Energy budgets in the populations of *Crangon crangon* L. (Crustacea) and *Cardium glaucum* (Poiret) (Mollusca) in the Gulf of Gdańsk*

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Energy budget
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ANNA SZANIAWSKA
Institute of Oceanography,
University of Gdańsk,
Gdynia

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Abstract

The energy budgets for *Crangon crangon* and *Cardium glaucum* populations in the Gulf of Gdańsk were calculated. The population of *C. crangon* consumes 56 666 $\mathrm{Jm^{-2}year^{-1}}$; the energy consumed by the *C. glaucum* population is much less – 10 474 $\mathrm{Jm^{-2}year^{-1}}$. The total productivity of *C. crangon* (12 066 $\mathrm{Jm^{-2}year^{-1}}$ is much higher than that of *C. glaucum* (904 $\mathrm{Jm^{-2}year^{-1}}$). The annual respiration of *C. crangon* is much higher than that of *C. glaucum*. *C. crangon* females assimilate about 40% of the energy consumed (males only 19%). In *C. glaucum* 28% of the energy consumed is assimilated.

1. Introduction

When studying the functioning of aquatic ecosystems, it is important not only to become acquainted with individual life processes, but also with overall functioning at the population level and its significance. An organism and its population can be studied from the point of view of its role in the ecosystem and its utilization of the energy gained from food. In this context, it is important to know the rate of production of organic matter by the dominant populations of the species. The growth rate of individuals may also be a good index of the influence of environmental factors on the organism (Bayne and Widdows, 1978; Widdows *et al.*, 1979a; Bayne and Worrall,

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1980; Vahl, 1980). Measurements of the productivity of the separate elements of the trophic network constitute part of the basis of estimating the dynamics of the ecosystem. A knowledge of the amount of energy utilized in metabolic processes is also necessary and respiration may be an index of this. A species could be represented by the equation

$$C = P + R + FU, \tag{1}$$

in which C represents energy consumption, P the productivity (*i.e.* anabolized energy), R the respiration (*i.e.* catabolism), P and R make up the assimilated part of the food ratio (A). Energy dissipated and not utilized by individuals or the system (Klekowski *et al.*, 1967; Petrusewicz and Macfadyen, 1970) are given by FU.

The aim of this paper is to define and present the energy balance of species common in Baltic inshore waters (*e.g.* the Gulf of Gdańsk), such as *Crangon crangon* (Crustacea) and *Cardium glaucum* (Bivalvia), and to discover which of the species is the best energy converter.

2. Material and methods

The material which was used to calculate the productivity of *C. crangon* was taken from the Gulf of Gdańsk in 1976, whereas that of *C. glaucum* was calculated from animals collected in the Gulf of Gdańsk the previous year (Crisp, 1984). The calculation is based on a knowledge of the sum of energy increments in consecutive length classes over period of a year in all the individuals in the population studied. The annual productivity P ($\mathrm{Jm^{-2}year^{-1}}$) was obtained by summing the monthly productivities.

Oxygen consumption in *C. crangon* was measured with a flow respirometer. Knowing the biomass of an average individual in consecutive months of the year, the relationships between the mass of an individual and oxygen consumption, the number of individuals per 100 $\mathrm{m^2}$ of sea bed, and the quantity of oxygen consumed by the population during a month or year could be calculated. Separate calculations were done for males and females.

Oxygen consumption by the *C. glaucum* population was calculated on the basis of Brock and Kofoed's data (1987). Oxygen consumption was measured at 6 different temperatures over a 6–9 hour period, with simultaneous measurements of filtration rates. The quantity of oxygen consumed by the two species was converted into energy units by applying the oxycalorific coefficient: 1 $\mathrm{cm^3}$ oxygen = 19.88 J (Thompson and Bayne, 1974).

A knowledge of the food consumption of the *C. crangon* was necessary when calculating the food intake. According to Wiktor (1980), the main nutrient components of the species are crustaceans (41.1%) principally *Neomysis integer* and Polychaeta, *e.g.* *Nereis diversicolor*, of known energy values. During a year, the stomach weight of *C. crangon* constitutes 12% of the animals' wet weight (Phil and Rosenberg, 1982). Knowing the size of populations per 100 m^2 of the bottom of the Gulf of Gdańsk during one year, the wet biomass of individuals, the weight of stomach contents and the food composition, it was possible to define the annual food consumption of the whole *C. crangon* population. In the case of *C. glaucum* it was necessary to know the rate of filtration (Marcinkowska, 1976), the water content (mg wet weight per dm^3 of water) and the energy value (11.42 Jm g^{-1} dry weight of suspended matter in the water in order to calculate the energy intake of an individual.

3. Results

3.1. Consumption

During one year, *C. crangon* females consume 37 906 $Jm^{-2}year^{-1}$ (Fig. 1), whereas the food intake energy of males is just over half that amount — 20 760 $Jm^{-2}year^{-1}$ (Fig. 2). The whole shrimp population consumes 56 666 $Jm^{-2}year^{-1}$ (Fig. 3). Consumption was lowest in winter and highest in June–July and September–October.

The energy consumed by the *C. glaucum* population is much less – 10 474 $Jm^{-2}year^{-1}$ (Fig. 4).

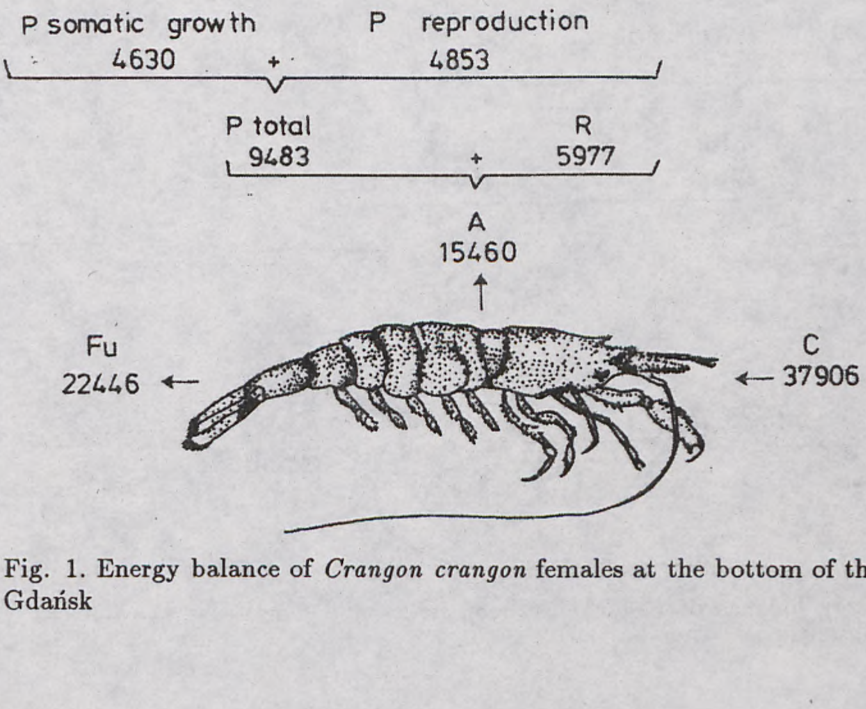

Fig. 1. Energy balance of *Crangon crangon* females at the bottom of the Gulf of Gdańsk

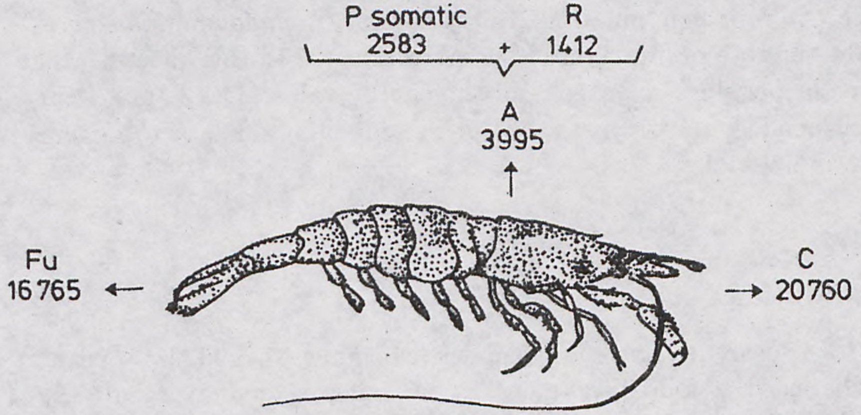

Fig. 2. Energy balance of *Crangon crangon* males at the bottom of the Gulf of Gdańsk

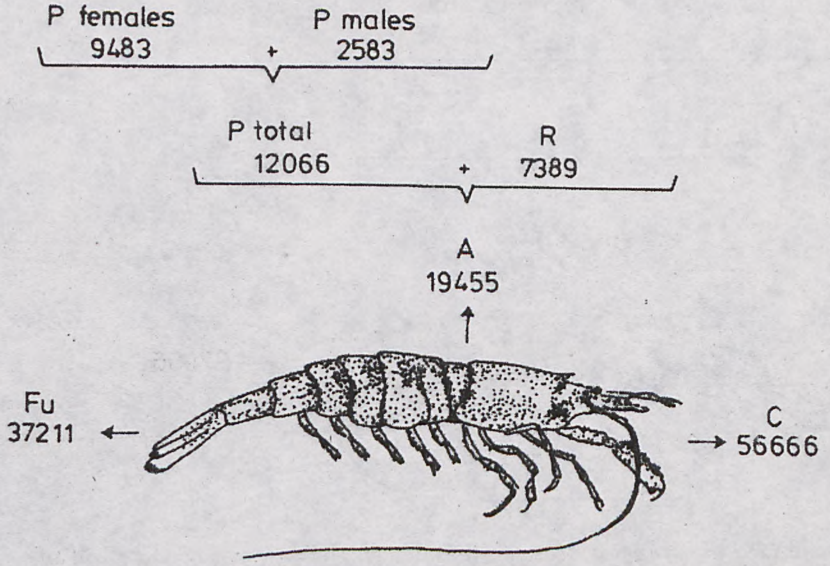

Fig. 3. Energy balance of *Crangon crangon* males and females at the bottom of the Gulf of Gdańsk

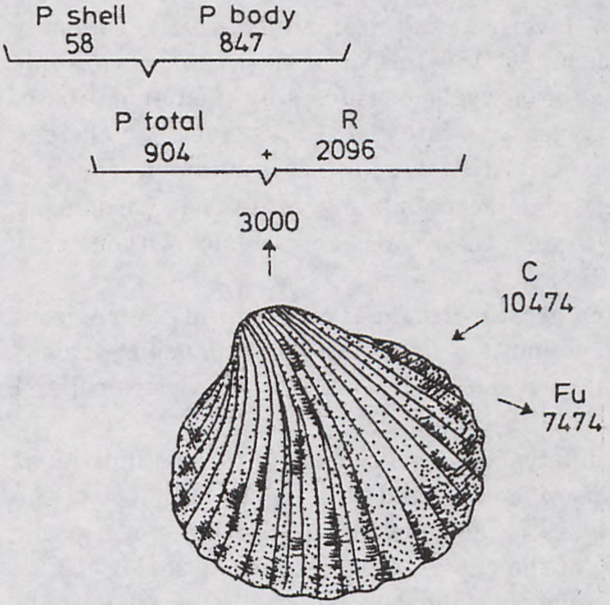

Fig. 4. Energy balance of *C. glaucum* at the bottom of the Gulf of Gdańsk

3.2. Productivity

In the *C. crangon* population, the annual productivity of females is higher than that of males (Figs. 1, 2). Related to body mass increments this amounts to 4630 $\mathrm{Jm^{-2}year^{-1}}$, that is almost half, despite the fact that males constitute about 50% of the whole population. The presence of females with eggs, which are found in coastal waters from May to the beginning of October, has an important influence on the size of the population's productivity. The amount of energy consumed in connection with annual egg production is high and amounts to 4853 $\mathrm{Jm^{-2}year^{-1}}$; it is almost equal to the annual productivity related to body mass increments of females. Altogether, *C. crangon* females produce a 9483 $\mathrm{Jm^{-2}year^{-1}}$, which is 4 times more the annual productivity of the males.

The annual productivity of *C. glaucum* population amounts to 904 $\mathrm{Jm^{-2}year^{-1}}$ and is the sum of the productivity of cockles amounting to 57 $\mathrm{Jm^{-2}year^{-1}}$ and body amounting to 847 $\mathrm{Jm^{-2}year^{-1}}$ (Fig. 4).

3.3. Respiration

The oxygen consumed by the *C. crangon* population is calculated from the number of individuals found in a known area of sea bed in particular months and the average mass W (g) of an individual animal by applying the dependence $R = 0.19\ \mathrm{W}^{0.78}$ ($\mathrm{r} = 0.80$), where R is the rate of oxygen consumption (ml O_2 $g^{-1}h^{-1}$) (Hagerman and Szaniawska, 1989). Annually the *C. crangon* population consumes 7389 Jm^{-2}. Of this, females consume 5977 $Jm^{-2}year^{-1}$ – 81% of the total oxygen consumed by the population of this species. Males consume oxygen at a rate of 1412 $Jm^{-2}year^{-1}$. Oxygen consumption by the *C. crangon* population was highest in summer, when the water temperature was highest and the population contained reproducing females, which consume more oxygen than males and females without eggs (Szaniawska and Wołowicz, 1984).

Taking into account the temperature changes observed in the environment during the year and the population dynamics of *C. glaucum*, the annual oxygen consumption by the cockle per 1 m^2 of sea bed was calculated at 2096 $Jm^{-2}year^{-1}$.

A distinct, sex-dependent difference in energy expenditure on individual life processes is observed in *C. crangon*. Females assimilate *ca.* 40% of the energy consumed, males barely 19%. Females also utilize more energy for the population processes (25% of the energy consumed) than males (12%). This is understandable, considering that female productivity covers not only the production of body mass, but also that of the new generation. Males utilize about 64% of the energy assimilated for the production of body mass; by contrast, of the 61% of the energy assimilated by females, half is expended on production connected with reproduction, the other half on the production of body mass. In males, *ca.* 80% of the energy consumed is not utilized for metabolic or production processes; This is much more than in females, which excrete and secrete only *ca.* 60% of the energy consumed.

In *C. glaucum*, 28% of the energy consumed is assimilated. That consumed by the body and shell constitutes barely 9% of the energy intake. Only 30% of the energy assimilated is expended on body and shell growth. This is much lower than in *C. crangon*.

4. Discussion

Animals take in energy as food, then utilize this energy in metabolic processes for the production of body mass, reproduction and respiration. Individuals from the Gulf of Gdańsk population of *C. crangon* take up 56 666 $Jm^{-2}year^{-1}$, whereas individuals of the species inhabiting the Kattegat and Skagerrak consume from 74 222 to 296 888 $Jm^{-2}year^{-1}$ (Phil and Rosenberg, 1982), *i.e.* about 1.3–5.2 times more. The higher food and energy consumption by *C. crangon* individuals from waters more saline than that of the Gulf of Gdańsk is an effect of the greater body size attained by such individuals.

Energy consumption by populations of the two species discussed is highest in summer and autumn, when the populations boast large numbers of individuals of greater body size, characteristic of an environment with high temperatures and easy access to nutrients. The lowest food intake is recorded in winter, owing to the meagre supply and the low water temperature, which lower the animals' metabolic rate. Temperature is known to have an important influence on the quantity of food consumed. A lowering of the environmental temperature by 12–14°C results in a food intake decrease of 0.4% in large *C. crangon* individuals and of 8% in small ones (van Lissa, 1977). Laboratory studies have shown that hungry sandy shrimps can scour 20 m^2 per hour in search of food (Dahm, 1976). The quality and quantity of food consumed is evident from a study of stomach contents of the animals. In the case of *C. crangon* from the Gulf of Gdańsk, 76% of individuals had empty stomachs (Wiktor, 1980). Unfortunately, this study was conducted an animals caught during the day; this species is known to feed in the evening and at night. Its metabolism is rapid and undigested food remains and metabolic products can be excreted within two hours (Phil and Rosenberg, 1982). On the basis of diurnal averages means, Phil and Rosenberg (1982) found that 26% of *C. crangon* individuals had empty stomachs in autumn and as many as 35% in summer.

As compared with the quantity of energy consumed by *C. crangon*, *C. glaucum* consumes much smaller quantities of food. The energy value of the food (10 474 $Jm^{-2}year^{-1}$) is also low, *i.e.* *ca.* 5.6 times less than in the carnivorous *C. crangon.* Similar observations have been made in other species of molluscs and clearly demonstrates the importance of food quality in the energy balance of filter feeders.

As in other crustaceans, biomass increments in *C. crangon* are related to moulting. Growth begins immediately after the shedding of the old exoskeleton and ends when the new one has hardened (Lockwood, 1968). In the Gulf of Gdańsk *C. crangon* moults every 10–12 days (Arendarczyk, 1974); in winter, however, the moult cycle takes rather longer to complete.

In *C. glaucum* energy increments are a continuous process, their rate (as in *C. crangon*) depending upon the age of the individuals and the water temperature.

The productivity of *C. crangon* in the Gulf of Gdańsk is less than in other regions studied. A very high level was reported in the Kattegat and Skagerrak, approaching 3.8 g of organic compounds per m^2 in July and August (Phil and Rosenberg, 1982). During the same period, the productivity of this species in the Wadden Sea was 3.1 g of organic compounds per m^2 (van Lissa, 1977), which is the highest productivity recorded in European waters. Both values concern the summer period when productivity is highest. Evans and Tallmark (1979) state the annual productivity of *C. crangon* in Gumarfiord to be 0.5–1.8 g of organic compounds per m^2 $year^{-1}$, which is similar to the annual productivity of this species in the Gulf of Gdańsk ($0.12\ \mathrm{g} \cdot \mathrm{m}^{-2}\ \mathrm{year}^{-1}$). The low productivity of *C. crangon* in the Gulf of Gdańsk may be due to the low salinity of the water (7.5 psu), the lowest of all the study areas compared.

The *C. crangon* population consumed four times more oxygen than that of *C. glaucum*, which is understandable in view of the former's more active mode of life. The more sedentary *C. glaucum* have a lower metabolic rate and, as in the majority of molluscs, their respiration can be anaerobic part of the time, so the whole the population consumes less oxygen to satisfy its energy requirements.

There are the differences in the amounts of energy assimilated by males and females of *C. crangon* (Tab. 1). Characteristic of the males is the poorer assimilation of energy, which is half of that observed in females. As the other energy efficiency indices are also higher in females, males are obviously worse energy converters.

Table 1. Energy efficiencies in populations of *C. crangon* and *C. glaucum* from the Gulf of Gdańsk

Species	A/C	P/C	P/A
Crangon crangon			
female	0.41	0.25	0.61
female + male	0.33	0.22	0.62
male	0.19	0.12	0.64
Cardium glaucum			
female + male	0.28	0.09	0.30

C. glaucum is not as good a converter of energy as *C. crangon*. The quantity of energy excreted and secreted constitutes about 70% of the energy consumed and it is similar to the values noted in *C. crangon*. The other coefficients of efficiency in the *C. glaucum* population are lower than in that of *C. crangon*.

One of the reasons why molluscs are less productive than crustaceans may be the fact that molluscs are herbivorous. Diatoms predominate in the food of *C. glaucum* whereas the predatory habits of *C. crangon* may be responsible for the higher productivity biomass ratio. A lower ratio of productivity to energy assimilated than in carnivores (Humphrey, 1979) is known to be characteristic of herbivores.

Changes in the quantity of energy assimilated and many other life processes are strictly dependent on temperature and the trophicity of the environment. These two factors have the greatest influence on the energy transfer flow in benthic organisms. Respiration and productivity increase with temperature within a certain range (Widdows *et al.*, 1979b). Abundance of nutrients in the environment will result in increased productivity, although above the critical point (excess nutrients) the efficiency assimilation decreases (Bayne and Widdows, 1978; Widdows *et al.*, 1979a,b). If the nutrient supply is insufficient or lacking altogether, the consumption and absorption of energy in many invertebrates are less than the quantity of energy consumed in metabolic processes.

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