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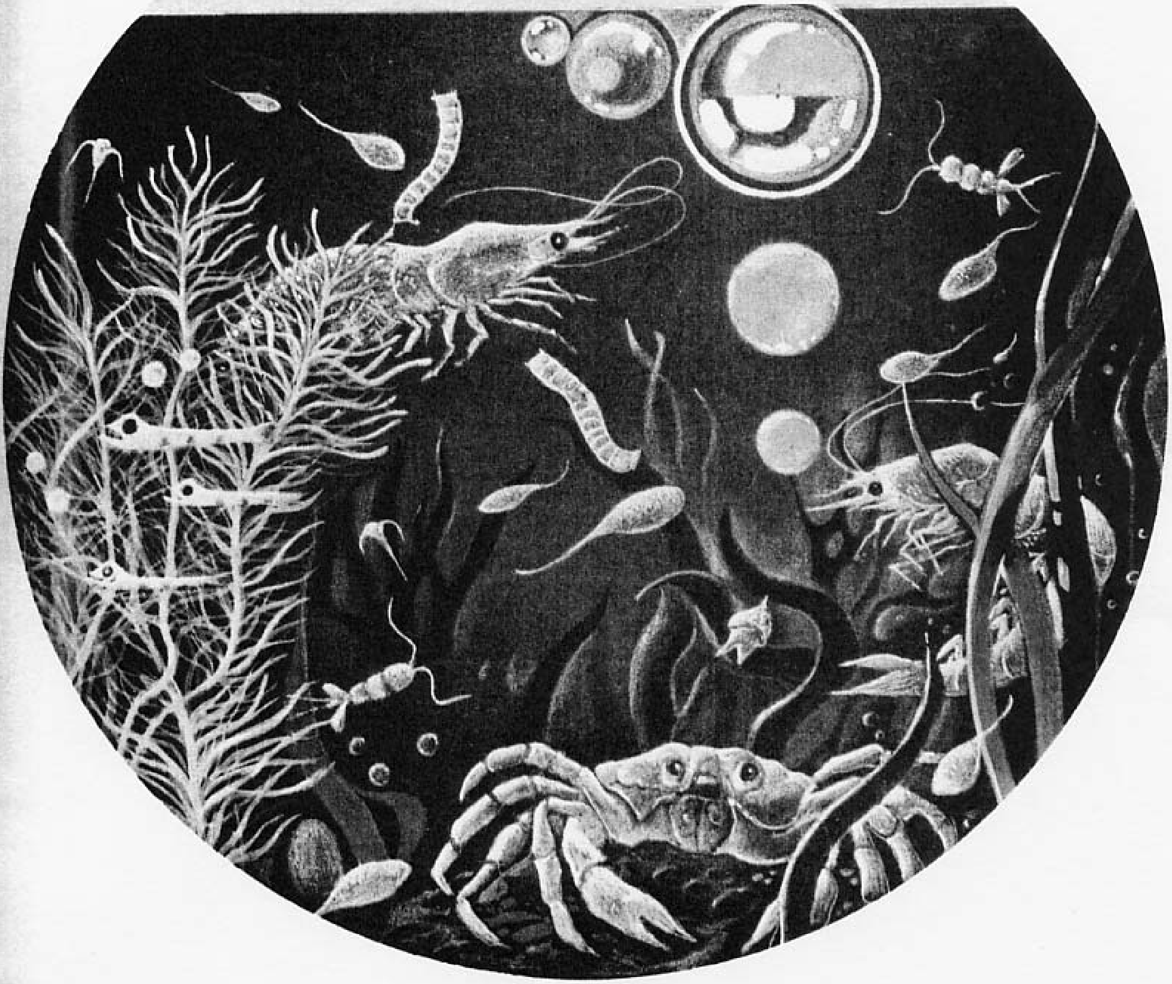

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CONTENTS

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Growth and Production of Amphipods in Rivers of the Southern Maritime Region (Soviet Far East)*

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The somatic growth of male amphipods in the rivers of the southern Maritime Region is of the parabolic type and that of females is described by an S curve. The combined rate of somatic and generative growth is described by the same power function for both sexes. The changes in ash content, caloric content, relative dry weight, and salinity of hemolymph in the period between molts were investigated. The somatic and generative production of the amphipods and their *P/B* coefficients for the year are estimated.

Gammarids play a leading role in the functioning of benthic communities of many salmon rivers of the southern Maritime Region. But this group is the least studied of all invertebrates inhabiting the streams of the region. For example, there is practically no information on the reproductive cycle or life cycle of rheophilic amphipods or on their rates of growth and production. In addition, the extensive literature on various aspects of crustacean biology [4, 5, 12, 13, 15, 16] contains only fragmentary data on changes in their dry weight, ash content, and caloric content in the period between molts. Investigations of this type are of special interest in production studies, since the main changes in weight and size of crustaceans depend on the periodic molting.

We investigated the growth and production of river amphipods, making a detailed study of their biology and of the changes in live and dry weight, ash content, and caloric content in the interval between molts.

MATERIALS AND METHODS

The investigation was performed in 1985 and 1986 in the middle section of Kedrovoy River in the area of the Kedrovaya preserve. The river is 8–10 m wide and a maximum of 0.6–0.8 m deep in this area, with a current velocity of 0.5–1.0 m/s; it had a gravel and rubble bottom. The mean summer temperature is 12–13 °C. The amphipods are represented by a population of *Gammarus lacustris* [6], but I.I. Dedyu reports (oral communication) that a previously unknown species occurs in the southern zone of the Far Eastern region.

The rate of growth was studied in individuals of various weight. Then specimens were placed in net bags or glass containers, which were then placed in the river. The food supplied was decomposed leaf litter. The specimens were weighed on a torsion balance after drying with wads of paper. The absolute growth rate (dW/dt) was calculated for time intervals (t_1, t_2) with the same length as the period between molts.

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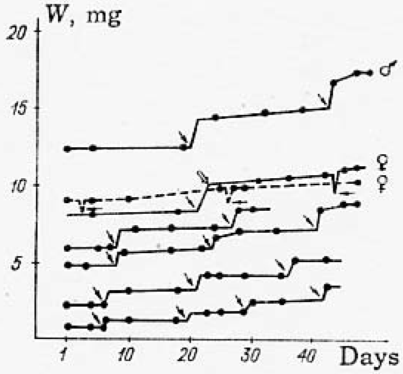

Fig. 1. Increase in live body weight (W) of individual specimens. Arrow shows time of molting; double arrow shows instant of first egg-laying in females.

The change in ash content, caloric content and dry weight of the specimens in the period between molts was investigated in individuals weighing about 20 mg. The salinity of the hemolymph was determined at the same time. The time at which the exuvia was cast off was determined visually; samples of hemolymph were taken at specified times after molting, after which the specimens were dried in an exsiccator at 80 °C and weighed. The ash content and caloric content were determined respectively by combustion in a muffle furnace and by bichromate oxidation, using the technique of Ostapenya [7] (T.M. Tiyunova, analyst), and the salinity of the hemolymph was determined cryoscopically [11] by N.V. Aladin.

Production was estimated in quantitative collections of benthos made by personnel of the Laboratory of Freshwater Hydrobiology, Biology, and Soil Institute in 1979 and 1980. The production of the gammarid population was calculated as the sum of the weight gains of its component individuals. The instantaneous production rate of each age group (P_i) was defined as the product of the derivative $d\bar{W}/dt$ and the mean abundance $\bar{N}$ of the group. The production rate of the entire population P' of age groups P_i was determined by summation:

$$P' = \sum_{i=1} P_i \qquad (1)$$

The annual production (P) was calculated at the time integral of function (1):

$$P = \int_{t}^{t_n} P'(dt) \qquad (2)$$

The abundance of each age group per m^2 of bottom was derived from the densities and size composition of the populations. The relationship between the length (L) and body weight (W) was calculated with the allometric growth equation

$$W = aL^b \qquad (3)$$

where a and b are constants. The parameters of the equations were found by the method of least squares, and the confidence intervals by the methods of Umnov [10].

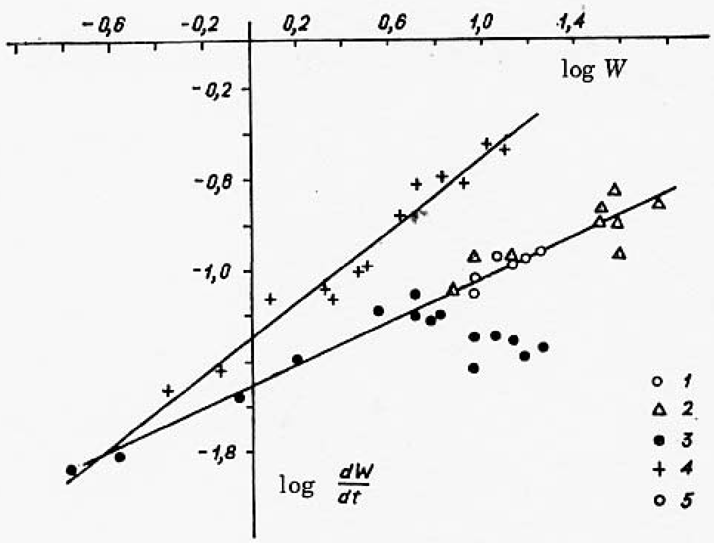

Fig. 2. Absolute rate of somatic growth (log $\frac{dW}{dt}$, mg/day) in immature individuals ((1) dark circles in figure), mature males (2) and females (3), and males with high growth rate (4)); and rate of somatic and generative growth of female amphipods (5) versus weight (log W, mg) at 12 °C. Bilogarithmic plot.

RESULTS AND DISCUSSION

In most rivers of the southern Maritime Region, amphipods are the dominant group: for example, in the Kedrovoy River, they account for an average of about 15 percent of the abundance and 20 percent of the biomass of the benthic community. They have a 1-year life cycle and inhabit all biotopes of the rivers. They are detritus-feeders, but predation and cannibalism occur if there is a shortage of food.

Sexual maturity occurs at a body weight of 7 to 8 g. Newly born individuals weigh about 0.12 mg, and ultimate weights of males and females are, respectively, 75 and 33 mg. The gammarids reproduce throughout the warm season. Males are always more numerous in the population. Each female lays about 7 or 8 clutches of eggs in the course of the season. The developing juveniles leave the marsupium of large females after 1 to 3 days and that of younger females after a few hours. The female then molts, and about 45 to 50 minutes later lays a new clutch of eggs. The number of eggs per clutch is closely correlated with body weight and can be approximated by linear equation

$$N_i = -2.44 + 1.39W_f \quad (4)$$

where N_i is the number of eggs per clutch and W_f is the weight of the female, mg.

At a mean temperature of 12–13 °C, the eggs are carried for about 30 days, regardless of the size of the female. In large females, the period between molts is 35 days. At the same temperature, the first molting of newly born juveniles occurs on the eighth to tenth day. The exoskeleton is cast off in seven to ten seconds; it usually accounts for 8–10 percent of body weight, but in large males it may be as much as 14 percent of body weight. We found that if the females were

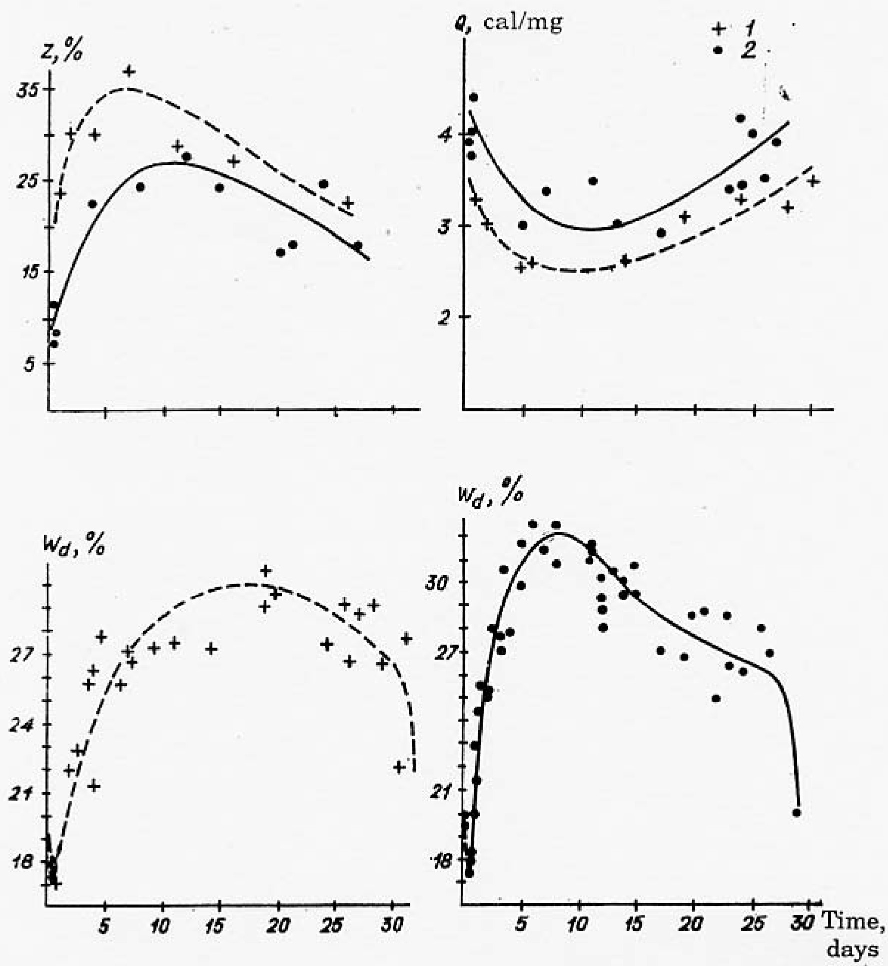

Fig. 3. Ash content (Z), caloric content (Q) and relative dry weight (W_d) of male (1) and female (2) amphipods in period between molts.

weighed immediately before molting, with excessive drying, they exhibited a delay in molting, and in one case molting failed to occur.

In immature individuals and mature males, the change in dry body weight (dW/dt) during growth is stepwise as a result of periodic molting (Fig. 1). More than 90 percent of the weight gain in the period between molts occurs in the first day. In mature females, the change in live weight shows a distinctive pattern. After emergence of the juveniles, the weight of the female drops sharply, but 24 hours after molting it returns to a level comparable with that before egg-laying. The subsequent rather smooth weight gain largely results from the development of the eggs that the female carries.

The stepwise increase in body weight made it necessary to determine the mean values of dW/dt at times (t_1, t_2) separated by an interval equal to the period between successive molts. This approach made it possible not only to determine the rates of somatic and generative growth, but also to identify the particular type of growth. For example, it is currently assumed that most crustaceans, including amphipods, have an S-shaped growth curve regardless of sex [1, 2, 9, 12], usually described by the Bertalanfi equation

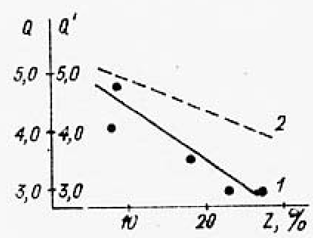

Fig. 4. Ash content (Z) and caloric content of dry matter (Q, cal/mg, (1)) and or organic matter (Q', cal/mg (2)) of female amphipods.

$$\frac{dW}{dt} = mW^n - kW \tag{5}$$

where ($-kW$) is a factor expressing the slowing of the growth rate; and n and k are constants. But during the juvenile period, when sexual products are not yet developed, the relationship between dW/dt and W is approximated by a power function [3]. The rates of weight gain in males, estimated from the total weight gain in the period between molts, did not indicate any significant slowing of growth, even after the onset of maturity (Fig. 2). It appears that the rate of testes development by males has practically no effect on the rate of somatic growth. If so, the growth of the males of this species is parabolic.

In contrast to the males, somatic growth in mature females slows markedly in the reproductive period. But the combined rate of somatic and generative growth does not differ significantly from the rate of somatic growth in the males. As a result, the relationship between the combined rate of somatic and generative growth dW'/dt and the individual body weight can be approximated in all cases by the same power function:

$$\frac{dW}{dt} = 0.031 \pm 0.003\ W^{0.47\pm0.04} \tag{6}$$

It is obvious that this equation describes the mean rate of growth of individuals in the population. In addition, we attempted to evaluate the maximum possible individual growth rate under particular environment conditions. For this purpose, we observed the brood from a single female, consisting of ten individuals. Although the juveniles were maintained under identical conditions and had an excess of food available, even at the time of the first molt, two individuals, which later proved to be males, had a much greater growth rate than the main group: for example, two months after spawning their body weights had reached 3.46 and 3.57 mg. The weights of the other individuals at this time were 1.62, 1.63, 1.74, 1.93, 1.94, 2.00, 2.03, and 2.22 mg, an average of 1.9 mg or only about half that of the fastest-growing males. Using data collected over a 6-month period, we obtained the equation

$$\frac{dW}{dt} = 0.049 \pm 0.003\ W^{0.79\pm0.05} \tag{7}$$

from which it is evident that the rate of somatic growth of the fastest-growing individuals was significantly greater than the mean growth rate of males in the population: for example, at the onset of maturity (with a body weight of about 7 g), their growth rate was nearly three times the mean (see Fig. 2).

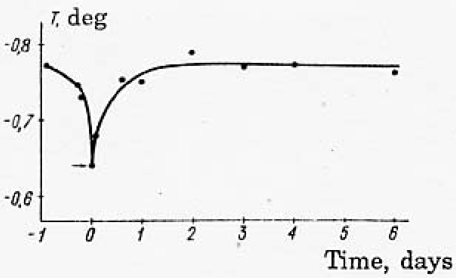

Fig. 5. Salinity of hemolymph measured at its freezing temperature (*T*), female amphipods in period between molts (arrow shows time of molting).

In individuals of the same size, the ash content, caloric content, and relative dry weight (that is, its ratio to live weight) were, respectively 7–37 percent, 2.6–4.4 cal/mg dry weight, and 17–33 percent. Significant ranges of variation of these values had been previously observed in other groups of crustaceans [14]. In the case of the amphipods, the variations are related to sex, and also on regular processes taking place in the period between molts. For example, the ash content in the period between molts (20–30 days long) ranged from 7 percent to 28 percent in females and from about 10–15 percent to 37 percent in males. The lowest ash content of both sexes (Fig. 3) occurred immediately after molting, and the highest ash content occurred on the 7th to 12th day. There followed a smooth decline in ash content, to 17 percent in females and 22 percent in males at the time of the next molt. It is clear that the lower ash content of the females over the entire period between molts results from the low ash content of eggs, which, according to Khmeleva and Golubeva [13], is only 2 percent of their dry weight.

During the period between molts, the caloric content of males was 0.5–0.8 cal/mg (relative to dry weight) less than that of females. This difference resulted from the high caloric content of the eggs. But regardless of sex, the caloric content of males and females was greatest at the time of molting and lowest on the 8th to 13th day after molting (see Fig. 3).

Thus we see that the caloric content and ash content of the amphipods are inversely related. The calculated caloric content of organic matter also shows a decline with increasing ash content (Fig. 4).

The relative dry weight was essentially the same (about 20 percent) in both sexes immediately after molting and reached its lowest value an hour later (see Fig. 3). In the subsequent hours and days, the relative dry weight increased markedly, reaching its maximum on the 6th to 10th day after molting in females and on the 17th to 22nd day in males. There followed a gradual decline in the relative dry weight; this figure declined earlier in females, owing to the great increase in volume of the eggs. Interestingly, several hours before the next molt, the relative dry weight was 26–27 percent in both sexes, then fell sharply to about 20–22 percent immediately after molting. These data indicate a pronounced decrease in the relative dry weight immediately before molting, the separation of the exuvia, and a subsequent rapid increase in body weight in the first hours after molting result from an increase in the water content of the tissues. At the time of molting, there was a significant decline in the salinity of the hemolymph (Fig. 5). But 15 hours after molting, the salinity of the hemolymph had been fully restored.

It is evident that the change in the relative dry weight as a result of direct uptake of water occurs only during molting and in approximately the next hour.

Thereafter, the process apparently becomes more complex, depending in particular on changes in the ash content and caloric content.

The mean values of the ash content, caloric content, and dry weight between molts were used to calculate the production of the population. The ash content was 27 percent in the males, the caloric content was 2.92 cal/g relative to dry weight and 4.05 cal/g relative to organic matter, and the relative dry weight was 22 percent. The corresponding values for females were 21.7 percent, 4.36 and 4.42 cal/g, and 27.8 percent.

To evaluate the production of aquatic invertebrates as the sum of the individual weight gains, we must know the mean body weight of an individual in each size group. The size groups were chosen arbitrarily at 1-mm intervals on histograms of the linear size. To determine the mean weight of an individual in each group, we derived the allometric growth equation

$$W = 0.024 \pm 0.002L^{2.791\pm0.023} \quad (8)$$

There were 17 measurements and the weight range was from 0.12 to 63 mg. The exponent is fully consistent with the values obtained previously for *G. lacustris* by other investigators [1, 9].

The annual production of the amphipods was evaluated from late April to the second half of November, when the water temperature in the river exceeded 4 °C, since below this value no significant growth occurred. The combined somatic and generative production over the course of the year was 11.9 g/m^2 or 10.2 $kcal/m^2$. Since the mean annual biomass was 4.4 g/m^2. The annual *P/B* coefficient was 2.7, fully consistent with the values presented in the literature for *G. lacustris* [8, 9].

The mean weight of an individual in the population ($\bar{W}$, mg) proved to be inversely related to specific production (C_b, $days^{-1}$); for a mean water temperature of 12 °C, the relationship is described by the equation

$$C_b = 0.051 \pm 0.002W^{-0.81\pm0.03} \quad (9)$$

It is evident that this equation can be used for rapid evaluation of production over specific time intervals.

CONCLUSIONS

The amphipods inhabiting salmon rivers of the southern Maritime Region have a 1-year life cycle. The increase in body weight is stepwise as a result of periodic molting. Over a time period equal to the interval between molts, the somatic growth of males is parabolic and that of females is described by an S curve. But the combined rate of somatic and generative growth can be expressed by the same power function for both sexes.

There were great variations in ash content, caloric content, and relative dry weight in individuals of the same size. These fluctuations are the result of regular processes in the interval between molts. The pronounced decline in relative dry weight immediately before molting, the separation of the exuviae, and the subsequent rapid increase in dry weight in the first hours after molting result from an increase in tissue water content, accompanied by a decline in the salinity of the hemolymph.

The above data, together with information on the size structure of the population, were used to determine the cumulative annual somatic and generative production and their *P/B* coefficients, which were respectively 10.2 $kcal/m^2$ and 2.7. We determined the relationship between the mean body weight of the population and the specific production, which can be used to evaluate the production of gammarids during specific time intervals.

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