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Title: **The problem of the co-existence of *Arctodiaptomus bacillifer* (Koelb.), *Acanthodiaptomus denticornis* (Wierz.) and *Heterocope saliens* Lill.**

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The problem of the co-existence of Arctodiaptomus bacillifer (Koelb.), Acanthodiaptomus denticornis (Wierz.) and Heterocope saliens Lill.

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Translated by: W.J.P. Smyly

In freshwater environments of modest size and without notable ecological structure, there is usually present only one diaptomid species. When two or more diaptomid species are present in the same habitat, generally their body dimensions are distinctly different. Hutchinson (1951) considers that such a fact may be verified since, although diaptomids are essentially filtering organisms, there is some evidence that swallowing of food may be selective, especially as regards the dimensions of the ingested particles, in as much as the larger particles, rejected by the smaller diaptomid species, can be used by the larger sizes of species living with them.

In lakes of high mountains, co-existence of two diaptomid species should be considered quite exceptional. The reasons for that are to be sought in the lower number of species capable of surviving in these extreme environmental conditions, and moreover the poorer quality of the algal food, and the enforced overlapping of biological cycles brought about by the very short period for which water-life is possible, causes leading finally to severe competition.

There are only four examples of co-existence of Arctodiaptomus bacillifer (Koelb.) and Acanthodiaptomus denticornis (Wierz.)(Fig.1), those in our country situated at higher altitudes:-

Lej Nair (m.1860), Engadine, Switzerland (Imhof 1891)
Lac de Darbon (m.1816), Chablais, France (Dussart 1948)
Lago di Monscera (m.2071), Domodossola, Italy. (Tonolli 1949)
Lago delle Valli Inferiore (m.1950), Schilpario, Italy (Tonolli 1951)
together with the analagous evidence for Lago Goktscha (m.1900 approx.) Armenia, reported by Richard (1895).

The altitudinal zone of distribution of these two species, in our region, does not overlap except in part (roughly between 1800 and 2200 m.), bacillifer being found higher up and denticornis lower down (Pirocchi, 1944). The altitude of the surroundings at which cohabitation of the two species has been observed is therefore more or less at the lower limit of distribution of bacillifer. This fact acquires greater significance when account is taken of the altimetric

distribution in relation to the lacustrine character on the southern slopes of the alpine hills. As the work of Morandini (1933) and of Zucchi (1947) has shown, there is a progressive and clear-cut increase in the number of lakes up to the altitudinal zone between 2200 and 2400 m. followed thereafter by a regular decrease in numbers. If we were to attribute only a casual significance to such cohabitation, we should logically expect a greater frequency around the upper limit of the altitudinal zone of distribution common to the two species. One has the impression instead that denticornis can cohabit with bacillifer only when the appropriate environment is found near the lower limit of distribution of bacillifer.

For none of the five waters cited above was it known, if in the pelagic zone, the two species were found contemporaneously and for how long; it seemed almost certain that bacillifer always reached the adult stage before denticornis. Undoubtedly, in this we can see a manifestation of the same reason which determines the difference in the altitudinal distribution of the two diaptomids. The variation of the lacustrine temperature in the summer season would determine the possibility of existence in one particular place - but in different and successive periods - of two related species but having different limits of altitudinal distribution and hence different thermal needs.

In Lago di Monscera (Tonolli, 1949) it has been observed that the population of bacillifer adults can be completely replaced by a population of denticornis, also adult, in a very short-time (in only ten days in 1947). In the single lake of Goktscha (Richard 1895) and of the Valli Inferiore (V. & L. Tonolli 1951) individuals of the two diaptomids have been found in the same samples. It would appear of interest therefore to establish whether the cohabitation of the two diaptomids should be regarded practically as a seasonal succession, or indicating an overlap of populations which might be the means whereby the population of bacillifer comes to be eliminated from the pelagic zone. The problem is made more interesting by the fact that in three of these five lakes (Lej Nair, Lac de Darbon and Lago di Monscera) the presence has been ascertained in the pelagic zone of Heterocope saliens (Fig. 1). The extraordinary predatory activity exerted by this species on other mesoplanktonts is known (Elster, 1936; Burckhardt, 1944) and on the other hand it is known also that this species is not found very frequently in lakes at high altitudes: for example (V.and L. Tonolli 1951) in 148 Italian lakes of high altitude, Heterocope was found only three times, compared with 45 records of bacillifer and 10 of denticornis. Consdiering the rarity of cohabitation by bacillifer and denticornis, the presence of Heterocope in three of the five known places, acquires considerable significance.

All these considerations persuaded us to analyse this relationship from closer to. It was decided to examine the lake of Monscera (2071 m Val Bognanco, Domodossola) because it was more easily accessible and for it there were already numerous observations recorded. In the summer season of 1953, we made altogether

19 visits, arranged thus: 1, 17, 24, 29 May: 4, 10, 14, 20, 27 June; 4, 10, 15, 21, 25, 29 July: 4, 17 August; 15 September; 6 October. Collection of plankton was made with quantitative vertical hauls in the centre of the lake where there was maximal depth and also with horizontal net-tows.

Data on the morphological characters and population of the lake of Monascera can be found in preceding publications (Tonolli 1947 & 1949). It is enough to say here that the lake of Monascera, with a very restricted profundal zone is subject to strong oscillations of level which can affect estimates of population density per unit volume of water, directly through modification of available space and indirectly on those characters of the lake (area, volume), through which the atmospheric climate exerts influence on the lake.

On the 1st May the lake was still frozen over and the fragility of the ice-cover made sampling impossible. On 17 May nauplii stages I & II were found, as many as of bacillifer as of Heteroscope, and bacillifer II nauplii more numerous than stage I. On 24 May, bacillifer & Heterocope had already reached the first copepodid instar and by 29 May, the fourth copepodid instar; the most numerous individuals of Heterocope were slow developers. On 29 May, nauplii (I to IV) of denticornis were found for the first time. Heterocope & bacillifer reached the adult stage contemporaneously on 4 June (only females) and on the same date there was slight progress in the development of denticornis as shown by the presence of a few nauplii in stage V. By 10 June, adults of bacillifer and Heterocope had increased noticeably in numbers among which there were now some males: denticornis proceeded in its slow development, there being now a few nauplii stage VI. On 14 & 20 June there was little difference from the preceding picture except that some bacillifer females now had eggs. On 27 June, denticornis had reached copepodite stage II and III. On 4 July, the sex-ratio in bacillifer and Hetercope started to change in favour of the males, and denticornis reached copepodite stage IV. The situation was unchanged on the 15th July: however, one began to find individuals of bacillifer with damaged joints, antennae, furcal rami, etc. Such evidence can be certainly attributed to the predatory action exerted by Heterocope saliens: numerous dissections of these organisms have shown the presence in their digestive tracts, chitinous fragments derived from bacillifer. On the 21 July, there were present stage V copepodites and some adult males of denticornis. On the 25th and 29th July, adults of denticornis were even more numerous, while population densities of bacillifer began to decline rapidly and after 4th August, bacillifer was always absent. On 17 August, the jetsam of shallow hauls indicates the presence of a new hatch in the pelagic zone of nauplii of denticornis. On the 15th September and on 6 October once more there were only adults, males and females, of denticornis and of Heterocope but only in small numbers.

As regards the populations of the other principal species of zooplankton inhabiting the pelagic zone of the Lake of Monscera (Chydorus sphaericus, Cyclops vernalis, Daphnia longispina), we will say that, while the complete participation of the first three in the biocoenosis amounts to around 5% on each date, Daphnia longispina, at first very scarce, increased progressivley in density until eventually at the start of August it forms 90% of the total population and stays at this level up to the end of the autumn.

Fig. 2. shows the abosulte values of the counts on the vertical hauls in numbers per cubic metre of filtered water, limited to the three copepods under discussion.

The pelagic population of the Lake of Monscera has been studied, though much less frequently, in three other years. We take the opportunity to report the observations relating to our problem.

In 1945, three visits were made: on 21 June, bacillifer was present in all stages of development and among adults, females were most numerous; Heterocope was also present, for the most part not mature. On 19 August, Heterocope had disappeared and the most frequent organism was denticornis, which follows Heterocope. On 19 October, Daphnia predominated but there was some denticornis and Heterocope.

In 1946, on 30 June, there were nauplii, metanauplii and copepodites of bacillifer and Heterocope. On 14th July, most bacillifer had reached the last copepodite stage with a preponderance of females: Heterocope was still not mature. On 30 July, all the bacillifer were adults, with males outnumbering females; Heterocope were now also mature. On the 12th August, not a single individual of bacillifer was found and once again there were mature denticornis and Heterocope. On 28 September and on the 13 October, there were still present, but scarcer, individuals of denticornis and adults of Heterocope, of both sexes. On the 29th October, with the lake already partially frozen, only denticornis was found.

For 1947, we have the results from eight visits distributed from 30 June to the 14 November. In this year, bacillifer was present as adults, predominantly males, on 30 June, and thereafter we found no more; the sex ratio suggests that at this time, the population was already in decline. Heterocope was present with adults from 30 June to 14 September; in contrast, denticornis was already present with adults numerous on 10 July and it was found finally in the last samples taken on 14 November.

Compared to 1953, we have therefore an earlier appearance of denticornis adults in 1945 and in 1947 and a greater persistence of bacillifer in 1946. If we study (Table 1) the monthly means of atmospheric temperature recorded at an observatory situated at 1504 metres in the adjacent Valle Antrona, we see that these later and earlier appearances are disposed exactly in relation to the thermal differences in summer in each year.

So, for all these years in the lake of Monscera, as also in the lake of Darbon, for the year (?) in which observations were made, bacillifer did not persist during the entire summer season. Populations of bacillifer in lakes situated at the same altitudes but not inhabited by denticornis invariably, in contrast, persist into the start of winter, and in most of these lakes have a clear and conspicuous second summer generation.

The lake of Monscera is without doubt to be regarded as a warm lake considering the altitude at which it lies, and especially a lake in which, through the summer lowering in water level, there is a greater seasonal thermal range than its physiographic characters would allow if the water-level were held constant. The same is true of the Lake of Darbon and this would suggest therefore that the possibility of these two diaptomids might perhaps be traced back to this small amount of variation in the thermal lake climate. It cannot however, be thought that the scarcity of bacillifer in mid-summer can be attributed to excessive temperatures for this organism, because in warmer lakes than Monscera, namely lakes which reach higher maximum temperatures, the populations of bacillifer, not in competition with denticornis, surmount the warm period normally.

If we consider the period for which adult bacillifer live in the pelagic zone, we find that in Lago di Monscera they live at most for two months whereas in the other lakes of the same Val Bognanco this period is at least three months and ranges from three to five months.

Premature scarcity of bacillifer in Lago di Monscera can be attributed then either to competition for food, set up with the arrival of denticornis in the pelagic zone, or to predation exercised by Heterocope, to which bacillifer succumbs more readily than denticornis which is larger in body-size.

The observations on the temporal sequence, athwart which is displayed the biological cycles of bacillifer and Heterocope in Lago di Monscera allows a major significance to be attributed to the second hypothesis. Fig. 2 shows clearly how these two populations start off together. The naupliar upsurge is greater ÷ more than twice as much for bacillifer than for Heterocope; however, compared with Heterocope, bacillifer suffers heavier mortality in passing through the various larval stages preceeding the adult form, the initial proportions of which are gradually attentuated. It is apparent then that the maturation of the different stages of development occurs in the two organisms at much the same time: the sex ratios of the adults undergo the same variations during the ageing of the populations and also a certain similarity has been noted in the population densities.

One could consider then this concomitance as having originated in a reciprocal adaptation between the predatory species and its prey which entails for bacillifer the necessity to curtail its biological cycle (with the laying of resting eggs) before the pressure of predation becomes too strong and for Heterocope the opportunity to exploit a favourable food situation.

Moreover, the fact, which we have stressed that in three of the five lakes in which cohabitation of the two diaptomid species occurs, Heterocope has also been found, gives also more support to our interpretation.

We may conclude then that the possibility of cohabitation of bacillifer and denticornis in one and the same place depends on three factors, which are clearly seen in the Lake of Monscera and probably, to a lesser degree, in the other lakes.

In the first place, altitude: a lake situated within this altitudinal zone, in its thermal summer vicissitudes, offers, during the stage of initial warming-up, conditions suited to the cold - stenotherm bacillifer, and in the second stage- that of maximum temperatures and the ensuing abatement - conditions appropriate to the needs of denticornis. It should be noted also that at this altitude the bacillifer in this lake experiences higher temperatures than those usual for its more elevated populations; we will have therefore for that reason only a reduction in development time of the individual adult.

Secondly, we should consider the probability that competition for food between the two diaptomids would have selectively increased the earlier individuals of bacillifer and the comparatively later individuals of denticornis; in this regard we note that in lakes of this kind we have never found, nor have we found any examples in the scientific literature, a population of bacillifer already adult and in full reproductive acitivity at the end of June, as can take place in Monscera.

In the third place, then, predation pressure, which becomes more evident in the damage to bacillifer, especially when the former shares the pelagic zone with denticornis, works in the same way as the selective process determined by competition for food between the two diaptomids.

We can also consider that Heterocope or some other predator, - may indeed enable denticornis to become established in a place already colonized by bacillifer, in as much as it brings about the elimination from the pelagic biocoenosis of this diaptomid exactly when the ambient conditions become more favourable for denticornis.

The ambient conditions without doubt assume a major role in determining the basis of a possible cohabitation, directly and also indirectly through a diverse capacity for endurance by bacillifer. An example of this can be furnished by a crude experiment carried out in the summer of 1950: in two occasions, in July and August, we have stocked a lake in the neighbourhood of lake Monscera, and situated at a similar altitude (the lake of Agro, 2041 m) but deeper and colder and in which bacillifer is abundant, with about 1500 adults of Heterocope and 7000 of denticornis

collected from lake Monscera. In relation to the volume of lake of Agro, this input corresponds to one individual, respecitvely, per about 20 and 5 mc of water. Repeated sampling, carried out in the following years failed to catch a single individual of these species.

Translator's note mc = metro cubo = cubic metre.

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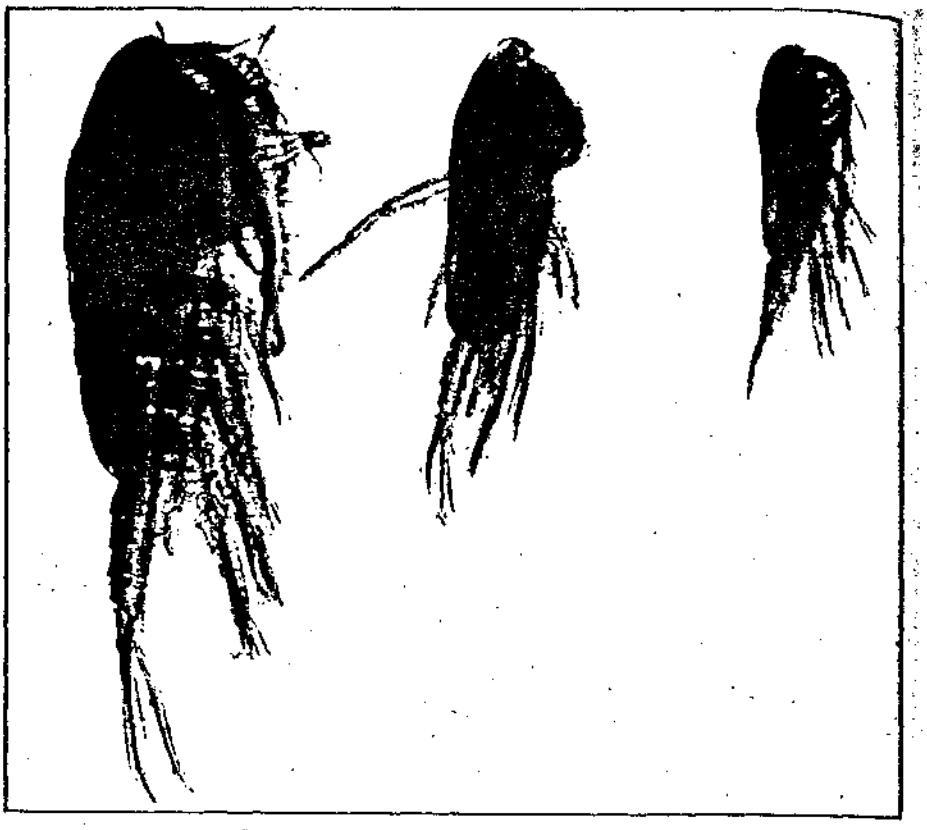

Fig. 1. From left to right : males of

Heterocope saliens, Acanthodiaptomus denticornis and Arctodiaptomus bacillifer.

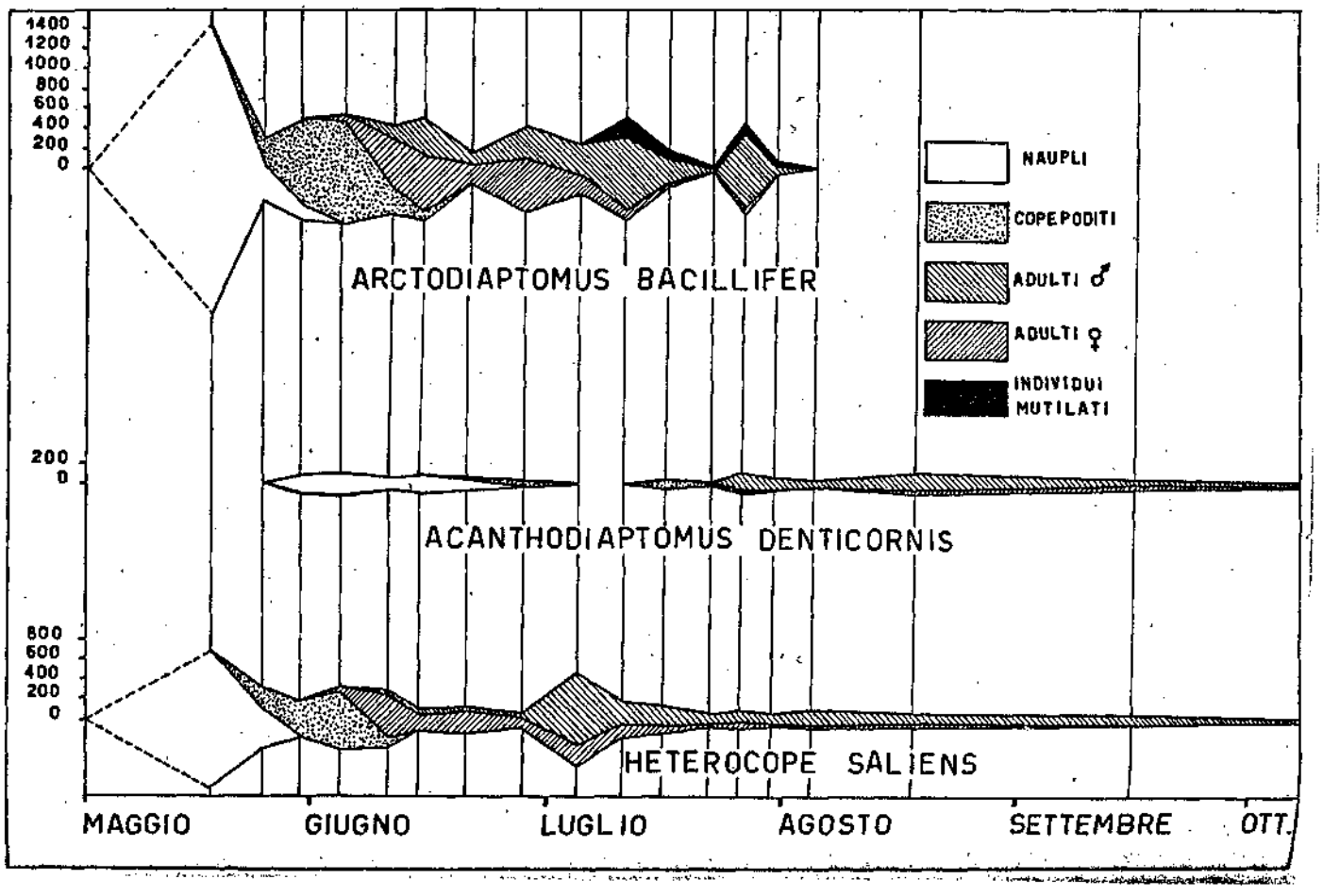

Fig. 2. Density values of the vertical samples as numbers per cubic metre of filtered water.
[The months given on the base line of the figure itself are respectively:- May, June, July, August, September and October.]

	1945	1946	1947	1953
Maggio MAY	10,2 Cº	8,6 Cº	11,6 Cº	10,6 Cº
Giugno JUNE	15,3	11,5	15,8	10,0
Luglio JULY	18,2	16,8	18,2	16,2
Agosto AUGUST	15,3	16,4	18,7	17,5
Settembre SEPT.	12,0	13,8	12,1	12,1

Tabella 1.

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.