

Interpretation of growth-curves for animals from running waters

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With 5 figures and 1 table in the text

Introduction

In 1963 the author published a paper on growth and life-cycles of some invertebrates from the springs Rold Kilde (Fig. 1) and Ravnkilde (Thorup 1963). Growth-curves of *Baetis rhodani* Pict. are presented (Fig. 2). It is remarkable that the mean size of the animals from Rold Kilde decreased during winter. This was explained by the disappearance of large nymphs, which is obvious from the previously published histograms. Also, growth stoppage during winter was suggested, which was well known from other studies of the same species (Macan 1957, Hynes 1961). The species in Ravnkilde also shows a growth stoppage during winter, but no decrease in mean size. In the paper from 1963 no attempt was made to discuss the differences between the growth-curves from the two localities.

Locality and methods

The studies, which here shall be reported, have been undertaken in Rold Kilde. A description of the spring is given by Nielsen (1942). It must be emphasized that important ecological factors as temperature, oxygen content and chemistry vary little throughout the year. The samples, which have been used for the growth studies, were taken through two years at six stations as shown in Fig. 1. Station I is situated in a tributary originating from one of the small springs which constitute the spring-complex Rold Kilde. So, Station I is closest to and Station VI farthest from the source.

Sampling was done by lifting stones of about fist-size, holding a sieve downstream and adjacent to the stone to catch dislodged animals. The content of the sieve was emptied into a tub in which the stones were cleaned for animals by means of a brush. Each sample consisted in 10 stones. The samples were preserved in 4% formalin at the locality and sorted by hand in the laboratory. Head width of each animal was measured by a stereomicroscope with an eyepiece micrometer. Because of inadequate sampling, small size groups are disregarded in the following discussion.

Results and discussion

The graphs in Fig. 3 illustrate the increase in mean size of *Baetis rhodani* throughout the year at the six stations. A growth stoppage, and even a decline, occurs at the lowermost station, whereas no stoppage, at most a retardation, occurs at the uppermost station. Samples for the former studies in Rold Kilde were taken close to Station VI and in Ravnkilde about 50 m downstream from the spring area. Thus the results from the earlier studies are in good agreement with the present.

Temperature conditions are often thought to affect the shape of growth-curves. But temperature measurements during the present investigation period (Tab. 1) have only revealed differences of more than 1°C between the six stations in a few cases during summer. Differences of this magnitude

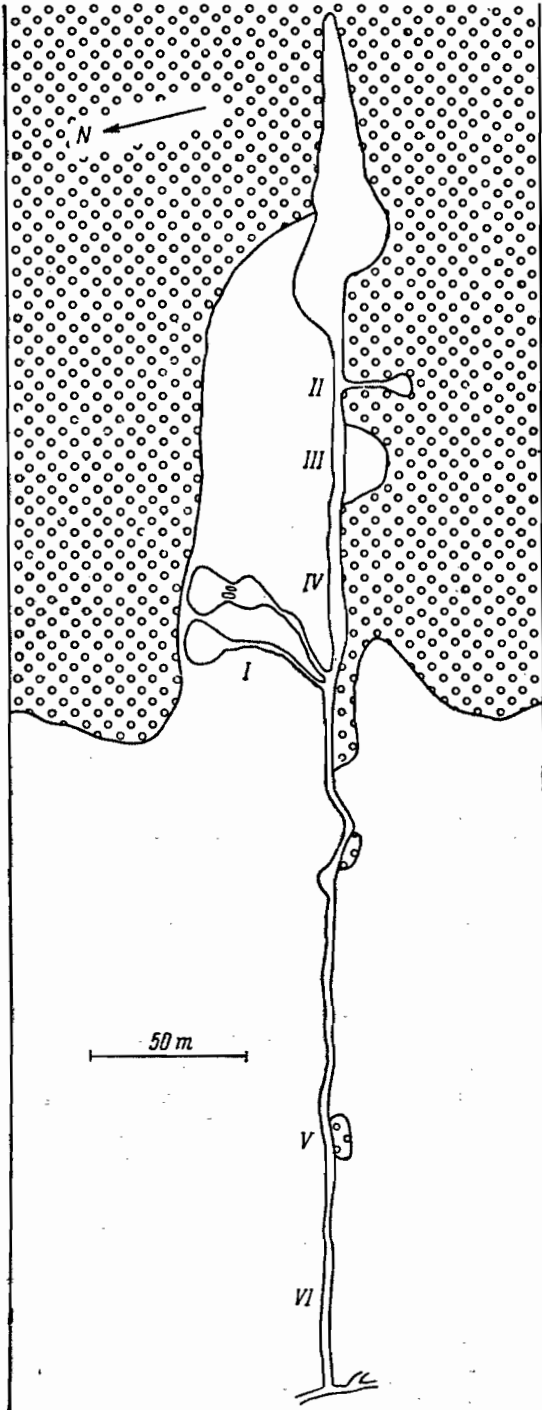


Fig. 1. Diagram of the spring Rold Kilde.
Stations and area covered with forest illustrated.

cannot be responsible for the demonstrated differences in growth pattern. The same is the case with oxygen concentration. This is close to the saturation point at all stations throughout the year.

In an earlier paper (Thorup 1966) it was demonstrated that the frequency values during summer were higher in exposed than in shaded

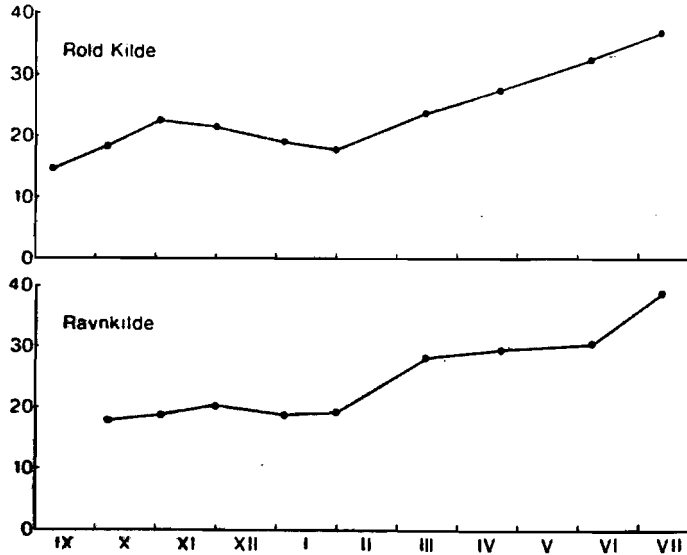


Fig. 2. Mean size of the winter generation of *Baetis rhodani* Pict. from, Rold Kilde and Ravnkilde.

Ordinate shows width of head capsule in micrometer units (10 units equals 0.25 mm).

areas. This was thought to be due to food conditions, as stomach contents of animals from this locality indicated that *Baetis* feeds on epiphytes. The shading, however, does not change gradually along the stream, as Stations II, IV, and V are shaded, and Stations I, III, and VI exposed. Thus, no correlation exists between shading and the shape of the curves.

It is, therefore, difficult to attribute differences in growth at the six stations to environmental factors. The curves may not illustrate differences in growth, but rather some other biological phenomena.

Tab. 1. Temperature ($^{\circ}$ C) at five stations in Rold Kilde during the period of investigation.

Station	1965						1966				
	1 IV	29 IV	29 VI	30 VI	1 VII	16 IX	9 XII	2 II	3 III	3 VI	14 XII
I	5.6	9.8	10.6	9.2	9.3	9.4	5.6	5.0	6.5	9.7	4.8
II	6.1	7.8	8.7	8.7	8.1	8.9	6.1	5.8	6.9	8.3	5.2
IV	6.0	8.3	9.1	9.1	8.3	9.4	5.7	5.4	6.7	8.6	4.8
V	5.8	8.7	9.7	9.2	8.4	9.5	5.7	5.4	6.6	8.8	4.8
VI	5.7	8.8	10.2	9.4	9.0	9.7	5.5	5.2	6.6	9.3	4.6

The differences in the shape of the curves could be explained by a higher death-rate of the small size groups in the upper stations. Such differences, however, must also be justified by differences in ecological conditions.

In Fig. 4 results from frequency analyses (Thorup 1970) at the six stations through the years 1964–1966 are illustrated. It is seen that

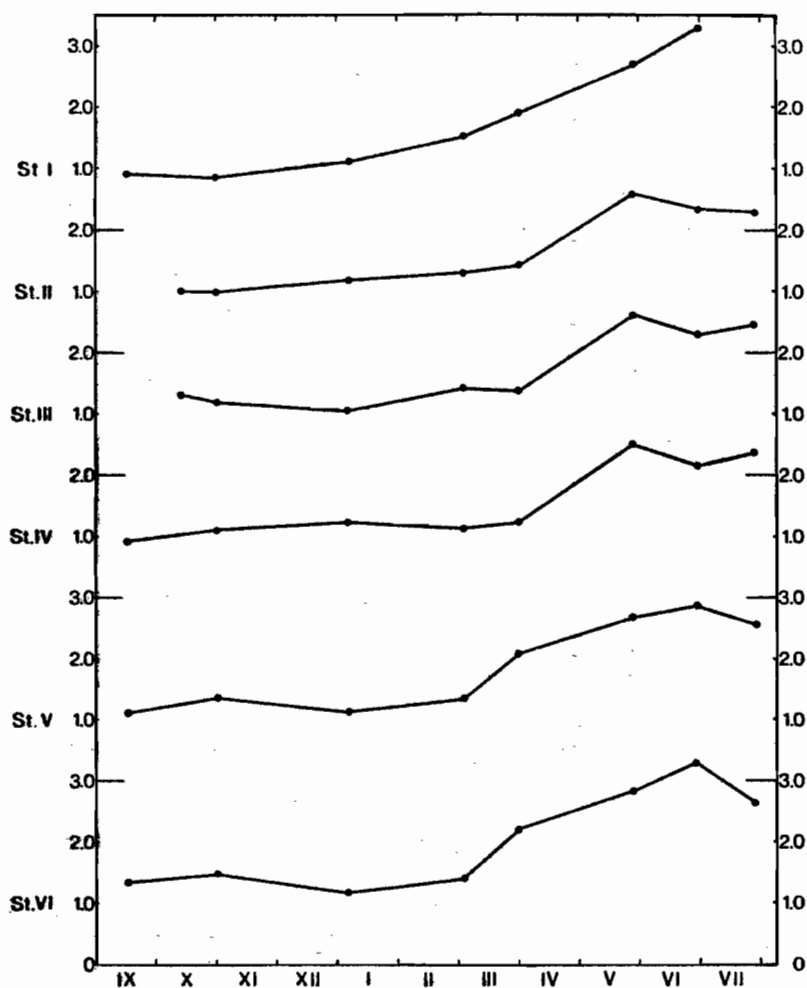


Fig. 3. Mean size of the winter generation of *Baetis rhodani* Pict. from six stations in Rold Kilde.

Ordinate shows width of head capsule in micrometer units (1.0 unit equals 0.33 mm).

whereas the frequency is constantly high at Station VI all through the investigation period, great fluctuations occur at Station I. The Stations II to V show intermediate conditions. The curve for Station II is explained by the species' life-cycle, as described in the author's 1963-paper. Shortly after egg laying in spring and autumn the species occur in large numbers and inhabit every stone at the station, resulting in high frequency values. In the periods in between the frequency values decrease, probably because the population is drifted downstream.

Station I differs from Station II in that only one maximum occurs a year. During summer this station is completely overgrown with vegetation. Therefore the egg-carrying females do not recognize it as a watercourse and no eggs are deposited here in the autumn. 1966 seems to be an exception to this in that a winter generation begins this year.

In Stations V and VI only slight minima occur, presumably as these stations are continuously supplied with animals from upstream. The remaining stations show intermediate conditions. Thus, the figure indicates

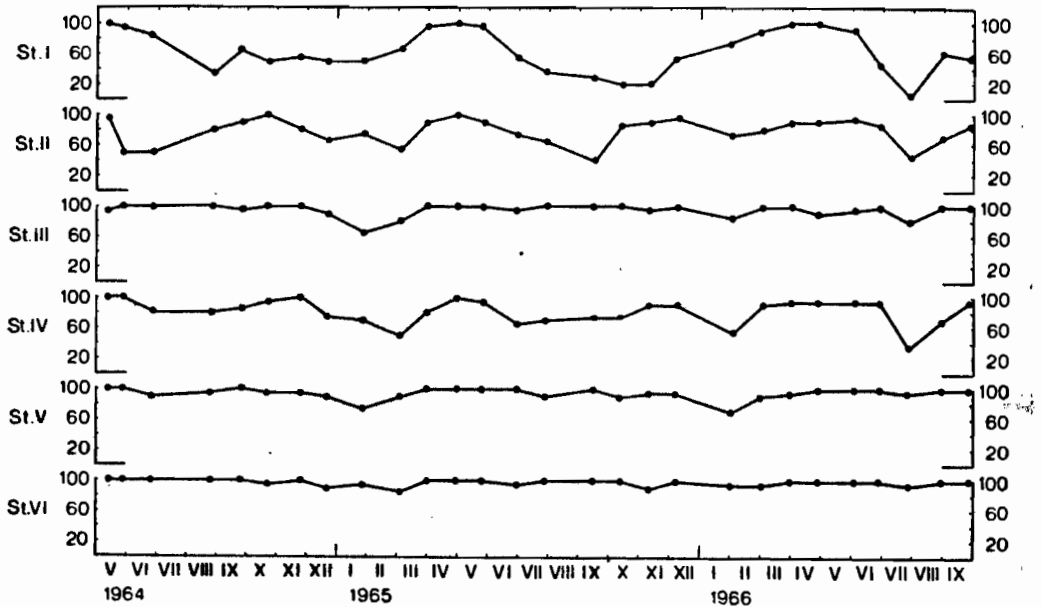


Fig. 4. Frequency values through 28 months for *Baetis rhodani* Pict. at six stations in Rold Kilde.

that drift occurs in the springbrook and alters the bottom fauna quantitatively.

Our next problem is whether the size distribution is the same in the drift and in the bottom fauna. Macan (1957) found for *Baetis* and Müller (1966) for *Baetis* and *Simulium* that drift-rate increased just before emergence and pupation respectively. This may indicate that large animals are more prominent in drift than small ones. Anderson (1966) found that the high drift-rate of Ephemeroptera, Plecoptera and Simuliidae during night was mainly due to an increase in number of animals more than 3 mm long. This seems to show that different size groups may be differently influenced by drift. Unfortunately drift samples have not been taken in the present study, but an analysis of the size distributions (Fig. 5) on which the curves are based, indicate some changes which can be explained by drift-rates being different for different size groups.

From the November samples it appears that the mean size increases down the springbrook. This is mainly due to increase in maximum size from Station I to Station VI, but also to decrease in number in the small size groups through the stations. The explanation for this could be that

the new generation starts earlier in the lower stations than in the upper. It could also be due to faster growth in the lower stations. Both of these explanations imply different ecological conditions at the six stations. But no ecological factor influencing the life-cycle has been observed to vary gradually through the springbrook.

Studies on the life-cycle of *Baetis* (M a c a n 1957, T h o r u p 1963) show that the flying period is long. According to M ü l l e r ' s theory on colonization cycle (M ü l l e r 1954), the eggs are mainly deposited in the upper part of the spring and drift carries the nymphs downstream as they grow up. The average age, then, is higher at the lower stations than at the upper and histograms like those for November will appear.

As mentioned it cannot be ascertained whether there is a growth stoppage or not in the population. If there is continuous growth during winter a displacement from smaller to bigger size groups must occur in the histograms from one date to the next during winter. This is what appears in the histograms for Station I from November to May, although another cause might be responsible. Histograms from the other stations show a similar less pronounced growth stoppage during winter.

This is partly explained by the fact that large animals disappear from the lower stations between November and January. Whether this is due to predation, migration or drift is uncertain. All predators are found in the spring throughout the year and this effect is only observed during winter.

The disappearance of larger individuals from the lower stations was not observed between January and March. In these cases an import of small individuals from the upper stations may be responsible for the seeming growth stoppage at the lower stations. It is in this period that the minimum in frequency values occurs at the upper stations.

If no growth takes place during winter, the increase of the mean size at Station I may be due to disappearance of the smaller individuals here and partly also at Station II. In the same way the decrease of the mean size at the lower stations is due to import of small individuals from upstream. This import and export is most easily explained by drift.

Brinck (1949) stresses that growth curves cannot be used for calculating growth-rate because of considerable variation around the mean value. The present study shows in addition that the so called growth-curves are of limited value, as they can vary considerably depending on where the samples are taken, even when it might be assumed that the samples come from the same population. M a c a n (1957) emphasizes the fact that overpopulation can cause an elimination of a number of specimens from a given locality, eventually resulting in an altered size distribution. In Rold Kilde such an elimination seems to occur in the upper part of the springbrook and, further, it seems to take place by drift.

M a c a n (l. c.) prefers to present results of growth studies as kite histograms. But these, also, can be difficult to interpret. Size measurements alone cannot be used to determine growth pattern of species in running water. Studies of import and export to and from the sampling station appears to be an important condition for the determination of the growth pattern of a species.

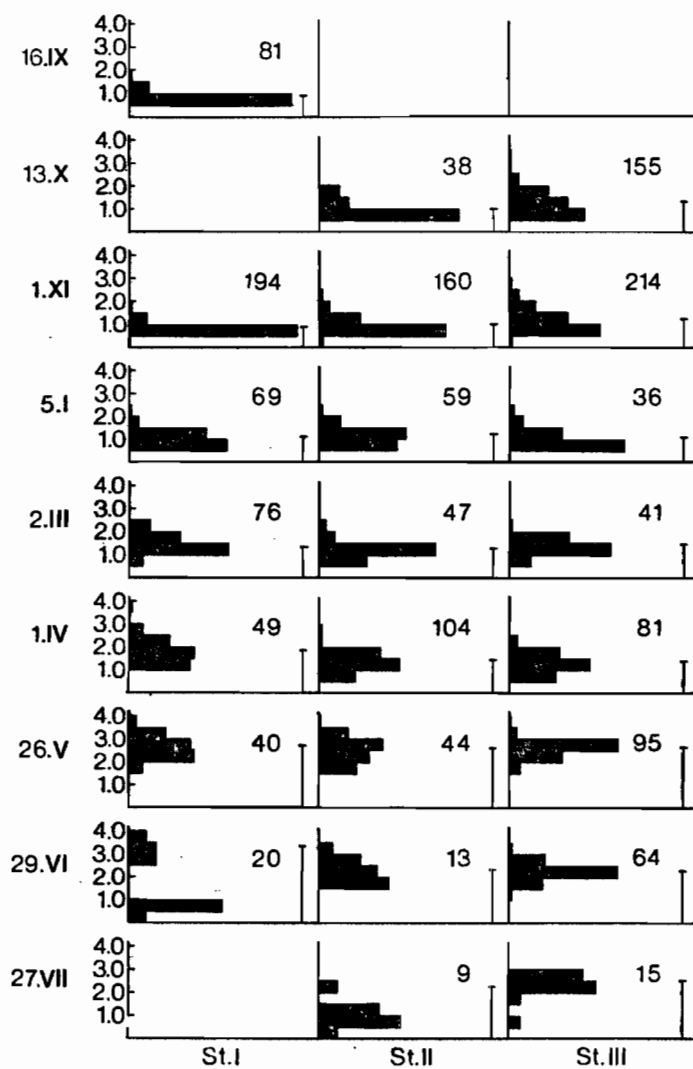
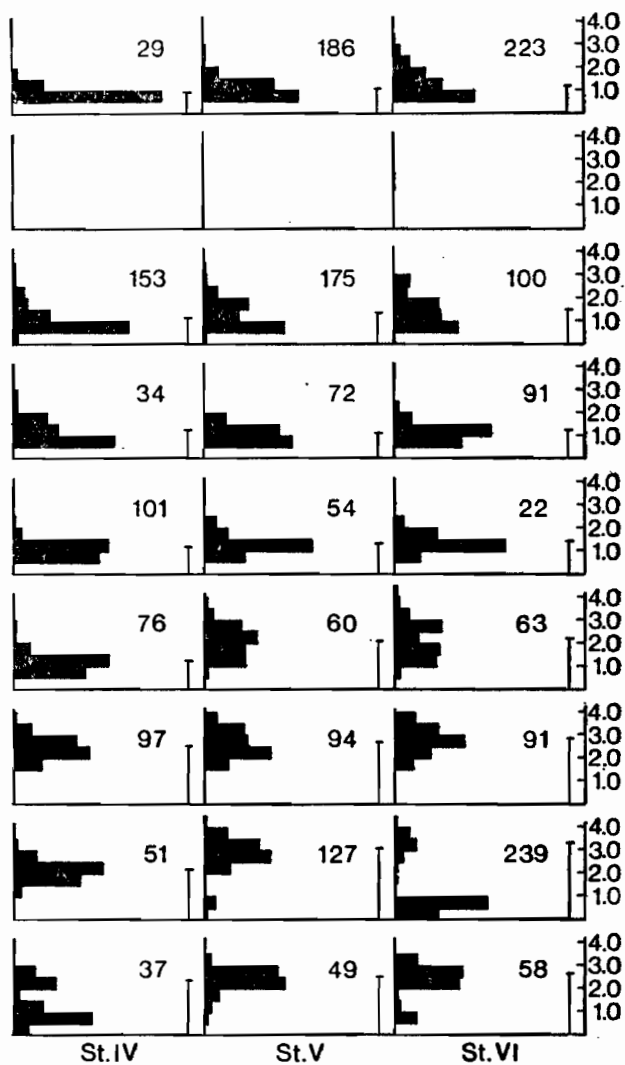


Fig. 5. Percentage size-distributions of the winter generation of *Baetis rhodani* Pict. at six stations in Rold Kilde.



Ordinate shows width of head capsule in micrometer units (1.0 unit equals 0.33 mm). The figures indicate number of specimens per sample. The vertical bars indicate average size of specimens in the sample

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