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High pH and the abundances of two commonly co-occurring freshwater copepods (Copepoda, Cyclopoida)

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Mesocyclops leuckarti increased relative to *Thermocyclops oithonoides* in fertilized experimental enclosures, whereas *Th. oithonoides* seemed to outcompete *M. leuckarti* in nonfertilized ones. The most reasonable factor to explain the numerical relationship between the two closely-related species was a selective pH effect : high pH favouring *M. leuckarti* and vice versa. In the lake the two species showed an historical development supporting the above hypothesis. *M. leuckarti* was the dominating species when the lake experienced highest pH during the peak eutrophic phase. Following recovery of the lake, *Th. oithonoides* is again becoming the more dominant species. This contrasting relationship to high pH may be the reason for the varying vertical distribution of the two species in lakes. Since *Th. oithonoides* is recorded below *M. leuckarti*, with a lower pH, temperature and food abundance, this results in the observed slower development and a more K-selected life history.

Influence d'un fort pH sur l'abondance de deux Copépodes coexistant dans les eaux douces (Copepoda, Cyclopoida).

Les densités de population de *Mesocyclops leuckarti* augmentent par rapport à celles de *Thermocyclops oithonoides* dans des enceintes expérimentales enrichies, tandis que *Th. oithonoides* semble dominer *M. leuckarti* dans les enceintes non enrichies. Le facteur le plus vraisemblable qui puisse expliquer la relation numérique entre ces deux espèces étroitement liées est l'effet sélectif du pH : les forts pH avantageant *M. leuckarti* et vice versa. La succession de ces deux espèces dans le lac appuie cette hypothèse. *M. leuckarti* était l'espèce dominante durant la phase eutrophe lorsque le lac présentait un pH élevé. Au cours de la régénération du lac, *Th. oithonoides* redevient l'espèce dominante. Cette situation antagoniste par rapport au pH peut expliquer la distribution verticale de ces deux espèces dans les lacs. Le fait que *Th. oithonoides* soit dominée par *M. leuckarti* dans des conditions de faibles pH, température et abondance de nourriture, expliquerait son plus lent développement ainsi que son cycle biologique de type stratège-K.

1. — Introduction

Several investigations concerning population dynamics of limnetic zooplankton have been carried out in which parameters such as temperature, oxygen concentration, metal ions, nutrients, toxic substances and vertebrate/invertebrate predation have been analysed to explain differences in competitive ability and population density of the various species of zooplankton. The ecological importance of extreme pH values, frequently observed in eutrophic lakes and ponds, has only been offered minor interest.

The few studies on this subject deal almost exclusively with cladocerans. Bogatova (1961) ; Ivanova (1969) and Walter (1969) all claimed that the upper pH limit for cladocerans was 10.5-11.5. Ivanova (1969) showed relatively large differences in optimum pH values (measured as filtration rate) between various cladoceran species, but most species had an optimal physiological balance around neutral pH.

As far as we are aware, no study has been published of the investigation of the relative abundance of cyclopoid copepods in relation to high pH, even though a number of investigations have been performed in eutrophic localities with fairly high pH.

In this study, the response of the cyclopoid copepods *Thermocyclops oithonoides* and *Mesocyclops leukarti* to artificial eutrophication was tested by

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short-duration experiments in fertilized and unfertilized bags in Lake Gjersjöen.

Both species have similar ecology and often cooccur in oligotrophic (Sarvala 1979), mesotrophic (Patalas 1954 ; Faafeng and Nilssen 1981) and eutrophic lakes (Patalas 1954 ; Gliwicz 1969 ; Karabin 1978). In oligotrophic and slightly mesotrophic lakes, *Th. oithonoides* seems to be the more dominant of the two (Sarvala 1979 ; Faafeng and Nilssen 1981), while the relationship in eutrophic and hypereutrophic lakes is more obscure. *M. leuckarti* occured in all kinds of lakes in Western Pomerania in Poland, including mesotrophic to strongly eutrophic lakes (Patalas 1954). When *M. leuckarti* and *Th. oithonoides* co-occured in eutrophic lakes the latter was most frequently found in deeper waters (Patalas 1954 ; Gliwicz 1969). In lake Gjersjöen *Th. oithonoides* strongly dominates over *M. leuckarti*, and is found deeper than the latter, in agreement with the above findings (Brabrand et al. in prep.).

Lake Gjersjöen has been monitored since the early 1950's, and since 1958 by the Norwegian Institute for Water Research, thus permitting interpretation of the lake's history during the last two decades. There have been strong oscillations in the numerical relationship between the closely-related cyclopoid copepods *M. leuckarti* and *Th. oithonoides*, probably due to changes in the trophic status of the lake (cf. Faafeng and Nilssen 1981).

2. — Study area

The experiments were performed in the meso-eutrophic Lake Gjersjöen, SE-Norway (59° 47' N, 10° 47' E) (area = 2.7 km², max. depth = 62 m). Due to increased sewage deposition, the lake developed from an oligotrophic lake in the early 1950's to highly eutrophic conditions in 1972, when a sewage treatment plant was built (Faafeng and Nilssen 1981). Since then, there has been a slow improvement and a slightly lower pH, but the lake still exhibits phytoplanktonblooms being mainly dominated by blue-greens.

The zooplankton community is at present dominated by small species, caused by the intense predation of a huge stock of planktivorous roach (*Rutilus rutilus*) (Brabrand et al. 1979). Among the cyclopoid copepods, *Th. oithonoides* is at present the dominant species, as in the 1950's, with *Mesocyclops leuckarti* and *Cyclops scutifer* as subdominants. The opposite relationship was observed during the eutrophic peak. These changes may be related to the pH development in the same period (fig. 1).

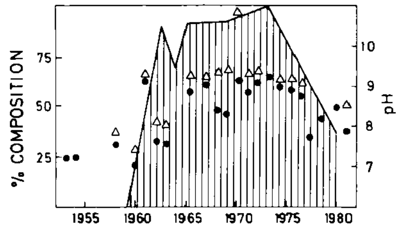

FIG. 1. Lake Gjersjöen, 1953-1980. The relationship between *Mesocyclops leuckarti* (vertical lines) and *Thermocyclops oithonoides*, related to pH. Black dots : highest recorded pH value from integrated samples 0-10 m, during summer. Triangles : highest recorded pH in epilimnion during summer. Data based on Faafeng and Nilssen (1981), and internal publications from Norwegian Institute for Water Research (NIVA).

3. — Materials and methods

The experiments were carried out in polyethylene bags, 135 μm thick. We used 12 bags with a diameter of 1.5 m, depth 4.2 m and a volume of about 7 m³. The bags were closed at the bottom and placed in a wooden framework, anchored in the pelagic zone. The experiment lasted for four weeks, 25.7-28.8.1980. The bags were filled by means of a water pump and vertical net-samples from 15-0 m were added using a 45 μm plankton-net with a diameter of 27 cm.

Twice a week zooplankton samples were taken, while phytoplankton-samples were taken three limes during the experiment. All samples were taken from 0, 1, 2 and 4 m depths using a modified van Dorn sampler as described by Blakar (1978). Water from all depths was mixed, and two 5 l samples were filtered through a 45 μm net for collecting the zooplankton. 100 ml water from the mixed sample was taken for phytoplankton-analysis. Both zoo-and phytoplankton were fixed with Lugol's solution. Chemical analyses of NH_4 was carried out at the Norwegian Institute for Water Research by reaction with hypochlorite in an alkaline solution, and measured by a Technicon autoanalyzer.

A solution of ammonium nitrate and ammonium hydrogenphosphate, which gave a final concentration of 3200 and 660 $\mu g\ l^{-1}$ respectively, was added to half the bags.

Pre-adult roach (5-7 cm) were added to two of the bags in order to detect a possible selective predation on the two species. 12 fish were added to each bag.

4. — Results

Phytoplankton: A relatively stable total volume of algae was observed in unfertilized bags throughout the experimental period, whereas the fertilized bags showed a considerable increase (fig. 2). At first there was a bloom of *Synedra* spp., but this soon collapsed. Then there was a sudden increase of chlorophyceans, such as *Collodictyon triciliatum*, *Golenkia* spp., *Scenedesmus quadricauda* and small, ellipsoid, unidentified green algae (ca. 4-5 $\mu m \times 3\ \mu m$). There was also a marked increase of the cryptophyceans, especially *Cryptomonas* cf. *pyrenoidifera*. The Cyanophyceae occured in similar densities and species composition in both fertilized and unfertilized bags, as did the Dinophyceae and Chrysophyceae (Tab. I).

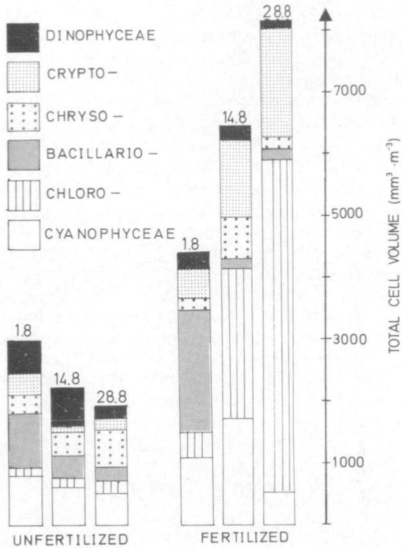

FIG. 2. Development of the different algal groups in fertilized and unfertilized bags. Mean values of 5 bags for each group.

Table 1. Total cell volume (mm^3 m^{-3}) of the different algal groups in unfertilized (U1-U5) and fertilized (F1-F5) bags.

	U1			U2			U3			U4			U5		
Date	1.8	14.8	28.8	1.8	14.8	28.8	1.8	14.8	28.8	1.8	14.8	28.8	1.8	14.8	21.8
Dinophyceae	699	402	113	410	875	715	815	530	330	18	652	164	695	947	105
Cryptophyceae	57	33	23	427	258	137	542	204	363	55	24	98	643	31	25
Chrysophyceae	242	371	1005	347	1493	603	197	162	450	296	795	317	345	720	1718
Bacillariophyceae	886	140	76	740	391	191	795	366	186	184	395	22	994	512	195
Chlorophyceae	108	99	187	67	208	218	63	166	203	69	168	294	194	80	242
Cyanophyceae	527	346	28	747	384	1117	820	231	2066	663	539	209	991	500	239

	F1			F2			F3			F4			F5		
Date	1.8	14.8	28.8	1.8	14.8	28.8	1.8	14.8	28.8	1.8	14.8	28.8	1.8	14.8	28.8
Dinophyceae	49	18	86	41		87	414			416	288		105		
Cryptophyceae	320	1277	3650	134	2497	891	392	1029	2554	26	771	978	392	1386	1526
Chrysophyceae	208	454	52	142	252	76	176	804		480	163	35	184	1394	359
Bacillariophyceae	1742	8	94	541	35	33	1386	190	208	586	3173	549	1762	75	77
Chlorophyceae	191	2832	3115	159	4092	2309	257	819	7037	101	1049	9394	366	3764	4142
Cyanophyceae	763	4684	574	674	967	770	1174	2292	2709	380	1730	576	1071	875	319

Species composition was almost identical in all the bags, but a great variance in the total volume of the various species was observed. The only species of algae which occured almost solely in fertilized bags was the small ellipsoid green algae. They were recorded in huge numbers in all fertilized bags, with a recorded maximum of 46 × 10^7 cells l^{-1} or 9394 mm^3 m^3.

pH : Simultaneously with the increased algal biomass in fertilized bags, there was an increase in pH. When the study was initiated all the bags had a pH of about 9.5-9.7, which agreed with the pH in the lake epilimnion at that time. In unfertilized bags a slight increase in pH was found during the first week (up to 10.0), before the pH became stable at about 9.5 (fig. 3). In fertilized bags, however, a sudden increase in pH took place and within a week the pH became stable at about 10.6-10.7. The highest recorded mean value was 10.7, with upper and lower values of 10.5 and 10.9 respectively. Also between fertilized bags, there was fairly good agreement between pH readings. The development of pH and species composition of cyclopoid copepods (mean values) is shown in fig. 4.

Zooplankton :The only crustaceans which showed a strong response during this short-term experiment were *Th. oithonoides* and *M. leuckarti*. In the unfertilized bags the former of these species accounted for about 70-90 % of the cyclopoid numbers, as in the lake. In fertilized bags, however, there was a strong decrease of *Th. oithonoides* following the pH increase. After the first 10 days, both species showed low densities, then a sudden increase of *M. leuckarti* was observed. At the end of the experiment *M. leuckarti* accounted for 90-100 % of the copepods in 4 of the 5 fertilized bags (Tab. 2). In bag F2, the fertilized bag having lowest pH (fig. 3), the relationship between the two was 1 : 1. In bags F4 and F5, which experience highest pH, *Th. oithonoides* disappeared. The relation between *Th. oithonoides* and pH is shown in Fig. 5, where it is evident that a high pH favours *M. leuckarti* and vice versa.

Table 2. Percentage of *Th. oithonoides* in unfertilized (U1-U5) and fertilized (F1-F5) bags at start (S) and end (E) of the experiment.

U1		U2		U3		U4		U5	
S	E	S	E	S	E	S	E	S	E
95.0	98.8	91.6	71.4	80.7	99.0	71.5	81.0	81.8	83.0
F1		F2		F3		F4		F5	
S	E	S	E	S	E	S	E	S	E
71.4	6.9	94.0	50.5	71.1	2.2	70.1	0	58.1	0

In the two bags containing fish, both species were almost equally eliminated due to fish predation. These bags are therefore not included in the figures and tables.

While *Th. oithonoides* produces few clutches with few and large eggs (8-15 per clutch) and has a relatively long generation time (ca. 2 months in Lake Gjersjöen), *M. leuckarti* has a larger clutch-size (20-30 eggs), with small eggs. In fertilized bags *M. leuckarti* had an extremely short development time, in some bags with water-temperatures 16-20° C the development from late nauplii to adult female occured within two weeks.

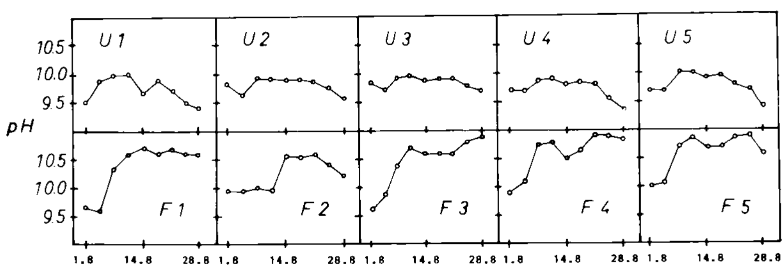

FIG. 3. Variations in pH in unfertilized (U1-U5) and fertilized (F1-F5) bags.

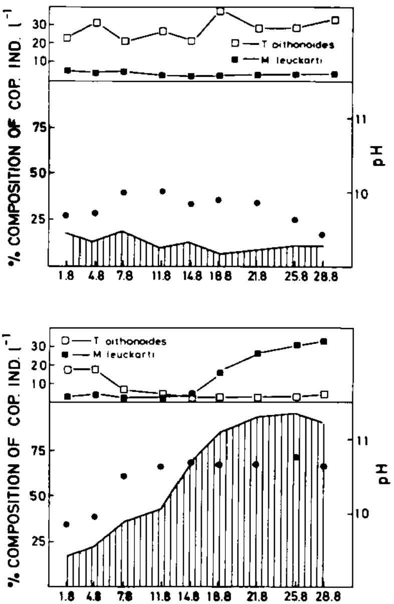

FIG. 4. Relationship between *M. leuckarti* (vertical lines) and *Th. oithonoides* in unfertilized (upper) and fertilizes bags (lower). Mean values. pH indicated as black dots.

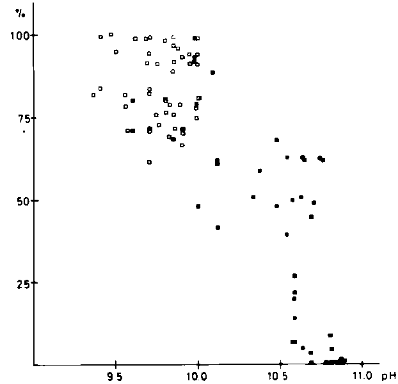

FIG. 5. Relation between pH and *Th. oithonoides* (as per cent of total number of cyclopoid copepods). Open squa res : unfertilized bags. Filled squares : fertilized bags.

5. — Discussion

Species dominance within the cyclopoid community was obviously related to nutrient perturbations, both regarding longterm changes in the lake and short-duration experiments in the bags. Several factors may have caused this :

a) A selective toxic effect caused by algal blooms.
b) Selective vertebrate or invertabrate predation.
c) Selective toxic effects from the fertilizers added.
d) A change in available food, thus favouring one of the species.
e) An increase in pH, affecting only one of the species.

a) Release of toxic substances from certain bluegreens is known from the early 1950's (Lefèvre 1950) and later verified by several authors (Shilo 1964 ; Gentile and Maloney 1969 ; Arnold 1971). The bluegreen species found in the bags were *Anabaena* cf. *tenericaulis*, *Anabaena solitaria*, *Oscillatoria agardhii* and *Oscillatoria limnetica*. The occurrence of these species was, however, very similar in both fertilized and unfertilized bags. The biomass of bluegreens was in fact higher in some of the unfertilized than some of the fertilized bags.

The only algal groups which always occured in greater numbers in fertilized bags, were the Cryptophyceae (represented by *Cryptomonas* spp. and *Rhodomonas lacustris*) and the Chlorophyceae (represented mainly by small ellipsoid and coccoid species). Within the chlorophyceans, some species might be suspected to cause toxic effects (Skulberg pers. comm.). Nevertheless, an algal toxin affecting *Th. oithonoides* but not the closely-related species *M. leuckarti* would be an interesting observation in itself and will be pursued in further studies. During the historical development of Lake Gjersjöen no increase in the above algae was observed however, something which may indicate that a high pH is more important for the numerical relationship between the two species.

b) Fish predators could have favoured *M. leuckarti*, the larger of the two species. In the two bags with fish added, however, both species were almost equally reduced. Invertebrate predators like *Leptodora kindtii*, *Chaoborus* and large cyclopoid copepods occurred only sporadically and in similar densities in all bags.

c) The same amounts of ammonium dihydrogenphosphate and ammonium nitrate were added to similar bags in a spring and autumn experiment without lethal effects on either *Th. oithonoides* or other species (Hessen unpubl.). However, in these experiments, maximum pH never exceeded 9.0 in any bag.

d) One could expect a fairly similar food choice from two such closely related species, with resulting strong competition. Advanced stages of development are omnivorous with food items including algae, nauplii, small copepodid stages of cyclopoids, small cladocerans and rotifers (Fryer 1957 ; Gliwicz 1969 ; Karabin 1978 ; Nilssen 1978). Considering the large numbers of small and medium-sized algae (5-50 μm) and the large number of rotifers, one would expect an adequate food supply for both species.

It is important to note that all stages of development of *Th. oithonoides* showed a strong decline during the first week, while increase of *M. leuckarti* was first observed in the last half of the experimental period (cf. fig. 3 and 4). A theory based on competitive exclusion therefore has to be rejected in this case.

e) Of all possible explanations, the pH seems to be the most reasonable to account for the observed patterns in the bags. Moreover, as far as the long-term changes in Lake Gjersjöen are concerned, pH and algal biomass are the only parameters which are closely-related to the observed changes within the cyclopoid copepods (cf. Faafeng & Nilssen 1981).

Even if the pH seems to be of major importance, it is unclear whether the pH-effects act directly or indirectly, or only as an additional stress-factor. The physiological effects of high pH are no straightforward, but it is clear that the ion-exchange among many zooplankton species is strictly pH dependent (Potts & Fryer 1979 ; Nilssen & al. 1983). Many copepods showed a good sodium balance up to about pH = 9.5 ; above this pH they showed a net loss (Nilssen & al. 1983).

The equilibrium $OH^- + NH_4^+ = NH_4OH$ is strongly influenced by the pH, and thus will produce more NH_4OH at a high pH (Hutchinson 1957). At pH = 7, the $NH_4 : NH_4OH$ relationship is 300 : 1, whereas the corresponding value at pH = 9.5 is 1 : 1. NH_4OH was toxic for a number of tested organisms (Trussel 1972). In fertilized bags the concentration of NH_4-H exceeded 200 $\mu g l^{-1}$. A strongly selective toxic effect due to the combination of high pH and high concentration of NH_4-N might therefore be a reasonable explanation in the short-duration experiments. During the pollution peak in the lake, however, NH_4-N never exceeded 100 $\mu g\ l^{-1}$. The influence from pH alone seems therefore to be the decisive factor affecting the numerical relationship between the surveyed populations of *Th. oithonoides* and *M. leuckarti*.

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