ACTA HYDROBIOL.	33	3/4	241—251	KRAKOW 1991

Feeding of the freshwater bryozoan *Plumatella fungosa* (P a l l.). 2. Filtration rate, food assimilation, and production of faeces

Maciej Kamiński

Warsaw University, Zoological Institute, Department of Hydrobiology,
ul. Nowy Świat 67, 0-046 Warszawa, Poland

Present address:
Warsaw University, Branch in Białystok, Institute of Biology
ul. Świerkowa 20 B, 15-950 Białystok, Poland

Manuscript submitted June 21, 1991, acepted October 15, 1991

A b s t r a c t — Investigations have shown the mean filtration rate of natural seston by *Plumatella fungosa* to be 2.2 cm^3 mg^{-1} d.w. of a colony h^{-1}. On the basis of experiments using artificial food (Sephadex), a strong dependence of the filtration rate on concentration and particle size as well as on the size of the zooids was determined. Assimilation of food was estimated at 41.6%, the mean time of food passage through the gut at 3.2—4.6 h, and the defecation rate at 0.13 mg d.w. of faeces mg^{-1} d.w. of a colony 24 h^{-1}.

K e y w o r d s: Bryozoa, Phylactolaemata, *Plumatella*, feeding, filtration rate, assimilation, production of faeces.

1. Introduction

The filtration mechanism and the feeding physiology of freshwater bryozoans (Bryozoa, Phylactolaemata) is not very well known. In the investigations so far attention has been paid above all to food composition and the possibility of selection by the bryozoans of the food particles available in the suspension (R a d d u n, J o h n s e n 1983, K a m i ń s k i 1984, 1991). In the littoral of the eutrophic lakes of central Europe certain species of bryozoan, especially *Plumatella fungosa* (P a l l.), attain a large biomass and are probably a significant element of these biocoenoses. To determine the role which may be played by the Bryozoan in the circulation of matter in freshwater ecosystems it is necessary, *inter alia*, to know the amount of seston removed by these animals

from the profundal zone and the rate of introducing detritus of faecal origin into the bottom sediments.

The aim of the present work was to determine the filtration rate, the time of passage of particles of seston through the gut, assimilation of food, and the amount of faeces produced by the freshwater bryozoan *P. fungosa* in one of the eutrophic lakes in Poland.

2. Study area, material, and method

The investigation on the feeding of the bryozoan *P. fungosa* were carried out in summer (June—September), in the period 1980—1983. The filtration rate of the seston particles by the bryozoans and consumption and assimilation of food were determined by laboratory experiments, carried out on colonies collected from the littoral of the eutrophic Lake Mikołajskie (Kamiński 1991). The colonies of bryozoans (on the average 3.5 g of dry weight) together with a fragment of the substratum occupied by them were placed in 14 dm^3 vessels filled with water from the epilimnion of Lake Mikołajskie. Prior to 60 minute experiments the animals were adapted for 3 hours to the laboratory conditions. During the adaptation period the water in which the animals were kept was gradually changed every hour with fresh water taken directly from the lake. At the start of the experiments and immediately after their completion the concentration of seston in the experimental vessels was determined by the weight method (filtration using filters of 0.45 μm pore diameter). The filtration rate was calculated according to the formula (Gauld 1951):

$$P = v \frac{\lg C_o - \lg C_t}{0.4343\ t}$$

where:

v — water volume per unit mass of the animals,
C_o and C_t — initial and final concentration of the seston,
t — duration of the experiment.

The consumption of food (C) was calculated from the difference in seston concentration before and after contact with the bryozoans, with known water volume (V) using the formula: $C = V (C_o - C_t)$. Food assimilation (A) was determined according to the formula: $A = C - F$, in which F denotes the mass of the excreted faeces. The efficiency of assimilation (E) was calculated according to the formula: $E = \frac{A}{C} 100\%$.

The filtration rate of *P. fungosa* was also studied in experiments using artificial food — a suspension of spherical particles of Sephadex (G-50 Superfine). This method was employed earlier by Bullivant

(1968) in his investigations on marine bryozoans and by Gliwicz (1977) in investigations on the feeding of lake zooplankton. The diameter of the particles forming the suspension of artificial food varied from under 3 to about 50 μm, the those in the fraction 30—40 μm decidedly dominating. The experiments were carried out in closed cylindrical vessels of 120 cm^3 capacity. The vessels were filled with aerated filtered water from the lake, a suspension of artificial food and also fragments of the stocks of *Phragmites australis* with small (some hundreds of zooids) colonies *P. fungosa* then being added. For each of the 3 experimental series suspensions of different particle concentration were prepared — from 0.4 to 25.0 particles in 1 mm^3. From the moment of restarting filtration, determined by way of direct observation of the advancing lophophores, the animals grazed for 40 minutes. To prevent sedimentation of the particles the vessels was slowly revolved in the vertical plane by 180° every 5 minutes. On completion of the experiment, all colonies were preserved in 4% formalin and then, after preparation of the guts of the particular zooids, the number and size of the isolated particles were determined. 35 individuals from each colony were taken for examination. On the basis of measurements of body length and the filtration rate calculated for the particular zooids, the correlation between these values was analysed (Żuk 1989).

The defecation rate of the bryozoans was examined in short-lasting (0.5—1.0 h) field experiments. Colonies of *P. fungosa* immediately after being taken from the lake, together with a fragment of the substratum, were placed in open 12 dm^3 containers filled with lake water collected at the site of the bryozoans' occurrence. After a predetermined time of exposure the dry weight of the bryozoan colonies and that of the excreted faeces were determined. To establish the diel dynamics of faeces production field experiments were carried out in which 0.5 h measurements of the mass of the excreted faeces were conducted every 2 or 3 hours within the whole 24-hr period. During the periods between the measurements the substrata inhabited by bryozoans were exposed in the lake at the stations from which they had been collected.

The time of food passage through the digestive tract of *P. fungosa* was investigated in laboratory experiments carried out at natural concentration of the seston. The experiments consisted in short-lasting (10 min.) placing of the bryozoans colonies in vessels containing lake water enriched with a suspension of artificial food. After this time the colonies, together with the substratum, were carefully washed in water without suspension, and then placed in vessels filled with unfiltered lake water. The colonies were transferred to new vessels every hour. The faeces removed from the colonies during the successive hours of the experiment were examined under the microscope and the number of the artificial food particles excreted was recorded. The

experiments were continued until at least 90% of the Sephadex particles consumed together with the food (had been removed from the colonies).

3. Results

The filtration rate of the bryozoan *P. fungosa* feeding on natural seston, determined in five laboratory experiments, showed values from 1.09 to 3.95 cm^3 mg^{-1} d.w. h^{-1} (table I), the slowest filtering rate being

Table I. Results of laboratory experiments on the feeding of P. fungosa using natural seston and artificial food particles

Natural seston			Artificial food particles (concentration 10 particles mm^{-3})		
initial concentration of seston mg d.w. dm^{-3}	filtration rate cm^3 mg^{-1} d.w. h^{-1}	assimilation of food %	diameter of particles µm	filtration rate cm^3 mg^{-1} d.w. h^{-1} mean	range
3.5	1.95	51.8	5—10	0.11	0.05—0.18
4.0	2.50	35.7	11—15	0.24	0.13—0.30
4.5	1.65	46.8	16—20	0.46	0.22—0.56
4.6	3.95	41.4	21—25	1.01	0.48—1.31
6.2	1.09	32.5	26—30	1.76	1.06—2.22
			31—35	1.85	1.22—2.33
Mean	2.23	41.6	36—40	1.56	1.02—2.11

seen with the highest concentration of seston. In the experiments where artificial food was employed a distinct dependence of the filtration rate on the food concentration, dimensions of the suspension particles, and the size of the zooids was determined. In the studied range of changes in food concentration an increase in the particle density was accompanied by a decrease in the filtration rate. In spite of the falling filtration rate the food ration of the zooids increased (up to a concentration of 6.1 particles mm^{-3}) (fig. 1). The filtration rate was dependent on the size of the individuals. An increase in the body length of the zooid (from 1.3 to 3.6 mm) was accompanied by an increased filtration rate. The dependence between the size of the individual and the filtering rate resembled a linear function (fig. 2). The relation between the size of the individual and the filtration rate of the particles was determined at various concentrations of artificial food. In each case it was statistically significant ($P<0.01$), the correlation coefficient having values from + 0.85 to + 0.92.

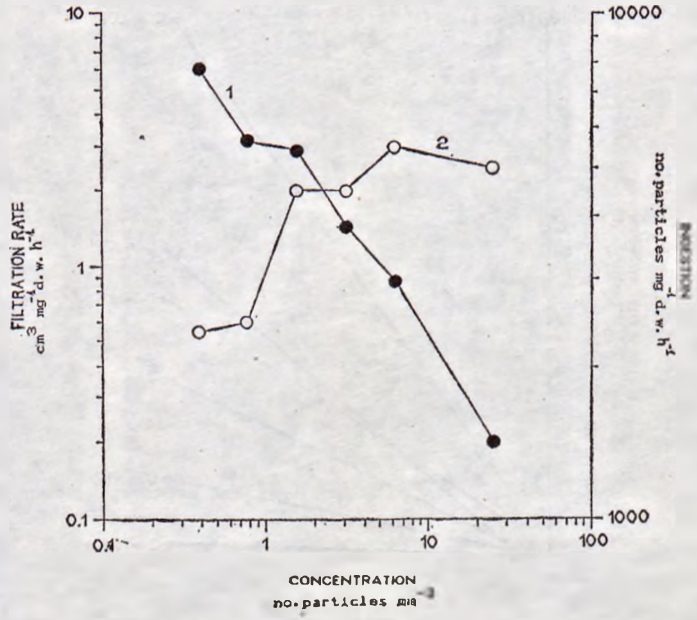

Fig. 1. Filtration rate (1) and food ration (2) of *P. fungosa* at various concentrations of artificial food. Results of a laboratory experiment, August 1980

Particles of various size were filtered from water at various intensity. In the case of artificial food particles, at a concentration of 10 particles mm^{-3} the highest filteration rate was recorded for particles of 31—35 μm in diameter, and the lowest for those with the smallest dimensions (5—10 μm) (Table I).

The time of passage of the seston particles through the digestive tract of the zooid *P. fungosa* investigated in five laboratory experiments varied greatly. The first particles of artificial food which included a small admixture of the natural seston appeared in the faeces after about 50 min. With time a steady increase was observed in the proportion of the Sephadex particles voided by the colonies with respect to the total number of these particles swallowed by the bryzoans at the start of the experiment. Half of the particles left the digestive tract within 3.2 to 4.6 hours, and 90% within 6.0 to 7.0 hours (fig. 3). The great differentiation in the time of passage of the food through the gut of the zooids was connected with the transport mechanisms of food particles from the mouth opening to the end section of the gut observed in vivo. The filtered and successively swallowed suspension particles were constantly mixed in the large and muscular caecum with the food particles already present there. Hence the end section of the gut, sometimes referred to as the rectum, where successive faeces are formed and

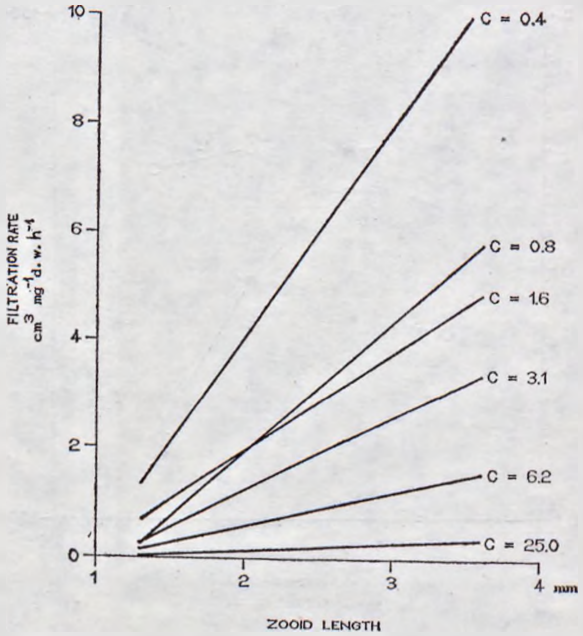

Fig. 2. Relation between the body length of the zooids of *P. fungosa* and the filtration rate, at various concentrations (C) of artificial food (number of particles mm^{-3}). Results of laboratory experiments, August 1980

enveloped in a peritrophic membrane, might contain not only the remnants of undigested food but also particles freshly swallowed by the zooid.

The bryozoans excrete faeces of large dimensions, compact, in the shape of elongated drops. On the basis of the measurements of more than 200 excrements of *P. fungosa* it was determined that the mean length of the faeces was 940 μm (320—1400 μm) with a width of about 280 μm (130—500 μm). The size of the faeces depends on the size of the zooid. With low concentration of the food the thickness of the faeces distinctly diminishes while their length remains unchanged (constant length of the peritrophic membrane). The mass of a single faeces determined on twelve occasions was $3.2 \pm 0.8 \times 10^{-3}$ mg d.w.

Defecation observed in large colonies of the bryozoans was continuous In the field experiments no distinct, diel rhythms in the voiding of faeces were recorded, although irregular variations in their production rate were observed (fig. 4). The faecal mass voided by a colony of *P. fungosa*, determined in the field experiments (140 replications) amounted on the average to 0.13 ± 0.05 mg d.w. mg^{-1} d.w. of a colony $24\ h^{-1}$. Considering the relatively short time that the injested seston particles remained in the gut, and the absence of a distinct, diel defecation

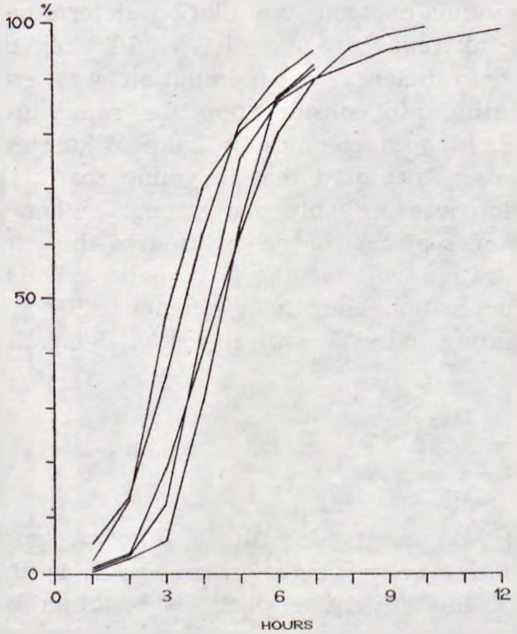

Fig. 3. Time of passage of natural seston (doped with an admixture of artificial food) through the gut of *P. fungosa* expressed as a cumulative proportion (%) of excreted food particles in the successive hours of observation. Result of laboratory experiments, 1980 and 1982

rhythm, it may be assumed that the bryozoans feed continuously and the filtration rate of the food does not significantly change within 24 hours.

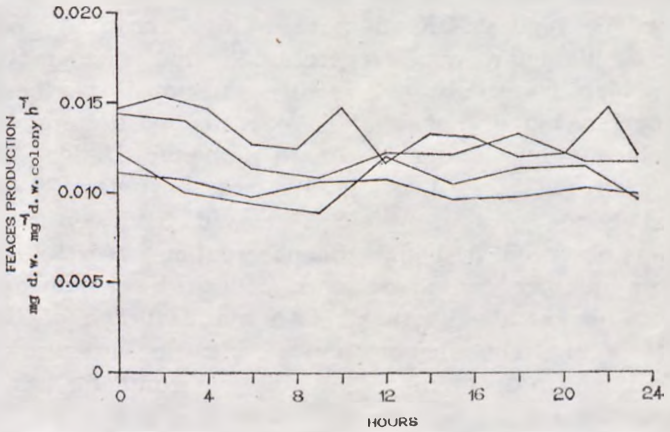

Fig. 4. Diel changes in the rate of faeces production by *P. fungosa* in Lake Mikołajskie. Results of field esperiments — July 1980 and August 1983

The absolute value of food assimilation determined experimentally amounted on the average to $3.0 \pm 1.1 \times 10^{-3}$ mg d.w. mg^{-1} d.w. of a colony h^{-1}. The efficiency of assimilation was estimated at 41.6% (32.5—51.8%). Taking into consideration the rapid growth rate of the biomass of the *P. fungosa* colonies in Lake Mikołajskie (Kamiński, unpubl. data), it was calculated that in young zoaria the absolute value of food assimilation was probably many times higher than in the older multi-layered colonies of this bryozoan used in the experiment.

The mean filtration rate of the bryozoans calculated on the basis of the rate of defecation and the efficiency of food assimilation was close to the filtration rate of natural seston determined in laboratory experiments.

4. Discussion

The filtration rate observed with *P. fungosa*, amounting to a few cm^3 per 1 mg of dry body weight in one hour, is similar to the rate of consumption of the suspension particles by other littoral or pelagial filter feeders — freshwater sponges, rotifers, cladocerans, copepods, and bivalves (Jørgensen 1966, Burns 1969, Jashnov 1969, Stańczykowska 1977, Frost 1978), although higher values, amounting to more than 10 or even many more than 20 cm^3 mg^{-1} d.w. h^{-1} have been determined for certain species of Cladocera (Haney 1973). Worthy of note is the diverse filtration rate of particles of different size. As regards natural food, in the course of grazing *P. fungosa* positively selected the smallest particles (under 20 μm) and particles measuring from about 40 to 170 μm (Kamiński 1991). In experiments with artificial food the result obtained was different from that in the field observations: the highest filtration rate was recorded for particles 31—35 μm in diameter, which represented that size fraction of the suspension which is usually not readily consumed by the bryozoans. In the nannoplankton of Lake Mikołajskie the most numerous fraction were the cells of algae under 20 μm in diameter. Under experimental conditions, with the highest availability of particles 30—40 μm in diameter, a change in the preferred size of food consumed by the bryozoans was observed. Although this observation needs to be confirmed by a greater number of experiments, it can be assumed that such behaviour of the examined animals is a manifestation of the strategy of optimal foraging. The phenomenon of filtration orientation towards the food fraction most abundant in the environment has also been observed with the filtering copepods (Wilson 1973).

The dependence between the particle concentration and the filtration rate as well as the food ration on the filter feeders is well known and

well documented. Both in the presented experiments carried out on *P. fungosa* and in investigations on the feeding of marine bryozoan from the genus *Zoobotryon* (Bullivant 1968) it was found that an increased concentration of particles in the suspension is accompanied by a decrease in the filtration rate and an increase in the food ration. The food ration of the filter feeders increases to maximum values, reached at the so-called concentration of saturation, and then becomes stabilized. In the experiments with artificial food it was found that the concentration of saturation for *P. fungosa* is very high, amounting to about 6.1 particles mm^{-3}.

The time of passage of food through the gut of *P. fungosa* was found to be relatively short. Dumortier and van Benden (1948, after Marcus 1926) defined the time of food passage through the digestive tract of this bryozoan as 2—3 hours. Becker (1937) established that the food particles remain for 15—20 seconds in the esophagus, a „longer time" in the caecum, and about 30 minutes in the end section of the gut, when large quantities of food are found in the environment. The various time periods during which the food particles remain in the gut (from several minutes to several hours) found in the present investigations, undoubtelly affects the efficiency of the digestive processes.

The data referring to the biomass of *P. fungosa* in Lake Mikołajskie (Kamiński, unpubl. data), food assimilation, and rate of production of faeces permit an estimation of the mass of seston removed by these animals from the profundal zone and the mass of faeces introduced during that time into the bottom sediments. It was calculated that in 1983 *P. fungosa* (at a mean biomass 11.9 kg d.w. ha^{-1}) in the littoral zone of Lake Mikołajskie filtered about 15 tons d.w. of seston and introduced into the bottom sediments about 8.8 tons d.w. of faeces. A comparison of the rate of faeces production by the bryozoans with that of other groups of the littoral fauna in Lake Mikołajskie (Pieczyńska et al. 1984) revealed that *P. fungosa* introduced into the bottom sediments about twice as much faecal matter as fish and water birds. Higher values for the production of detritus of faecal origin were determined in this lake for bivalves (Stańczykowska 1977) and for snails (Kołodziejczyk 1983). The consumption by the bryozoans of a considerable amount of seston and the production of large quantities of detritus may be an indication of the vital importance of this group of animals for the circulation of matter in the littoral of his lake.

5. Polish summary

Odżywianie się słodkowodnego mszywioła *Plumatella fungosa* (Pall.). 2. Tempo filtracji, asymilacja pokarmu i produkcja fekalii

Badania nad odżywianiem się *Plumatella fungosa* prowadzono w latach 1980—1983 na koloniach występujących w litoralu eutroficznego jeziora Mikołajskiego. W eksperymentach laboratoryjnych stwierdzono, że średnie tempo filtracji naturalnego sestonu wynosi 2,23 cm^3 mg^{-1} s.m. kolonii h^{-1} (tabela I). Eksperymenty z wykorzystaniem sztucznego pokarmu (Sephadex G-50 Superfine) wykazały uzależnienie tempa filtracji od koncentracji zawiesin, średnicy cząstek pokarmowych oraz wielkości zooidów *P. fungosa* (tabela I, ryc. 1, 2). Cząstki sestonu pobrane przez mszywioły pozostawały w jelicie od kilkudziesięciu minut do kilkunastu godzin, przy czym średni czas pasażu pokarmu wynosił 3,2—4,6 godziny (ryc. 3). Asymilację pokarmu oceniono na 41,6%. Na podstawie doświadczeń terenowych nad dobowymi zmianami tempa wytwarzania fekalii wysunięto przypuszczenie, że mszywioły odżywiają się w sposób ciągły, a tempo filtracji pokarmu nie zmienia się istotnie w ciągu doby (ryc. 4). Biorąc pod uwagę dane o biomasie *P. fungosa* w jeziorze Mikołajskim, tempie filtracji i masie wytwarzanych fekalii obliczono, że w ciągu sezonu mszywioły te odfiltrowywują w strefie litoralu około 15 ton s.m. sestonu i wprowadzają do osadów dennych około 8,8 ton s.m. fekalii.

6. References

Becker G., 1937. Untersuchungen über den Darm und die Verdauung von Kamptozoen, Bryozoen und Phoroniden. Zeitschr. f. Morph. u. Ökol. d. Tiere, 33, 72—127.

Bullivant J. S., 1968. The rate of feding of the bryozoan *Zoobotryon verticillatum*. New Zealand J. Mar. Freshwat. Res., 2, 111—135.

Burns C. W., 1969. Relation between filtering rate, temperature and body size in four species of *Daphnia*. Limnol. Oceanogr., 14, 693—700.

Frost T., 1978. In situ measurements of clearance rates for the freshwater sponge *Spongilla lacustris*. Limnol. Oceanogr., 23, 1034—1039.

Gauld D. T., 1951. The grazing rate of planktonic copepods. J. Mar. Biol. Assoc. UK, 29, 695—706.

Gliwicz Z. M., 1977. Food size selection and seasonal succession of filter-feeding zooplankton in an eutrophic lake. Ekol. pol., 25, 179—225.

Haney J. F., 1973. An in situ examination of the grazing activities of natural zooplankton communities. Arch. Hydrobiol., 72, 87—132.

Jashnov V. A., 1969. Praktikum po gidrobiologii. Moskva, Vyshaya Shkola, 438 pp.

Jørgensen C. B., 1966. Biology of suspension fedding. London, Pergamon Press, 357 pp.

Kamiński M., 1984. Food composition of three bryozoan species (Bryozoa, Phylactolaemata) in a mesotrophic lake. Pol. Arch. Hydrobiol., 31, 45—53.

Kamiński M., 1991. Feeding of the freshwater bryozoan *Plumatella fungosa* (Pall.). 1. Food composition and particle size selection. Acta Hydrobiol., 33, 229—239.

Kołodziejczyk A., 1983. Występowanie Gastropoda w litoralu jeziornym i ich

znaczenie w produkcji i przekształcaniu detrytusu [Occurrence of Gastropoda in lake littoral and its role in the production and processing of detritus]. Warszawa, Uniw. Warsz., 101 pp.

Marcus E., 1926. Beobachtungen und Versuche an lebenden Süsswasser-bryozoen. Zool. Jahrb., Abt. f. Syst., 52, 279—350.

Pieczyńska E., D. Balcerzak, A. Kołodziejczyk, Z. Olszewski, J. Rybak, 1984. Detritus in the littoral of several Masurian lakes (sources and fates). Ekol. pol., 32, 387—440.

Raddum G. G., T. M. Johnsen, 1983. Growth and feeding of *Fredericella sultana* (Bryozoa) in the outlet of a humic acid lake. Hydrobiologia, 101, 115—120.

Stańczykowska A., 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. Pol. Arch. Hydrobiol., 24, 461—530.

Wilson D. S., 1973. Food size selection among copepods. Ecology, 54, 909—914.

Żuk B., 1989. Biometria stosowana [Applied biometry]. Warszawa, PWN, 425 pp.