

Schriften des Vereins für Geschichte des Bodensees und seiner  
Umgebung, 87. Heft 1969.

Translated by P.L.Nock.

INVESTIGATIONS ON THE VERTICAL MIGRATION OF PLANKTONIC CRUSTACEA IN THE  
BODENSEE-OBERSEE.

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The vertical zoning of the planktonic crustacea in a lake is the expression of a complex set of different factors. Besides the measurable, external influences such as light, temperature, acid and CO<sub>2</sub> stratification, a particularly large part is played by internal factors, which co-ordinate a specific reaction in each species depending on state of development, age and sex. Supporting this extensive, predictable, annual course of diurnal depths and the daily vertical migrations, whose extent is again dependent on external conditions, primarily of course on the amount of light. The individual factors mentioned, however, are here also of great significance.

Within the scope of a long-term study of the planktonic copepoda of the Bodensee, some day and night series were in 1963 also carried out in the Obersee, in order to obtain at least volumetric data on the extent of the daily migrations of these creatures. Although Weismann (1877) had already referred to this phenomenon, the number of further investigations on the Bodensee still remained relatively small. After the studies of Hofer (1899) and two 24-hour series of Auerbach (1934), Elster (1936, 1954) above all supplied data on the vertical migration of Heteroscope borealis and Eudiatomus gracilis, which had meanwhile disappeared from the Bodensee. Some studies are valid for the genera Cyclops s.str. (1964, 1967) and Mesocyclops (1968) in the Obersee as well as Diacyclops bicuspidatus in the Untersee (1965).

Where possible pump traps were attached to the final net series on each north or south station in a section from Meersburg to Staad. These made possible a precise analysis of the layers, with a vertical distance of one meter and a pumping capacity of 40-50 litres per degree of depth. Unfortunately this combined method could only be carried out on 21/5/63 and 11/10/63; for the other profiles the comparatively rough division of the depth profile in 5-metre stages (up to 30 m, then in 10-metre stages) had to suffice. On comparing the catches from the pump and the net, on 21/5/63 there was obtained an average obstruction factor in the net of about 1.5,

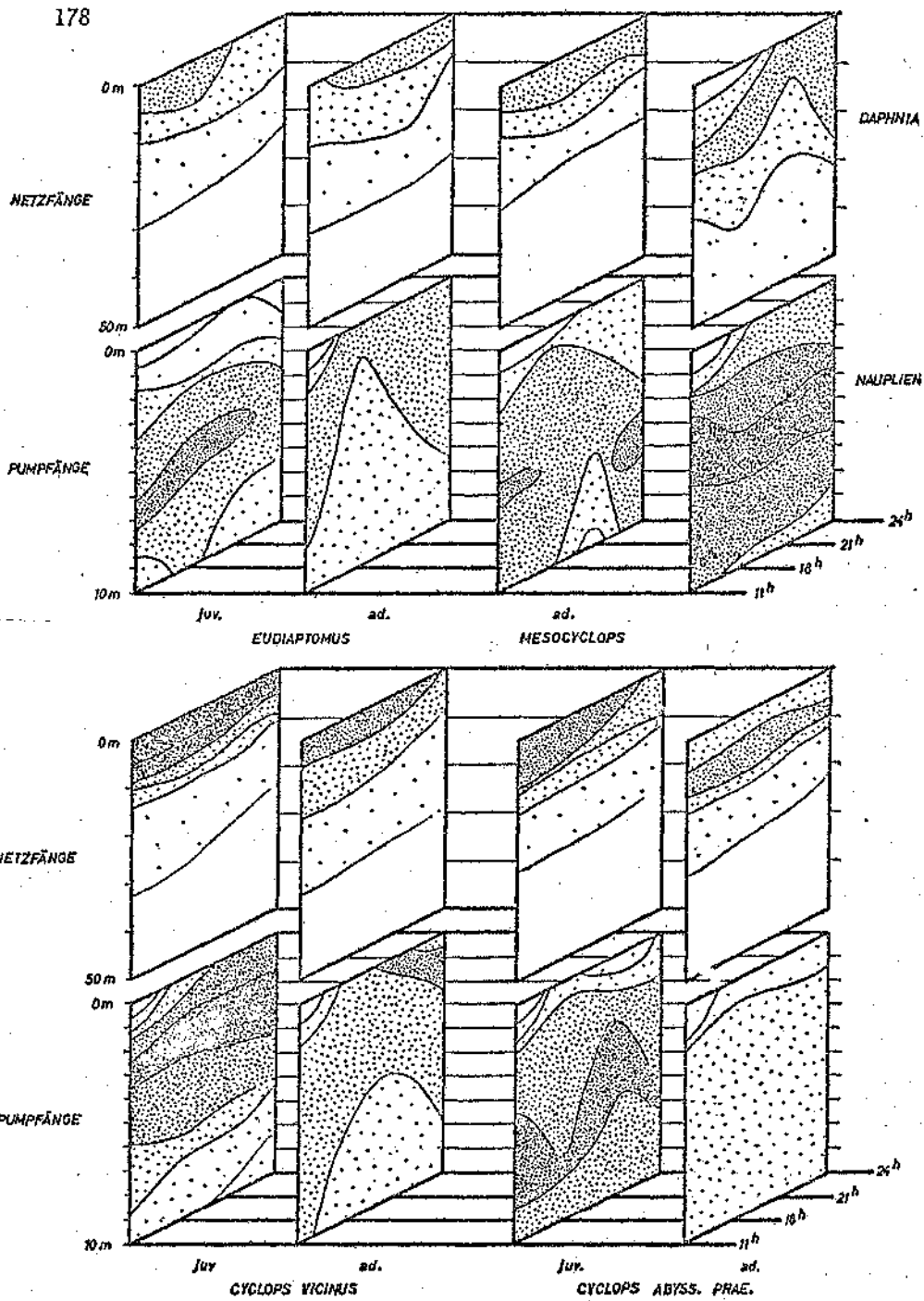


Abb. 1: 21. Mai 1963

at which, however, very strong differences appeared in the individual groups for counting.

The numerical values in the diagrams signify thickness per cu. m.; the day profiles are in the foreground, the night series are produced behind them.

The series of separate experiments.

The limnological situation in the year 1963 was characterised by an exceptional event for the Bodensee-Obersee - "Seegfrörne" [? freezing of the lake] - The almost complete icing-up of the Obersee was noticeable for a long time in extraordinarily low temperatures, which for example in May stood at  $3.7^{\circ}$ .

a. On May 21st the surface water between Staad and Meersburg had warmed up to about  $10-13^{\circ}$ , the values in a depth of 10 m. varied between 4 and  $10^{\circ}$ . The mass of water, consequently, was in a strong hydrodynamic motion, to which the planktonic organisms were likewise subject. In spite of this situation, unfavourable for a series of investigations, the pump and net catches allowed a migration to be recognised for most species (Fig. 1).

In a cloudless sky the animals in the afternoon mostly settled in the zone between about 10 and 20 m., at which the uppermost decimetre was practically free of plankton. Already at around 18 hours the animals could be observed directly beneath the water surface; in the series around midnight some forms (Mesocyclops) finally began to sink back already into deeper layers. Most of the groups showed this termination of the daily migration, with Eudiaptomus at any rate only the full-grown animals. Remarkable is the remaining - if also negligible - migration of the Nauplii, in which only a small part of the population took part. The maximum in about 5 m. of depth remained unaltered thereby, although from the minuteness of the Nauplii a vertical amplitude of migration of 1 m. should be looked on as an astounding achievement.

That the events of this day showed only relatively small migrations lies - as already mentioned - with the stratification of the crustaceans, which up to this time in any case lay close to the surface. With the increasing warming of the water and the formation of a stable metalimnion, some

species, especially Cyclops abyssorum and Eudiaptomus, left the epilimnion during the day, so that the ~~amplitude~~ amplitude of migration of these animals becomes larger towards autumn.

b. Already by July 17th this separation into species living in the epilimnion and the metalimnion by day was being extensively performed. The lake surface had warmed up to almost  $23^{\circ}$ , a definite thermocline ~~(indicated by a double line)~~ lay between 15 and 20 metres. Unfortunately in this investigation, as also in the following ones, only two profiles could be carried out, in the early afternoon and before midnight, so that there was no possibility of the situation near the surface being considered after the start of darkness. The species composition of the plankton had greatly altered, as on the one hand Cyclops vicinus had entered its summer diapause (Einsle 1967), while on the other hand the cladocerans were engaged in a rapid development. This group, living predominantly in the epilimnion, naturally permitted no details through the coarse method of net capture (Fig. 2), although however the effect of the migration was plainly recognisable. The uppermost 5 m. were visibly preferred at night, especially by Daphnia and Leptodora.

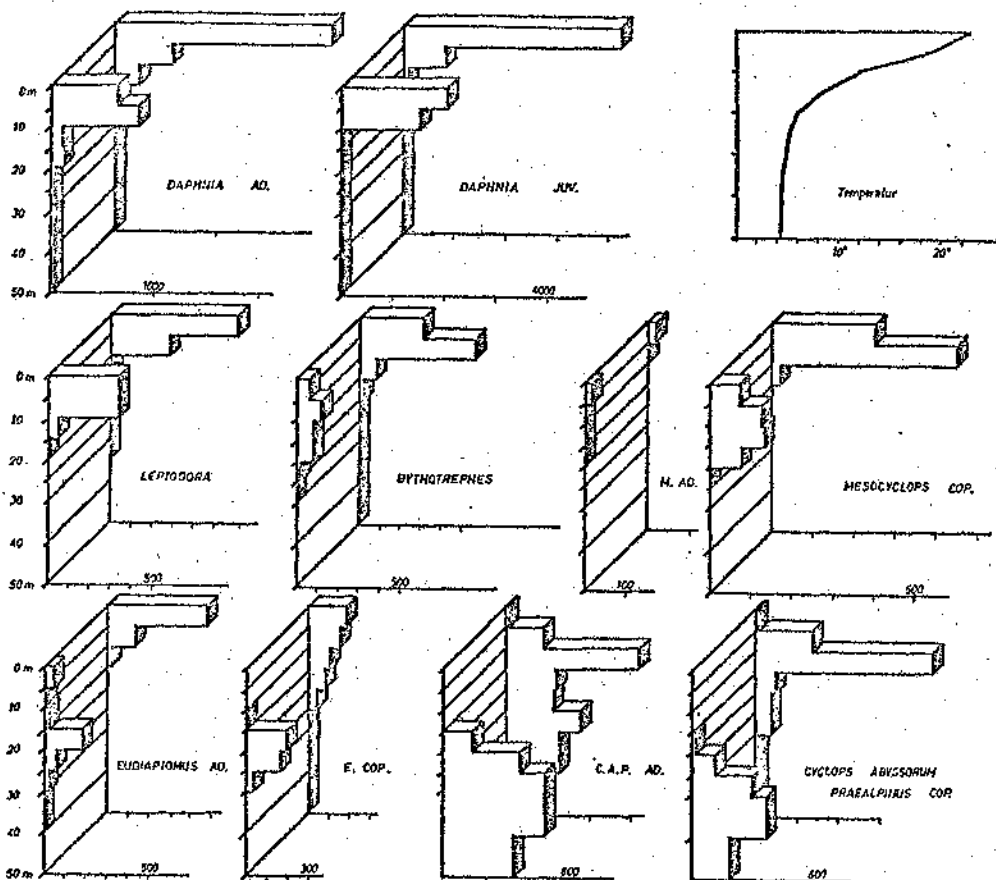


Abb. 2: 17. Juli 1963

With the copepods the displacements of the depth maxima were very plain and visibly recognisable, ~~xxxxxxx~~ apart from the Mesocyclops leuckarti, which lives more in the epilimnion. Cyclops abyssorum praecalpinus and the copepodidae of Eudiaptomus had completely left the upper 15 m. during the day, and during the night just between 10 and 15 metres; with Eudiaptomus even in the uppermost 5 m. definite maxima resulted. These creatures, then, had in a few hours surmounted a vertical difection of 10 and more metres with a temperture difference of 16-18°.

c. Up to July 30th (Fig. 3) the epilimnion had increased to a size of 10 m, at which the upper 8 m. showed almost the same temperature at around 20°. Also with this series of investigations the cladocerans and Mesocyclops were limited to these epilimnial zones, so that their migrations cannot be definitely established with the net. In addition it came about that - caused mainly by currents dependent on the wind - during the night double to five-fold thickness amounts were found compared with the day series. In any case the daily maximum with the cladocerans lay between 5 and 10 m., in the night,

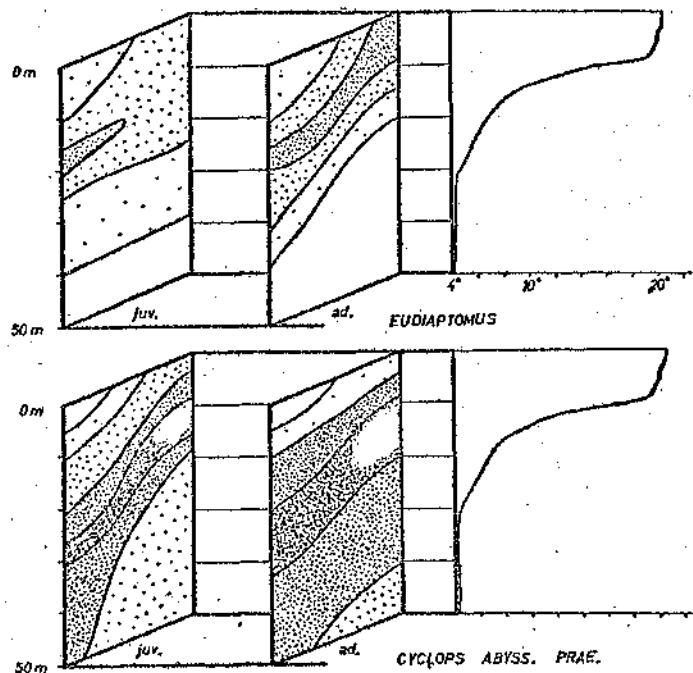


Abb. 3: 30. Juli 1963

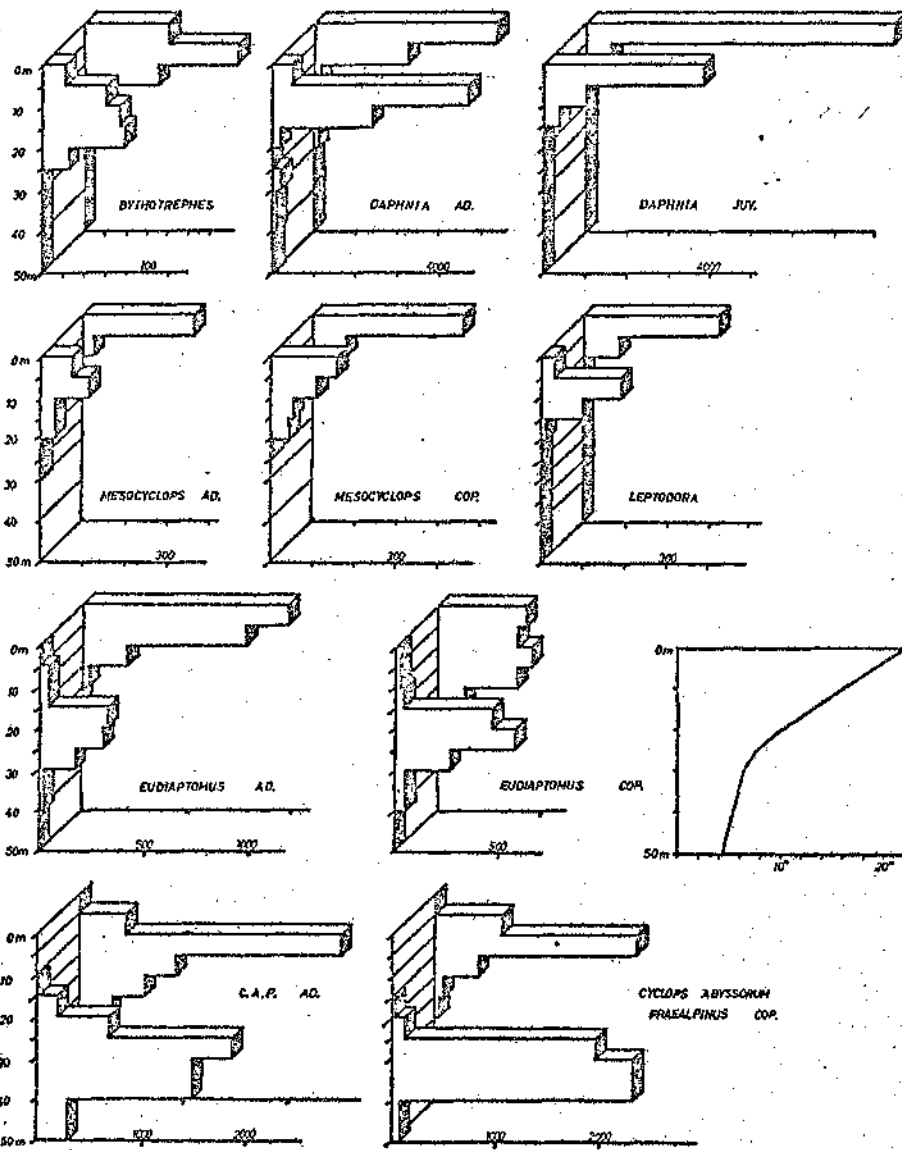


Abb. 4: 5. August 1963

however, between 0 and 5 metres. The population of Mesocyclops, numerically weak at this time, was divided proportionately during the day in the upper 15 m., but at night collected completely in the epilimnion, the zone between 10 and 15 m. was thus completely deserted.

A definite migration was again observed with Cyclops abyssorum praecalpinus, which during the day lived extensively beneath 20 metres; the maxima of both age groups lay between 20 and 30 metres. Around midnight the animals had attained a high maximum with relatively large numbers in thickness between 10 and 15 m., while especially with the Copepodidae the zone below 20 metres was now hardly inhabited. That the uppermost 5 metres should contain only few Cyclopidae should be attributed probably to the "midnight decrease" (Siebeck 1960) in the starry and moonlit night.

An equally definite vertical migration was also determined for Eudiaptomus gracilis, which showed only small numbers for thickness, and which during the day reached their maximum in the layer between 15 and 20 metres; the upper 10 m. contained only a few individuals. In the night now the adult animals especially had collected in the upper 10 m., the zone below 20 metres was completely deserted. Like Cyclops, Eudiaptomus gracilis therefore also overcame the thermocline and with this a temperature difference of 10-15°. d. With the series on August 5th, as is frequently the case in the Obxersee, no genuine epilimnion formed with a thermocline lying beneath it, but the temperature decreased proportionately from the surface to around almost 30 m. For this reason the crustaceans were not narrowly stratified, but were distributed over larger ranges in a vertical spread. The day series were made under a cloudless sky between 14 and 16 hours, the night profile under bright moonlight between 22 and 24 hours. It should also be observed here that with some forms, sinking had already begun again, and so these differences compared with the whole amplitude of migration should be neglected.

The diurnal distribution of the Daphnia population (D. longispina hyalina and galeata) (Fig. 4) <sup>showed</sup> the difference due to age in the vertical stratification. While the adult animals lived predominantly between 5 and 15 metres, the young daphnia preferred the upper metres in the afternoon, which then in the night contained almost 8000 young per cu. m. The adults also at this

time had risen up to the surface layers (about 4000 animals/cu. m.) and had almost deserted the zone between 10 and 15 m. A precise statement is of course only possible with the cladocerans, and just with pump catches. The representation in Fig. 4 accordingly considerably blurs the actual situation; and so during the day the zone was doubtless directly beneath the surface, thus the uppermost 50-100 cm. were practically free of zooplankton.

The large predatory cladocerans Leptodora kindti and Bythotrephes longimanus sought out greater depths during the day than Daphnia; above all Bythotrephes showed the highest density values between 15 and 20 m., Leptodora stood somewhat higher with the centre of gravity at 5 to 15 metres. In the night both species ~~visibly~~ evidently migrated upwards, Leptodora especially reached values of at least 300-400 animals per cu. m. Bythotrephes had likewise removed its living depth to the upper 15 metres, the inhabited zone of the maximum formed during the day was extensively deserted.

Among the cyclopids the warmth-loving Mesocyclops leuckarti had approached the temperature curve in its daytime distribution, only the adult animals avoided somewhat the uppermost layers (here also the graph (Fig. 4) shows the average density of the uppermost interval for the net). In the night, however, both age groups migrated upwards, where they occupied the 0-5 metres layer in their overwhelming quantity.

Eudiaptomus gracilis, on the other hand, was during the day already in deeper layers, the adults and the copepodidae lived mostly between 15 and 30 metres, and so at temperatures of under 10-12°. The occurrence of vertical migrations in the night was then very surprising, as the adults especially populated the upper 10-15 metres which they avoided during the day. The copepodidae also attained a similar performance, in which the first stages were distributed more over the whole water column, without the development of the maxima found with the older copepodidae. Obviously their ability to swim was still too small for them to be able to complete a uniform migration.

A great impression was made in turn by the vertical migration of Cyclops abyssorum praealpinus, which in the afternoon attained large density numbers of between 25 and 40 metres; the upper 15 m. were practically free of Cyclops. In the midnight series the layers between 10 and 15 metres were mostly strongly populated, between 5 and 10 metres at least several hundred animals



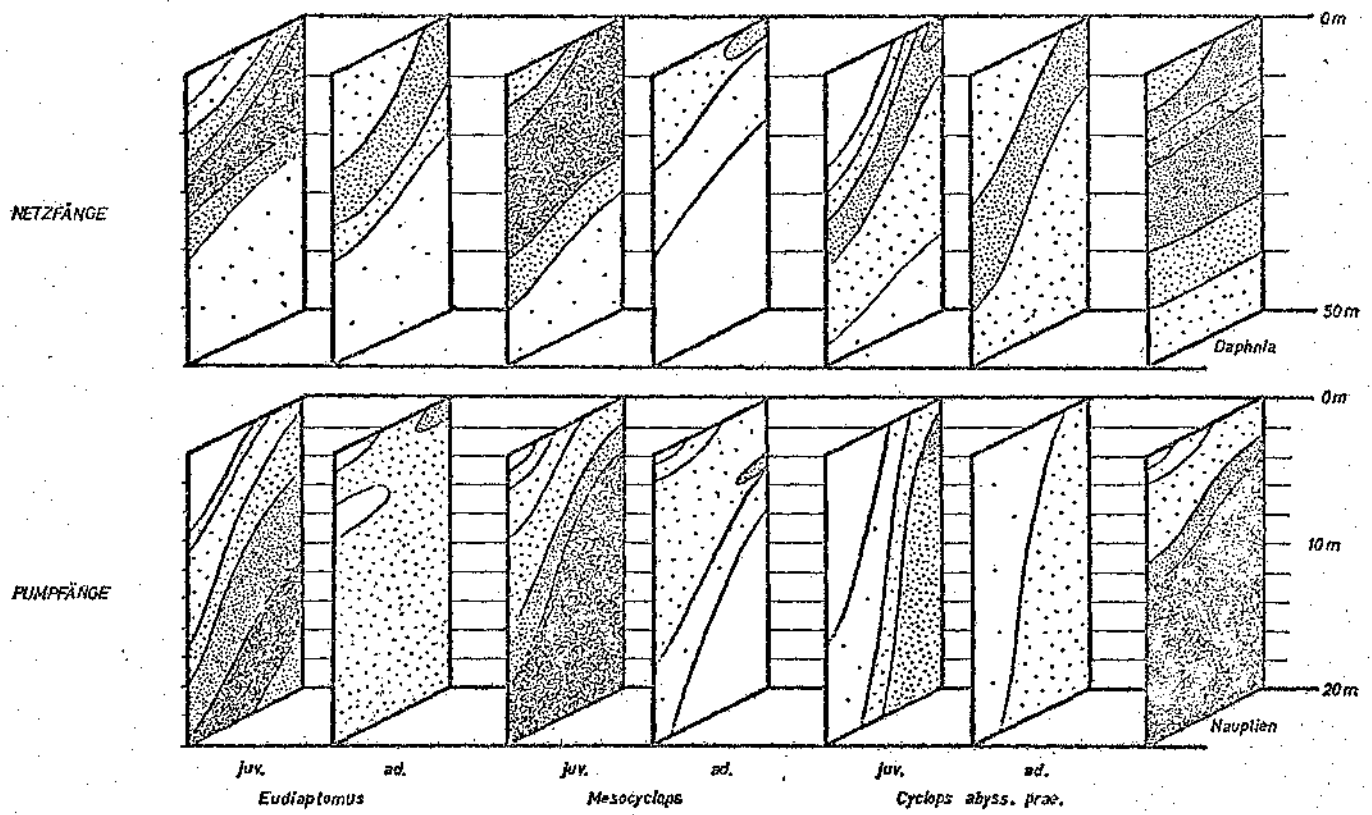


Abb. 5: 11. Oktober 1963

Per cu. m. were encountered. Amongst the copepodids there were dominant - as is the rule in summer (Einsle 1964) - the older copepod stages by far, so that the distribution pictures for all age groups appeared quite similar. The few primary stages at hand likewise migrated in a vertical direction and thereby completed differences in depth of at least 15-20 metres.

e. With the last series of the year 1963, on Oct. 11th the water temperature fell finally <sup>from</sup> almost  $14^{\circ}$  on the surface proportionately to  $4.0^{\circ}$  at a depth of 50 m.; thus no form of thermocline was recognisable. Above a lake depth of about 100 metres a pump and net series was carried out before Staad in the afternoons (14-16 hours) in sunny weather, and similarly at night (21.15-22.30 hours). A ~~clear~~ <sup>definite</sup> flow of water indicated a certain restlessness in the body of water, which was then also reflected in the numerical values, since in the night double to threefold amounts of plankton were found (Fig. 5).

The net catches produced for the copepodids<sup>5</sup> a day depth of between 10 and about 30 metres, and only Cyclops abyssorum praealpinus was also to be found in deeper layers. The population of Mesocyclops at this time consisted substantially of older copepod stages, the number of adult animals was decreasing strongly. As this age composition was already tending towards the winter stagnation of development (Einsle 1968), the preference for warmth of this generation was not so highly pronounced as in the early summer.

All three species carried out very impressive migrations by day, leading to small maxima in the upper 5 to 10 metres. From the pump series, which analysed the upper 20 m. yet more minutely, it can be seen that these accumulations lay in a depth of 1 to 2 m., only the adult diaptomidae were found immediately below the surface. Again, the behaviour of Cyclops abyssorum was very conspicuous; during the day it was practically completely lacking in the uppermost 20 metres, in the night, however, it lived preferably just there. In this case also the amplitude of migration is very noticeable from 20 to 20 metres, although the temperature difference was relatively small ( $6-7^{\circ}$ ).

The numbers of the cladocerans on Oct. 11th were decreasing strongly, so that a graph diagram was possible only for Daphnia (young and adult animals).

The maximum at a depth of between 10 and 15 metres was also maintained during the night, only a small part of the population migrated in the direction of the surface. This corresponds to the general experience, that the intensity of the migration by day decreases with the subsidence of a yearly cycle or the dying-out of a generation.

In the pump tests a migration - if also trifling - of nauplii was in addition indicated: the density of 3000 nauplii/cu. m. lay during the day at a depth of 5-6 m., while at night, however, it lay directly below the surface, where in turn no nauplii were found by day. Likewise the horizon of 12,000 nauplii/cu. m. from a depth of 9 m. by day ~~was~~ had been removed to 5 m. by night, so that an amplitude of migration of the nauplii of about 4-5 metres can be considered - a thoroughly remarkable achievement with the small size of these stages.

#### Discussion and conclusion.

The five series of investigations, in spite of the afore-mentioned reservations about the insufficient accuracy of the net catches, gave a clear picture of the day migrations of the planktonic crustaceans in the Bodensee-Obersee. Without at this point going into a discussion of the whole phenomenon, from which there has arisen already a quite extensive literature (Gushing 1950, Ringelberg 1964), a survey of the migratory behaviour of the Bodensee animals should be made in an exclusively descriptive manner, especially in order to gain a clearer conception of the amplitudes to be expected. Knowledge about the daily completed animal differences, including temperature, is of the greatest significance just for the analysis of ~~the~~ population dynamics (Elster 1954), for example in determining in situ the exertions and the speeds of development of the plankton-living population.

According to the depths normally occupied by day, the crustaceans (Cladocerans, Mesocyclops, Cyclops vicinus) living mostly in the epilimnion are fundamentally different from the forms preferring the metalimnion (Eudiaptomus gracilis) and the hypolimnion (Cyclops abyssorum). As has already been mentioned in an earlier publication (Einsle 1967), the individual consequences of the migrations are of the highest significance for the different species. The forms living in the light-receiving epilimnial zones

evidently seek to obtain the illumination preferred in the day through swimming upwards; they reach the surface of the water before or with the onset of dusk and begin the "midnight sinking" quite soon. The amplitudes of migration of these groups are obviously smaller than those of the remaining crustaceans, about that of Cyclops abyssorum praealpinus, which during the day lives in quite dark layers of water.

These somewhat speculative discussions of course do not pay attention to the fact that it is not the endeavours of the animals to obtain a characteristically optimum light condition alone which sets off the vertical migration. There is widespread ignorance about the influence of the length of day, the range of temperature variation and above all the biologically-conditional state of a population, whether it stands therefore at the end or at the beginning of a generation cycle. These questions cannot be solved without greater ~~experimental~~ expenditure on investigations.

In conclusion therefore it must be determined for the planktonic crustaceans of the Obersee, that all species make daily migrations at least from spring to autumn, which can constitute only a few metres or, however, also distances of 30-40 metres depending on the specific daily depth.

1. The cladocerans Daphnia hyalina, Daphnia galeata as well as the Bosminids live preferably in the epilimnion, so that their migrations do not attain very large dimensions. Leptodora and Bythotrephes do however stay somewhat deeper during the day, although their density numbers are mostly too small to verify the migration.

2. Of the copepodidae Mesocyclops leuckarti and Cyclops vicinus likewise live in the upper layers of the water, and show, however, generally definite migrations. On the behaviour of the numerically very weak summer generation of Cyclops vicinus no certain evidence can be obtained.

3. Eudiaptomus gracilis, particularly with the males, very clearly completes relatively large vertical distances in a short time; the animals appear mostly directly beneath the water surface already in the evening dusk, and then however sink back little below.

4. Without doubt the most impressive migrations are observed with Cyclops abyssorum praealpinus, especially in summer and autumn, when the population remains during the day at a depth of 30-50 metres, in order to arrive at high maxima in the night between about 5 and 15 metres.

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### **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.