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The vertical distribution of zooplankton in the Goggaussee (The influence of algae and Chaoborus flavicans).

HERZIG A. & MOOG O.

Carinthia II, 166/86, 373-385 (1976)

Translated by L. Heller

Introduction

The Goggaussee, a small, shallow, meromictic lake (700m long, 150m wide, max. depth=12m, mean depth=6m; FINDENEGG 1963), was the site of a week long study (19-26 May 1974) of the limnology department of the University of Vienna. The study comprised pollen analysis and palaeolimnological studies on the one hand, as well as a stock-taking of physiochemical factors, primary production, bacteria, zooplankton, zoo benthos and fish on the other. With the exception of the zooplankton, the results have already been published (LÖFFLER et al 1975).

A meromictic lake, with its anoxic deep water, restricts the vertical distribution of most zooplankton. With a few exceptions (several protozoa, rotifers and Cyclops - species; resting stages; eg. HERZIG & POWELL 1972, RUTTNER - KOLISKO 1975) the organisms are confined to those water layers rich in oxygen. At the time of study, however, the high phytoplankton density -- in particular the alga Synedra nana found in greatest numbers between 1.5 and 3m-presented a hindrance to the animal organisms. There was also an oxygen - bearing layer of 7m, this again separated by the "Synedra-horizon " into a 1.5m upper and 4-5m lower layer.

The aim of the study was to pursue the vertical distribution of the rotifers and Crustacea in diurnal cycle, thereby grasping the influence of the algal horizon and the nocturnal presence of the predator Chaoborus flavicans in the upper water layers.

Method

Sampling equipment consisted of a motor-pump (two-stroke petrol motor, make: Libelle - O, 1.5 PS), to which a sampling tube (diameter 1 inch made by Sempertt) had been attached and whose orifice was made wider by a funnel. The samples were taken at intervals of one metre with a delivery rate of 10 litres/min.

The times of the sampling : 20 May : 16.30, 21.00, 24.00 / 21 May ; 12.00, 15.30, 18.30, 21.30, 23.45 / 22 May : 1.15, 3.15, 5.15, 9.30, 11.15.

For the migration of Chaoborus flavicans the dates of SCHIEMER et al (1975) were used (21.30^{1/4} May). On the 20 and 21 May the weather conditions were stable and fine , and on 22 May a break in the weather brought almost constant cloud and rain.

Results

Zooplankton in general : those expected to be most influenced by the seasons were copepods and rotifers and less so cladocera. It was, therefore all the more surprising that rotifers were almost exclusively to be found (99.7% of individuals, 93% of zooplankton mass) and the crustacea presented an " insignificant rest ". To this a relatively large Chaoborus - population added their number (Table 1.). Moreover, the absence of a calanoid copepod was striking - this also being reported by FINDENEGG (1963) (an explanation

will be considered later). Cyclops strenuus abyssorum and Mesocyclops leuckarti formed the main portion of the crustaceans (adults and copepodites 79.6%, Nauplii 15.5%), whereas Daphnia longispina only formed 3.4% of the remainder; 1.5% consisted of Ceriodaphnia pulchella, Bosmina longirostris and Chydorus sphaericus.

Table 1. Density of individuals, biomass, percentages and corresponding confidence limits (95%) for 20/21 May 1974.

Individuendichte	m ²	95 % VG.	%
Zooplankton gesamt	8.145 × 10 ⁶	9.774-6.788 × 10 ⁶	
Rotatoria	8.120 × 10 ⁶	9.906-6.655 × 10 ⁶	99.7
Crustacea	25110	30132-20925	0.3
<i>Chaoborus flavicans</i>	5445	8448-3509	

Biomasse (mg Trgew.)	m ²	%
Zooplankton gesamt	650	
Rotatoria	605	93
Crustacea	45	7
<i>Chaoborus flavicans</i>	1270	

Individuendichte = density of individuals

VG. = confidence limits

Trgew. = dry weight (abbr.)

Zooplankton gesamt = all zooplankters

The most numerous rotifers were Keratella cochlearis (37%) and Filinia longiseta (30.2%); likewise Anuraeopsis fissa (15.7%), Polyarthra dolichoptera (11%) and Keratella quadrata (4.6%) Trichocerca birostris, Gastropus stylifer, Asplanchna priodonta, Synchaeta pectinata, Synchaeta sp. and Hexarthra sp. comprised the remaining 1.5%.

Under a meter quadrat, 8.145×10^6 individuals were found, resp. 650 mg dry weight biomass (0-11 m). It appears from a comparison of the density of individuals in the Klopeiner See with that of the Längsee, which were sampled in May of 1971 and '72 (HERZIG & POWELL 1972, HERZIG et al. 1973), that approx. the same number of crustacea were to be found in both lakes. The density in the Goggausee on the other hand, was disproportionately low. The rotifers in the Goggausee are ten times as numerous as those in the Klopeiner See (Table 2.)

Table 2. Comparison of counts of individuals in three meromictic lakes in May (Goggau: 20/21 May 1974, Klopeiner S. 8/9/10 May 1971, Längsee: 29/30-May 1972)

	m ²		m ³		
	Total	Total	Crust.	Rotat.	% Rot./Crust.
Goggausee (0-11 m)	8.145 × 10 ⁶	740000	2283	737717	99.7/0.3
Klopeiner See (0-25 m)	2.983 × 10 ⁶	119300	35790	83510	70/30
Längsee (0-10 m)			28800		

The abundance of Chaoborus flavicans amounts to $5445/m^2$. SCHIEMER et al. (1975) found $11,000/m^2$ ($110/100\text{ cm}^2$) attributing this variation to the different methodology. To show how large this population can be, several examples are quoted: SMYLY (1972) gives $500-5200/m^2$ for the years, 1956-1968 in Esthwaite Water, (Lake District, England); KAJAK & RANKE - RYDICKA (1970) mention $300/m^2$ for a eutrophic and dystrophic lake in Poland and denote this as a low density, but indicate that this species can reach over 100,000 animals per m^2 . In the Längsee, where this species likewise occurs, c. $400/m^2$ were to be found in May 1972 (SCHIEMER 1973). The density of this organism in the Goggausee can

therefore be considered to be rather high.

It is noticeable, that in the Goggausee few crustaceans, a great many rotifers and many chaoborids are to be found, whereas calanoid copepods are completely absent. It has now been stated on several occasions, that chaoborids alone are in a position to decimate the zooplankton stock and in particular the crustaceans, in a short time. (KAJAK & RANKE - RYBICKA 1970, ANDERSON & RAASVELDT 1974). It is also likely that the absence of a diaptomid and the low crustacean density is associated with the high number of individuals of Chaoborus flavicans.

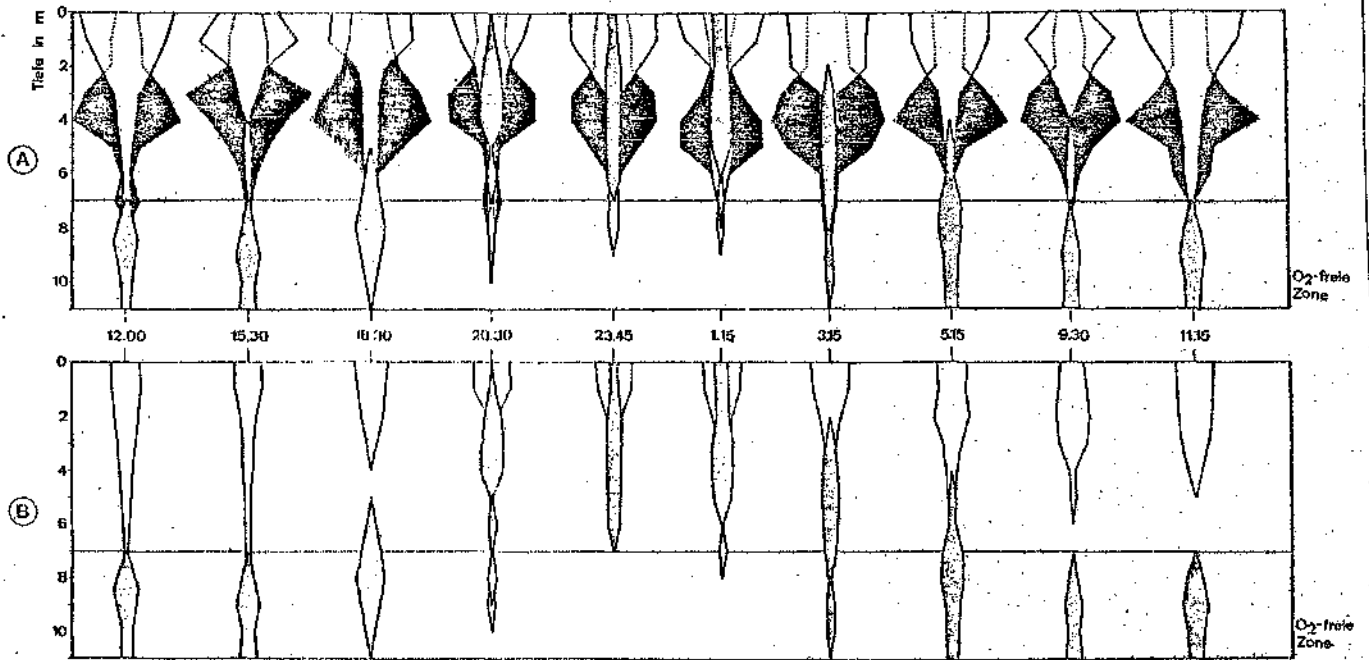


Abb. 1a: Vertikalverteilung von *Keratella cochlearis* [white box], Rotatoria-Rest [stippled box], und *Chaoborus flavicans* [cross-hatched box] (die Zählwerte dargestellt als $\sqrt[3]{\frac{N}{k_{30}}}$, der Maßstab für *Chaoborus flavicans* ist doppelt so groß wie der der Rotatoria)

1b: Vertikalverteilung von Crustacea [white box] und *Chaoborus flavicans* [cross-hatched box] (Zählwerte dargestellt als $\sqrt[3]{\frac{N}{k_{30}}}$)

Fig. 1a. Vertical distribution of *Keratella cochlearis* [white box], rest of Rotatoria [stippled box], and *Chaoborus flavicans* [cross-hatched box] (The counts shown as $\sqrt[3]{\frac{N}{k_{30}}}$. The scale for *Chaoborus flavicans* is twice that of the rotifers).

Fig. 1b. Vertical distribution of crustacea [white box] and *Chaoborus flavicans* [cross-hatched box] (counts shown as $\sqrt[3]{\frac{N}{k_{30}}}$)
 Tiefe in m = depth in m. freic Zone = free zone

The vertical distribution in the diurnal cycle.

At the time of the study, conditions were given as stipulated in BERGER (1975) & DOKULIL (1975). In Fig. 2a these are once more briefly shown. The turbidity is striking (1.5m On average), the oxycline at 7m and the biomass maximum of *Synedra nana* between 1.5 and 3m (values of 5 to 6.3 mg/l). This high phytoplankton biomass is also the reason for the low transparency. The euphotic zone reaches to 3.1m.

Crustaceans & Rotifers: The greater part of the crustaceans are to be found between 0 and 2m (Figs 1b,2a). In Fig. 1b the distribution of the crustaceans is shown at different times; it is evident, that only a minimal migration takes place and the invasion of the *Chaoborus* - population into the region of the crustaceans during the hours of darkness is very small.

In Fig. 2a the mean depths of the crustacean population are added according to time. These mean depths (S) Of a population can be calculated as follows (c.f. HOFMANN 1975):

$$S = \frac{\sum_{z=0}^H N_z \cdot z}{\sum_{z=0}^H N_z}$$

S.... mean depths of the population

N no-of individuals of a species
Z in the depth Z

Z.... depth in meters

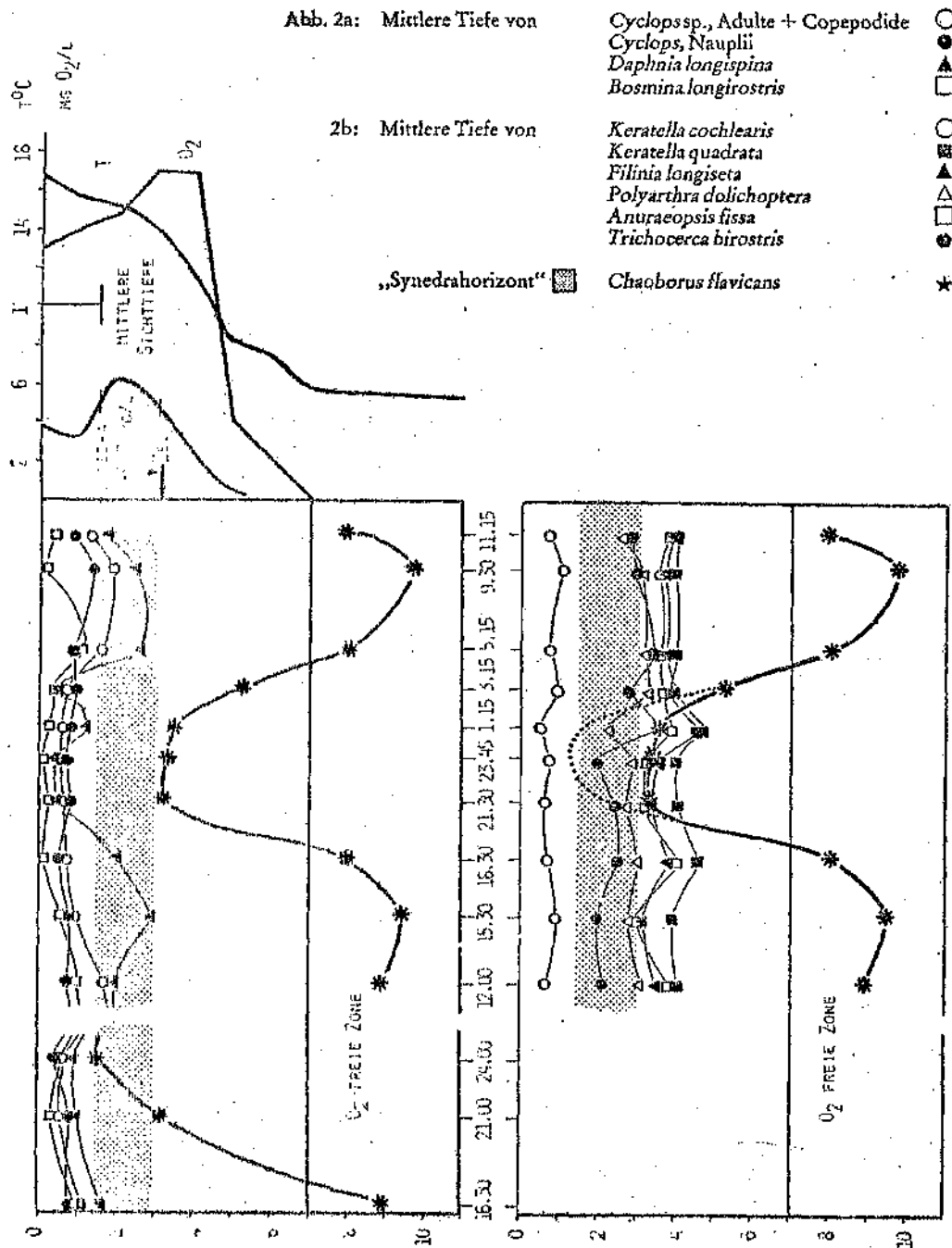
(1)

From a solution of this calculation it follows, that with the exception of *Daphnia longispina* all Crustacea remain above the most dense *Synedra* - horizon and show little displacement (Fig. 2a). Table 3. shows the minimal day - night differences..

Table 3. S - Values of the most important species:
Day, night and twilight hours.
Dämmerung = twilight

S in Metern	Tag (8-18)	Nacht (20-3)	Dämmerung (4-6/18-20)
Crustacea	1.00-1.82	0.62-0.74	0.73-1.42
<i>Cyclops</i> spp.	0.95-1.88	0.60-0.70	0.73-1.59
<i>Cyclops</i> Nauplii	0.79-1.40	0.53-0.89	0.65-0.94
<i>Daphnia longispina</i>	1.68-3.25	0.44-1.00	2.00-2.57
<i>Ceriodaphnia pulchella</i>	1.00-2.50	0.10-0.55	1.00-2.00
<i>Bosmina longirostris</i>	0.10-1.00	0.10-0.70	0.12-1.05
<i>Keratella cochlearis</i>	0.67-1.08	0.52-1.00	0.75-0.82
<i>Keratella quadrata</i>	3.94-4.10	4.01-4.59	4.00-4.58
<i>Amuretopsis fissa</i>	3.02-3.93	3.20-3.87	3.69-3.89
<i>Polyarthra dolichoptera</i>	2.62-3.08	2.29-3.29	2.97-3.26
<i>Filinia longiseta</i>	3.14-4.00	3.43-4.70	3.73-3.80
<i>Chaoborus flavicans</i>	7.93-9.69	1.50-5.25	7.00-8.00
<i>Chaoborus flavicans</i> (23./24. Mai, SCHUBERT et al. 1975)	8.60-9.70	2.78-5.00	7.40-8.76

Fig. 2a Mittlere Tiefe von = mean depths of
Mittlere Sichttiefe = mean euphotic zone



The rotifers occur in two separate layers, causing only a small amount of overlap (Fig. 1a, 2b). *Keratella cochlearis* is only to be found in great numbers from 0 to 2m. However none show a clear diurnal migration (at most 0.5 - 1m.) (Table 3). *Apparently the clear division between *Keratella cochlearis* and the remaining rotifers and it seems, as with the crustaceans, the algal population presents a barrier.

Fig. 1. shows the low percentage of animals penetrating the deoxygenated zone. *Keratella cochlearis* has a maximum, 0.4%, the remaining rotifera, 0.8%, and the cyclopids, 0.5%. On the other hand in the Klopeiner See, *Keratella cochlearis* had a second maximum in the strongly deoxygenated zone. (HERZIG & FOWELL, 1972). RUTTNER - KOLISKO (1975) observed similar results in the Lunzer Obersee.

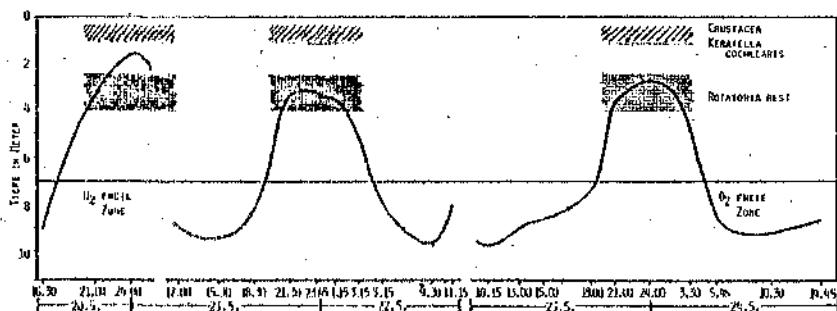
* Translated literally.

Chaoborus flavicans: The diurnal migration agrees very well with the findings of other authors (eg. TERAGUCHI & NORTHCOTE 1966, GOLDSPIK - & SCOTT 1971, PARMA 1971 for Chaoborus flavicans; LAROW 1970 for Chaoborus punctipennis; WOODMANSEE & GRANTHAM 1961 Chaoborus albatrus).

The light is sometimes suggested as "Zeitgeber", and the oxygen, temperature and the abundance of food organisms modify the migration. According to TERAGUCHI & NORTHCOTE (1966) the most essential factor is the oxygen situation then the temperature and finally the presence of prey, the latter being of lesser significance.

In the Goggausee the definite displacement of the population in the deoxygenated water layers begins at dusk (18.00) and towards 21.30 the first individuals can already be observed in the upper layers. Between 23.00 and 1.00 the majority of animals are near the surface, then the downward migration sets in and in the half-light of dawn only a few remain in the oxygenated region (Fig. 1,2,3).

Fig. 3: Migration of Chaoborus flavicans and the depth distribution of the prey (shown as the mean depth of the corresponding population). (23/24 May from SCHIEMER et al. 1975).



According to Fig. 2 and 3 the majority of the animals are between 1.5 and 3m. The sojourn in the oxygenated water lasts 9 - 10 hours. During the day they are all between 7 and 11m (bottom) the maximum lies at 8 -9.7m.

During the migratory phase, the Chaoborus - population completely overlaps that of the rotifers (with the exception of Keratella cochlearis). This means that the chance of coming into contact with their food supply is greatest at this time, for the majority of the chaoborids do not reach the bulk of the crustacea and Keratella cochlearis. The importance of this fact will be discussed later.

As can be concluded from all figures, no distinct diurnal vertical migration exists - apart from Chaoborus flavicans and Daphnia longispina. The influence of the high algal population certainly plays an essential role in this. This permanent extreme stratification can be substantiated with the help of a coefficient, the "Schichtungsgrad" (B) of a population ("degree of stratification"). This can be calculated as follows:

$$B = \frac{1}{\sum_{z=0}^n p_i^2} \quad P_i = N_i \cdot N_i^{-1} \quad (2)$$

P_i is the constituent found in the depths Z of the species i of the total population of this species. LEVINS (1968) and LANE & McNAUGHT (1973) denote this value as 'Nischenbreite' ("niche breadth"). In this case it ought, as with HOPMANN (1975), to be considered as the degree of stratification.

A low B- value is, therefore, to be equated with extreme stratification and vice versa.

In this way we found for the crustaceans daytime values of $B = 3.1-3.7$, for the nights $B = 2.1-2.3$. There is no distinction between day and night ($B = 2-2.5$) for Keratella. This holds for the other rotifera ($B = 2-2.9$). For Chaoborus flavicans the strong stratification throughout the day ($B = 2-3$), compares with a weaker ($B = 3-4.5$) during the night. At this time they are also distributed in the upper 0 - 7m.

The zooplankton in the Goggausee is, therefore permanently extremely stratified, with only insignificant displacement, distinct migrations with a migratory amplitude of several metres cannot be ascertained. Only Chaoborus flavicans shows a clear distinction between day and night.

Chaoborus flavicans and food availability in the Goggausee:

Chaoborids feed chiefly on zooplankton, insect larvae and oligochaetes. Crustacea and rotifera are the preferred foodstuffs of Chaoborus flavicans; GOLDSPINK & SCOTT (1971) mention a benthic food source as least significant. Experiments have shown their preference for copepods as opposed to cladocera. However, if the cladocera are present in the form of small Daphnia, they are caught just as readily (eg. KAJAK & RANKE - RYBICKA 1970, SWUSTE et al. 1973, ANDERSON & RAASVELDT 1974). As for the copepods, the diaptomids are taken most easily, Cyclops nauplii represent a foodstuff taken up most easily. KAJAK & RANKE - RYBICKA (1970) found the following in their experiments; 80% of nauplii were eliminated, 61 - 73% of copepodites and adult copepods and 34% - 53% of cladocera. The consumption of rotifers is mentioned in almost all works, but only PARMA (1971) gives two species, which were actually caught (Notholca squamula, Keratella quadrata). Rates of intake of crustacea are available (eg. KAJAK & RANKE - RYBICKA 1970, SMYLY 1972, ANDERSON & RAASVELDT 1974, SCHIEMER et al. 1975) but not for rotifers.

PARMA (1969) emphasizes further the influence of feeding on the development up to the time of pupation. If food is insufficient, up to 50% and more of the larvae die and do not reach pupation.

Table 4: Food intake (c) and body weight (w) in Chaoborus flavicans and Chaoborus americanus.
(4th Larval stage)

Art. (Autor)	C/Tag	µg Trgew. W. LIV	C in % W
<u>Chaoborus flavicans</u> (KAJAK & RANKE-RYBICKA 1970)	14-36	320-380	3.6-12.5
<u>Chaoborus flavicans</u> * (SCHIEMER et al. 1975)	2-42	190-240	0.9-18.0
<u>Chaoborus flavicans</u> (SMYLY 1972)	-40		
<u>Chaoborus flavicans</u> (PARMA 1971)		388-400	
<u>Chaoborus americanus</u> (ANDERSON & RAASVELDT 1974)	10-20		

Art = species

Tag = day

Trgew. = dry weight (abbr.)

* Feeding rates from SCHIEMER et al. 1975 were chosen, the counts of individuals calculated from dry weight (according to weight - length regression, in prep. by HERZIG); the activity time is assumed to be 6 hours.

Lack of food can, besides, lengthen the duration of the development period. Starvation experiments of SIKOROWA (1966, Chaoborus alpinus, Chaoborus - crystallinus) show how long these animals (according to species 19 - 83 days) can live without food.

SCHIEMER et al. (1975) determined food intake rates for the Goggausee population. Crustaceans were taken as prey. A comparison of these results with those of other authors shows a relatively good agreement (Table 4.)

If the chaoborids in the Goggausee want to eat crustaceans, then they must penetrate to the upper water layers (0-1m) during the hours of darkness, to find their prey in sufficient concentration, which, in the experiments of SCHIEMER et al. showed the lower limit of the food supply (in experiment: 28 μ/L ; in nature: 12-35 μ/L). As can be seen from the migration of the animals (Figs. 1, 2, 3) this only occurs for a small percentage (1-26%-20/21 resp. 21/22 May; -34% - 23/24 May); the Chaoborus population overlaps that of the rotifera far more (with the exception of Keratella Cochlearis).

To show this overlap of the two populations, the index (α) of this overlap can be calculated.

Where P_i as in (2) and i and j are 2 species.

$$\alpha_{ij} = \frac{\sum_{z=0}^n P_i \cdot P_j}{\sum_{z=0}^n P_i^2} \quad (3)$$

This was used a great deal as "coefficient of competition" by LEVINS 1968, LANE & McNAUGHT 1973): however in this work it is to be taken as "overlap of occurrence" (COLWELL & PUTUYMA 1971, HOFMANN 1975). The results are compiled in Fig. 4. It is shown quite clearly, that an insignificant overlap of the Chaoborus population with crustaceans and Keratella cochlearis is found during the hours of darkness, and only that between Chaoborus and rotifers is of real importance.

The chaoborids which take crustaceans as food, can only do so in the time from 21.30 to 3.30, which means 6 hours of eating activity. For the rotifers it was 10 hours (18.00 - 6.00). If one takes the slowest intake rates found by SCHIEMER et al. and transfers them to the given situation in the Goggausee, then 11.4mg (dry weight) of zooplankton could be removed by the Chaoborus population daily. However, only 45mg of crustaceans are available (under a meter quadrat); the food requirement, then, must be taken from the larger constituent of zooplankton, the rotifers (605mg/m³). How far a diet of rotifers is sufficient cannot be ascertained and does not emerge from any literature on the subject. It is noticeable, however, from a comparison of the larval weights (L IV, 9-11mm) with those from other waters (KAJAK & HANKE - RYBICKA 1970, PARMA 1971), that the animals in the Goggausee are essentially lighter (Tab. 4). This fare of rotifers, therefore, seems not to be optimal. In spite of this probably undernourishment of Chaoborus flavicans, the number of this species to be found in the Goggausee is considerable.

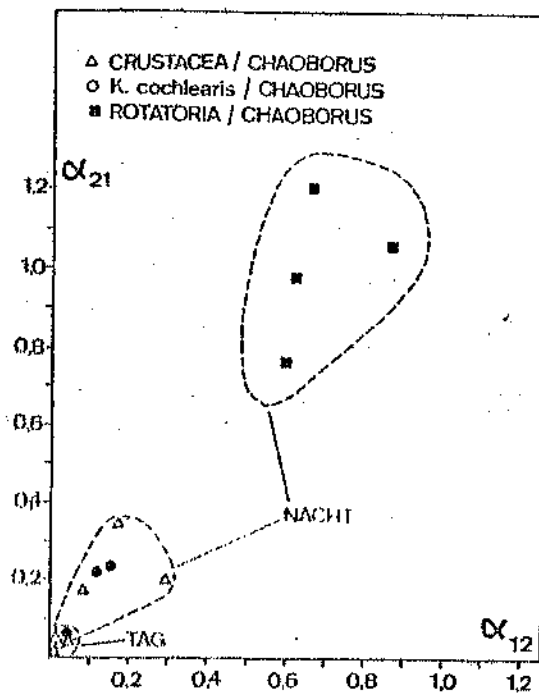


Abb. 4: Grad der Überlappung durch *Chaoborus flavicans*.

Summary

1. In May 1974 the zooplankton consisted of 99.7% rotifers, the rest were crustaceans.
2. A dense algal stratum (*Synedra nana*) divided the mixolimnion into an upper region (0 - 1.5m), where the crustaceans and *Keratella cochlearis* reside, and a lower (2 - 7m) region, where the rest of the rotifera form a layer.
3. The plankton was extremely stratified day and night, only *Daphnia longispina* and *Chaoborus flavicans* followed a diurnal vertical migration.
4. Abundance of crustaceans and rotifers as well as the experimentally deduced rates of food intake (SCHIEMER et al. 1975) of *Chaoborus flavicans* form the basis of a discussion of the food availability of this species.

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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.