

[Translated by F. Spaun]

Translation of
 "Über die Populationsdynamik von
Eudiaptomus gracilis Sars und
Heterocope borealis Fischer im
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B. Eudiaptomus gracilis Sars.

1. Duration of the development of eggs.

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Experimental research.

a) Material and method.

Newly caught, not too heavily concentrated plankton samples were transported live from the Bodensee (Lake Constance) to Falkau within a few hours and by night during the warm season of the year. Then a greater number, several hundred *Eudiaptomus gracilis* females, which carried no egg sacks, and a similar number of males were isolated and distributed among several bowls containing 50 - 100 ccm Bodensee water, each bowl receiving from 50 to 100 pairs. The water in these maternal bowls was renewed daily by about 90%. At the same time the animals were fed with a few drops of bright green chlorella - or mixed algae culture. Dead individuals were picked out once or twice daily. As soon as females with egg sacks could be spotted under frequent controls of the maternal bowls, they were caught and distributed in special culture bowls, so that the duration of development of the eggs under certain environmental conditions could be observed. 1 - 4 females, that were found with egg sacks under/in the same control interval were put together in a culture bowl containing 25 to 50 ccm water. Feeding was as for the maternal bowls.

Since the possibility of varying reaction norms had to be taken into account for the different seasons (different generations), four experimental groups were run at different times (October and November 1950, April and August 1951). In October 1950 similar material from the Schleinsee was examined, a small, moderately eutrophic lake about 10Km inland from Langenargen.

b) Egg production of the isolated females.

Table 1. gives a synopsis of the egg amounts produced by the isolated females. In all experimental series, by far the most eggs were laid in the first four or five days by the isolated females, after that only a few. The maternal bowls were kept, now warm, now cool. On the first three experimental groups, neither a significant influence of temperature nor the influence of day or night, could be observed on the rate of egg production. In August 1951 fewer egg sacks were formed during ex-

posure to cold (7 - 9°C.), but here one has to take into consideration that the whole life process is slowed down with lower temperatures, so that the relatively few numbers must not lead one to the conclusion that warmth has a stimulating, or cold, an impeding effect.

Within the first 24 hours after isolation, the number of eggs per sack in October 1950 and August 1951 averaged eight to nine, in November 1950 and April 1951 only about five, which was probably effected by the respective condition of the population in the Bodensee. Where a sufficient number of eggs was laid several days after isolation, a decrease in the number of eggs per egg sack for these cultures became apparent, especially in August 1951, when the decrease amounted to 50%. Possibly the reason for the cause might be found in insufficient nourishment of the females, or in the produce of the metabolism, event. it may be a space factor. The percentage of egg laying females in the cultures varied from between 5.5% (Nov. 1950) and 33.3% (August 1951).

c. Dependence of the development duration upon outside factors.

Basis of calculation.

Table 2 shows the results for the separate experiments, ordered according to the average temperature of the cultures. Since, with the exception of one thermostat which could only be used for the highest temperature experiment, no apparatus was available for setting constant temperatures, stages, or gradings of temperature were achieved by the expedient method of locating the experimental bowls in various places. Unfortunately it was not always possible to avoid relatively strong diurnal amplitudes in the various experimental series. The lowest temperature, according to the season of the year, was in the cellar of the station, or in a cystem fed by spring water. In both these places the daily range of temperature was small (in the cellar it varied from 0.1 to 0.5°C. in the cystem it was practically 0). In the cystem the experimental bowls stood in a flat, enclosed tin, half filled with water, which floated on the water of the cystem. The cystem itself was covered by a heavy cement lid. The experiments in the darkroom were subjected to small diurnal variations, whilst those which were situated in rooms known as the 'laboratory' were subject to a stronger variation in the course of the daily rhythm; the variations in the attic, especially in the north-facing double glazed window, were quite considerable. In the cold storage chamber variations were irregular being a succession of slow-warming and rapid cooling periods. The strong variations in the "heating chamber" - boiler house - were also irregular. With the thermostat the temperature remained within a range of 1°C.

The average temperature as given in Table 2 can have differing interpretations. Therefore the measured minimum and maximum temperatures are given for each single bowl between the time of isolation of the egg carrying females and the appearance of the last nauplius, for each experiment, also the magnitude of the daily range/amplitude. In the calculations of the average temperatures, the temperature in the maternal bowls between the last but one control and the isolation of the egg

carrying females, was taken into consideration, i.e. the temperature even before the beginning of the actual experiment. This would explain why the average temperature for cultures subjected to the same temperatures may differ, especially when the experiment temperature constancy is great the average temperature may even lie outside the minimal and maximal temperatures (e.g. Table 2 No.21).

The development duration was calculated as follows: the minimum time was the number of hours between the discovery of the egg sack, i.e. isolation of the egg-carrying females, the last control before birth of the first nauplius; the maximum was the number of hours between the last control before the formation of the egg sack- i.e. the last but one control before isolation of the egg carrying female, and the first control at which the last 'experiment' egg was laid. The average is the average of both values, taking into account a strong distribution and the time at which the majority were born; hatched. (meaning could be 'laid').

The development duration, in hourly stages, was calculated by multiplication of the respective average temperatures with the number of hours, from control to control, and finally summed up. Minimum and maximum values were calculated hourly but in the same way, but had to be omitted from table 2 owing to lack of space.

b) Results.

In general, all eggs of a female were laid in relatively short time, frequently within a few hours. Also individual females of the same experiment showed little differentiation in the development time of their eggs. The differences between the minimum and maximum values are determined by the varying time intervals between the laying of the egg and hatching, which may be determined by environmental factors, and the time of the following control. The actual distribution is smaller.

Let us next examine, if, apart from temperature, there are other factors, either in nature or in the experiment, which respectively can vary or change the duration of development significantly (to our purpose). The relatively small quantities of water cannot be of any account in the experimental bowls, since in larger bowls (about 100 cm³ per female) the times were the same as for the smaller bowls containing four to five females in 10 cm³.

Also the health and nourishment-condition of the mother after the formation of the egg sack is without significance since the eggs of females that died in the experiment or of females that were not too fungified- hatched simultaneously to those that still had a healthy, actively swimming mother. Similarly there was no difference between fed and un-fed cultures, -the egg sack, or single eggs lying on the floor, or on egg sacks carried by their mothers. There could not have been a lack of oxygen in the flat experimental bowls. Since there is also no oxygen deficiency in the Bodensee Obersee, the subject of development retardation through lack of oxygen was not investigated further.

In general only those eggs, or egg-sacks produced by mothers in the first three days after being caught, were used in the experiments. In

some cases, when material was scarce, eggs laid after the third day in captivity (> three days) were used, partly, even when the number of eggs per egg sack had begun to decrease - Table 2: No. 1 (7 days), 16 (4 days), 25 (5 days), 26 (4 days) and 59 (5 days). Most of these experiments revealed a somewhat longer development period than those conducted at the same temperature but which used earlier laid eggs, - even though the variation scales for the compared experiments do largely coincide. The differences are negligible, almost on the error margin, and will not need to be considered further. From the physiological development angle, however, this question deserves further investigation. Of note was, that after a longer period of captivity (> three days) the number of eggs per female and egg production in general not only declined considerably, when conditions were unfavourable, but also an increasing percentage of laid eggs died.

The four different experiment series - using material of the different seasons, gave almost identical results. The variation margins of comparable experiments (similar temperature in Table 2), coincided in all cases, - in most cases almost completely. The majority of the August experiments gave somewhat higher average values than the April experiments, whilst the October and the November values, at least in the lower or the middle temperature range, were closer to the April values. The difference in the average values are, however, so negligible they will be of no further account to us here. The question of variable reaction norms in the different seasons is still to be a subject of research. Those few comparison values obtained from material sampled from the Schleinsee coincided likewise to the variation margin given for the Bodensee animals, but on an average are lower. These differences are still within the error margin of the 'method' and are again of no significance to our problem. The question, if the rate of development of Copepod eggs is type-specifically the same in all waters, or if the same types/species develop differently in different waters must still be the subject of further research.

As a result of the of necessity differently located cultures, those experiments which had high or low temperatures were in darkness, those having more average temperature were mostly exposed to normal daylight. A glance at table 2 will show that the light- and dark experiments can be ordered clearly into a consistent curve. Some experiments conducted for comparison in the middle temperature range, e.g. table 2 No. 35 and 36 (light) and 39 and 41 (dark), show clearly, that normal daylight, i.e., a normal day and night rhythm or total darkness do not significantly affect the rate of development.

Finally the effect of water of varying quality in the experimental bowls was investigated. Bodensee (B) and Schleinsee water (S) had a carbonate hardness varying from 6 - 7 DH° , and in the experimental bowls had a pH rating from 7.5 to 7.6. Against this - table 2, No. 37, 38 and 39 44 Falkauer spring water was used (Q) of only 0.7 DH° and pH 5.8 - 5.9 at the beginning, rising towards the end of the experiment to 6.0. In addition it was weakly (humos) humic? By addition of HCl to Q, also B, the pH value could be adjusted to 5, 6, or 7, and through $Ca_3(PO_4)$, to 8.

But it seems that pH and calcium content do not have any effect on the rate of development. With a pH of 5 several eggs died during their development, and those hatched died within a few hours or days respectively. In the spring water and mixed water as with all pH values between 5.8 and 8.0 they lived just as long as in the Bodensee water.

It seems that temperature is a key factor upon which further observations and calculations will have to be based. A comparison of experiments having almost constant temperature with those subjected to strong fluctuations shows, that the determining factor is the average temperature. Special investigations will have to show how development is affected by different fluctuations of the same average temperature, and whether the differences are marked enough to be considered in our work. It must be mentioned that also in nature adult animals are subjected to temperature fluctuations, which vary with the seasons, but which are most marked in summer, when there may be a considerable temperature range. At the moment only the average temperatures will suffice to our purposes.

Fig. 1 A shows in graph form the dependence of the rate of development upon temperature, but because individual values are so dispersed, we took the average development duration of several individual experiments conducted at the same temperature taking into account the respective number of eggs. Unfortunately the graph line between 5.6 and 4.75°C. is determined only by a single experiment with 5 eggs, this because we did not have the apparatus during the (warm) seasons of the year which could maintain a temperature which averaged below 4.75°C. The continuance of the curve had thus to be 'extra' plotted hypothetically. Unfortunately calculations on egg production in winter do not thus have a very firm basis, and it is hoped to conduct additional experiments to fill the gap. But from the form of the curve it seems unlikely that the eventual corrections will change the present picture much.

In fish-biology it has been customary to calculate development time in "degrees of a day", even though more recent investigations by Ammann (1948) and Steinmann (1950/51), have shown that the product of temperature and development duration is by no means constant. According to Ammann e.g. Sand 'felchen' eggs require, with an average temperature of 3.2°C. 345, and by an average temperature of 7.3°C. 568 day degrees. Changes in temperature and day degrees run parallel to one another. Things are different, however, with *Eudiaptomus gracilis* ! Also here the product of temperature degree times hours is by no means constant for various temperatures, but decreases with increasing temperatures, as shown in table 2 and Fig. 1B. Between 4.75°C. and 23°C. the number of hour-degrees decreases by about half, whilst the absolute number of hours decreases to about 1/9. More information concerning these relationships will be given on the basis of more extensive research material, when this is available. In future we will not speak of hour-degrees.

The curve 1A serves as the basis for all subsequent calculations. In order to enable a better comparison with parallel experiments in other waters, table 3 gives development times interpolated for whole degrees.

2. The replacement coefficient of eggs in nature.

2. The renewal/replacement coefficient of eggs in nature.

It is more difficult to determine the absolute figure for egg production in nature. For this we need the absolute egg number/m² and the development duration, respectively, the knowledge of when and in what time the quantities of eggs contained in the plankton samples hatch and become replaced by new eggs. In this section we will deal solely with the replacement coefficient, which was calculated from the development duration of eggs at various depths for periods of 10 days. Through multiplication of the known egg quantities with the renewal coefficient it would then be possible to obtain the absolute egg production over a period of 10 days. We chose the 10 day value for the sake of easy calculation of production over any desirable interval.

The bases for calculation are illustrated again in table 4 using the example from the 22. 8. 1934:

Table 4: Calculation of the renewal coefficient of the eggs.
 Catch: 22.8. 1934 Obersee, Hùhe,, Langenargen.
 Averages obtained from pump- and net samplings.
 Weather: 9/10 cloud varying to 5/10, cumulus, some sunshine,
 wind SSW 0 - 1, time 15.45 - 18.00.

From the individual 'closing'(draw?) net and pump samples the absolute number of eggs under 1m² was calculated separately for each layer - and from the simultaneous temperature measurements, the average temperatures as also the development duration of eggs for each depth layer was calculated. From the number of eggs and from the development duration one is able to find out, for each layer, the absolute increase of nauplia in 10 days. Egg as well as increase-numbers for all depth layers were summed up and the total increase was calculated as a percentage of the egg numbers. The hundredth part of this value gives the development coefficient for 10 days for the whole vertical column, under the condition, that the vertical distribution during these ten days has remained constant. But this assumption cannot hold. Table 4 shows how greatly the rate of development of eggs changes with depth. In winter, vertical differences do not exist owing to the absence of significant temperature stratifications and the diffuse scattering of the egg carrying females, especially after heavy storms, over all depths. During the warm season, and as long as the lake has temperature stratifications, the differences in the vertical distribution of eggs must be considered in relationship to their spatial distribution in various parts of the lake, also time, as a factor in the daily rhythm as well as various meteorological and hydrographical conditions. This is only possible to a certain degree owing to the continuously changing conditions of the lake. Concerning the vertical distribution of the Bodensee Zoo-plankton, more detailed information will be given separately. For our immediate purpose, all (closing) net and pump samples taken from the Obersee from 1932 till 1935 were tabulated, as in table 4, and on this basis average values were formed for the periods under consideration. Lokal differences were partly taken into account, but the great majority of samples were taken from the middle

Obersee, i.e. from the region between Langenargen, Roschach, Romanshorn, Friedrichshafen. The Uberlinger lake often showed deviations in its hydrographical and biological stratifications; in relation to the open Obersee, its area, and thereby its influence on general conditions, is small. From the open Obersee a great number of calculations from its central area should be sufficiently representative.

The daily vertical migration of the egg laying females was taken into consideration when several 24 hour investigations showed, when they were analysed, that changes from day to day occurred, within a variation band of the vertical distribution, at the same hour, provided that similar weather and hydrographical conditions prevailed. The average values of vertical series conducted at different times throughout the day and under varying meteorological conditions reflect quite closely, for a given period, the predominant average conditions between morning and evening in the lake. In several cases the egg carrying females were lowest in the morning, and then rose during the day, but especially during the afternoon, a little higher. At about midday the 'average depth' was reached, which corresponded to the daily mean. So, most samples were taken at this time, when there was an average daily distribution. Moreover, especially with differentiated pump samples, the constant change in the vertical distribution of the females is only slightly reflected in the renewal coefficient (E_k) of the Eudiatomus eggs, since the greater part of the mother animals constantly (i.e. day and night), stays in the warmer zone of the lake, resp. in the Epilimnion. From November, even from October onwards till - often into the middle of May, there is no difference whatsoever between the day and night values of the E_k . Then the daily amplitude of the E_k increases till the high summer daily minimum of plankton, which was ascertained in most years. When, in autumn, the zooplankton is higher also during the day and the upper layers of the lake begin to cool, the daily amplitude of the E_k , resp. the rate of development, decreases. Table 5 gives an example of the daily amplitude in the high summer of 1932 and includes a thunderstorm which also gave rise to wind towards evening, which, in the course of a whole night drove a proportion of the mother animals from the surface layers of the lake, (0 - 5 m.). The few 'exhibits' obtained by depth-samplings could have entered the net at the surface which was unavoidable owing to the waves and the darkness. They are of no import to our observations. But even if all mother animals had concentrated in the upper 5m., the E_k could not have been significantly higher than in the late afternoon.

In the calculations of the daily average values one could assume generally that the greater part of the mother animals were concentrated at night, from sunset to sunrise, in the upper 10 m., by calm, in the upper 5 m; of the lake. The daily values, sunrise to sunset, taking into consideration the length of day and the temperature stratification, resp. the daily amplitude of the coefficient, were corrected/adjusted.

Fig. 2 gives the average monthly mean of the E_k for the years 1932 - 1935; the minimum lies in the months from January till March, - the maximum in the months July and August. The sharpest increase takes place in May and June; the sharpest decrease in October and November.

In individual years the course of the E_k curve may be quite different,

- as shown by Fig. 3. In order that a fuller understanding of this will assist future calculations and observations, this curve will briefly be analysed:- The winter minimum is the most regular section of the curve. The other sections of the curve vary from year to year. The Ek is dependant on the state and thickness of the Epilimnion (wind and cool weather) and also esp., on the presence of a surface-"leaping"- layer(?) (still and sunny weather), and also on various vertical distributions of the mother animals in the different years.

In 1932 we found, during quiet, sunny, weather, above average surface temperatures and below average (10- and 20-m.-) temperatures. Till September, the surface "leaping" layer maintains itself. The mother animals remain at a very high level even during the day. Their life process is hastened by the higher temperatures of the layer inhabited by them, so that we found in the year 1932 the shortest development time and the highest Ek values of all the years under study. Even in December the Ek curve lay above the mean.

1933. From April till June, considerable exchange in the upper layers was increased by strong winds and the surface temperature was lower, - however, the 10 and 20 m. levels had a higher temperature than in the preceding year. To this we had to add the diffuse distribution of the mother animals till May. Only at the end of June did the female animals concentrate during the day in the upper layers provided the weather was calm. The Ek values therefore increased strongly at this time. The renewed decline in June and August was caused by the occurrence of an unusually cold spell in the weather. Cooling of the upper water layers and the descent of the female animals to lower depths occurred thus simultaneously. Even though the surface temperatures as well as the temperatures of the next depth layer down to a depth of 20 m. sunk a little more by the end of September, it was only then that the Ek values reached their maximum, since, at this time all mother animals were now concentrated in the top 5 m. ! This distribution was also maintained throughout October, but now a rapid decline of the Ek values set in as a result of the rapid cooling of the lake. Below average surface temperatures in December caused exceptionally low Ek values to be registered.

1934. In spring, temperatures at 0 - 5 m. depth rose more quickly than in 1933, but in the lower levels they were significantly colder. Since the females, partially and in varying percentages remained in the colder layers, the spring ascent of the curve was flatter. In July the majority of female animals were found in the lower or the middle part of the "leaping" layer; * That explains the low value of the July Ek, when ~~the day time~~ compared with the other years, even though the surface temperature was high! Only in August did the female animals remain during the day in the upper layers. The curve reached in this month the yearly maximum, which, however is below the maximum for 1932 and 1933. The cooling of the lake in September and the markedly diffuse distribution of the female animals gave rise to an interim minimum, whilst in October, a second maximum is reached as the mother animals concentrate in the upper water layers. The notable decline in the second half of October was again caused by cooling of the lake and more diffuse distribution of the female animals.

In the middle of November 87% of the eggs were found again in the upper 5 m. so that the steep incline of the curve was temporarily interrupted.

The year 1935 provided us again with some very different results: Strong storms caused intensive circulation in March so that the plankton (zoo plankton) was distributed evenly at all depths. Also April was cold and stormy and circulation continued at deep levels in the lake. As the temperature was very much below average the April values of the Ek were comparable to those of winter! However, the maximum of the year was attained already at the end of June! The maximum is the lowest of the compared years - the lake had not reached its maximum warmth and also the female animals were not concentrated in the upper layers to the same extent as in the other years at the time of the maximal Ek values. The following decline was effected by the depth-migration of the mother animals. Only in the Uberlinger see-lake were conditions different: In this lake temperature at depth was considerably higher this year and the mother animals remained higher up so that the Ek value was almost, more than double that of Lausenargen. How long these conditions in the Uberlinger lake were at variance with those of the Obersee, was, unfortunately, not determined. Calculations for the year 1935 were based almost exclusively on samples taken from the middle Obersee. No adjustments were thus calculated for the Uberlinger lake. The autumn values of the Ek were again approximately normal.

Already this short summary shows that the life rhythm of the Eudiaptomus population differs from year to year: sojourn in higher temperatures does not only cause the eggs to develop more rapidly, but also accelerates the life process of the whole population insofar as its members remain in the warmer regions.

Let us now examine how these differences affect propagation or destruction.

II Fundamentals of Population Dynamics.

1. Calculation Basis.

As has already been mentioned, it is only with great reservations that single samples can be used for biological production calculations. Thus, from the beginning, samples taken within a short time (within a week or 10 days) were grouped (single "group values" given in Figs. 4 - 7). But also these mean values showed themselves to be partly dissimilar because some of them were based on too few individual samples. For this reason, monthly averages were calculated; namely from the 15th to the 15th, so that the mean values would be valid for the first of each month. Unfortunately this results in a considerable flattening of the curves and the disappearance of some individual details. When faced with the difficulty, however, of providing plankton data which is representative for the whole lake, it is nevertheless better to obtain averaged values for biological production calculations over a longer period, than to have many individual values which in themselves could deviate considerably from the true average. It might be recommended for future work that a number of samples necessary in the calculation of the true average value, are pooled to facilitate the work of counting, so that it will be possible

to obtain the average values from the outset, provided naturally, that one can dispense with an analysis of the locational and temporal differences for individual samples.

Difficulties also arose in the comparison of the closing net samples taken in steps, with the 0 to bottom samples, since the stepped samples had a lower clogging-up factor. From a number of simultaneous parallel samplings which were distributed over the whole research period, a curve could be constructed to show the strongly variable differences between the 0 - bottom and the stepped samples, according to which, correction factors were calculated for the intermediately placed individual closing net samples - without a simultaneous 0 to bottom control. Insofar as values are given in the curves which are based but on a few or single samples only, then they are marked by an *.

It must be stressed again that one must not expect too much from these numerical values. Quite apart from difficulties arising from the apparatus, the constantly changing, complicated plankton distribution necessitates certain reservations to be made. Individual details in the curves would therefore cause uncertainty, but the assumption might be justified, that they reflect actual conditions, at least generally.

The absolute increase in the population per month was determined by multiplication of the average number of eggs for the resp. month, with the threefold value of the calculated egg reproduction rate (E_k) over a period of 10 days. The calculated increase minus the observed actual difference in the population provided the number of destroyed animals per month (VZ).

2. Annual means.

Table 6 shows the composition of the population under one square meter in averages of monthly means for the years 1933 till 1935, (all monthly means).

The monthly increase and destruction figures (the negligible difference between the two is explained by the differences in population at the beginning and at the end of the period of observation) are therefore of the same magnitude as for the average total population, that means, the average length of life of all individuals was about one month, The number of eggs is on average about twice as great as that of females. The E_k (Development coefficient) of the eggs averages 3.3/month. Each female thus produces on average about 6.6 eggs per month. The total number of Nauplia which hatched in one year was about 80 times greater than the average number of females, resp. 40 times greater than the average number of adult animals of both sexes. If the E_k of the adults were known, we could calculate from the numerical relationship of the hatched Nauplia: adults approaching puberty, the average destruction figure from one generation to the next.

Table 6. Average values for the year.

If the destruction figure (VZ) were 0, resp. if all animals died as adults at the physiologically determined age, then the percentage of the development stages would reflect the relative development, resp. the length of life of the group concerned. If, on the other hand we knew the length of the individual stages, then it would be possible for us to determine from the numerical relationships the VZ of each single development stage. Both ways are recurrently described in literature. It is impossible, however, to deduct from laboratory experiments the skinning intervals in nature, since these, apart from temperature, depend also among other things on nourishment conditions which could hardly be reproduced or compared (among others, Elster 1936), nor is it possible to deduce from *situ* observations, i.e. from samples, statistically the rate of development, as will be described below. In general, we can however, assume from experiments with other species of Copepodes, that skinning intervals lengthen with increasing age, that under similar environmental circumstances the Copepodit-Period is longer than the Nauplius-Period and that the maximal age of the adult animals is again longer than the Copepodit-Period. Then the reduction of the average figures for Nauplia- till adult, is a first indication, that the VZ is already quite substantial during the development period. Thus the turnover coefficient is highest for the younger stages and sinks considerably as the animals get older. It is therefore not possible to apply the expectancy of life of a newly hatched Nauplius, which was given above to be about one month, without further consideration to the whole bio-mass of the population. In order to understand these relationships a little more fully, we will have to examine the individual years more fully.

3. Variations in the Population of Adults.

Figs. 4 - 7 (S. 590/1) show the individual monthly means of development stages which could be distinguished during counting, more faintly are also included the individual group values for 1932-34, so that apart from the monthly means upon which all calculations are based, it will be possible to consider several details.

Our research work was begun with the assumption that all curves would show a clear rhythm in the yearly cycle, so that it would be possible to see propagation periods, the development and the death of individual generations. Then one would have to analyse how the biological rhythm 'fitted' into the hydrographical rhythm. Comparative experiments in other lakes were to show the plasticity of the biological rhythm of the individual species depending on different environmental conditions.

A first glance at the totality of curves from 1932-35 revealed, however, an unexpectedly different picture. The curves were so different from year to year and apparently were quite independent from one another, that at first sight it was difficult to find any parallels between the years. The most regular curves were for the adult animals. At all times fully grown male and female animals occur in the lake. Two maxima were found in all years: a larger in winter and a smaller one in summer. Table 6-7 shows not only the time but also the numerical magnitude (individuals within 1 square meter) of the individual maxima for the years of research.

Table 7 Extreme values of adult population.

The time and magnitude for the first maximum lies fairly constantly in February, the first minimum varies in time between May and July also quantitatively. The figures in Table 7 are lower as the minimum is later. One could assume that this is a result of the continuing losses of the winter generation and the delayed ascent of the summer generation, the few figures in hand are not sufficient, however, to allow any conclusion to be based on them. The summer maximum occurred in three of the four years in July with an noticeably constant number of individuals of 36000 to 39000. Only the year 1934 deviated entirely, both in time and quantity (25000) in month IX. The delayed and low value of the first minimum indicates that the whole development rhythm was shifted forward this year, and it now seems more likely that the conditions for development for the animals during the second summer maximum were abnormal. Also the second minimum in 1934 was somewhat delayed in comparison with the other years but has considerably greater numbers than that of 1932 and 1933. Here the cause is without doubt the delayed maximum which had not subsided completely, whilst the winter generation which in 1935 attains the highest maximum for all the compared years is already in coming.

Is this relatively weak, but nevertheless clear and relatively constant rhythm of the adult population variation, to be explained primarily as the biological cycle, or is this rhythm dependant on environmental conditions? Is the variable height of the individual maxima a result of the variable egg production of the preceding generation? In order to be able to answer this question we will have to investigate the individual propagation periods as well as the destiny of individual generations during the time of research.

4. Propagation-intensity and Egg-production.

Let us first find out ^{the} production of a single female in the yearly rhythm. The average number of eggs per egg sack i.e. per "Gelege" is very variable in the individual months, variations occur also from individual to individual and may be considerable. Unfortunately only a small part of the original Countings-lists which contained data on the number of eggs per egg sack, were saved. Some periods do not have, therefore, sufficient statistical material. Nevertheless it is possible to read the following general characteristics from the available data:

The number of eggs per egg sack in the Obersee can vary from 1- 14, in seldom rare cases to 15. The most frequent number on average is 6. Egg sacks with 6 eggs or less can be found at any time of the year, even when all cases were exempted, in which part of the "Gelege" -Total number of eggs- had been laid, which could be seen from the empty envelopment jackets or from the arrangement of the eggs. The greatest egg numbers, especially values above 10, do not occur when the average values are low.

The yearly cycle begins mostly with a weak January maximum (average 5 - 6). There follows a decrease to a minimum at the end of the winter

period (average 3 - 4), mostly in March, in the case of 1935 - as a result of the strong (lake) circulation, till April. After this minimum the number of eggs increases rapidly with the increasing stability of the lake in summer so that an early summer maximum is reached in May - June, (mostly between, in 1934 7-8, 1932 and 1935 8-10). This is again followed by a decline which was variable in the compared years. In summer we often found strongly varying values within a few weeks having short lived intermediate maxima of different heights. Quite regularly such an intermediate maximum occurs in September, especially noticeable in 1935. In all years there was a strong decline in egg production/numbers till an autumn minimum was reached at the end of October to November (Average 3-4), from which, during December, there is an ascent towards the January maximum.

If we were to ask for the causes for these fluctuations, we know as yet too little about the effect of purely physiological factors, e.g. of the individual age, of *Eudiaptomus gracilis*. Special investigation is here necessary. Some incidental observations speak for this, that the "Primiparae" lay at first relatively fewer eggs than the older animals, but we have no indication that the "Gelege" of old females show declining egg numbers.

It is also not possible to define a clear relationship between the rhythms of population density, and the number of eggs per "Gelege". The maximal number of eggs per egg sack were mostly observed during the period of ascension before the maximum population is reached. The early summer maximum minimum of females produces the highest egg numbers, the autumn minimum of females with the minimum number of eggs (page 570 4th para.).

But it can be said with certainty that environmental factors, especially the nourishment factor, have great influence. This is shown not only by the above described culture experiments (Side 555, and table 1), but also by a comparison of the egg number of *Eudiaptomus gracilis* of the oligotroph Obersee with those of the eutrophic Untersee, in which the values attained are at times almost double those of the former and where maximal numbers of >30 are reached. Yes, under certain limitations it is possible to take the mean number of eggs as an indicator of the trophic-ness of a lake, resp. the favourable or unfavourable nourishment conditions of a lake. Also the rhythm of the number of eggs per "Gelege" in the Obersee seems to be intimately related to its hydrographical rhythm and its consequences. This is indicated by the minima at the end of the winter circulation and again in high-summer, at a time, therefore, when most animals are especially deep and thus swim during the day in layers poor in nourishment. After the extraordinarily intense and prolonged circulation of the lake in 1935, also the average numbers remained low for a long time, and even in April egg sacks containing only one egg were most frequent as a group! The November minimum which occurs in November of all years cannot be easily explained, since, for the time-being, we know too little about the nourishment conditions at this time.

The percentage of egg-carrying females can also not be stated accurately, since the lists for this have mostly been lost. From table

from table 8 we can, however, read the quotient, total number of eggs: number of females, and by dividing with the average number of eggs per egg sack calculate the approximate percentage of egg carrying females. In common for all years, the quotient minimum - total number of eggs: number of females, lies in November. There follows (1933 very weak) a winter ascent, a (1935 especially marked) interim minimum in March (1935 also in April), and relatively high summer numbers reaching their maximum in September. Also in May (1932 and 1934) resp. in (1932! 1935?) June an early summer maximum may be distinguished. The total egg numbers/females run approximately parallel to egg numbers/egg sack, this depending more on the propagation intensity of the roe carrying females, and less on their proportion to the total female population.

If we divide the total number of eggs /total number of females, by the average number of eggs per "Gelege", we find that in winter about one half, in January 1935 nearly all females carried one egg sack. In spring and early summer the percentage can decrease to about 25% and remain about the same until autumn. In November the proportion of egg carrying females may sink as low as 10 - 20%. If we are to assume that the pauses between two Gelege are dependent on temperature in the same way as the rate of development of eggs, then the percentage of egg carrying females can also be a scale to show the number of 'roe-mature' females. Then the percentage of fully mature females would be lowest in November. In January and February the winter generation of adults consists almost entirely of fully mature animals, whilst in other seasons there is a changing and in general somewhat higher percentage of young, not yet mature (or too old?) females.

The total numbers of eggs and their variations can be seen in Fig. 4-7. If we compare these with the curve of the adults we can see notable differences. The proportion of females to the total population usually amounts to 50% in most months- all months, taking into account samples from all depths and as great as possible a number. Independantly, resp. not in agreement with the adult curve, varies the percentage of egg carrying females and above all the egg numbers/ Gelege. The number of eggs from which the new generation is to grow is thus not entirely dependent on the number of the parents, but from the beginning also on the environmental conditions encountered in the lake. Certain features of the adult curves are also reflected in the egg-number curves, above all the two maxima, but even these vary from year to year in both quantity and time. In every year the main maximum in January-February and the minimum in November recurs in the egg number curves. The spring, resp. early summer maximum is absent only in 1935 as it was delayed by two months. A September maximum is not recognisable in all years. In general the stock of eggs shows a falling tendency between early summer and late autumn. Since we will have to investigate certain details later, the reader should refer now to Fig. 4 - 7 and table 11.

We find a very different picture when, instead of considering the quantity of eggs at any given time we consider the absolute production of eggs. Here the relationship between the winter and the summer maximum is completely altered by the shorter development times in summer:

1933 and 1934, - in these years the winter maximum appears only as a subsidiary peak, in 1934 as merely an episode in the general ascent of propagation intensity till the summer maximum. At the beginning of our research in July 1932 the propagation intensity reached 366000 eggs per square meter which was also the absolute highest maximum attained during the period of research. In 1933 the maximum lay in June (226000), in 1934 in May (189000). In 1934 we could also distinguish a notable autumn maximum, namely in September, with 150000. The year 1935 did not quite conform to this pattern: the winter maximum of 156000 is nearly double the winter maximum of the two preceding years. The decline towards the spring minimum in April (61000) is marked, the ascent towards the summer maximum (July 301000) is steep. The considerable decline in egg production which could be observed in all years after the summer maximum, was interrupted^{as} in 1934, by an intermediate maximum in September (169000), but this maximum is not so sharply defined as in the year 1934. Thus it can be seen from the outset that the differences in egg production in the course of the year are much greater than the population variations of the adults, and that the temporal and quantitative differences are also considerable from year to year.

In table 8 the quotients, egg-production/number of females, is given. These figures signify the monthly egg production of the individual female in winter, since in this season nearly all females are 'laichreif' - carrying roe (?). In summer, as has already been mentioned, there is a greater percentage of ~~not~~ in roe (or also, not any more in roe). That is why at this time the number of eggs for each mature female still increases a little. The egg production of the individual female per unit of time, is, as we can see, determined in the first place by the temperature of the inhabited layer, and this function is modified by other environmental factors, above all conditions of nourishment. Not only the carrying time of the eggs is shortened, but also the intervals between spawning, as is shown by dividing the egg production numbers by the egg numbers/Gelege: In winter there may be as much as four week between two spawnings, in summer the time is 10 - 14 days at the most, and these summer numbers are maximal values! Table 8 also shows the variations in fertility of the females in the individual years, especially in summer (1932 July, 1934 July).

5. Increase, Development and Losses.

We know now that eggs are produced in over abundance, but also that this production does not occur evenly, that in the course of the year we can expect certain maxima and minima. When, at what stage and what causes the reduction of the younger generation? If we knew this, we would have the key towards solving, at least partially, the secret of productivity in the Bodensee Obersee with respect to *Eudiaptomus gracilis*!

a) Interpretation of graphs/curves and tables.

If we were to try, in order to approach this problem, to observe individual generations from one propagation maximum, by way of Nauplia and Copepodites to the next maximum of the adults, we are faced with

considerable difficulties, as can be shown by a glance at Figs. 4 - 7. In order to interpret these curves correctly, we will have to take into account some general considerations. Let us make the following simplified assumption: constant number of eggs = 100, i.e. hatched eggs are constantly being replaced by newly laid eggs; other losses during the whole development period, also in later stages, would be impossible. The longevity - the development times for the eggs, for Nauplia, Copepodites and adults respectively three, six, nine and nine days. Then the population numbers are constant, the magnitude of the numbers being proportional to the development times of the respective stage, i.e. the longevity of the adults.

We now increase the temperature to such an degree that the development time of the eggs is halved, and assume that the development and life processes of all other stages have the same temperature coefficient. The number of eggs would remain constant because accelerated hatching is substituted by increased propagation. The same applies also for the other stages: the stocks remain unchanged, only the 'turnover', the "speed of the cycle" of the succession of generations is increased, just as a certain segment of a circulation system will contain the same amount of water all the time independantly of the speed of the flow.

Should I alter the temperatures for the individual development periods, in various directions, resp., in varying degrees, e.g. higher for Nauplia, lower than for the eggs of adults for Copepodites, so that the development time is increased for Nauplia and decreased for Copepodites but the propagation per unit of time remains constant, - the same would occur as if I reduced or increased the diameter of one or the other segment of water in the circulation model; the constant 'stock' of the segments is correspondingly decreased (Nauplia) or increased (Copepodites).

Should egg production not be constant in time, but would show maxima and minima, these relationships would become more complicated. Instead of long theoretical deductions a simple example is given in table 9 from which we can interpret the following vital information:

1. If x eggs are laid in y days and the development times for the eggs be z , the times for the Nauplius and Copepodite periods be z_2 and z_3 days, then the corresponding stages which originate from the eggs of the time $y = y + (z_1 - 1)$ resp. $y + (z_2 - 1)$ days, etc..
2. The height of the maxima of successive development stages are no longer a pure function of the relative development times, but depend on the shape of the curve on each side of the maximum, resp., on the period of observation.
3. Only when successive stages are of the same length of time are the differences between the maxima, or any other characteristic curve-points equivalent to the development duration of the stages. with varying development, resp. longevity of the successive stages, so also the differences between the maxima is modified according to the form of the number curve of the younger stage.

4. If, in a limited time of propagation (y) a total of x eggs is laid whose development duration is z days and if we are to undertake daily stock counts, then the sum of all daily stocks would be $EB = z \cdot x$. Let us compare two development stages B_1 and B_2 of the same "wave of propagation", with the development times z_1 and z_2 , then $EB_1 : EB_2 = z_1 : z_2$.

5. The average level of stock

$$\frac{EB}{\text{no. of stock counts}}$$

increases with the duration of the respective stage, however, not simply proportionally to the development duration.

Let us now apply this conception to our Eudiaptomus curves! We must not compare statistical with dynamical values: not the curve of absolute egg production, but the curve for egg stocks is the determining factor for the shape of the Nauplia curve! This because egg production is calculated from stock \times "rate of turnover" resp. renewal coefficient. Whether the temperature coefficient found for the eggs applies also to the development rate and longevity of all the other stages and the adults, is as yet unknown. In the meantime we will assume, that it is of the same magnitude, that the duration of all stages is affected similarly by similar temperature changes.

We still have to ascertain whether all stages inhabit the same layer, i.e. inhabit the same mean temperature layer. This must be the case in winter in all years, since either all vertical differences in temperature cease in this period (December till March), or the homotherm Epilimnion is so deep that it must include the layers inhabited by all stages. During the remaining time the 'habitation' temperature of the eggs and the mother animals must be identical, since the eggs are carried by their mothers.

Nauplia greatly prefer to concentrate in the upper 5 meters, and during their maximum occur in several summer profiles in 2 - 4 m., even sometimes 1 - 2 m. depth. There is, besides, a greater or lesser percentage is distributed throughout the whole vertical migratory zone of the mother animals, i.e. within the birth zone, and it appears that Nauplia mainly from the middle and older stages prefer the surface layers, resp., to have reached these.

During the day the Copepodes remain mostly between the Nauplia and the adults; the younger C. stages are more similar to the Nauplia in their vertical distribution, the older ones more similar to the adults. But there are many exceptions in individual vertical profiles, and Nauplia can occur just as deeply as the mother animals, Copepodes even deeper.

After the winter circulation it is the adults that rise to the upper layers first, whilst the Nauplia are diffusely distributed in much greater depths than the mother animals and the Copepodites. One gains the impression that the upper layers, especially in spring and after stormy weather, are colonised mainly by newly hatched Nauplia.

On average Nauplia occur somewhat higher than the mother animals during the day, the Copepodes occur between the two. Adults and Copepodites migrate during the night to the surface, the Nauplia- even those inhabiting deeper layers- do not partake in this nocturnal migration. Quite on the contrary, the distribution becomes more diffuse during the night, a proportion sinks by one or more meters, the mean habitation layer is displaced downwards, and at night may be lower than that of the adults. In the whole-day mean, therefore, the differences of the habitation temperatures are still further decreased.

We can thus state the following: Assuming that the temperature coefficient of the development and life-process-rate is similar for all stages, then the Bx values obtained for the eggs (comp. Fig. 2 and 3, S. 563/4) are a relative 'yardstick' also for the acceleration of the rate of development of the other stages during the time when in summer there is limnological stratification. With Copepodites acceleration is not significantly greater than for adults, but with Nauplia, however, - at least partially, it is notably greater. The stock of Nauplia are relatively somewhat ^{tea} lower from April, or May till October resp. November in comparison with the other stages, since the Nauplius-Period is relatively much shortened. But the differences do not appear to be very large.

In conditions of undisturbed development we thus have to expect the following curve: a maximum of the stage x is followed by a maximum of the stage $x + 1$, after a mean development duration dependent on x but the interval may not be exactly equivalent to this, - which is numerically as high above the x maximum as the period $x + 1$ is long compared to x . Were we to form quotients from the stocks $Bx + 1$, then the new propagation maximum is preceded by specially low values $Bx + 1 / Bx$, (the minimum occurring mostly with maximum Bx), which lead up to the maximum values as soon as the main body of the younger generation has developed beyond the stage x to stage $x + 1$. In order to facilitate the interpretation of Figs. 4 - 7, the quotients $Bx + 1$ are given in table 10, and in table 11 the lowest and the highest $Bx + 1 / Bx$ time and the height of the maxima and minima of all enumerated stages is given for the research years. The two tables differentiate themselves in their mathematical construction: In table 11 the highest and the lowest mean values calculated upon the first of each month i.e. for the first of each month, are given. In table 10 the mean individual numbers for the whole month (from the 1st till the 30 resp. 31) are taken as a basis.

b) The Nauplius-Period

Let us next compare the Nauplius and egg stocks. Not taking into consideration small details, we can see that the Nauplia curves broadly repeat the egg-stock curves (Figs. 4 - 7). The winter maximum lies just one month later than the egg maximum and occurs in the months February or March. In 1934 it continued until the beginning of May but the possibility here exists that a summit was not reached in April.

Table 10.

In this year the decline in the numbers of Nauplia was delayed by the unusual second egg maximum at the beginning of May. In all years the Nauplia and egg numbers show a falling tendency throughout the year, but in some years both curves are temporarily interrupted or levelled by interim maxima. The maxima of both curves occur in November, resp. in Decembr.

Table 11: Maxima and minima of the development of Eudiaptomus gracilis in the Bodensee- Obersee. 1932 (Maxima in heavy type, minima in normal type).

Table 11 gives the absolute numbers of the extreme values, table 10 gives the quotients of both curves. In the years 1933 and 1935 the N (Nauplius) quotient attains the expected maximum in March and then declines strongly to a June minimum. In 1935 the quotient remained almost constant till November as both curves run almost completely parallel to one another, in 1933 the quotient increases till autumn (IX and X), only then to decline in December to a low minimum; this is maintained also throughout January 1934. What does the behaviour of the quotients signify? The winter maximum is the result of retarded development due to lower temperatures so that the Nauplia maximum can only be reached when the egg numbers begin to fall. On the other hand development is so fast in summer that both maxima can occur within the same month. Thus the summer maxima of 1935 had no effect upon the quotients. The low values in summer are notable, however, because it seems quite improbable that the duration of the Nauplius period is of the same order as the carrying time of the eggs, resp. only 1.2 - 1.5 times greater! The small variations of the habitation temperature would certainly not suffice to cause this low coefficient. With the flatness of the curves in summer we find that the relationship of the monthly stock-means corresponds to the relationship of the duration of both stages. Thus the mean longevity of Nauplia, according to daily calculations, would have the following magnitudes for the individual months:

1933: V=12; VI=5; VII=5; VIII=6-7; IX=7; X=9; XI=18. Before and after this time it is not possible to calculate Nauplia times since the egg-curves are not sufficiently flat, even the May value could have been artificially large owing to the presence of "winter remnants" of Nauplia, or the December value could be too small owing to the then renewed increase in egg numbers.

In the case of summer 1935 our calculations are uncertain since interim maxima occurred at this time. But the constancy of the quotients in just this year would enable one to calculate roughly the mean longevity of the Nauplia from the carrying time of the eggs $\times \frac{N}{E}$:

1935: VI=6; VII=6; VIII=6 - 7; IX=7; X=8 - 9; XI= 12 - 13.

These values are almost identical for both summers. But in 5 - 6 days, as far as can be ascertained from aquarium observations - by a mid summer average temperature of 20°C. in the uppermost habitation layer - it is not possible for a complete succession of VI Nauplius stages up to the I

Copepodite, to take place. It seems that during this time only the first two Beta Nauplius stages were reached. This would mean, however, that a large part of the Nauplia dies before reaching the I Copepodite stage. We will return to this question later.

In the year 1934 egg- and Nauplia curves are flatter than in 1935. An adjusted calculation for Nauplius-duration should also be possible here. But the quotients show a deviating course (table 10). Correspondingly the Nauplius times are:

1934: V=12 - 13; VI=9; VII=12; VIII=7; IX=5; X=7; XI=19. The high value for November is resultant of especially low lake-temperatures, which also considerably prolongs the egg carrying times. Also the June value is influenced by below-normal habitation temperatures, but, this was not the case with the enormously high July temperatures. Greater longevity at equal temperatures leads one to expect that a relatively high percentage of Nauplia reach the Copepodite stage. In actual fact the Copepodite numbers do rise - more strongly for individual values than in monthly means, (fig. 7) - especially steeply in their ascent in the second half of June! In 1934, from July to September, the $\frac{C}{N}$ are the highest of all the compared years! This supports the view that the short average Nauplius duration is determined only through the death of a greater number of Nauplius.

When thus, at the beginning of July 1932 the strong egg maximum was only faintly repeated in the Nauplius curve, and the $\frac{N}{E}$ stood at record depth in June and July, then this phenomenon can best be explained - again by a high mortality rate. Nevertheless one has to consider the fact that the Nauplius-period which is descended from this egg-maximum generation occurs at a time of strongly rising lake temperatures so that the development rate of Nauplia is accelerated more than that of the eggs.

C) The Copepodite-period.

Let us now go a step further and compare the Nauplia with the Copepodite curves. In the sequence: adults-eggs-Nauplia, the stock curves of successive stages could easily be separately deduced. The relationship of the next stages: Copepodites:Nauplia and adults:Copepodites, can only be distinguished with some difficulty from the curves as a glance at figs. 4 - 7 shows.

In the years 1932 and 1934 it is possible to distinguish from the Copepodite curve 2 annual maxima, of which the first falls in spring or early summer (comp. also with table 11), whilst the second falls in autumn. The relative height of both maxima varies for individual years; only in 1933 is the first maximum (end of May 87000, resp. monthly mean for 1. VI 78000) higher than the second maximum (beginning of November 80000, resp. month mean for 1. XI= 64000).

In all other years the autumn maximum of the Copepodites is notably higher than the spring maximum; the minimum between the two maxima is only flat and appears to be more of a temporary delay in the ascent of Copepodite numbers from the winter minimum to the autumn maximum. This is

especially true for the year 1935. In this year it is possible to detect from individual values in May, July and November short-lived interim maxima of increasing height, before the abnormally high peak is reached in the 2nd decade of October with almost 150000 specimens. But the monthly means do show an almost perfect continuity for the increase from April to October.

This autumnal increase of Copepodites does not in any year appear to be related to the curve showing the quantity of Nauplia. The increase of Copepodites occurs when Nauplia numbers are steadily declining, also, even when small secondary maxima of Nauplia-numbers occur in summer or autumn there appears to be no direct correspondence either numerically or temporally with the increase of Copepodite numbers.

At first sight one would think, especially when reflecting on the years 1934 and 1935 (Figs. 6 and 7) that the Nauplia of the spring maximum would reach the C (Copepodite) stage only gradually in the course of the summer, this resulting in a bulge before further development to the adult stage can take place in autumn or winter. There are, however, weighty objections against such an interpretation which is based merely on the superficial comparison of statistical magnitudes. Let us consider further the characteristics of the curves themselves: The attested C. maximum in the second half of May 1933 (fig. 5) follows the pronounced winter maximum of Nauplia after a period of three months. The autumn maximum of the Copepodites in November would have to depend on either the N (Nauplia) maximum now 8 - 9 months back, or on the very flat interim maximum of the Nauplia in September, i.e. 6 - 8 weeks back. These interpretations seem the more probable.

In 1934 the discrepancy becomes still more obvious (fig. 6). The high spring maximum of Nauplia is followed after 4 - 6 weeks by a relatively flat C maximum, but the very weak Nauplia interim maxima occurring with the 'summer decline' at the beginning of August and at the end of September, are followed by a significantly higher and uniform C. maximum. With individual group maximum values, simultaneous interim-maxima of the Copepodites and the Nauplia correspond. In the monthly means the difference in time is 2, resp. 0 months. If one were to assume that the very gentle decline of the C-curve till June, resp. till the middle of July, were to be based on the following - that the Copepodites remained as such till the autumn and that the second maximum was supported to a certain extent by/on the first, even so there would remain a glaring discrepancy between the

Quotients $\frac{1.N-Max.}{1.C-Max.}$ and $\frac{Summer-N-Max.}{2.-1. C-Max.}$
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In addition it is inexplicable why Copepodites of the 2nd maximum should live 5 months shorter, resp. should develop more quickly than those of the 1st maximum, because the Copepodite numbers decline sharply after reaching the maximum at the end of October.

1935 (Fig. 7) finally we will have to observe with great care, the short-lived variations of the individual group values since they originated from a rather limited area - from the middle of the Obersee in front of

Lansengren. Observed realistically the interim maxima of the Nauplia and Copepodite numbers in July, September and October occur in the same month. In the monthly means of 1935, the noticeably high spring maximum of Nauplia is not shown at all in the C-curve, and the record maximum of the Copepodites in October is likewise resultant from the small interim summer maxima, - or one should conclude that the high C-maximum in October is likewise resultant from the equally unusually high N-maximum in February and March, i.e. after 7 - 8 months!

In looking retrospectively at the Copepodite periods of the years 1933-35 we seem to be faced with many contradictions: If, as has been shown earlier (table 9 s. 575), that the intervals between the peaks, as the maximum proceeds through the development stages, does not exactly correspond to the development duration of the younger stages, in fact, is primarily dependant on the duration of the older compared stages, we find, in comparing the years, among them quite different minimum lifetimes for Nauplia, which in some cases amount to half a year and whose varying duration appears in no wise related to the different habitation temperatures; this does not have to be demonstrated further in detail. We obtain the same result when we compare not just the peaks but the "necks" as they rise to the maxima, as can be seen from figs. 4 - 7.

Let us now take the results from the comparison of egg- and N-curves and also avail ourselves to the absolute production figures, then we have before us a demonstrative example of the errors which can result from a merely superficial comparison of the stock-curves: the average longevity of Nauplia in summer amounts to only a few days, the stock of Nauplia in the time between the maxima of the N- and C- curves is partly replenished/renewed several times, and on this ground alone it is not possible to relate the interval between the peaks to the development times! Moreover, at present, whilst we know nothing of the actual development times, the question is open, as from what period those Nauplia originated which later form the maxima of the C- curve. The above calculated values on Nauplia-longevity are average values. A great proportion of the Nauplia obviously dies before reaching this age- average age-, a part dies later, and of the total again only a fraction reach the C- stage. The larger the numbers of Nauplia, the greater, naturally, the possibility of a larger number reaching the C- stage. But in such a case the course of the N- and C- curves would have to show regular/recurring relationships, and the peaks, resp. the ascents of both curves would have to follow one another in a period of time independently of the habitation temperature. That in many cases it is not possible to determine such an equal, even if temporally somewhat varying trend in the curves, may have two reasons:

1. The number of Nauplia reaching the C- stage can vary independently of the already existing stock of Nauplia, and also depend on the beneficial or unbeneficial influence of the environmental conditions.
2. The longevity of Copepodites can vary in the course of the year, since at various times, as is the case with Nauplia, differently great percentages die, i.e. before the last skinning. This percentage of prematurely

dying Copepodites would have to vary a great deal more than that for Nauplia, whose stock-curve, as we have seen, runs more or less parallel to the egg-curve. Also variations in the habitation temperature could not explain away the deviations of the C-curve, even if the autumn maximum of the Copepodites may appear a little too high through this, that further development within the C-period takes place more slowly than in the preceding N-period as a result of the cooling of the habitation layers. But since the autumn maximum of the Copepodites is reached in some years already in September, at a time when the habitation temperature has not dropped much, and since the C-curve annually (and particularly) in November, drops when there is the strongest decline in the habitation temperatures, this temperature effect cannot be great and certainly not decisive.

Unfortunately it was not possible for us to calculate the longevity of the Copepodites in the same way as for the Nauplia. That all, or nearly all counted eggs hatch at a certain time, has been proved experimentally. But, what percentage of the stock of Nauplia reaches the C-stage, this is the open problem! Nevertheless a glance at the $\frac{C}{N} Q$ in table 10 is instructive:

The pronounced winter maximum of Copepodites with the quotient < 1 , partly even < 0.1 , can be found in many years from January to March 1935 (literal translation). Since during this period, the minimum habitation temperature falls simultaneously, we have to give to this minimum a special significance. Only 3 months after the ascent of the $\frac{N}{E} Q$ the $\frac{C}{N} Q$ begin to rise.

This ascent is maintained throughout the whole summer- unimportant interim maxima occurring only in August 1932 and July 1933- culminating in a high autumn maximum in November. The fall to the winter-minimum is very steep. This behaviour of the $\frac{C}{N} Q$ purports, however, (this the more so since it is

not related to the habitation temperatures), that either an increasing percentage of the N-stock reaches the C-stage in the course of the summer, or, that the average longevity of the Copepodites increases in the course of the summer, briefly, that the development in the course of the summer, on average, carries on into older and older stages, the "barrier" in the course of development moves backwards! (literal translation). Whether this is the case only with Nauplia, or resp. primarily with the Copepodes, cannot be ascertained on the basis of our present knowledge!

Originally it was planned, by counting the individual skinning stages, to analyse this problem more accurately, but this intention could not be realised owing to the outbreak of the war, the loss of gathered material, and change in the field of my activity. Similar research is in progress for Black Forest lakes and further research is also desired for the Bodensee.

d) The Adults.

If one recalls the characteristics described above for the development course, especially the changing silhouettes of the Copepodite quantity curves in the individual years, then one is surprised to find the above-described relatively regular rhythm for adults in the annual cycle. In many cases it is impossible to relate directly the adult curves to the Copepodite curves. Neither the dependence of longevity upon temperature, nor the increase and decrease of Copepode numbers, resp. their replenishment from Nauplia, can explain the rhythm of the adults. Let us analyse the individual years:-

In 1932 Copepodite numbers increase in September and October whilst the number of adults remains constant. In November and December, Copepodite numbers decrease a little more than adult numbers increase. Here it is completely impossible for the adults to have only a short natural life. Much rather, everything seems to indicate, even the egg-numbers that from November onwards we see the rise of the adult winter generation whose maximum lies in January resp. February with regard to the number of specimens and egg production, i.e. three months after the Copepodite maximum. The decrease in adult numbers from February to May 1933 would give the impression to their natural mortality rate, resp. give expression to the total losses of the adults since replenishment from the Copepodes must at this time certainly be very small. This all would indicate that the winter generation is uniform, and that the mean longevity of the adults in winter lasts several months, presumably at least a quarter year. The quotient of the maximal monthly means $\frac{A(I\ 33)}{C(X\ 32)}$ is 0.73 .

1933: The feeble increase in adult stock from May till July, resp. end of June, can be explained by the increased supply from the Copepodite stock which itself had increased strongly. The interval between the maxima is about one month, the quotient (month middle) $\frac{A}{C} = 0.6$. After the maximum

is transgressed, both curves show a similar course, then the adult curve lapses increasingly behind as the habitation temperature sinks, and reaches its maximum (January 1934) two -in monthly averages- three months after the C- maximum. The quotient of the maximal monthly averages $\frac{A(I\ 34)}{C(IX\ 33)}$ is 1.02 .

In 1934 we find at first the relationships to be similar as in the preceding year. The Copepodite maximum at the beginning of May was not able, however, to halt the decline in adult numbers which continued until the middle of July. Copepodite and adult numbers decrease together from the beginning of May till the middle of July. The number of Copepodites increases considerably more strongly than the number of adults who have their maximum somewhat earlier than the Copepodites. Neither the almost simultaneous and possibly unreal interim maxima of the individual group maxima group values (Fig. 6), nor the temporally inverse maxima of the monthly means can be related to one another. Should one assume that the adults of the August and September maximum originate from the first C-

cont. Should one assume, that the adults of the August- September maximum originate from the first C- maximum at the beginning of May, then the time interval for the maxima of four months is much too long in comparison to the summers of 1932 and 33. Either the interpretation of the summer maximums for the above-mentioned years was wrong, or the maximum of 1934 must be given another meaning!

From the end of September onwards there is a strong reduction in the number of Copepodites, whilst adult numbers decrease only slightly and temporarily. From the middle of October the stock of adults increases only slightly till the end of December, whilst the number of Copepodites continues to decline sharply till the end of the year. In this period many Copepodites of the last skinning die.

1935: Only in January and at the beginning of February, i.e. when the Copepodites have reached their minimum, do adult numbers increase strongly again. Here the explanation must be found from prevalent hydrographical conditions and from the position of the sampling station. This particular case must show again how careful one has to be when relating curves of successive development stages. As has already been mentioned several times, the full circulation of the lake that winter in 1935 was especially intense. Zoonlankton was distributed in all lake parts, almost uniformly and in all depths and one can assume that in the course of the winter there was not only a vertical but also a considerable horizontal exchange of water masses. The quantity of Plankters underneath one square meter of the lake surface was thus approximately proportional to the depth of the water, near the end of the winter of 1935. If we thus assume a uniform distribution in the upper layers prior to the beginning of full circulation, then, after the onset of the horizontal and vertical exchange, the number of individuals in shallower areas is reduced below one square meter, in areas of below average depths, however, there is an increase. But most of the samples in the year 1935, especially those that were taken in winter, were from areas of below average depth in the middle of the Obersee, namely from depths ranging from 180 to 250 m.. This points out, that the considerable increase of adults and the aforementioned above-average height of the adult winter maximum of 1935 is not only the result of conditions of production, but also the result of local transportation and 'bunching'.

Unfortunately we do not have sufficient lateral and cross sections for 1935 to be able to determine the horizontal arrangement of the locally different adult numbers. In our curves (Fig. 7) the reduction of adult numbers, those taken primarily from the middle Obersee, was a little steeper than in the previous years. But also the number of Copepodites remains minimal till the end of April, so that the increase in adult stock from the Copepodites may have been later than usual this year. However, the time and the magnitude of the adult minimum VI = 19000 is not unusual. While Copepodite numbers varied in detail but showed a steady increase in their mean monthly values, the adults reach a clear summer maximum about the 10th July, that is, after a short period of ascent, then to fall again, even though Copepodite numbers continue to increase unchanged. With respect to time and height, the summer maximum (VII = 39000) is com-

pletely normal and shows no traits, neither of previous unusual hydrographical conditions, nor of the previously deviating form of the Copepodite curve! Also the decline in adult numbers from the middle of July to the middle of August resp. till the middle of October, can be explained neither from the number of Copepodites nor from the lake temperature. Probably there is a relationship between the high number of Copepodites in late summer and autumn, and the relatively flat form of the autumn adult minimum (IX-X each 17000). Unfortunately our research was ended in December 1935, so that it is not possible to state whether the abnormally high numbers of Copepodites in autumn 1935 resulted in a correspondingly high number of adults in the winter of 1936.

Let us now take another look at the $\frac{A}{C} Q$ in table 10. Only in winter, from December to March (1935 till April) are the values above 1, that means, there are more adults than Copepodites. From April, resp. May, the quotients remain < 1 sinking at times even to 0.1 - 0.2. Even adult summer maxima hardly show any significant rise in the quotients, if at all. The values then also remain < 1 . Here we are not assisted by the argument, that with increasing C- numbers the A- stocks lag behind, so that quotients of simultaneous monthly means would necessarily show to low a result because the quotient is < 1 also for periods of falling C- numbers (VII and VIII 32; VI, VI 34)!

Again we are faced with two explanations: Either the average longevity of the adults is shorter than that of the Copepodites, being only $\frac{1}{2}$ to $\frac{1}{4}$ of the C- time, or, only one part of the Copepodites reaches the adult stage! If the first explanation were correct, then we have to take into account the great differences in the average longevity of the adults in order to explain the discrepancies in the course of the C- and the Adult curves. If we apply to eggs and to adults the same magnitude of the temperature coefficient for life-rate, then the "turnover" of adults in mid summer is 5 - 6 time quicker than in winter. As has already been mentioned the longevity of adults in winter is, on average, at least three months, if anything longer, perhaps up to six months. Purely physiologically, three winter months would correspond to about 2 - 2 $\frac{1}{2}$ summer weeks. Yet we know too little about the actual longevity of grown up Eudiaptomus gracilis. Perhaps research on morphological or any other age indicators, such as worn mandible- chew-chamber(?) etc. can help us further. It must also be mentioned, that even under the most unsuitable life conditions in the small and over populated mother bowls (comp. S. 5), all Eudiaptomus adults caught from the Obersee and kept in August at a temperature of about 17°C. were still allive after 9 days; in December at 16 - 18°C., that is, under summer temperatures they were for the most part lively and fresh. What age the animals had when caught- we do not know. The natural longevity resp. physiologically determined life- expectancy in nature must be greater than 2 - 3 weeks even under summer habitation temperatures.

The second possibility, that from time to time a varying proportion of Copepodites dies before the last skinning, is the more probable not only because of the irregularity between the A- and C- curves, but also

because of the irregularity between the N- and C- curves, which supports this view. We can suppose that both factors - the varying longevity of the Copepodites and adults, as also the varying percentage of Copepodites which attain the last skinning - play a part, though for the time being we cannot estimate their individual roles.

Total Stock and Mortality Numbers.

If we comprise into one stock all the development stages of Nauplia till the adult stage (without egg- numbers), and relate this to the absolute Nauplia production, then we should be able to note the total mortality rate within the population - in the course of the year. The rule seems to confirm a winter or spring maximum primarily of Nauplia, and a mid- summer or autumn maximum primarily of Copepodites. The deviations of the year 1933 (fig. 5) depend above all on the different courses of the C- curve.

If we compare the monthly arrival of Nauplia, with the differences at the beginning and at the end of the respective month, then the differences between them gives us the mortality rate within that population for the month. In figs. 4 - 7 mortality and production, = the rising generation, curves are given for the whole period of research. At first sight we are struck by the almost completely parallel course of the two curves! With few exceptions the maximum and minimum of both curves occur at the same time and any exceptions are confined to one or two cases in the winter months. These also in their absolute height- agree to such an extent as to be remarkable! The common factor of both curves is only the development and life-rate -both depending on temperature in the yearly rhythm, and which must affect propagation, age, resp. death in the same way. Additionally, however, the propagation curve/rising generation curve is dependant on fluctuations in the stock of eggs, and the mortality curve -is dependant "a priori" upon the stock of over-aged animals. The fact that birth and death in a population are not merely a function of temperature, is shown by the winter months of all research years, the summer values of 1934m and a little less clearly, summer and autumn of 1935. Let us just try to deduce the mortality number (VZ) from the death of over-aged animals, and we will find that our endeavours are baulked even if we were to regard the total stock of adults as over-aged. If only adults die, then the quotient would be $\frac{VZ}{EKA}$ = the renewal coefficient of the adults per month, $\frac{30}{EKA}$ (resp. $\frac{31}{EKA}$) = the mean longevity of adults in days. What we thus obtain is shown in table 12 taking the year 1934 as an example:

Table 12

It is quite improbable that in May and June stocks of adults are respectively renewed more than ten times, resp., that the mean longevity of the adults is not quite three days. This does also not explain why the VZ curve follows the propagation curve in all its details.

If losses were to occur only at the conclusion of the development cycle of adults, then the quotient $\frac{VE}{\text{total stock}}$ give the Ek for the

total stock, 30 the duration of the "cycle", i.e. the whole duration of development from the Nauplius till death, in days for the "Geschlechtstier". The corresponding values for 1934 are shown in table 13:

Table 13.

Also these values are not creditable, in their absolute height (May!) as also in their variations, which cannot be made to harmonize with variations in the habitation temperature (comp. e.g. Fig 3). (Table 13: II, III, V, VII, XII)!

The assumption that the greatest mortality rate occurs at the end of a generation cycle must be wrong! It would not permit an interpretation of the individual curves in figs. 4 - 7 as we have seen. But agreement between the increase- and loss curves, would indicate that earlier development stages, mainly Nauplia, suffer losses. The life span between birth and death must be very different for single individuals, but it is relatively short for the majority of individuals. Only a fraction reaches the C- stage and only a part of this, puberty. This explanation of the VZ- curves is, at the same time, the key to the understanding of other curves, as has been repeatedly indicated. The agreement between egg- and Nauplia curves can now be explained in the same way as the deviations of the C- and A- curves. Not the development time itself determines "the time position" of the maxima; not the absolute egg- production itself determines the strength of numbers of the rising generation, but the beneficial or detrimental effect of development conditions determines selection and destruction. These regulating environmental factors are something which is foreign, changing, "animose" in the biological rhythm of the species; they check any wave of increase of stock which had developed under beneficial conditions - before it is able to reach its goal; a new generation of 'Geschlechts tiere'; they put up development barriers and open "Development sluices" in a rhythm which can be modified by many factors. Nutrient conditions certainly play an important part. What is meant exactly in detail under the heading 'beneficial' or 'detrimental' environment, we do not yet know.

6. Losses through the Rhine Effluent at Konstanz

Until now we have not taken into consideration all groups of factors which could have a bearing on the calculated losses. Three possibilities must be considered:

1. Mortality in the lake. This loss factor, has been repeatedly mentioned in previous sections. It was to have been investigated more closely with the help of "Sinktöpfen" (sinking pots?) at various depths and by control after a short "exposition" time. The war prevented the carrying out of this research.

2. Losses due to fish feeding by fish and other enemies. It was planned to determine the magnitude of this factor, and work was begun only to be hindered again by the war.

3. Losses through the effluent Rhine at Konstanz. To answer this question we can avail ourselves to a series of samplings taken from the effluent Rhine at Konstanz between July 1934 and December 1935. Net-samplings from the lake Rhine were made using the plankton net, which, when the boat was stationary, was held into the current immediately behind the Rhine bridge at Konstanz- for one minute. The speed of the current was measured and so the amount of fished water could be calculated. The same correction factors were applied as for the net catches from the lake, although the relative speed of the current passing through the net, resp. passing by the net, was two to three times greater in the river than in the lake. Since defects of the net increase as the current increases, we must expect from net catches, values which are too low. We also used a number of pump samplings which were calculated on the same basis as the lake samplings. Thus, from simultaneous net- and pump samplings average values were used.

Fig. 8

Eudiaptomus quantities (monthly means per cubic meter) in the lake Rhine (Konstanz).

It might also be mentioned, that contrary to expectations, the net-factors which were determined by control-samplings, did not differ very much for the lake Rhine.

On a number of sampling journeys comparative samplings were taken during the forenoon and night, mostly one or two hours after dark, in some cases at nearly midnight. In these cases the mean from the day and night values was used for the calculation. We must, however, take into account, that the daily rhythm of plankton transportation in the lake Rhine does not necessarily reflect the daily rhythm of the lake since some forms which during the day remain at lower levels only rise towards evening and thus be transported into the shallower waters of Konstanz bay, and from the entrance to the bay to the Rhine bridge in Konstanz may need a variable length of time from fall to fall (case to case?). In the main the rhythm of plankton transportation in the lake Rhine is affected by local vertical migrations of plankton in Konstanz bay itself, immediately in front of and within the suction zone.

Let us next compare the stock curves (numbers are for cubic meters) for the lake (comp. fig. 6 and 7), with the plankton numbers (per cbm) in the Rhine (Fig. 8, different scale !): We are immediately faced with great differences in the curves of the two places. Maxima and minima occur partly at a different time and in other relative quantity proportions. The reader will be asked to contend himself with the figure as we will not describe and analyse differences in individual details, because the causes for these differences can easily be seen (see below), but do constantly change, so that the curves from the lake Rhine reveal more the variation possibilities as hard and fast rules than anything else.

Plankton transportation in the lake Rhine is primarily affected by the changing vertical distribution of the zooplankton which here gives quite different results as for the lake-stocks, since only those organisms are caught which are in the suction area of the Rhine. Changing meteorological conditions can in a short time give rise to great differences. Also horizontal differences in the concentration of plankton as effected by wind and 'tilted' layers, cause a locally different plankton concentration, in front of, and in the bay of Konstanz. Finally the depth of the suction zone of the Rhine varies in the course of the year but its extent/magnitude and rhythm has not been fully clarified: Note: Comp. Auerbach 1952.

For the same reasons the differences between the day- and night samplings vary a great deal. Nauplia, which during the day usually remain quite high - very high, rarely show daily amplitudes in the lake Rhine which are outside the error margin. But Copepodites, and above all adult animals can attain at night ten times their day values, whilst at other times differences are negligible and day values may be even higher than the night values. It was therefore not possible to make a correction of the daily values to give a 24-hour-mean, where night samples had not been taken. All figures can therefore only give the approximate magnitude.

As an example of the differences between the Obersee and the lake Rhine curves, it may still be mentioned, that the winter maxima of 1935 are shown in the lake Rhine only very weakly or not at all. The reason lies with the repeatedly aforementioned full-circulation intensity which distributed plankton down to great depths and thereby reduced its concentration in the upper layers, that is, also in the suction zone.

Let us now calculate the total quantity of Eudiatomus which the Rhine drains from the lake in the individual months. In order to enable comparison with the calculations for the Obersee we will multiply the number of individuals/m³ with the total quantity of water which the Rhine has taken from the lake, and divide the obtained numbers by the surface area of the lake ($476 \times 10^6 \text{ m}^2$). Thus we obtain the loss per square meter of lake surface, which can be compared directly with the stock and mortality numbers of the lake. We could deduce the rate of flow from water gauge^{reeds} of the Obersee, as well as ^{the} empirical off-flow curve for the gauge.

The results from the calculations are shown in table 14. From it can be seen that in the individual months, especially in summer, the lake Rhine drains away a considerable part of the total Eudiatomus-stock from the lake. Thus 28% of the total stock were drained away in September 1934, and 97% of the average stock of Nauplia was lost. In other words, even the effluent alone gives a renewal coefficient for Nauplia of 2 for the respective month. This loss is replaced by the hatching of new Nauplia resp. over-compensated by 8000 specimens. In the winter months the percentual rates-of-loss through the Rhine are considerably lower and have no longer any weighty bearing, partly because of the low water of these months (comp. fig. 8), partly because of the diffuse distribution of plankton and the resultingly low concentration in the

suction zone of the Rhine.

But the percentual losses related to the respective stocks have a very different meaning for population-dynamics in summer and winter because of the variable development rate, resp. the higher development coefficient in summer. In the last two columns of table 14 the total loss of Eudiaptomus, including eggs, is related to the mortality figure which was calculated earlier. Here, however, we have a similar picture: In summer the calculated total losses for the lake as also the observed losses through the effluent are higher, and the proportion of the total losses passing through the effluent was in summer resp. autumn 1934 about one third, sinking to 10% as the flow of the Rhine decreases, and remaining very low in the winter months. One exception was in January for which the total loss numbers were unusually low since there began in this month a mass-hatching of Nauplia, whose longevity in the cold winter temperatures must extend beyond the end of the month. Also the stock of adult animals is on the increase and mortality as yet small. As a result of this, the absolutely small effluent losses still make up one third of the total losses.

That conditions can change quite considerably and do not allow any general conclusions can be learned from a comparison of the summer months of 1934 and 1935. The figures in table 14 show quite clearly that the rôle of the effluent in population dynamics of the Bodensee plankton, and especially on the forms living near the surface, can be very significant in times when the lake Rhine is in high water, and that the effluent in a single month can claim a quantity equivalent to a mean population density. Possible we do not even know some of the extreme values. A constant control of the effluent in research pertaining to population dynamics resp. production biology, is therefore absolutely necessary.

Translators Note:

Please substitute for the appropriate mis-interpretation:-
within one square meter = underneath one square meter.

7, Westbury Avenue,
Bury St - Edmunds,
West Suffolk.

Yours sincerely
F. H. Sporn.

Notice

Please note that these translations were produced to assist the scientific staff of the FBA (Freshwater Biological Association) in their research. These translations were done by scientific staff with relevant language skills and not by professional translators.