I refer, here, to a few of the experiments completed by my ex-pupils, R. Schröder and H. Eckstein.

The sensory reactions which initiate the vertical migration of zooplankton were studied by Schröder, using an experimental system which is shown in Fig. 1. A circular vessel (made of Petri), 30 cm in diameter, was placed in a vertical position. By means of a screen accordingly placed, the daylight was only able to fall horizontally on the animals, in such a way that the force of gravity and the light acted at right-angles to each other. The average position of the experimental organisms was, for that reason, conclusive with respect to the proportional influence of the geotaxis and phototaxis on the direction of swimming movement of the animals.

During the day, the greatest number of Daphnia longispina were found at an angle of $x=140^\circ$. This indicated a light positive phototaxis. In this case, nothing could be asserted concerning the geotaxis, since the animals were swimming with their heads in a superior position yet remained in the bottom of the dish. During the twilight, the phototactic behaviour of Daphnia reached its maximum. When the intensity of the light was becoming very low, a negative geotaxis appeared and the animals were found in the highest part of the dish, at an angle $x=0^\circ$. Intensities of light, even less than 0.03 lux provided by the moon or by a distant street-lamp, were sufficient to alter the reaction. This now produced a positive phototaxis or, during the night, a descent of the animals in the dish.

At daybreak, they sank towards the deepest parts of it, since the increase in the light intensity reduced the frequency of movement of the antennae and induced a positive geotactic reaction. Moreover, a rapid increase in the intensity of the light produced a negative phototaxis. After the light exceeded 100 lux and the rate of change
of the intensity decreased, the animals changed once more to positive phototaxis, resuming the normal swimming position maintained during the day. All these observations are also valid for the swimming behaviour of Daphnia in the natural environment.

The depth at which Daphnia magna maintain themselves in the lightly humic lakes of the Black Forest and in sub-alpine lakes, depends on the clearance of the water. The animals remain in the stratum or layer of water which receives 10-50% of the green part of the light which falls on the surface of the lake. Moreover, the colour of the water, that is, the nature or composition of the light, is of great importance. The experiments showed that Daphnia respond to light of equal strength, but of different colour, even as when they are exposed to white light of different intensities. The animals are more sensitive to blue light than to red. In lake Maggiore (Italy) which is most transparent to blue light, Daphnia descends to greater depths than in Lake Titi (Black Forest), whose maximum transmission is in the range of the longer wavelengths.

The reactions of Mixodiaptomus resemble those of Daphnia, while the behavious of Cyclops abyssorum exhibits a completely different pattern.

The vertical migrations of zooplankton were studied in the lakes, by quantitative sampling with a water pump, by direct observation underwater (diving), or by means of an echo-sounder. The sensitivity of this last was adjusted in such a way that great densities of zooplankton registered as layers or horizontal bands. At the same time the vertical displacements of the isotherms were determined, known as internal waves (Fig. 2). As a result of these studies, the following conclusions can be arrived at:

In Lake Constance a concentration of zooplankton frequently appears in water layers separated by conspicuous temperature gradients, that is, between the limits of one mass of water and another. Here the animals gather in the course of their vertical migration. Outside the thermocline, the zooplankton maintain themselves at a constant depth, in spite of a concurrent vertical displacement of water. Near to
and in the thermocline, the animals can be lifted out by vertical currents. If the vertical amplitude of the isotherm exceeds certain limits, the zooplankton leaves the thermocline (Fig. 3).

Ringelberg concludes that the vertical migration of zooplankton is not homogeneous (Fig. 5). This was confirmed by Schröder in his experiments with Corethra, whose vertical migration begins towards the evening, when the greatest decrease in light intensity occurs. The animals then move more rapidly than the corresponding isopleths of light intensity, (Fig. 4).

Likewise, the ecograms show a non-homogeneous distribution of zooplankton (Fig. 5). The formation of different spots or "clouds" of zooplankton, could be caused by small vortices or waves in the margins of the currents of water. Vertical correction currents could also influence the spatial distribution of the plankton.

By means of experiments with dyes, film and diving observations, Schröder detected certain slicks on the surface of the lake, in which the water flowed together radially and sank down like a funnel. These surface slicks of extraordinary nature, are identical to the "oil-stains" which have already been described by Forel. These stains are actually covered with a mono-molecular film of (grease?), which accumulates due to the flow of water.

After the work and observation of Otswald and Wasenberg-Lund, the maintenance of the plankton in a state of suspension in considered to be primarily of a passive nature. The same authors conclude that in temperate latitudes, the (cyclomorpha) is necessary to counteract the lowering of the viscosity of the water in summer. But nearly all zooplankton are not only transported by simple suspension, but also by an active swimming movement. The diaptomids, for example, swim with movements of their secondary antennae, mandibles and maxillae. Using a stroboscopic method, Schröder observed with Mixodiaptomus laciniatus a linear increase of the frequency of movement of these appendages, of 32.5 to 61 movements/sec. in the temperature range 9 to 23°C. It is assured, for that reason, that the lowering of the viscosity of the medium is at least compensated by a greater frequency of movement of the appendages.
According to Eckstein, the size of the body of *Eudiaptomus gracilis* decreases in summer, while the relative length of the primary antennae increases. These differences are very small to be effective in terms of the classic theory of the suspension of plankton. However, these morphological changes are used in the identification of different generations of adults of the course of studies of dynamics of population. In cultures of *Eudiaptomus gracilis*, Eckstein observed a greater intensity of colouration of the animals with the growth in the amount of available nourishment.

High concentrations of humic compounds exert the same influence. Animals grown at less than 12°C were bright red in colour, and deep blue at over 17°C. Those grown between 12°C and 16°C consisted of a mixture of red and blue animals. The red animals produced by cultures of low temperatures, turned blue if maintained for any length of time at more than 17°C. A promised range of future work presents the following questions and problems: What are the irritations or external stimuli which control the reactions of zooplankton in a relatively homogeneous pelagic environment? How do they locate their food? How do they recognise their partners? What do they do to escape from predators that approach them, such as fish? How do they react towards currents, vortices and waves?

In these cases, the optical senses are probably of minor importance, the irritation or mechanical stimuli being more of a major influence. For example I observed in an aquarium that *Heterocopa borealis*, which is a copepod with positive phototaxy, escaped immediately to the darkest part of the tank before the influence of a simple tapping (percussion).

If 100 males and 100 females are collected together in the same container, the males seized other males with the same frequency as they seized females. Apparently, it is only after the seizing the abdomen of the other specimen, when the active male takes account whether he has seized a male or a female. The chemical factors are probably not functional as stimuli; we are almost certain that the micro-waves or other oscillations emitted or reflected, good for the prey or the predators, are the main source of information.
The complicated systems of hairs and/or bristles, probably, contain the detectors of these micro-waves. As was demonstrated by Schröder, the "echo" of the micro-waves emitted by the secondary antennae and mandibles of *Mixodiaptomus laciniatus*, enabled the animal to avoid collision with a sheet of "plexiglass" introduced to the aquarium. If instead of "plexiglass" an opaque sheet of sound-dispersing and absorbing material was introduced ("stryropor" for example), there were frequent collisions. Moreover it was found that *Cyclops* is extremely sensitive to the acceleration and retardation of the surrounding water.

Our studies and experiments are still in their beginning and many interesting problems must be resolved before we have a satisfactory picture of zooplankton under their environmental conditions.

References


References (cont.)


Fig. 1
Diagram of the organization of the experiment.
(By Schröder, 1959)

Fig. 2
Vertical distribution of zooplankton, the temperature and condition of currents.

Fig. 3
Schematic ecogram of the vertical distribution of zooplankton, isotherms and temperature gradients.
Fig 4. Vertical migration of larvae and pupae of Corethra, areas of equal intensity of green light, current and temperature gradient (June 1960, Lake Gnaden) Schröder 1962.

Fig 5. Ecogram of a layer of plankton (Lake Constance 14-9-1959; 20:30 hrs, drifting at 10cm/sec) Schröder 1961.
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.