *Mysis relicta* spp. group consists of at least four sibling species with likely different histories and environmental preferences. *M. mixta* is yet another species.

In this essay, as in many bioenergetic studies, I will treat these species of mysids as similar ones. All of them were assumed to have similar response to temperature and at the moment it seems to be

difficult to evaluate how much of these adaptations are population- or species-specific. So, to increase the amount of available experimental data I will pool these species.

This does not imply they are the same – the differences remain to be uncovered.

QUESTION A: Do all the mysid populations have essentially the same energy budgets, as expressed by maximum ingestion rates, corrected for temperature, maximum body volume, energy conversion efficiencies, and energy allocation for growth vs. reproduction (κ)?

Yes, if temperature adaptations are concordant in all the processes, so that only the optimum temperature and thus the peak of the temperature curve is different (Fig. 2.18 in DEB book). If it is so, the precise estimation of mysid temperature history is not needed – the consistent value of energy conversion efficiency can be used, assuming that mysids in nature stay at the temperature they are adapted for.

No, if different strategies are adopted and consumption/"energy gain" rate is uncoupled with respiration/"energy use" rate. In this case we expect different assimilation efficiencies among arctic and temperate populations and in some cases also different investment in reproduction.

QUESTION B: Different curves of response (respiration, ingestion and gut residence time) to temperature have been obtained, resulting in uncoupled physiological processes and leading to "food-limitation" at higher temperatures. Are these curves applicable to natural conditions?

Yes, if experimental conditions for analysis of different responses are comparable and animals were adapted to experimental temperature.

No, if food-limitation was really possible in the laboratory conditions at higher temperature, so that consumption measure was not adequate, or mysids were not adapted to experimental temperature.

METHODS

The essay will be based on three already mentioned papers, including also additional published experimental data and application of bioenergetic models (Lasenby & Langford 1972, Sandeman & Lasenby 1980, Cooper & Goldman 1982, Halfon et al. 1996, Gorokhova 1999 PhD theses, ...).

I will analyze methods and the basic conclusions of the papers I-III in the light of the raised questions A and B.

RESULTS AND DISCUSSION

Paper I (Chess & Stanford 1999)

The paper aims to give theoretical explanations to the success and sudden increase of mysid populations after introductions, and their ability to alter food web (also analyzed in Chess & Stanford 1998). The authors rely on McLaren hypothesis (1963) on the energetic benefit of diel vertical migrations. They conclude that irrespective of food density the highest accumulation of lipids occurs at low temperatures and this might have implications for mysids reproductive success in the lakes where they perform diel vertical migrations.

- NOTES ABOUT METHODS: Mysids were collected from Flathead lake. Mysids were introduced into this lake from Waterton Lake. Flathead is a deep, oligotrophic lake, mysids migrate up to 14-15 C isocline in summer. For experiments mysids were collected from 110 m point, stored at 8 C, temperature changed by 0.5C/hour to the experimental temperature of 4, 8, 14, 20 C. Experiments were conducted in 1.5 L chambers, 10 mysids in each. Mysids were fed every second day with 0.5x, 1x and 2x densities of zooplankton, collected from the lake (from 30 m to surface) and acclimated for experimental temperatures in the same way. So, qualitatively, all the mysids were fed the same food and only quantity of the food was different. There was 12 different experimental conditions (0.5X, 1x and 2x food each for 4 temperatures).

NOTES ABOUT THE STUDY:

- a) There were no controls with ample food and the exact number of zooplankton consumed was not estimated. Actually it was showed that regardless of temperature and prey density FOR ALL EXPERIMENTAL SETS ALL THE GIVEN PREY WAS EATEN. This implies constant food limitation and hinders any conclusions about different strategies of energy allocation – at 4 C and 2x food density both biomass and percentage of lipid accumulated was the highest and this only shows that these animals had least food limitation. The second least food-limited sample is 8C with 2x densities if we assume approximate Q_{10} of 2-3 (the consumption in t difference of 4 C should increase up to 1.5 times and food was increased twice). Q_{10} refers to van't Hoff coefficient, which shows the increase in the rate of process/reaction with the increase of temperature at 10 C. At higher temperatures mysids might have been more limited by food and therefore did not accumulate lipids. The mortality at 14 and 20 C was very high, indicating that animals were not adapted to these temperatures and in most cases results from these sets were not presented. The amount of lipids accumulated in all the cases, except 4C and 2x food, was less than 20%. Throughout the year in Flathead Lake mysids usually have >20% lipids, however (Chess & Stanford 1998), which also might indicate food limitation in the experiment.
- b) Container effect must have been strong in the experiments, as 10 mysids were kept in 1.5 L container. It was indicated by Hansson et al. (in Gorokhova 1999) that interference among mysids occurred at the density of 20 mysids in 26.6 L, and their feeding rate was smaller to compare to 10 mysids/26.6 L. The container effect should be stronger at higher temperatures, as metabolism is increased.
- c) It was also indicated that feeding rate depends on prey escape response (Cooper & Goldman 1982), which must have been clearly lower at low temperatures. The prey response, however, might not have important effect in this case, as all the prey was consumed, unless the costs of foraging were important.
- d) No variance of calculated biomass, lipid density or energy conversion efficiency (ECE) values was presented in the paper, so it was impossible to trace back the variation and significance of the estimates. ANOVA to test the effect of prey and temperature was presented for all groups pooled and again individual variation remained unknown.
- e) The experimental design does not seem to test McLaren hypothesis, as animals were subjected to constant temperature and the results of coupled higher consumption at high t with assimilation at low t were not tested.

In conclusion, the results of the paper do not seem to confirm hypothesis on different energy assimilation efficiencies and different allocation strategies in the temperature gradient. Most of the differences could have been explained by the amount of available food (functional feeding response). Different allocation strategies are not needed to explain different fecundity of mysids in Flathead and Waterton Lakes either (Chess & Stanford 1998) – it was actually indicated that the experienced temperature is the same in two lakes and only amount of food consumed can explain higher size and fecundity in Flathead lake.

The McLaren hypothesis itself is a matter of dispute. It was shown that sculpins actually behave opposite – they feed in cold water and migrate to warm water to digest and thus gain more energy (Wurstbaugh & Neverman 1988, Hammar 1996).

If, however, we accept the conclusions of the authors that at low temperature mysids have different allocation strategies and accumulate more lipids instead of increasing body size to gain reproduction advantage – fecundity/egg size should be higher in arctic vs. temperate mysids at the same body size. This was not indicated by Lasenby & Langford 1972, Beeton & Gannon 1991 and also will be discusses later in this essay (Fig. 3 in this essay) – the correlation between brood size and length of female is best explained by lake productivity and thus functional feeding response.

Paper II (Chipps 1998)

Important conclusion is that consumption rate has a dome-shaped response curve, whereas gut evacuation rate increases to the power function. This implies that at some certain temperature relative gut residence time is the highest as well as food assimilation efficiency, whereas with the increased temperature assimilation efficiency should decrease, because gut evacuation rate is uncoupled to consumption (if assimilation efficiency is directly related to gut residence time).

- NOTES ABOUT METHODS: The natural conditions of the lake (Pend Oreille, Idaho) were not described, so it is not clear what conditions mysids have been adapted to. Before experiments animals were kept at 8C for 2-4 weeks, temperature changed 1-1.5 C/day and adaptation to experimental temperature (4, 10, 15, 18C) was allowed for 1-2 days. Consumption at these four temperatures was measured for a wide mysid size ranges. Gut evacuation rate was measured at 4, 10 and 15 C. To compare specific consumption, the individual consumption was divided by mysid $DW^{0.41}$.

NOTES ABOUT THE STUDY:

- a) There is a mistake in Table 1 – mean *Mysis* mass is 10 times smaller (0.0005 g instead of 0.005 g).
- b) Standardization of specific consumption by $DW^{0.41}$ seems to be artificial and it did not give good results for another experimental set on *M. mixta* consumption (Gorokhova 1999). It was shown in DEB that consumption is proportional to surface area and standardizing by square of total length (TL^2) or $DW^{2/3}$ gave different results. The individual consumption standardized by TL^2 for *M. mixta* decreases with the size by 15 % (0.1-8 mg DW and 3.6-15 mm TL) whereas if standardized by $DW^{0.41}$ it increases 250 % (calculations are presented upon request).
- c) I have standardized the mean specific consumption, given in Table 1 in Chipps 1998, by surface area (Total length estimated from DW, assuming $DW=0.15 \times WetW$ and shape correction function 0.24 for WW or 0.13 for DW). The obtained specific consumption values were highest at 15 C and not for 10 C, as concluded by Chipps (Fig. 1).
- d) Gut residence time (GRT) was measured at three temperatures 4, 10 and 15 C and allometric equation presented, also indicating that gut residence time was not correlated to consumption. However, it was not indicated to what measure of consumption GRT was compared (absolute or standardized from the first experiment on consumption or to some consumption estimate in the same experiment on GRT).
- e) The scaled response to temperature of surface-area standardized consumption and gut evacuation rate ($GER=1/GRT$) both increased with increased temperature up to 15 C (Fig.1 in this essay). The extrapolation of GER above this temperature range can not be performed, because mysids apparently were not adapted to higher temperature, as indicated by sharp decline in consumption (the same sharp decline at 18 C could have been observed for GER, but it was not measured).

To conclude, the results do not seem to confirm the hypothesis of uncoupled feeding and GER at higher temperature. The both scaled responses increased for temperature values 4-15 C. Calculated Q_{10} between 4 and 15 C for both feeding and GER is similar (2.0 and 1.8). This coefficient is, however, different for two temperature intervals 4-10 and 10-15 C: 3 and 1.3 for feeding and 1.7 and 2 for GER. In principal, it is reasonable to assume that GER for the temperature-adapted animals depends on ingestion rate, which is consistent with DEB and also observed by Murtaugh (1984). This implies that also energy conversion efficiency should be similar in the range of reasonable temperatures. Energy conversion efficiency can of course depend on other things, additionally to ingestion and gut evacuation rate. However, only these two aspects are taken in this paper and also analyzed here.

As a practical implication of the conclusions from the paper, one can also think of migrating mysids – they often forage in the surface water of 14-15 C and stay there for several hours. The disassociated consumption and GER should be very costly and restrict them from such temperatures. More experimental data of consumption and GER under different temperature and food densities is needed to test the raised hypothesis. If, however, such uncoupling is taking place at 14-15 C,

assimilation efficiency and composition of faeces should differ at different temperatures (I am not aware of such experimental data).

Paper III (Rudstam 1989). The bioenergetic model for mysids was presented in 1989 and later used to estimate consumption of *M. relicta* in Kootenay lake (Kokanee population restoration project by lake fertilization, Ashley et al. 1996-1999?), Ontario and Michigan Lake (Johannsson et al. 1994), the Baltic Sea (Mohammadian et al. 1997).

- NOTES ABOUT METHODS: Assumptions: egestion=15% of consumed food energy, excretion=18% of assimilated food (includes 10 % of excretion and 8 % of moulting costs) and specific dynamic action (SDA) =18 % of assimilated food. Model is based on two response curves to temperature – consumption (dome-shaped) and respiration (exponential) (Fig. 2 in this essay).

NOTES ABOUT THE STUDY:

- a) The respiration curve was obtained from Sandeman & Lasenby 1980: The experimental animals in that study were collected from Kootenay Lake and kept at 5C for up to three days. The experimental temperature (5, 10, 15C) was reached over the period of several hours, acclimatization allowed for 1 h before experiment. Kootenay Lake is a deep lake, in the summer time surface temperature reaches 17-18 C, without sharp thermocline (Ashley et al. 1999). Therefore the experimental temperatures are in the range mysids encounter during vertical migrations. Q_{10} for respiration for all the temperature range was about 2.3.
- b) The consumption curve was fitted for maximum consumption at 10 C and $Q_{10}=2$. The values of 50 % consumption at 0 C and 1 % consumption at 16 C does not look realistically, however. Mysids are likely still to feed actively at 16 C not only in the lakes (Chipps 1999), but also in the Baltic Sea (...). The author, however, has mentioned himself (pers. comm.), that mysids can live for some period at as high 17-18 C, so probably parameters for the curve were changed in later application of the model.
- c) Excretion (both including moulting costs and excretion of nitrogenous waste) probably should be related to the maintenance costs as nitrogen waste originates from constant protein turnover (DEB – p. 127). If diet is rich in proteins, nitrogen can be excreted also as a result of assimilation, but this is probably not the case with mysids. They are likely to have mixed diet and respiration quotient was estimated to be around 1 (Ranta & Hakala 1978, Branstrator et al. 2000, Hansson..., Viherluoto 2000) .

To conclude, consumption response to temperature change does not look realistic. If excretion costs are also taken to be proportional to maintenance and not to the feeding, the growth rate above 14 C should decrease even more, because maintenance costs increase sharply. In general there is much evidence that mysids can stand higher temperatures and this does not harm them so much. It was noted already by Holmquist (1959): "the culture experiments showed that *M. relicta* endured 0C as well as 18 C, if only the temperature was kept constant. The mysids captured in the Arctic were also kept for some weeks at 17-18 C..."

It would seem reasonable to assume that in the range of temperatures population is adapted for, mysids can couple their physiological processes and maintain similar energy conversion efficiency and hence the responses of all the processes to the temperature should have similar shape.

Notes on some additional related studies:

Paper IV: Lasenby & Langford 1972 – comparison of growth, life history and respiration of *M. relicta* in Arctic and Temperate Lakes.

- a) No difference in respiration rate at 2-8 C temperatures in two lakes was noted, even if annual temperature in arctic (Char) lake is 0.8 C to compare to 5.3 in temperate (Stony) – no metabolic compensation of cold-adapted populations was noticed, which was the raised hypothesis.

- b) In both lakes mysids breed at size of 15-16 mm, but it takes two years to reach this size and maturation in arctic lake and one in temperate lake. Average fecundity in both lakes was 12 eggs/female, but in arctic lake, eggs were smaller (0.12 mg DW) and clutch size was more variable (5-22 eggs) than in temperate lake (0.2 mm and variation of 10-14 eggs). This could indicate more stochasticity in arctic lake, but also sample sizes were different (N= 75 and 22 respectively).
- c) The study is interesting, because it is one of the first attempts to estimate energy budget. It was concluded that the amount of energy, used for growth+respiration to reach maturity in one vs. two years is the almost the same in both lakes (39+156=195 and 28+170=198 kcal). The investment in reproduction in the temperate lake was almost twice as high as in arctic (14 and 8 kcal respectively). In another study, fecundity in Stony Lake was actually indicated to be as high as 17 eggs/female (Adare & Lasenby 1994). In any case, higher investment in reproduction in Stony Lake is best explained by different food availability and quality – mysids in Char Lake are mainly herbivorous, whereas zooplankton predominates in Stony Lake (Lasenby & Langford 1973).

The estimations of energy budgets can be compared to the ones in Paajarvi lake (Hakala 1978). For example, female reproducing in Lake Paajarvi in the first year needs 114 kcal for respiration and invests 35 kcal in production (growth and reproduction) – compare to 156 and 53 kcal in Stony Lake. The female, breeding only on the second year, respire 260 kcal and invests 50 kcal in production – this can be compared to Char Lake, correcting for Q_{10} . The average temperature mysids endure in Paajarvi is about 5 C, comparing to 0.8 C in Char lake. Thus the calculated Q_{10} for respiration is about 2.3, which is concordant with Q_{10} , estimated for other responses. These estimates, of course, are only very approximate because many parameters were not taken into account.

To conclude, this study seems to confirm the idea of similar energy budgets and energy allocation in both arctic populations and also ones in the temperate lake, experiencing diel migrations.

Paper V: Halfon et al. 1996 – Energy flow through the Lake Ontario food web: conceptual model and an attempt at mass balance.

Energy budget of *Mysis relicta* in Lake Ontario was estimated among many other species. It is only interesting to point out wildly varying assumptions about energy assimilation parameters – excretion in the model is assumed to be 3 % of consumption (compare to 10 % or 18 % if moulting is included in Rudstam 1989), egestion – 70 % of consumption (compare to 15 % in Rudstam 1989). *Mysis relicta* makes up only one of 14 compartments in the model, but in any case more precision should be aimed for. Authors also state, that confident precision of fish biomass can not be performed at present...

—

The exact answers to A or B QUESTIONS can not be given at this stage so far, so only some reflections are presented:

*The more likely answer to QUESTION B is that experimental condition for different response analyses were not concordant and in many cases extrapolation of the results was not justifiable. The lack of good experimental data still seems to be one of the obstacles for good bioenergetic models. Extrapolation of results beyond the range of tested conditions and also to the populations in nature was indicated as important source of errors also by Ney (1993) and I think it will stay a problem in the nearest future.

So far the models often fail to predict energy budgets of organisms in nature – estimates of predation rates on *Mysis* in Lake Ontario were 1.2-2.0 times the estimated production (Rand et al. 1995). Ney (1993) also indicates the difference of at least 50 % in the predicted and observed fish growth in four of six revised models (is the two-fold difference between predictions and observations a big difference or a very good prediction?).

*As to the answer to QUESTION A – I would like to conclude that different populations have similar energy budgets and concordant parameters of energy conversion efficiency and allocation over

the range of temperatures they are adapted for. As a crude evaluation of energy allocation to growth and reproduction I have collected some data on length of female vs. fecundity in different lakes (Fig 3 in this essay). No sophisticated analysis was conducted, but from the first glance a clear correlation of both larger size and higher fecundity to better trophic conditions is clear. Such a primitive comparison does not confirm uniform energy conversion efficiencies and allocation strategies, of course, as ingestion functional response was not evaluated.

CONCLUSIONS:

1. *M. relicta* spp. have rather wide temperature range where they are likely to be able to regulate different physiological processes. Uncoupled estimation of feeding and respiration rate does not seem to be very reasonable, hence. The simple approach would be to assume that mysids are adapted for the temperatures they occur and are able to maintain the same energy conversion efficiency and allocation of energy to reproduction. If the same Arrhenius temperature applies for all the processes the maximum response of consumption, GER and respiration in well-adapted animals should be at the same temperature (see Experimental design 1).
2. Much of the variation and adaptation is possible among populations. This hinders application of the same temperature-dependence curves for all the populations. Also if rates of different physiological processes change independently of each other it becomes impossible to apply model to the population in the nature, because of the difficulties to trace back all the experienced temperatures and find out at which place of the curve certain population is at certain moment. If, however, it is possible to prove the uniform energy budget and allocation strategies – the model becomes much more general and simple (Experimental design 2).
3. There seems to be a lack of data on mysids consumption over the temperature gradient. The comparison of mysids from different populations and temperature adaptations would be appealing.
4. There is no clear trend of arctic populations to have higher reproduction capacity at the same size. This implies that no compensation mechanism, to increase accumulation of lipids in costs of growth, occurs.

REMAINING QUESTIONS:

1. What happens when temperature rises above the range of adaptation? Does the respiration increase or decrease? Why such exponential curves on respiration have been obtained in the experiments?
2. What are the costs and possible implications of being steno- vs. eurythermic (living in arctic vs. temperate lake)? Costs of having enzymes for wide temperature ranges must be evaluated and are likely to be incorporated in the DEB equation on correction factor (2.21 formula in DEB book). Are the stenothermic organisms more efficient in their temperature range, because they can allocate higher proportion of enzymes adapted for this temperature?
3. How to incorporate into DEB the McLaren hypothesis (and the opposite observations on fish) on the benefits of vertical migrations: increased rate of feeding at high temperatures and reduced costs of maintenance, assimilating at low temperatures? Is it reasonable to assume that other factors, except for decreased metabolic costs play role here? Digestion rate, SDA should also decrease at low temperature. On the other hand, the organism must maintain a big variety of enzymes, which is likely to be costly.

REFERENCES:

1. Chess D. W, J. A. Stanford 1999: Experimental effects of temperature and prey assemblage on growth and lipid accumulation by *Mysis relicta* Loven. *Hydrobiologia* 412, 155-164.
2. Chipps S. R. 1998: Temperature-dependent consumption and gut-residence time in the opossum shrimp *Mysis relicta*. *J. Plankton Res.* 20, 2401-2411
3. Halfon A., N. Schito, R.E. Ulanowicz 1996: Energy flow through the Lake Ontario food web: conceptual model and an attempt at mass balance. *Ecological Modelling* 86, 1-36.
4. Lasenby D. C., R.R. Langford 1972: Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake. *J. Fish. Res. Bd. Canada* 29, 1701-1708
5. Rudstam L. G 1989: A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. *J. Plankton Res.* 11 (5), 971-983.
- 6....Other references are available upon request...

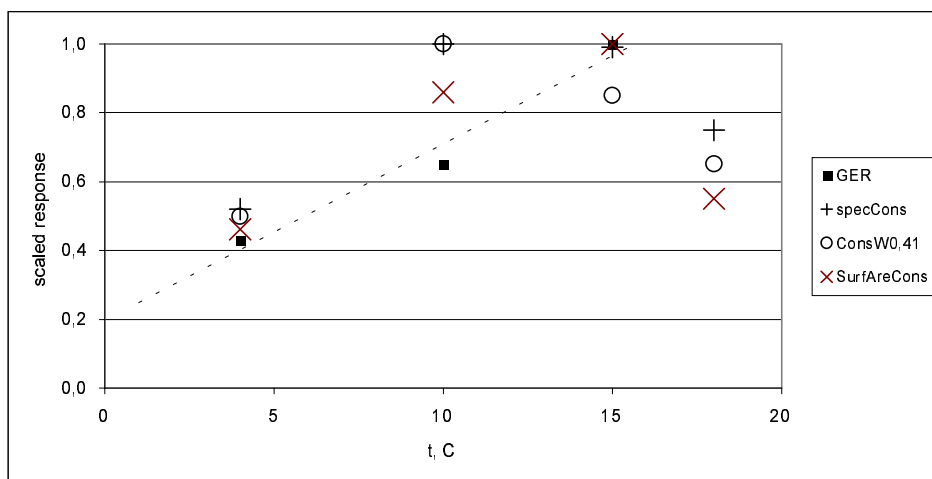


Fig. 1 Scaled response of consumption and gut evacuation rate (GER), calculated from Chipps, 1998. Indicated is the absolute specific consumption (g prey/g mysid/t) (specCons), specific consumption standardized by $DW^{0.41}$ (ConsW0,41) and specific consumption, standardized by the surface area (Total Length²) (SurfAreCons). The dashed line shows the trend of response of surface area standardized consumption and GER to the temperature gradient 4-15 C.

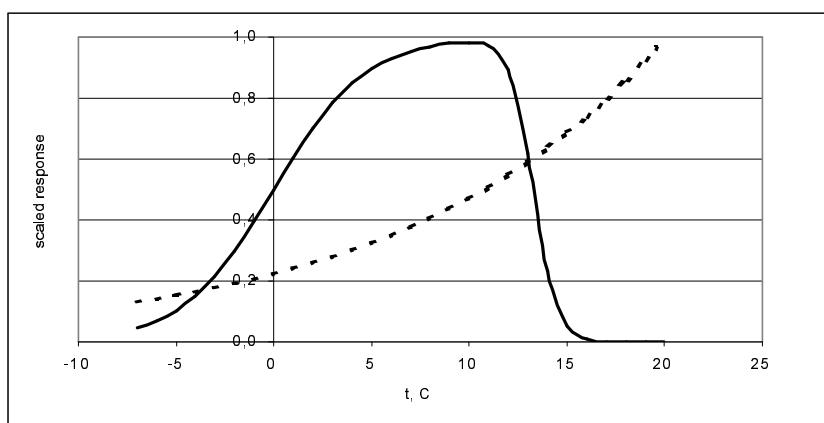


Fig. 2. Scaled response for consumption (entire line) and respiration (dashed line) used for the bioenergetic model of *Mysis* (Rudstam 1989).

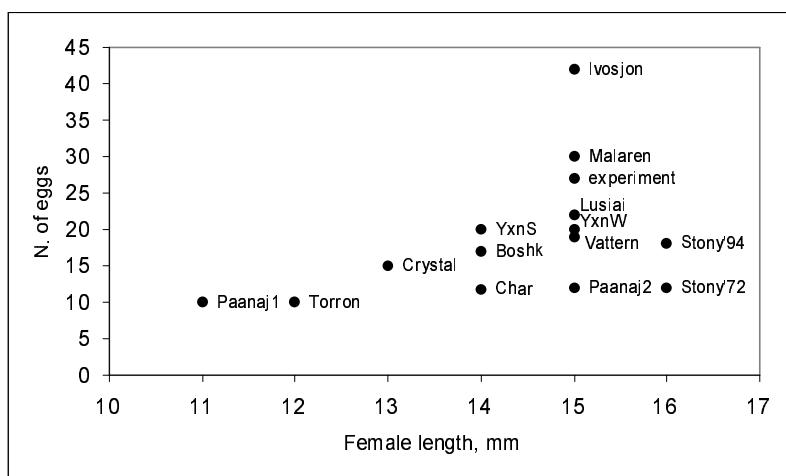


Fig. 3. Correlation of female size to fecundity in different lakes: Paanaj 1 & 2 – oligotrophic lake in Karelia (females maturing on the first and second year resp.) Torrion, Char, Boshk, Vattern – oligotroph. Crystal, Lusiai, Stony – mesotrophic. Yxn S & W – females breeding in summer and winter resp. Experiment – *M. mixta* fed with ample food. Malaren, Ivosjon – meso/eutrophic lakes. (references available upon request).