ANNAL. BIOL. TIHANY	43	105–116	HUNGARIA 1976

SEASONAL CHANGES IN THE FILTERING RATE OF *EUDIAPTOMUS GRACILIS* (*G. O. SARS*) IN LAKE BALATON

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Received: 15th March, 1976

The only filter feeding copepod of Lake Balaton, *Eudiaptomus gracilis* was first found by Richard in 1891 (Entz, 1897). From that time on this species is mentioned in all papers dealing with the crustacean plankton of this lake. However, only a few quantitative data are available on the nutrition, filtering rate, food uptake and incorporation of this species in other lakes, and until recently hardly any investigations of this type have been carried out in our lake. In 1972–73 we fed *E. gracilis* on algae obtained from pure cultures and determined the food incorporation in function of alga species, food concentration and season (Zánkai and Ponyi, 1974a, b; Zánkai, 1975). Detailed investigations on the population of *E. gracilis* were carried out by Ponyi et al. (1975). In order to get some estimate of the food uptake and the role of this population in the ecosystem of the lake, this paper deals with the filtering rate of adults under natural conditions.

Material and methods

20–28 hours before the experiments 2 litres of water were sampled from 0.5 m depth in the pelagial 300–500 m off shore in front of our Institute. From the sample 1.5 litre was filtered through a No. 8 net (pore size 300–320 μm) in order to remove larger for nutritional purposes unavailable animals, algae and other particles.

After this treatment 200 μCi $NaH^{14}CO_3$ (Isotope Institute of the Hungarian Academy of Sciences, spec. activity 57.1 mCi/mmole) was added to the water, and the bottle was replaced and incubated in the lake for 20–28 hours at a depth of 0.3–1.0 m depending on turbidity. In the laboratory this water was then portioned per 100 ml into smaller bottles. The latter had glass stoppers and were wrapped into aluminia sheets to prevent further photosynthesis. Of the same water 100 ml was passed through GF/C glass fibre filter and the particulated organic carbon content was determined by the wet oxidation techniques (Ostapenja, 1965).

In order to determine the specific activity of the food 3×50 ml water was filtered through membrane filters (Sartorius Membranfilter GMBH, pore size 0.2 μm), then the filters were washed by previously filtered, inactive lake water. This rinsing continued till the effluent became absolutely inactive. According to previous experiments rinsing with 250 ml was necessary.

The animals were collected immediately prior to the experiments by No. 6 net from the same area whence the water was sampled. Male and female adults were separated under stereomicroscope, and 8 – 20 individuals (males and females mixed) were placed into the bottles, containing 100 ml water. These bottles were then replaced into the lake.

In all experiments the feeding period lasted for 40 – 41 minutes. This time interval was chosen on the basis of the data of RICHMAN (1964) and KIBBY (1971) and of our experiments. Before the experiments on the filtering rate 15 – 15 *E. gracilis* adults were placed into 100 – 100 ml previously filtered (0.2 μm pore size) lake water, containing carmine pulver to determine the shortest time necessary for the food particles to pass through the alimentary tract (minimum Erneuerungskoefficient) (NAUMANN, 1921; RIGLER, 1971). The feeding periods were 40, 50 and 60 minutes. Most of the animals (10, 13 and 11 from the 15 – 15 – 15 individuals and 10 from 10 individuals) fed on the carmine particles, and the passage of these particles in the alimentary tract could be traced under a stereomicroscope. After feeding with carmine particles the animals were placed in Balaton water, filtered through No. 25 net. None of the animals released carmine within the first hour. In the third hour about half of the animals, after the sixth hour all depleted their guts. This was the 40-minute feeding period in our experiment was short enough to avoid loss of radioactivity through defecation.

After the feeding period the crustaceans were rinsed, killed by hot water and placed into scintillation vials, containing Bray solution. The radioactivity was measured by Isocap/300 and Packard Tri-Carb liquid scintillation detectors. In the case of the particles, filtered from the water the absolute radioactivity (dpm) was obtained by the channel ratio method, while in the case of animals a correction factor of 1.38 for self-absorption was also used (ZÁNKAI and PONYI, 1974b).

The filtering rate was calculated according to the following formula:

$$F = E \frac{R_2 \times 24}{R_f \times t},$$

where

F = filtering rate in ml.cop^{-1}.day^{-1},
E = self-absorption of adult animals,
R_2 = radioactivity of one animal,
R_f = radioactivity of food in one ml water,
t = time of feeding in hours.

Results

The investigations were carried out in fortnightly–monthly intervals from March 1974 to November 1975. This way the changes in filtering rate were followed throughout nearly two years by natural food and temperature conditions *(Table I)*. The minimum filtering value per animal per day was 0.01 ml water (0.4 °C; 1.43 μg C/ml), the maximum one 3.27 ml (21 °C; 0.8 μg C/ml). The seasonal (astronomical seasons) average filtering rates were the

TABLE I

Changes in the filtering rate of Eudiaptomus gracilis

Date	Water temperature °C	Organic C µg/100 ml	Number of samples	Filtering rate ml/cop./day ± S. D.
12. III. 1974.	5.6	89.7	4	0.28 ± 0.08
28. III.	10.0	–	4	0.04 ± 0.00
18. IV.	10.2	173.1	4	1.19 ± 0.38
9. V.	14.0	103.7	6	2.15 ± 0.78
31. V.	19.5	47.5	5	1.22 ± 0.72
13. VI.	15.0	80.6	5	1.04 ± 0.42
28. VI.	20.5	90.7	5	0.92 ± 0.29
16. VII.	23.0	144.2	5	0.83 ± 0.11
5. IX.	2.14	104.4	3	1.94 ± 0.39
11. IX.	18.0	80.5	2	0.62
26. IX.	15.0	79.1	4	0.87 ± 0.34
30. X.	6.5	87.0	5	0.75 ± 0.15
5. XI.	6.0	–	5	0.31 ± 0.04
10. XII.	5.0	99.4	5	0.16 ± 0.05
23. XII.	3.0	97.5	5	0.13 ± 0.04
9. I. 1975.	2.5	107.2	5	0.08 ± 0.06
22. I.	3.0	101.9	5	0.15 ± 0.05
13. II.	2.0	96.9	5	0.12 ± 0.07
5. III.	5.0	–	4	0.08 ± 0.01
21. III.	9.0	186.4	5	0.11 ± 0.07
27. III.	7.0	189.7	7	0.22 ± 0.03
15. IV.	9.0	153.7	7	0.12 ± 0.04
8. V.	17.5	91.9	7	1.61 ± 0.39
22. V.	22.3	95.2	8	2.36 ± 0.74
5. VI.	17.2	172.8	8	0.33 ± 0.12
25. VI.	27.0	60.8	8	1.27 ± 0.28
9. VII.	26.0	–	8	1.23 ± 0.35
25. VII.	23.5	112.4	8	2.18 ± 0.32
14. VIII.	24.0	42.2	8	1.34 ± 0.42
5. IX.	23.0	57.6	8	1.95 ± 0.43
19. IX.	21.0	76.0	7	2.93 ± 0.34
8. X.	14.5	155.2	8	1.48 ± 0.29
23. X.	12.0	67.3	8	0.47 ± 0.08
4. XI.	8.5	58.1	6	0.77 ± 0.19
28. XI.	0.4	142.9	8	0.12 ± 0.06

following: spring 0.96; summer 1.44; autumn 0.63; winter 0.11 ml/copepod/day. The difference between the summer and winter values is highly significant ($P \ll 0.001$).

The filtering rate of *E. gracilis* depends on water temperature, on the concentration of food and on the physiological state of the animals. A comparison of the filtering rate and the water temperature *(Fig. 1)* shows the two factors to be connected. This connection is especially close in periods with rapid temperature changes, i.e. in spring and autumn. In winter, parallel with low temperature, filtration is likewise slow. In summer filtration is usually intensive, but it varies much, and does not follow the changes in temperature.

By the statistical analysis (t – statistic) of the temperature effect on the filtering rate the direction of the temperature changes was disregarded.

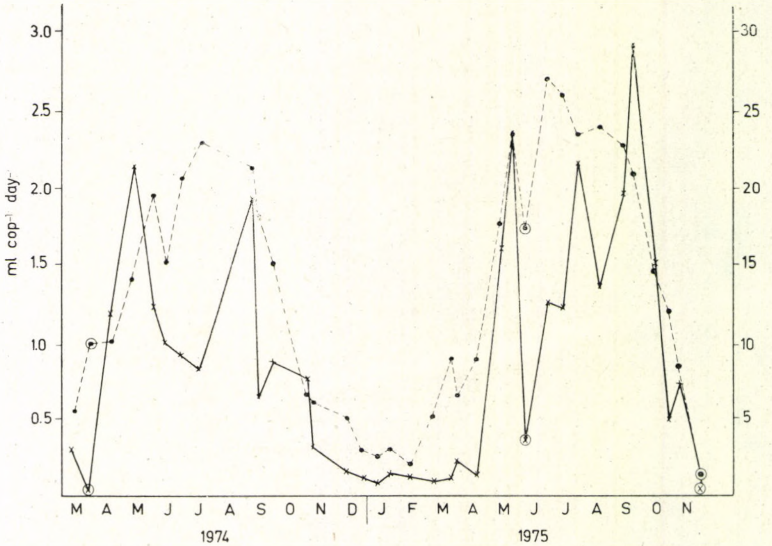

Fig. 1. The filtering rate of *Eudiaptomus gracilis* and the temperature of the lake during the experiments. (———— filtering rate, — — — — temperature, O storm)

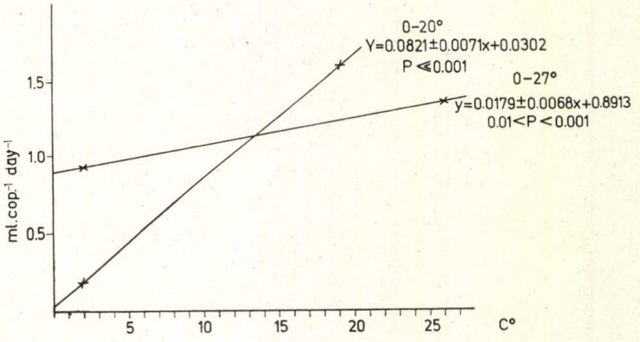

Fig. 2. The filtering rate in the function of temperature

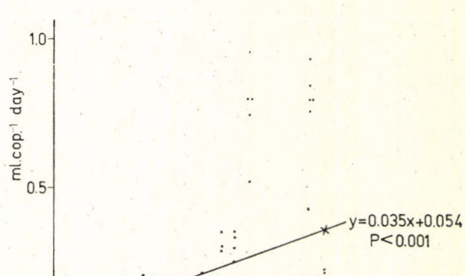

Fig. 3. Regression between filtering rate and temperature within the range of 0—10 °C

Taking into calculation the total temperature range of the lake (0—27 °C) the effect of temperature was significant ($0.01 > P > 0.001$) *(Fig. 2)*. For the 0—20 °C interval the two components are even more closely connected ($P < 0.001$). By dividing the total temperature range to intervals of 5 °C amplitude, it was found, that for a temperature change of 5 °C the filtration does not change unequivocally, and only a difference of 10 °C resulted in signif-

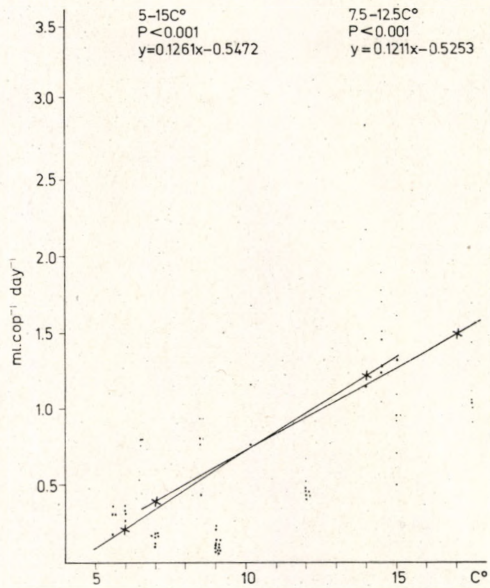

Fig. 4. Regression between filtering rate and temperature within the ranges of 5—15 and 7.5—17.5 °C

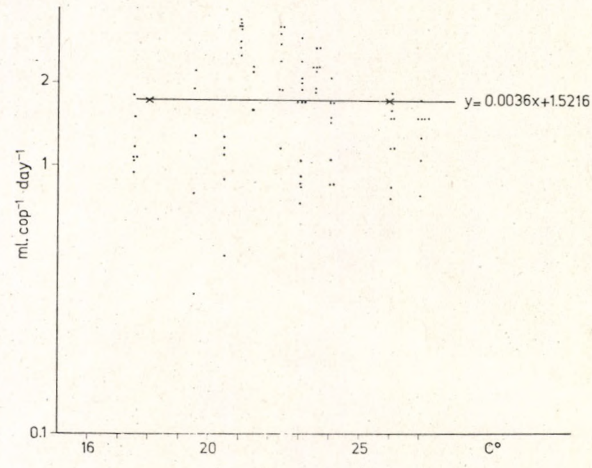

Fig. 5. Regression between filtering rate and temperature within the range of 17.5—27 °C

icant increase or decrease of the filtration. This statement is valid for the temperature intervals of 0–10, 5–15, 7.5–17.5 °C *(Figs 3–4)*. In the intervals of 15–25 °C and 17–27 °C filtering rate does not follows temperature changes, but it appears to be absolutely independent from it *(Fig. 5)*.

To get information on the concentration of food available to crustaceans, the particulated organic carbon content of the water was determined. This is proportional with the amount of algae and the suspended detritus, and thus

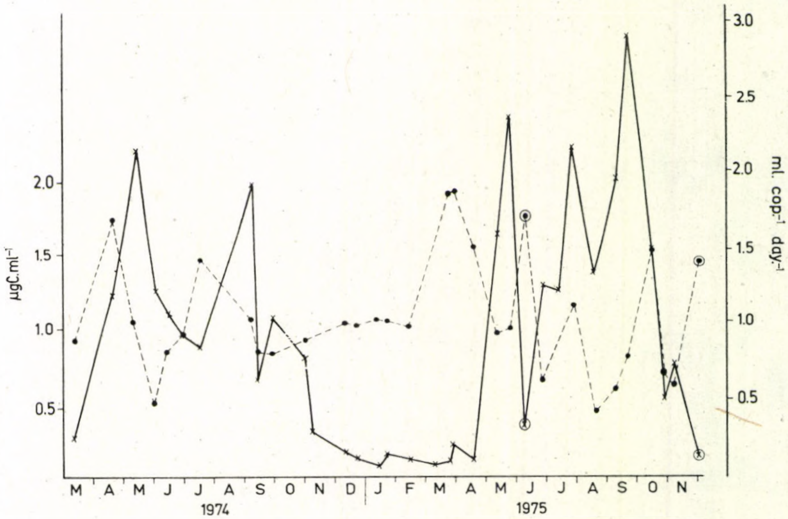

Fig. 6. The filtering rate of *Eudiaptomus gracilis* and the particulated organic carbon content of the water during the experiments. (———— filtering rate, — — — — organic C, O storm)

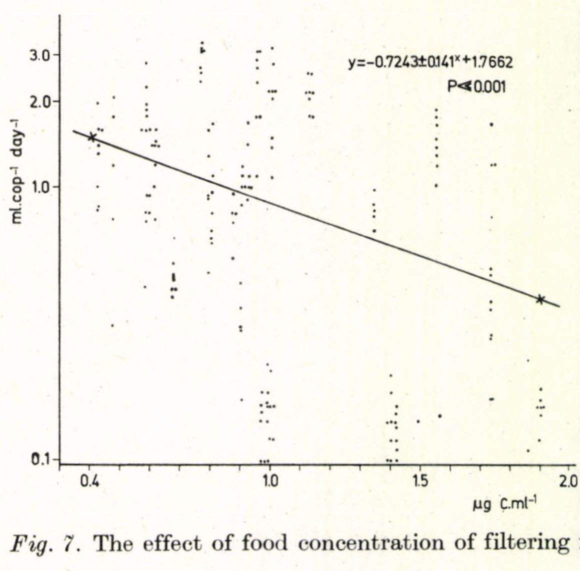

Fig. 7. The effect of food concentration of filtering rate

depends on the water movement. In the present study it varied within the range of 0.42 – 1.90 mg C/litre with an average of 1.05 mg C/litre *(Table I)*. In both years the lowest values were found in summer during long calms. During phytoplankton rises in spring (March, April) and autumn the organic carbon content attained a value of 1.5 – 1.9 mg/litre. The fairly constant autumnal and winter values fell within the range of 0.9 – 1.0 mg C/litre. This was doubled during storms. Disregarding the effect of temperature a negative correlation was found between food concentration and filtering rate: $y = (-0.7249 \pm 0.141)\times + 1.7662$ ($P < 0.001$) *(Fig. 7)*.

Filtration is influenced both by temperature and food concentration, however, sometimes these effects can be separated. In late autumn and in winter the temperature (0 – 5 °C) slows down the filtration (continuous line in *Fig. 1*) to an extent, that food concentration in this period (0.97 – 1.43 mg C/litre) had no effect on it. The effect of food concentration prevails in stormy periods (e.g. 4 – 5 June 1975 in *Fig. 6*). Before this experiment there were already strong waves for two days. The temperature did not change significantly, but the amount of organic and inorganic materials increased in the water, strongly inhibiting filtration. In summer (20 – 27 °C) the organic carbon content of the water varied from 0.42 to 1.12 mg/litre with the single exception of 16 July 1974 when it attained 1.44 mg/litre. In summer both low food concentration and high temperature contribute to low filtering rate.

The effects of body size and physiological conditions on the filtering activity are reflected by the high variability of the parallel values in summer *(Fig. 5)*. In addition the number of animals and the ratio of males to females varied too in the samples. In order to demonstrate physiological effects, in some experiments the filtering rate of females with and without eggs were separately studied *(Table II)*. After the experiment the animals were killed

TABLE II

The filtering rate of Eudiaptomus gracilis females with and without eggs

Date	Water temperature °C	Cop./100 ml	Filtering rate ml/cop./day
5. Sept. 1974	21.4	10	2.48 with eggs
		15	2.43 with eggs
		18	1.50 without eggs
		16	2.21 without eggs
		11	2.13 without eggs
11. Sept. 1974	18	16	0.79 with eggs
		11	0.71 with eggs
		18	0.64 without eggs
		17	0.62 without eggs
26. Sept. 1974	15	6	1.72 with eggs
		18	1.08 without eggs

in hot water and the eggs were removed to obtain crustaceans of the same size and self-absorption. The activity of egg carrying females proved to be 20 – 25 per cent higher.

Discussion

The quantitative aspects of the nutrition of filter feeding crustaceans can be characterized by their filtering and feeding rates (GUTELMACHER, 1974). The method of filtering rate measurement, used also in our experiments was described by NAUWERCK (1959). He demonstrated its usefulness in the case of *Diaptomus graciloides*, living in Lake Erken. The error of the method is supposed to be less than 20 per cent. Since that time the filtration and feeding of crustaceans were studied in many lakes (BELL and WARD, 1970; BURNS and RIGLER, 1967; SAUNDERS, 1969; 1972; DUNCAN, 1975). These works deal mainly with cladocerans, while until now the nutrition of only four fresh water calanoid species was studied under natural conditions *(Table III)*.

TABLE III

Filtering rates of fresh water calanoids feeding on natural foods

Species	Water temperature °C	Filtering rate ml/cop./day	Lake	Author
Diaptomus oregonensis	18±1	1.91±1.25 – 12.9±1.98	Lake Marion	MCQUEEN 1970
Diaptomus oregonensis	22 – 23	0.067±0.014	Lake Winnebago	RICHMAN 1964
Diaptomus oregonensis	3 – 24 – 2	0.0 – 1.4 2.1 – 2.2	Lake Heart Drowned Bog Lake	HANEY 1973
Diaptomus siciloides	10 20	1.0 2.0	Lake Severson	COMITA 1964
Eudiaptomus graciloides	0.2 – 17 – 0.2	0.3 – 2.8	Lake Erken	NAUWERCK 1959
Eudiaptomus graciloides	17.9 21.1	3.67 – 4.00 1.60 – 2.40	Lake Krivoe	GUTELMACHER 1973
Eudiaptomus gracilis	4 – 18 7 – 15	0.83 – 2.40 1.09 – 1.97	Queen Elizabeth II King George VI	KIBBY 1971
Eudiaptomus gracilis	5.6 – 27 – 0.4	0.04±0.00 – 2.93±0.34	Lake Balaton	ZÁNKAI, PONYI 1976

Our results are similar to the filtering rates obtained by KIBBY (1971) for *E. gracilis*, by NAUWERK (1959) for *E. graciloides*, by COMITA (1964) for *D. silicoides* and HANEY (1973) for *D. oregonensis*. GUTELMACHER (1973) found a higher filtering rate, but he used a self-absorption coefficient of 1.88, while this coefficient is only 1.42 according to KIBBY (1971) and 1.38 according to our measurements (ZÁNKAI and PONYI, 1974b). By correcting GUTELMACHER's data for our self-absorption coefficient the filtering rate for phytoplankton is 2.69 – 2.94 and for bacterioplankton 1.17 – 1.76 mg/cop./day. These data fit already into the range obtained by the authors listed above and also by us.

On the other hand Richman (1964) published much lower and McQueen (1970) higher values.

The effect of temperature on the filtering rate of cladocerans was studied by Burns (1966), Burns and Rigler (1967), McMahon (1965), Ivanova (1965) and Duncan (1975) under natural conditions. They found the filtration to increase up to a critical temperature, then to decrease again. This critical temperature varied between 20 and 27°C depending on the species. On the other hand, according to Ivanova (1965) temperatures above 5 °C have no effect on the filtering rate of *Daphnia pulex*.

In case of fresh water calanoids no work is known to us aiming to establish correlation between temperature and filtration. However studies, carried out for many months on the feeding of these crustaceans under natural conditions refer to the effect of temperature. Kibby (1971) measured the filtration of *E. gracilis* from March (4° C) to October (14.5 °C) and found it to depend more on temperature than on food. Nauwerck (1959) studied the annual cycle and mentioned the effect of temperature on the filtering rate, too. On the contrary Haney (1973), who studied *D. oregonensis* a whole year through, has found no correlation between filtering rate and body size or temperature. Our two-year experiences support the findings of Nauwerck (1959) and Kibby (1971) with the addition, that only temperature changes higher than 10 °C result in significant increase or decrease of the filtering rate. In our experiments the critical temperature was 19 ± 1 °C.

Filtering and feeding rates depend also on the quality, size, concentration and chemical composition of the food. It remains for further experiments to determine which materials and to what extent are available as food under natural conditions, and whether the feeding is selective or not.

In the case of *E. gracilis* such problems were studied by feeding the animals on algae, obtained from pure cultures, and determining the filtering and feeding rates and the incorporation of the food (Malovickaja and Sorokin, 1961; Schindler, 1971; Kibby, 1971; Infante, 1973; Zánkai and Ponyi 1974a, b). Another method to obtain information on the composition of the natural food is the analysis of the intestinal content. By this method other fresh water calanoids, e.g. *E. graciloides*, *E. coeruleus* (Bogatova, 1965), *Acanthodiaptomus denticornis* (Bogatova, 1965; Infante, 1973), *Mixidiaptomus laciniatus* (Infante, 1973), *Diaptomus shoshone* and *Diaptomus coloradensis* (Maly and Maly, 1974) have been investigated, but no data on *E. gracilis* are available.

As proved by Nauwerck (1962) *E. gracilis* can be cultured in lake water free of algae. Sebestyén (1959) detected $CaCO_3$ and detritus particles in the gut of *E. gracilis* collected from the stormy Balaton. These observations prove, that this species ingests besides algae also organic and inorganic particles, and obviously bacteria adhering to the surface of these particles may serve as food. Gutelmacher (1973) demonstrated that *E. graciloides* can utilize the bacterioplankton. According to Haney (1973) all suspended particles of the size of 0.45 – 30 μm are to be regarded as potential food for crustacean plankton. The nutritional value depends of course on the quality of the particles. Nauwerck (1959) and Richman (1964) regarded materials passing the No. 25 net as food. In these experiment we followed the method of Kibby (1971) and removed only the particles larger than 300 μm by filtration. According to Rigler (1971), since the presence of phytoplankton influences the filtering rate of *Daphnia*, a suspension of nannoplankton cannot be regarded as natural food supply. This statement may also be applicable to *E. gracilis*.

In this paper the quantity of natural food is expressed in terms of organic carbon. This is a rough estimate, but not less informative than the dry weight or caloric value of the seston, used by RICHMAN (1964) and KIBBY (1971). The dry weight would be very misleading in the case of Lake Balaton, because except for the frozen period this lake is frequently swirled up by waves and the water is rich in inorganic particles. Ingestion of such particles of low nutritional value is to be regarded as ballast feeding. In our opinion the organic carbon content includes all the materials that are regarded as food in the papers cited above. It can be used to demonstrate the correlation between the amount of natural food and filtering rate.

The effect of food concentration on the filtering rate of cladocerans was investigated by several authors. GUTELMACHER (1974) found a correlation, that could be described with an inverse S-shaped curve. The concentration limits were determined by IVANOVA (1970) as follows:

below 0.1 mg dry weight/litre filtration is maximal; from 0.1 to 7.5 mg weight/litre the filtering rate is inversely proportional to food concentration; above 7.5 mg dry weight/litre the filtering rate is constantly low. In Lake Balaton we found 0.4 – 1.9 mg organic carbon per litre. According to WINBERG's (1971) correction factor these values fall within the medium or normal range. Our experiments demonstrated that in this range, like in the case of cladocerans, the increase of food concentration decreased the filtering rate of the calanoid *E. gracilis*.

Summary

The filtering of *Eudiaptomus gracilis*, consuming natural food was measured in two–four weekly intervals in Lake Balaton from March 1974 till November 1975.

The filtering rate varied within the range of 0.01 – 3.27 $ml.cop.^{-1}.day^{-1}$. The seasonal averages showed in spring 0.96, in summer 1.44, in autumn 0.64, in winter 0.11 $ml.cop.^{-1}.day^{-1}$. The summer and winter values differ significantly ($P \ll 0.001$).

Filtering rate depends on temperature. The correlation is especially strong between 0 and 20 °C ($P \ll 0.001$). Temperature changes lower than 5 °C do not result in unequivocal changes in filtering rate. Temperature changes of 10 °C result in significant increase or decrease of filtration. The critical temperature is around 18 – 20 °C.

In order to get some idea of food concentration, the particulated organic carbon content of the water was determined. Its average was 1.05 mg C/litre, and varied within the range of 0.42 – 1.90 mg C/litre. An inverse relationship was found between this food concentration and filtering rate.

Egg carrying females showed 20 – 25 per cent higher filtering rates than females without eggs.

Acknowledgement

For the radioactivity measurements we are indebted to Dr. D. SZY physicist and his co-workers in the Radiophysical Department of Radiological Clinic, Semmelweis Medical University, Budapest.

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AZ *EUDIAPTOMUS GRACILIS* (G. O. SARS) SZŰRÉSÉNEK SZEZONÁLIS VÁLTOZÁSA A BALATONBAN

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Összefoglalás

A szerzők 1974 márciusától 1975 novemberéig 2—4 hetes időközökben mérték az *Eudiaptomus gracilis* szűrési rátáját a Balatonban, természetes táplálék fogyasztása mellett.

A szűrés sebessége 0,01—3,27 ml/cop./nap között változott. Évszakosan a következőképpen alakult: tavasz 0,96; nyár 1,44; ősz 0,63; tél 0,11 ml/cop./nap. A nyári és a téli évszakokban mért értékek szignifikánsan különböznek egymástól ($P \leqslant 0{,}001$).

A szűrés sebessége hőmérsékletfüggő, különösen szoros a kapcsolat 0—20 °C között ($P \leqslant 0{,}001$). 5 C fokonkénti hőmérsékletváltozásra a szűrés mértéke nem változik egyértelműen. A 10 °C-os hőmérsékletkülönbség szignifikáns növekedést ill. csökkenést okoz. 19 ± 1 °C felett a hőmérséklet növekedése hatástalan a szűrés mértékére.

A táplálékként számításba jövő anyagok mennyiségéről a víz particulált szerves szén tartalmának meghatározása útján tájékozódtak. Ennek mennyisége átlagosan 1,05 mg/liter, legkisebb érték 0,42; legnagyobb 1,90 mg C/liter volt. Az átszűrt víz mennyisége fordítva aránylik a táplálék koncentrációhoz.

A petezacskót hordozó nőstények 20—25%-kal nagyobb vízmennyiséget szűrnek át, mint a petenélküli egyedek.