ANNAL. BIOL. TIHANY	42	203–218	HUNGARIA 1975

INVESTIGATIONS ON PLANKTONIC CRUSTACEA IN LAKE BALATON VI. QUANTITATIVE CHANGES IN THE *EUDIAPTOMUS GRACILIS* POPULATION AT VARIOUS REGIONS OF LAKE BALATON

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Received: 3rd March, 1975

As regards number of individual and biomass, *Eudiaptomus gracilis* is the most important filter feeder of the planktonic crustaceans in Lake Balaton (SEBESTYÉN, 1960; PONYI, 1968; PONYI and P.-ZÁNKAI, 1972). On the one hand, its decided role has been borne out by those investigations proving that it serves as important food to fry, even fry of pike-perch on the other hand, as the only filtering copepode of the lake, its breeding goes on throughout the year, and all the developmental stages are present in each season. These facts called for detailed studies on this species.

This study presents data on *Eudiaptomus gracilis* on the basis of samples taken during the periods 1965–67, 1972 and partly 1973.

Time table sampling stations and methods

The stations are given in *Fig. 1* and the detailed description of the transversal sections can be found in previous papers (SEBESTYÉN, 1960; P.-ZÁNKAI and PONYI, 1970). The number of sampling sites of the separate sections were different. Samples were taken monthly from 1 point each of the section in 1965, 3–3 points in 1966–67 and 5–5 points in 1972–73. The sampling generally took place in the warm-water period, except some years when the samples were taken in early spring and late autumn.

Dates of sampling:

1965: 9–10 June, 1–2 July, 3–4 August, 7–8 September, 13–14 October.
1966: 17–18 May, 14–15 June, 26–27 July, 23–24 August, 21–22 September, 18–19 October, 15–16 November.
1967: 16–18 May, 20 June, 26 June, 19–20 July, 15–16 August, 19–20 September, 23 October, 26 October.
1972: 19–21 April, 17–19 May, 21–23 June, 24–26 July, 15–17 August, 26–29 September, 16–18 October.
1973: 25 April, 14 May, 4 June, 19 June, 2 July, 18 July, 7 August, 20 September, 2 October, 25 October, 13 November (only at section M).

Samples were taken within a 1–3 days period from the 77 km long Lake Balaton, thus even those of the far-off sections could be compared.

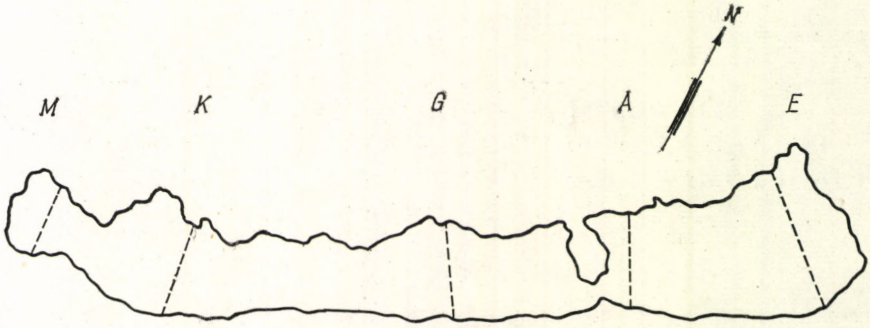

Fig. 1. Sampling places at Lake Balaton

The samples were taken with a water-column-lifting-filtering apparatus (SEBESTYÉN, 1960). For details on this method and the analysis of samples see PONYI and P.-ZÁNKAI, 1972.

Results

Surveying the data of *Eudiaptomus gracilis* samples taken in the periods of 1965—67 and 1972—73, it became evident that the density per litre of each life stage had considerably changed *(Figs 2—6)*. The quantitative fluctuation of the developmental stages was represented with curves. According to the pattern of curves the following eight types could be distinguished:

1. spring peak (abbr. T)
2. summer peak (abbr. N)
3. autumn peak (abbr. Ö)

These three types of curves showed only one peak;

4. peaks in spring and summer (abbr. TN)
5. peaks in spring and autumn (abbr. TÖ)
6. peaks in summer and autumn (abbr. NÖ)

In these types the number of developmental stages increased twice a year. Sometimes, between the two peaks, prior to or after them, a third increase was observed but because of its low value (1 individual/litre) it was disregarded.

7. peaks in spring, summer and autumn (abbr. TNÖ)
8. undefinite peak or peaks (abbr. B)

Of course, in the periods non-investigated or between the investigations further numerical increases or decreases might occur.

When examining the samples of 1 year and the frequency of patterns of the different developmental stages along the neighbouring transversal sections, the followings could be stated:

a) Identical pattern (N) at each of the five sections (from M to E) was shown once by males *(Table I) (Figs 2—6*, 1967).

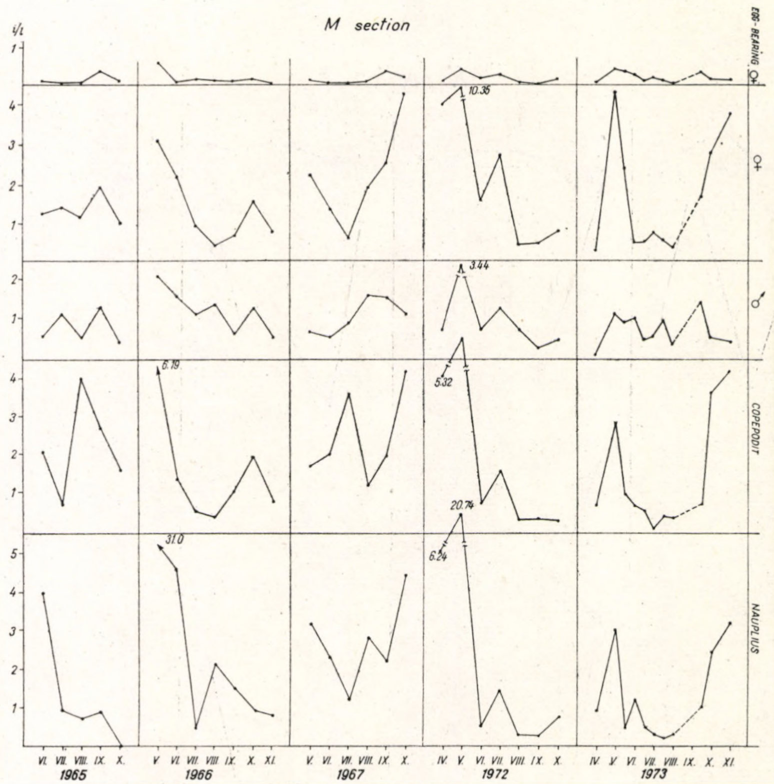

Fig. 2. Variation in the number of developmental stages of *Eudiaptomus gracilis* at transversal section *M* in five years

b) Identical pattern (TÖ) at four neighbouring sections (K-E) was also observed once produced by the copepodite stage *(Figs 3—6,* 1972).

c) Identical pattern at three neighbouring sections was found 5 times. One of them was shown by females (pattern N) in 1965, while other two by males: at sections M-G in 1966 (pattern T) and at sections K-A in 1972 (pattern TN) *(Figs 4—6)*. The nauplii showed also identical patterns twice: the first one (T) at sections M-G (1965) and the second one (TN) at sections G-E (1966).

d) Identical patterns of two neighbouring sections were observed 12 times, mostly shown by egg-bearing females (4 times) and females (4 times) *(Table I* and *Figs 2—6)*.

Items a—d clarify that the distribution of the developmental stages at the sections diverged very much within the same year. Not more than one-fifth of the so-called patterns showed uniformity.

By summing up the patterns of the different sections, it can be concluded that the seasonal variation of the developmental stages of *Eudiaptomus gracilis* differs section by section. While the spring peak is rather the characteristic of sections M-K (36—40 per cent), the summer peak is of higher frequency at sections A-E (25—40 per cent). The spring-summer development of the

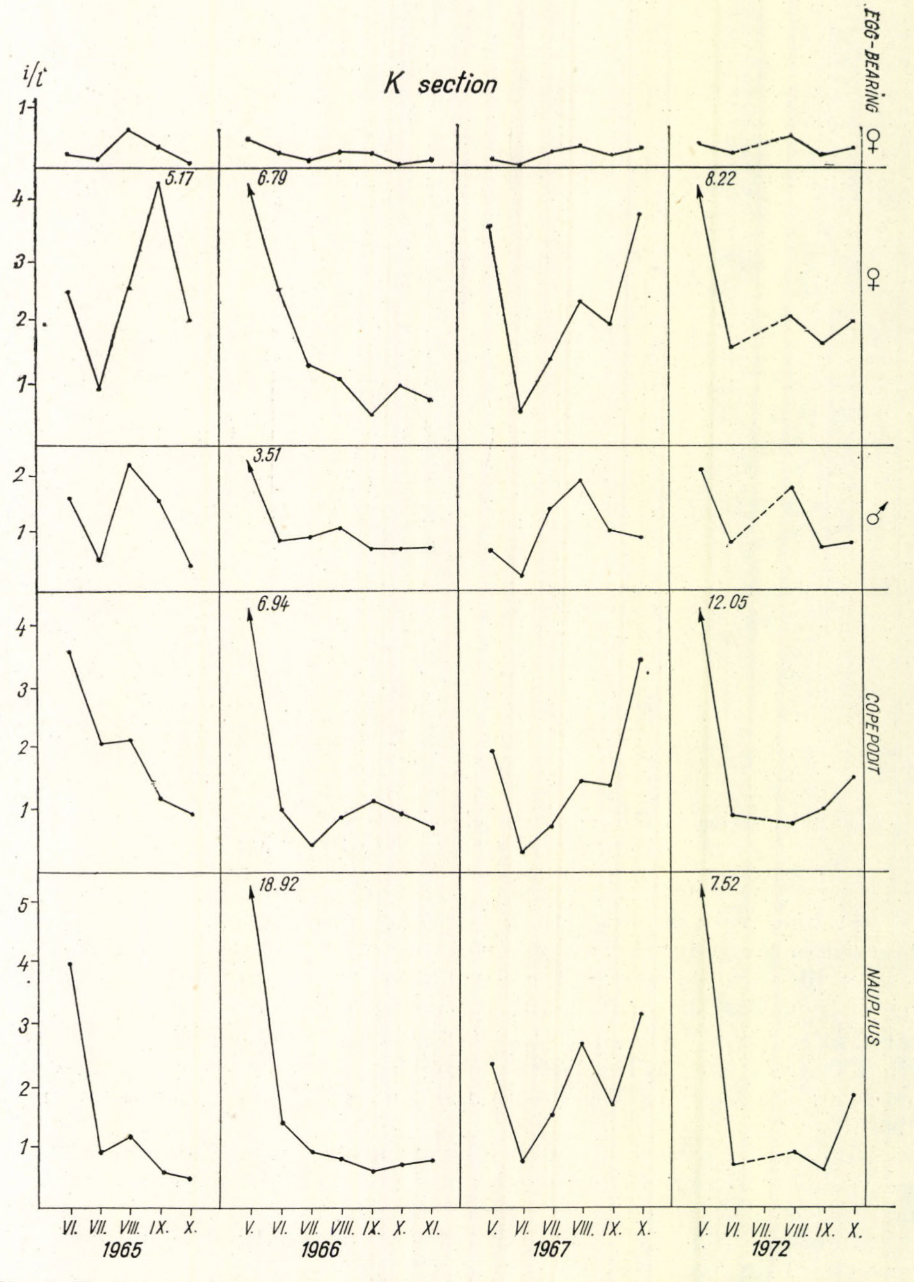

Fig. 3. Variation in the number of the developmental stages of *Eudiaptomus gracilis* at transversal section *K* in Lake Balaton in a period of four years

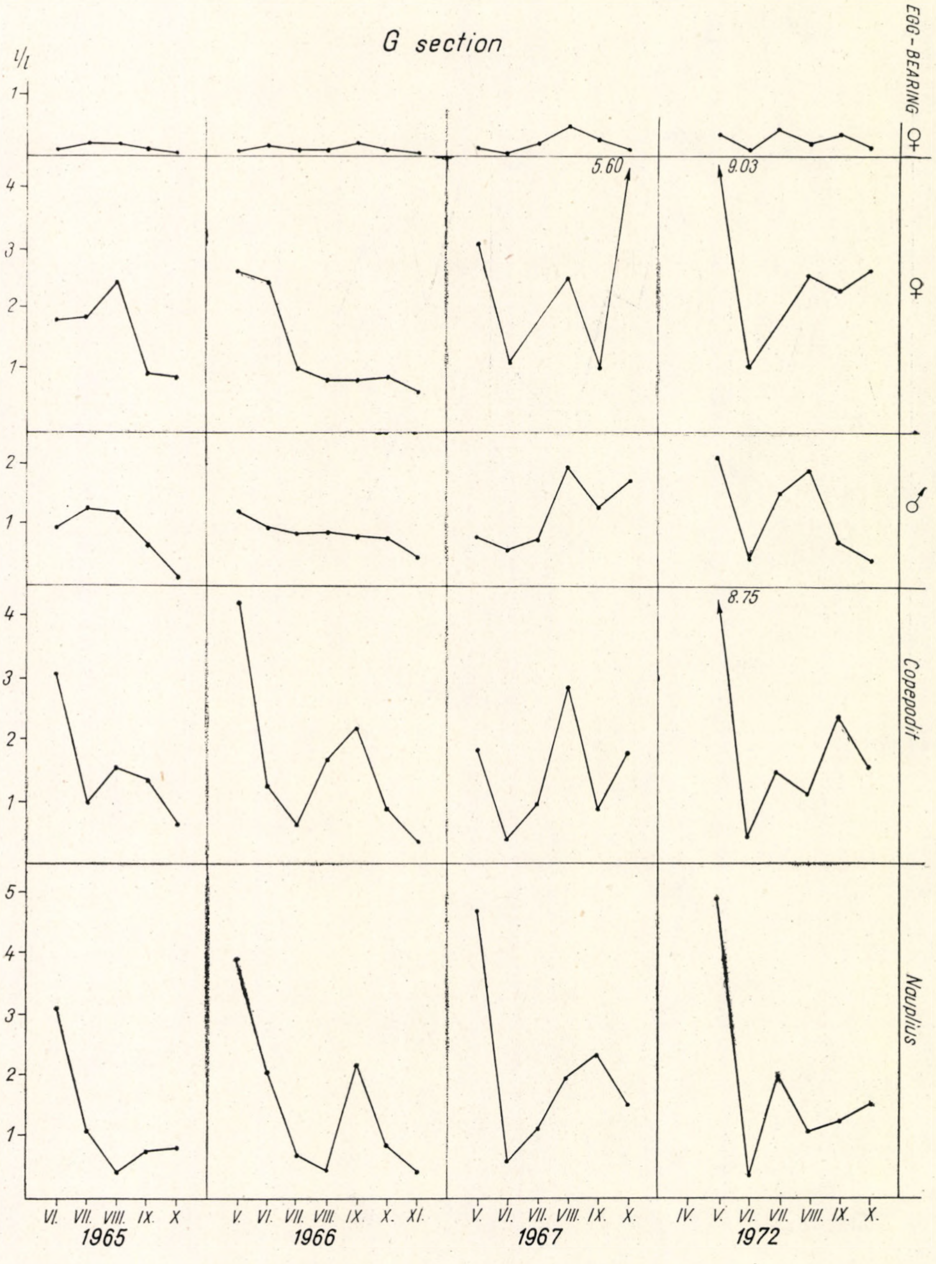

Fig. 4. Variation in the number of the developmental stages of *Eudiaptomus gracilis* at transversal section *G* in Lake Balaton in a period of four years

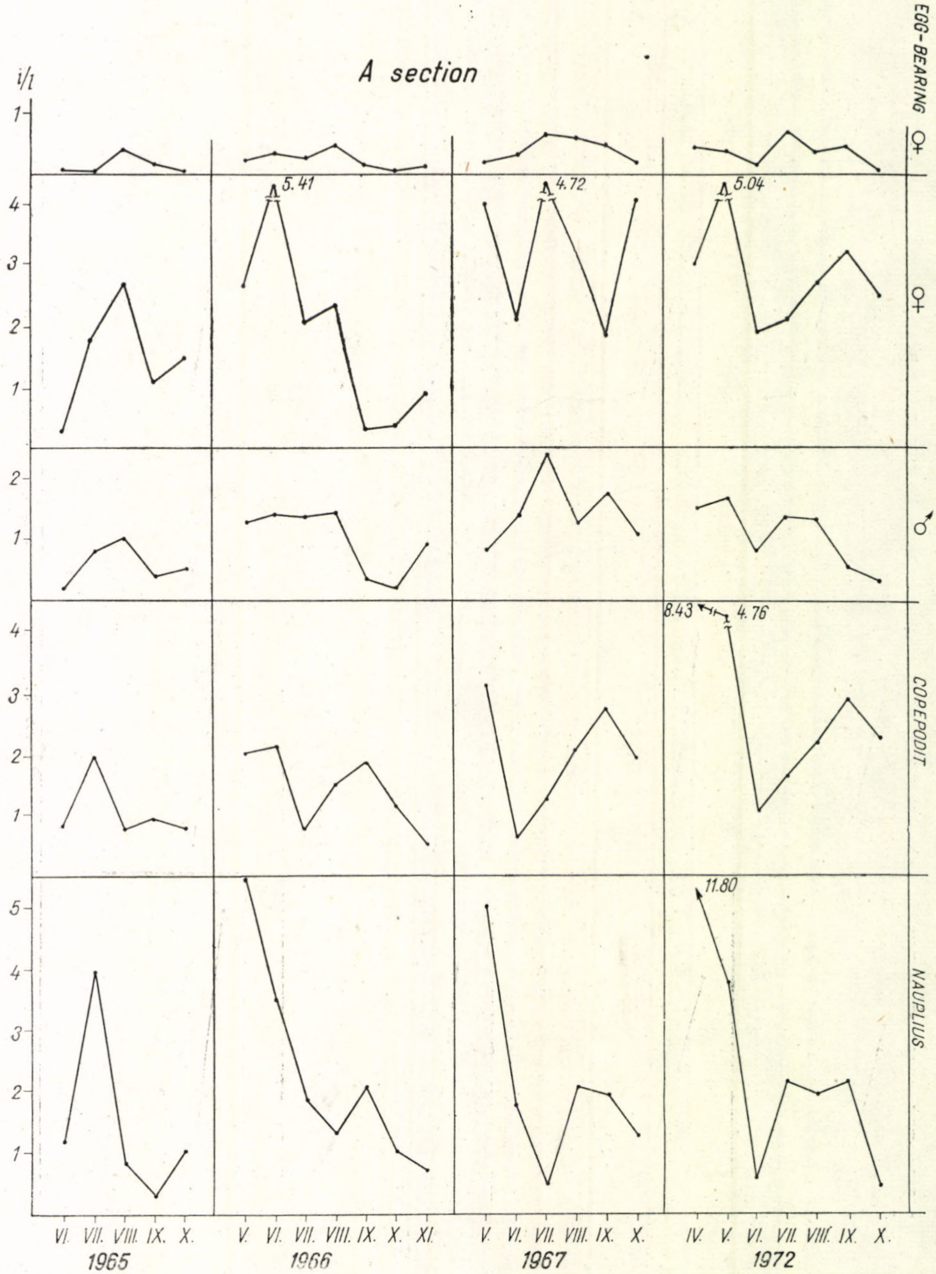

Fig. 5. **Variation in the number of the developmental stages of *Eudiaptomus gracilis* at transversal section *A* in a period of four years**

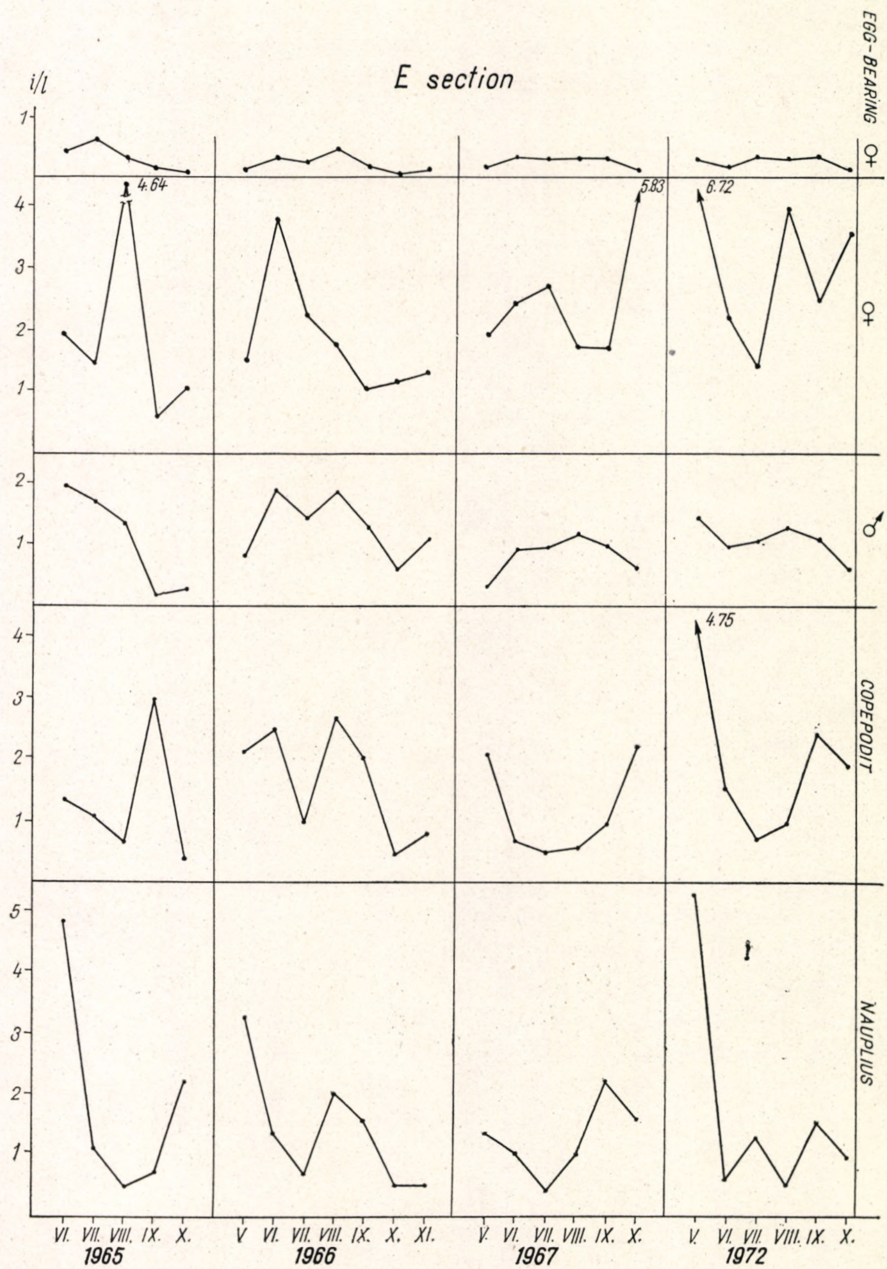

Fig. 6. Variation in the number of the developmental stages of *Eudiaptomus gracilis* at transversal section *E* in a period of four years

TABLE I

Distribution of patterns of the developmental stages of Eudiaptomus gracilis population at the sections investigated

yections		M	K	G	A	E
egg-bearing	1965	Ö	N	B	N	N
	1966	T	T	B	N	N
♀	1967	Ö	B	N	N	B
	1972	T	N	B	N	B
	1973	T	—	—	—	—
	1965	Ö	TN	N	N	N
	1966	TÖ	T	T	TÖ	T
♀	1967	TÖ	TÖ	TNÖ	TNÖ	NÖ
	1972	T	T	TN	TÖ	TN
	1973	TÖ	—	—	—	—
	1965	B	TN	N	N	T
	1966	T	T	T	B	N
♂	1967	N	N	N	N	N
	1972	T	TN	TN	TN	B
	1973	B	—	—	—	—
	1965	TN	T	TN	N	Ö
	1966	TÖ	T	TN	TÖ	TN
copepodite	1967	NÖ	TÖ	TN	TÖ	TÖ
	1972	T	TÖ	TÖ	TÖ	TÖ
	1973	TÖ	—	—	—	—
	1965	T	T	T	NÖ	TÖ
	1966	TN	T	TN	TN	TN
nauplius	1967	TÖ	TÖ	TN	TN	TÖ
	1972	T	TÖ	T	TN	T
	1973	TÖ	—	—	—	—

Explanation: T = peak only in spring N = peak only in summer Ö = peak only in autumn TN = peak both in spring and summer TÖ = peak both in spring and autumn NÖ = peak both in summer and autumn TNÖ = peak both in spring, summer and autumn B = other

populations is characteristic for sections G-A but in other regions of the lake, the spring-autumn peaks (20—28 per cent) are more common.

TABLE II

Percentual frequency of the patterns of the Eudiaptomus gracilis developmental stages at different areas of the lake

Transversal sections	M	K	G	A	E
T	36	40	20	0	15
N	4	15	20	40	25
Ö	12	0	0	0	5
TN	8	15	35	20	15
TÖ	28	25	5	25	20
NÖ	4	0	0	5	5
TNÖ	0	0	5	5	0
B	8	5	15	5	15

The quality of the population composition can be concluded in the best way by comparing the patterns of the copepodite and naupliar stages *(Table III)*. Both stages are mostly characterized by two peaks (62, 72 per cent). Spring peak was also noticed though in lower percentage. On this basis it can be stated that the number of *E. gracilis* increases in Lake Balaton twice in the warm-water period.

TABLE III

Percentual frequency of the patterns of nauplius and copepodite stages of Eudiaptomus gracilis in the whole Lake Balaton (1965—73)

	Copepodite	Nauplius
T	14	33
N	5	0
Ö	5	0
TN	24	33
TÖ	48	29
NÖ	5	5
TNÖ	0	0
B	0	0

When comparing the frequency of the different developmental stages of this population to one another *(Table IV)*, it was observed that the relative quantity of the largest forms (females and egg-bearing females) gradually

TABLE IV

Variation of the developmental stages iu the population during the three years investigated (May—October)

	M		K		G		A		E	
	average	%	average	%	average	%	average	%	average	%
1966										
egg-bearing	0.20	1.70	0.18	1.92	0.12	2.01	0.22	2.91	0.21	3.13
female	1.49	12.70	2.17	23.11	1.41	23.66	2.18	28.87	1.89	28.17
male	1.32	11.30	1.29	13.74	0.90	15.10	0.99	13.11	1.30	19.37
copepodite	1.91	16.30	1.86	19.81	1.83	30.70	1.59	21.06	1.77	26.38
nauplius	6.78	57.90	3.89	41.43	1.70	28.52	2.57	34.04	1.54	22.95
1967										
egg-bearing	0.14	1.64	0.17	2.44	0.21	2.84	0.35	3.80	0.24	3.85
female	2.22	26.00	2.22	31.85	2.52	34.05	3.31	35.98	2.70	43.27
male	1.04	12.18	1.02	14.63	1.16	15.68	1.43	15.54	0.85	13.62
copepodite	2.45	28.69	1.54	22.09	1.48	20.00	1.99	21.63	1.18	18.91
nauplius	2.69	31.50	2.02	28.98	2.03	27.43	2.12	23.04	1.27	20.35
1972										
egg-bearing	0.17	1.22	0.27	2.67	0.25	2.83	0.30	3.47	0.24	2.79
female	3.38	24.35	3.07	30.37	3.22	36.47	3.00	34.72	3.37	39.23
male	1.25	9.01	1.24	12.27	1.19	13.48	1.15	13.31	1.24	14.44
copepodite	4.03	29.03	3.21	31.75	2.65	30.01	2.31	26.74	2.04	23.75
nauplius	5.05	36.38	2.32	22.95	1.52	17.21	1.88	21.76	1.70	19.79

decreased from transversal section A to M retaining identical population levels at sections A-E.

The number of the individuals per litre changed inversely. As regards the average of three years, the total number of individuals is highest at section M (11.4) gradually decreasing towards section G (7.4). At section A it shows a low increase (8.4) but declines at section E again (7.2).

The variation in the egg-number/egg-sac of 100—100 animals was also worked up. The samples were netted simultaneously with those for quantitative purposes *(Table V)*. This value was found to decrease in each of the four

TABLE V

Variation in the number of eggs of Eudiaptomus gracilis at the five transversal sections of the lake in the four years of investigations

	M				K			
	1965	1966	1967	1972	1965	1966	1967	1972
IV.	—	—	23.5±4.5	16.9±3.8	—	—	21.8±4.4	—
V.	—	11.4±2.1	17.1±4.1	8.2±2.9	—	7.7±1.5	11.6±2.7	5.8±1.5
VI.	13.1±3.9	11.0±2.2	14.7±2.9	13.3±2.8	5.4±1.2	8.6±1.7	10.5±2.9	11.8±3.7
VII.	14.0±3.3	11.4±2.5	14.8±3.7	15.8±3.8	10.7±2.4	9.5±2.7	15.1±3.4	—
VIII.	13.8±3.3	15.5±4.3	12.8±2.3	18.2±3.8	9.9±2.5	8.3±2.4	9.9±1.7	11.8±4.1
IX.	10.0±2.9	10.7±3.1	11.0±2.9	17.8±5.7	5.6±0.3	4.5±0.0	8.9±2.1	16.6±4.1
X.	17.1±5.1	17.5±3.9	13.2±2.9	18.4±5.0	14.7±3.1	16.2±3.5	10.5±2.5	14.6±3.8
XI.	—	12.1±2.2	—	—	—	11.4±2.8	—	—

TABLE V *(continued)*

	G				A			
	1965	1966	1967	1972	1965	1966	1967	1972
IV.	—	—	13.7±2.9	—	—	—	10.6±2.5	—
V.	—	7.4±1.6	10.4±2.5	5.2±1.1	—	9.2±1.7	7.6±1.5	5.5±1.7
VI.	4.8±1.0	5.0±1.0	10.6±1.6	—	7.6±1.9	3.7±0.2	4.5±1.7	5.9±1.1
VII.	4.6±0.3	6.3±1.2	8.8±2.2	7.9±2.4	5.7±1.3	6.5±1.6	5.4±1.4	6.0±1.4
VIII.	4.1±0.0	5.4±0.0	9.1±2.0	6.0±1.0	5.1±1.1	5.2±1.0	7.0±1.5	6.3±1.3
IX.	6.2±1.1	4.0±1.4	4.6±0.0	8.9±2.4	5.3±1.0	4.4±0.0	5.1±1.1	7.4±1.5
X.	11.4±3.2	12.3±2.4	6.2±1.4	6.8±3.3	8.9±2.2	—	5.7±1.1	6.6±1.3
XI.	—	11.5±2.7	—	—	—	7.9±1.6	—	—

TABLE V *(continued)*

	E			
	1965	1966	1967	1972
IV.	—	—	10.9±2.1	—
V.	—	7.0±1.3	7.4±1.4	4.8±1.0
VI.	7.1±1.6	4.0±1.0	5.9±1.1	—
VII.	5.7±1.4	5.6±1.1	5.5±1.6	6.3±1.5
VIII.	4.4±0.3	5.0±1.0	4.8±0.0	4.9±1.5
IX.	5.3±0.0	5.5±0.0	5.5±0.0	4.9±1.5
X.	8.4±2.0	8.7±2.5	7.5±2.3	5.5±1.3
XI.	—	9.4±1.6	—	—

years in the direction from section M to A. The value of section E was identical with that of section A:

	M	K	G	A	E
egg-number/egg-sac average of 4 years	14.3	10.9	7.9	6.3	6.2

Discussion

Eudiaptomus gracilis is widely distributed and can be found in the British Isles, Scandinavia, the northern region of the USSR as well as in France, Germany, Austria and Eastern-Europe. Its distribution to the South is limited by the Alps (KIEFER, 1968a). In Hungary it is common both in small and large water bodies and fish-ponds (PONYI, 1956).

Its relatively wide distribution in Europe proves that this species has a wide ecological valency. Consequently, the development of its population is very variable. It is mentioned both in the old and the latest studies that this species is represented by its mono-, bi- or polycyclic type in waters of the same type, being geographically near to one another (SPANDL, 1926; ELSTER, 1954; KIBBY, 1971). The overwintering forms of this species as well as the cold- and warm-water forms are well known. In Lake Balaton the nutrition intensity of the cold- and warm-water forms diverges too (P.-ZÁNKAI and PONYI, 1974). The forms of the two seasons show similarly morphological differences. In the cold season a special protruding appendix appears on the third segment of the right antenna of the males, disappearing with the warming up of the water. This seasonal morphological deformation is regarded by some authors as the cyclomorphosis of this species (WOYNÁROVICH, 1938).

Its quantitative importance is underlined by the fact that this species constitutes 50 per cent of total population of plankton crustaceans in the warm-water period (May-October) (PONYI and P.-ZÁNKAI, 1972). Owing to the fact that *E. gracilis* can develop even three cohors in 40 days (WEGLENSKA, 1971), the life stages found in the monthly samples could not be related to each other. Thus the life stages of this population is evaluated separately. At a given place the increase and decrease in the population density of the species is expressed by the pattern formed by the majority of developmental stages.

The quantitative change of the developmental stages of *E. gracilis* in the lake is shown by patterns of 8 different types. Comparing these patterns to each other, it is obvious that even within the same water area different types alternate with one another during the same year. The water areas were compared on the basis of their patterns by adapting the formula of MARCZEWSKI—STEINHAUS:

$$S = \frac{w}{a + b - w} \times 100,$$

where $w =$ number of identical patterns at the sections compared; a and $b =$ number of diverse patterns separately at the two sections.

Accordingly, sections A and G show the greatest similarity, while sections G and K are the most diverse. The rate of similarity was identical between the two sections in the south-wastern basin (M and K) and the other two sections of the north-eastern basin (A and E). Evidently, as regards the development of the population, several diverse water areas can be distinguished in Lake Balaton.

TABLE VI

Patterns of the Eudiaptomus gracilis population at the different sampling stations of the lake shown by the formula of Marczewski—Steinhaus *(1965—67; 1972—73)*

	M	K	G	A	E
M	—	36.8	9.7	2.7	2.7
K		—	27.3	9.7	5.9
G			—	69.2	14.3
A				—	36.8

Earlier observations (Sebestyén, 1953; Ponyi, 1968) showed that the population of *E. gracilis* increased twice a year in the north-eastern basin. With special regard to the nauplii and copepodites, our present studies suggest *(Table III)* that the population may increase 1—3 times a year in Lake Balaton. In the larger lakes (e.g. Lake Constance) summer and autumn peaks were observed (Kiefer, 1968b), while in smaller water bodies only one spring peak was noted (Spandl, 1926).

Within the population the percentage of egg-bearing females was very low, hardly mounting up to 4 per cent in Lake Balaton. In his study on 42, mostly shallow lakes Smyly (1968) stated that this value rarely fell under 20 per cent in the warm-water period. In contrary the egg-bearing ones, the percentage of the adult females varied between 1.4 and 43.0 per cent in the population. In the period of four years, the data on individual number/litre and egg-number/egg sacs showed that the "production" of the species is probably the highest at section M, gradually decreasing in the direction to A *(Fig. 7)*. Simultaneously, the percentual distribution of adult and egg-bearing females was inverse. This phenomenon indicates that the degree of grazing by the fish is the highest at section M, gradually decreasing towards the north-east basin. This suggestion is supported by fishery statistics.

Studying the fluctuation in the number of individuals on *E. gracilis* populations from the thirties till recent years (Fig. 8) it is seen that this number (without nauplii) ranged in the period of 1936—38 from 12 to 22, while between 1946 and 1972 it was less than 7 individuals/litre.

When comparing *Figs 7* and *8* it was concluded that the density of fish and fry feeding on *E. gracilis* had increased in the lake. The suggestion that planktonic crustaceans of large body size are grazed intensively by fish is well supported by investigations in fish-ponds (Hillbricht-Ilkowska et al., 1973), establishing that the decrease in the biomass of crustaceans was followed in some cases by a decrease in the production.

According to the literature the egg-number/egg-sac value of *E. gracilis* is low in oligotrophic lakes and is high in eutrophic waters (Czeczuga, 1959; 1960; Steemann Nielsen, 1962). Thomas (1961) compared the egg-number of *E. gracilis* with the total ion-content of the water. He states that the egg-number of this species is more abundant in low ionic concentrations than in high concentrations. Our investigations showed an inverse picture for Lake Balaton *(Table VII)*.

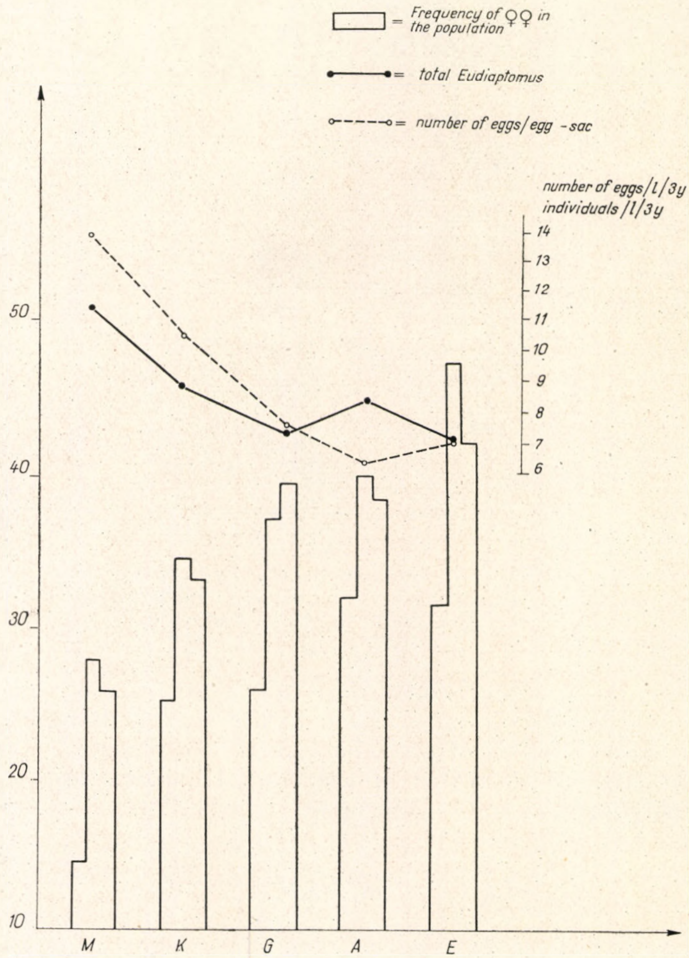

Fig. 7. Comparison of the egg-number/egg-sacs, total individuals and females at different sections of the lake

TABLE VII

Comparison of total ionic content to the egg-numbers of Eudiaptomus gracilis in four English lakes and in different regions of Lake Balaton

	THOMAS (1961) Total ion expressed in the % of maximum	egg-number		ORSÓS (1968) Total ion expressed in % of maximum	PONYI et al. (1975) egg-number
Windermere	100.0	8.71	BALATON M	100.00	14.30
Grasmere	88.8	9.30	K	97.74	10.86
Derwent	85.1	6.05	G	95.02	7.41
Ennerdale	64.8	10.53	A	93.52	6.27
			E	91.45	6.19

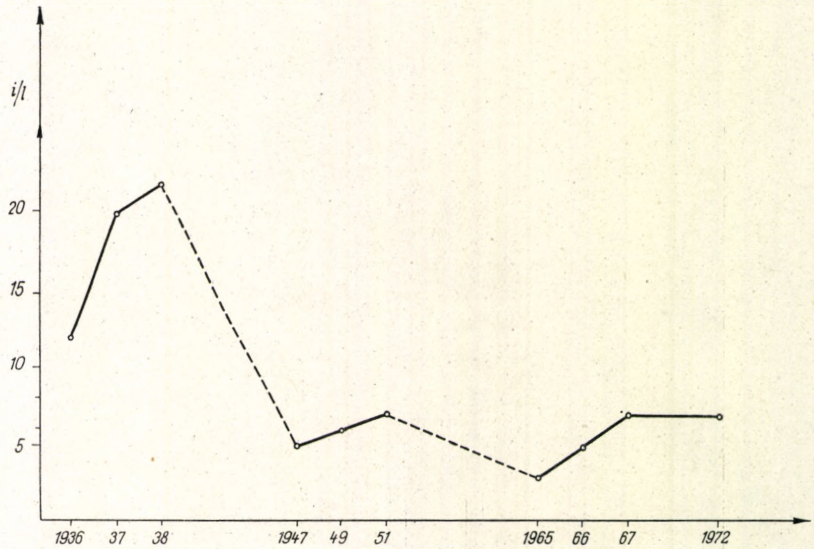

Fig. 8. Variation in the number of *Eudiaptomus gracilis* in May—October at transversal section *A* (without nauplii) on the basis of the data of SEBESTYÉN (1953; 1960), SEBESTYÉN et al. (1951) and ENTZ et al. (1937)

It is suggested that in case of Lake Balaton the increase in the egg-number of *Eudiaptomus gracilis* can be ascribed to the degree of trophyty, and the quantity of salt-content is of secondary part. The highest egg-number was found at the hypertroph region of the lake (HERODEK and TAMÁS, 1975) decreasing parallel with the degree of trophyty.

Summary

In the periods of 1965—67 and 1972—73 the authors investigated the variation of *Eudiaptomus gracilis* populations on the basis of samples taken monthly at water areas of different trophic level of Lake Balaton.

In the course of the investigation the following could be stated:

1. The development of the population of the species differs in space and in seasons. At the south-western end of the lake (section M) where the water quality is hypertrophic a spring peak of 36—40 per cent frequency was found, while in the other basin (sections A-E) summer peaks dominated (25—40 per cent). In the middle of the lake mostly spring-autumn peaks were observed (20—28 per cent).

2. Adapting the formula of MARCZEWSKI—STEINHAUS the patterns of the highest similarity were found at the mesotrophic areas (sections G-A), while those of the less similarity at sections K-G.

3. In the population the relative quantity of forms of large body size (females and egg-bearing females) gradually decreases from section A (mesotrophy) to section M (hypertrophy). Regarding the mean values of the period 1966—67 and 1972, it is seen that the total number of the species is the highest

at the south-west end of the lake (11 individuals/litre) gradually decreasing to the north-east basin (7.2 individuals/litre).

4. The egg-number/egg-sac was found to be the highest in the hypertrophic south-west basin (14.3) decreasing to 6.2 at the other end of the lake.

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CRUSTACEA–PLANKTON VIZSGÁLATOK A BALATONON VI AZ *EUDIAPTOMUS GRACILIS* (G. O. SARS) POPULÁCIÓJÁNAK MENNYISÉGI ALAKULÁSA A TÓ KÜLÖNBÖZŐ TERÜLETEIN

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Összefoglalás

A szerzők 1965—67 és 1972—73-ban a Balaton különböző, trofitásban eltérő vízterületein havi gyűjtések alapján vizsgálták az *Eudiaptomus gracilis* G. O. SARS populációjának változását.

A vizsgálatok alapján a következő eredményekre jutottak:

1. A faj populációjának kifejlődése évszakosan és vízterületenként is eltér egymástól. Míg a tó délnyugati végén a hypertróf vízterületen (M szelvény) a vizsgálati esetek 36—40 %-ában csak egy tavaszi maximum alakult ki, addig a tó másik medencéjében (A—E szelvények) egy csúcsú nyári maximumok a jellemzőek (25—40%). A tó középső részein a tavaszi, őszi kettős maximum kialakulása a leggyakoribb (20—28%).

2. A MARCZEWSKI—STEINHAUS-féle hasonlósági index segítségével az *Eudiaptomus gracilis* populációjának alakulását jelölő mintázatok alapján a legnagyobb fokú hasonlóságot a mezotróf vízterületeken (G—A szelvények), a legkisebbet a hypertróf és mezotróf vízterület találkozásánál (K—G szelvény) találtunk.

3. A populáción belül a legnagyobb testű alakok (nőstény és petés nőstény) relatív mennyisége az A szelvénytől (mezotróf) az M szelvényig (hypertróf) fokozatosan csökken. 1966—67 és 1972 év átlagát tekintve a faj összes egyedszáma a tó DNy-i végén a legnagyobb (11 e/lit.), amely fokozatosan csökken a tó másik vége felé (7,2 e/lit.).

4. A petezacskónkénti peteszám a tó DNy-i végén, a hypertróf vízterületen a legmagasabb (14,3), mely a tó másik végén 6,2-re csökken le.