Studies on Danish springs

Jens Thorup and Claus Lindegaard

Introduction

In his well-known textbook E. P. Odum opens the section on springs with the sentence: "Springs are the aquatic ecologist's natural constant temperature laboratory" (Odum 1971; p. 321). Although temperature is not the only ecological factor constant, it is undoubtedly the one that made European springs attractive to freshwater biologists during the first half of this century. For example, in the first studies on Danish springs (Nielsen 1942, 1950 a, 1950 b, 1951), constant temperature was considered an important factor determining faunal composition. In larger springs, factors such as current velocity, flow (Berg 1951) and chemical composition are also fairly constant. This means that springs, in comparison with other types of environments, "hold a position of importance as study areas

that is out of proportion to their size and number" (Odum 1971; p. 321). Investigating the significance of such constancy was the main goal of the spring studies reviewed for this paper.

The springs most intensively studied in Denmark are situated in Himmerland, an area in northern Jutland. Geomorphologically the landscape (Fig. 1) may be described as a relatively high lying plateau diagonally intersected by a deep valley in which the streams Lindenborg Å and Simested Å flow towards NE and SW, respectively. Most of the rain falling on the catchment area drains off through a number of large springs, the largest being Lille Blåkilde, Ravnkilde, Kovads Bæk, and Rold Kilde. Photographs of these springs are reproduced in Nielsen 1950 b, 1951 and Lindegaard et al. 1975.
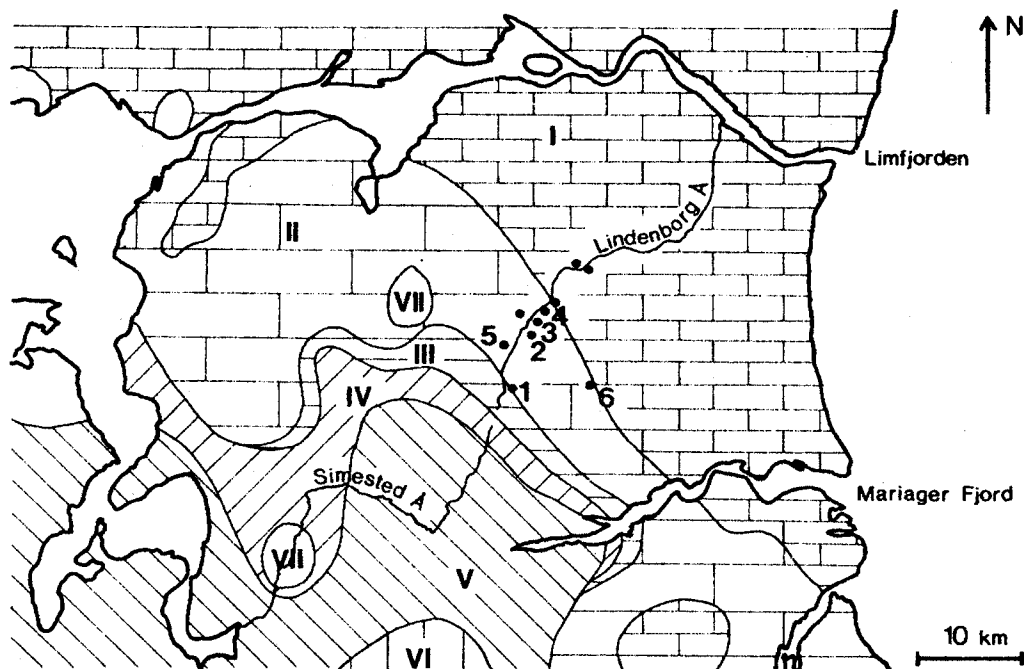

Fig. 1. Geological map showing the different Himmerland subsoil formations and major springs. 1: Limestone from Senonian; II: Limestone from Danien; III: Clay from Paleocene; IV: Clay from Eocene; V: Sand and clay from Oligocene; VI: Miocene; VII: Horsts of stone salts from Permian. Springs mentioned in the text are: 1: Rold Kilde; 2: Kovads Bæk; 3: Ravnkilde; 4: Lille Blåkilde; 5: Stubberup Vad; 6: Store Blåkilde.

The subsoil is composed of chalk deposits from the Cretaceous period, covered only with thin layers of glacial deposits and mold. Due to its porosity, the chalk subsoil provides for a large ground water reservoir which ensures constant water flow and current velocity throughout the year (Berg 1950). Rain water seeps rapidly through the upper layers without loosing much oxygen or gaining much carbon dioxide. Thus, ground water is rich in oxygen and poor in carbon dioxide. As a result, the spring water is generally also rich in oxygen (Table 1), except in some places where ground water seeps through thick organic deposits. Due to its paucity of carbon dioxide the ground water dissolves very little chalk and, even in places where spring water flows directly from the chalk beds, it is not particularly rich in calcium.

Table 1. Himmerland springs: Maximum and minimum oxygen concentrations (mg O_2/l; % saturation) measured over a 2 year period.

Spring	mg O_2/l min.	max.	% sat. min.	max.
Rold Kilde, Locality 6, source	10.61	11.50	88	95
Rold Kilde, Station 1, springbrook	8.66	12.41	73	100
Rold Kilde, Station VI, springbrook	10.99	12.73	95	101
Ravnkilde springbrook	10.60	11.73	92	102
Lille Blåkilde, source	8.66	9.79	72	82
Kovads Bæk, springbrook	12.62		100	

Chemical factors are summarized in Table 2. The high concentrations of NO_3^- and PO_4^{3-} in some of the samples are remarkable. These nutrients are undoubtedly indirectly responsible for the rich fauna of algalscrapers, for they allow a considerable production of sessile algae. A high Cl^- concentration is found in several places along the valley where a fault is found. Because of low iron concentrations no ochre deposits occur.

Zoogeography

Because of the special temperature conditions found in springs some zoogeographic phenomena are worth mentioning. Nielsen (1950 b) pointed out three types of relicts occurring in the springs: late glacial relicts which are cold-stenotherms, Atlantic relicts which do not tolerate very low temperatures, and Subboreal relicts which require high summer temperatures.

The late glacial relicts immigrated to freshwater shortly after the last glacial epoch. Large springs povided a refuge by sheltering them from increasing temperatures for where the water wells out the temperature is fairly constant at 7.5° C. Due to the strong current velocity and the large and constant discharge (Berg 1951) this temperature increases only slowly along the springbrook during summer. Today, the late glacial relicts have their main distribution in arctic and subarctic areas.

Apatania muliebris McL. is the most prominent species of this group. It cannot withstand temperatures much higher than that recorded in the springs and thus it is found in only a few of the largest springs (Rold Kilde, Lille Blåkilde). The isolated occurrence and the parthenogenetic propagation of A. muliebris have favoured formation of races and Nielsen (1950 a, 1963) and Schmid (1954) describe three subspecies, A. m. cimbrica Niels., A. m. intermedia Niels., and A. m. nielseni Schm. of which the first is considered to be the original form. Other species are regarded as glacial relicts too, but their main distribution today is not so restricted (e.g., Parachiona picicornis Pict., Plectrocnemia conspersa Curt., Silo nigricornis Pict.).

The postglacial warm relicts are reminiscenses of a fauna inhabiting the area during two warmer periods after the last glacial epoch. One group, from the Atlantic epoch, obtained shelter in the springs against low winter temperatures. There they live side by side with the glacial relicts. Examples are Agapetus fuscipes Curt., Wormaldia occipitalis Pict., and Odontocerum albicorne Scop. Their present European distribution extends farther north in the western part than it does in the central part of the continent.

The second group of postglacial warm relicts is from the Subboreal epoch during which summer temperatures were higher. Today these species have a more continental distribution than the former type, and they require higher summer temperatures than are normally found in Denmark. A few small springs at Stubberupvad are situated on slopes with considerable insolation and, due to their small discharge, water temperatures often exceed those of the air (further information in Nielsen 1951). Eubria palustris Germ. and Oxycera (Hermione) cfr. pygmaea Fallén are considered to be relicts of this type. Perhaps Protonemura hrabei Rauser, found in Rold Kilde and Ravnkilde, also belong to this

Table 2. Himmerland springs: Chemical data for October 1975 samples

Spring	pH	Alka-linity meq/l	Ca^{2+} mg/l	Fe^{2+} Fe^{3+} mg/l	NH_3-N mg N/l	NO_3^--N mg N/l	PO_4^{3-}-P mg P/l	Cl^- mg/l	COD part. mg O$_2$/l	COD dissolv. mg O$_2$/l
Rold Kilde, Station 1, springbrook	7.62	1.60	53	0.01	0.002	4.61	0.027	32	1.25	2.3
Rold Kilde Locality 6, source	7.54	1.46	60	0.01	0.002	9.72	0.042	34	0.04	2.0
Rold Kilde, Locality 7, source	7.88	2.32	72	0.01	0.002	8.79	0.099	27	0.29	2.0
Ravnkilde, springbrook	7.66	2.39	65	0.01	0.002	3.40	0.060	28	0.11	1.6
Lille Blåkilde, source	6.87	2.56	60	0.01	0.002	1.32	0.065	38	0.00	0.04
Kovads Bæk, springbrook	7.92	2.87	64	0.01	0.002	0.41	0.039	26	2.72	1.5

group (Thorup 1967). Further, Nielsen (1951) describes a number of *Atrichopogon* species from the springs at Stubberupvad of which all but one are known only from the type locality.
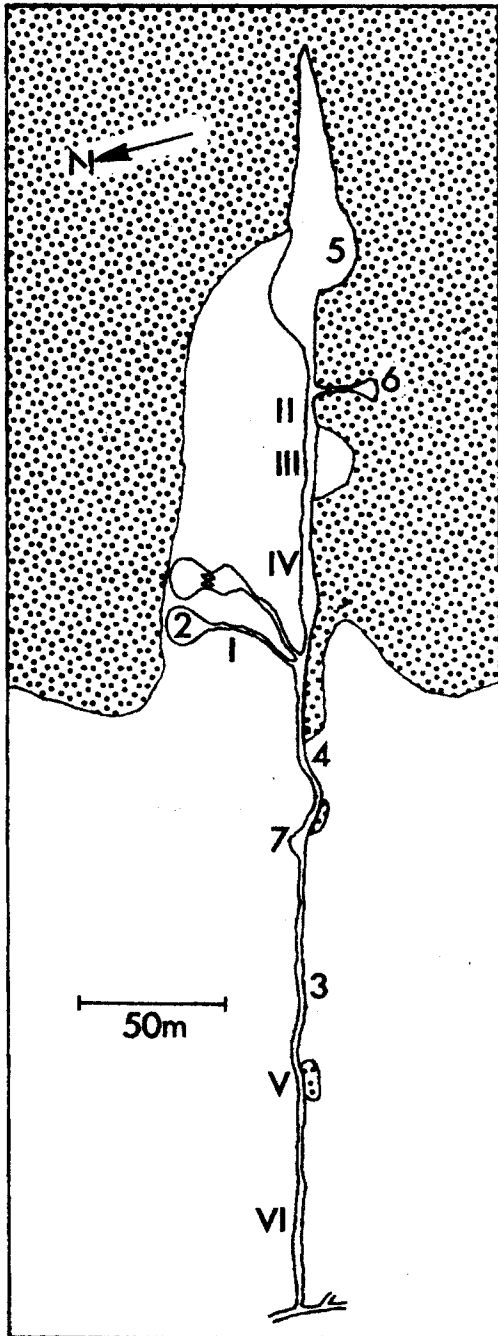

Fig. 2. Rold Kilde: Forested area noted by circles. Remaining area is open land. Sampling localities indicated by Arabic numerals 2-7. Sampling stations on stony bottom by Roman numerals I-VI, in the text grouped into Ia (= I), Ib (= II, III, and IV), and Ic (= V and VI).

Substrate relationships

Description of substrate types

The helocrene is the most common type of spring in the area, although some large limnocrenes and a few small and atypical rheocrenes are found. In the helocrenes a great variety of substrate types occurs (Thorup 1966, Lindegaard *et al.* 1975) which accounts for the large diversity of species found in these springs. For a study concerned with the dependence of faunal composition on substrate type, the most important substrate types in the spring Rold Kilde (Fig. 2) were sampled quarterly during two years. Some preliminary results of this study follow.

Substrate types sampled were:
Locality 1. Stony bottom (at Stations I-VI, later grouped into Ia, Ib, and Ic)
Locality 2. Emergent macrophytes from localities with low current velocity (10 cm/sec.)
Locality 3. Submerged macrophytes from localities with medium to high current velocity (50 cm/sec.)
Locality 4. Submerged mosses from localities with high current velocity (75 cm/sec.)
Locality 5. Emergent mosses from localities with low current velocity (10 cm/sec.)
Locality 6. Accumulations of dead beech leaves from localities with low current velocity (10 cm/sec.).

Ecological differences between sampling localities are mainly due to the substratum. Although factors such as food supply and current velocity are important they are likewise affected by substrate type. It is difficult to give more than a rough estimate of their value as they vary so much within a substrate. Also, light intensities interact with substrate type in determining whether a locality possesses vegetation or not. Most of the other physical and chemical factors do not differ substantially between the substrates studied. Only temperature varies independently of substrate type, but is dependent on insolation and discharge. However, as the sampling localities all are situated in or near springs, the differences in temperature between stations are small and of minor importance to faunal distribution.

Faunal Composition

An outline of the faunal composition on the different substrate types is given in Table 3. Because of the small distance between sampling stations (at maximum 400 m) located within the same water system, it is not surprising that nearly all species are found on every substrate type. However, the relative faunal composition differs very much between substrates and one can even characterize the fauna associated with each substrate type by means of character species according to Berg's definition (Berg *et al.* 1948, p. 286).

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Table 3. Rold Kilde: Tabulation according to substrate type of those species exceeding 1% of the total in November 1966 samples. Figures show percents of total

Stony bottom		Emergent macrophytes		Submerged macrophytes	
Baëtis rhodani Pic.	24.4	*Nemurella picteti* Klp.	30.0	*Dugesia gonocephala* Dugès	23.2
Odagmia ornata Meig.	20.5	*Gammarus pulex* L.	26.8	*Gammarus pulex* L.	22.6
		Oligochaeta	17.8	*Odagmia ornata* Meig.	21.0
				Chironomidae	10.8
Dugesia gonocephala Dugès	9.2	*Agapetus fuscipes* Curt.	9.9	*Eusimulium latipes* Meig.	4.2
Gammarus pulex L.	9.0	*Dugesia gonocephala* Dugès	4.0	*Baëtis rhodani* Pic.	3.1
Brachyptera risi Mort.	8.8	*Helodes minuta* L.	3.2	*Eusimulium costatum* Fried.	2.2
Agapetus fuscipes Curt.	6.7	Chironomidae	1.6	*Nemoura flexuosa* Aub.	2.0
Nemoura flexuosa Aub.	4.6	*Pericoma fuliginosa* Meig.	1.2	*Pericoma freyi* Berdén	1.9
Eusimulium costatum Fried.	3.1			*Helodes minuta* L.	1.9
Eusimulium latipes Meig.	1.8			*Amphinemura standfussi* Ris	1.4
Ancylus fluviatilis Mül.	1.5			*Dixa* sp.	1.0
Helodes minuta L.	1.4				
Chironomidae	1.2				

Submerged mosses		Emergent mosses		Beech leaves	
Odagmia ornata Meig.	24.1	*Gammarus pulex* L.	39.7	*Gammarus pulex* L.	49.2
Pericoma freyi Berdén	12.5	*Nemurella picteti* Klp.	18.4	Oligochaeta	13.1
Oligochaeta	12.4	Oligochaeta	13.4		
Amphinemura standfussi Ris	11.1				
Baëtis rhodani Pic.	7.9	Chironomidae	4.4	*Leuctra hippopus* Kmp.	9.1
Brachyptera risi Mort.	5.9	*Pericoma fuliginosa* Meig.	4.1	*Potamocypris wolfi* Brehm	8.5
Chironomidae	4.8	*Leuctra hippopus* Kmp.	2.9	*Nemurella picteti* Klp.	3.7
Dugesia gonocephala Dugès	4.5	*Helodes minuta* L.	2.2	Chironomidae	2.2
Wormaldia occipitalis Pict.	3.9	*Parachiona picicornis* Pict.	2.0	*Helodes minuta* L.	1.6
Gammarus pulex L.	3.1	*Pericoma blandula* Eaton	1.4	*Leuctra nigra* Kmp.	1.1
Leuctra spp.	3.0	*Dixa* spp.	1.2		
Rhyacophila fasciata Hagen	2.5	*Leuctra nigra* Kmp.	1.1		
		Dicranota spp.	1.1		

To further analyze the similarity between faunas of different substrates, "percentage similarity" (Whittaker and Fairbanks 1958) has been calculated for the fauna of each pair of substrates. We must take note that at the present state of the investigation some groups have not yet been identified to species. However, in our opinion the final division among the various species will not alter the main characteristics substantially.

An analysis carried out on the six samples from stony bottoms (Loc. 1) gave the percentage similarities presented in Table 4. Application of Mountford's (1962) method for classifying samples reveals the relationships pictured by the dendrogram in Fig. 3. The figure demonstrates that the percentage similarity between Stations V and VI, and between Stations II,

III, and IV is high (85 and 70, respectively), whereas the similarity between Station I and the other stations is low (46). This classification of the stony-bottom fauna

Table 4. Rold Kilde: Percentage similarities among November 1966 samples from stony bottom stations (see text for stations)

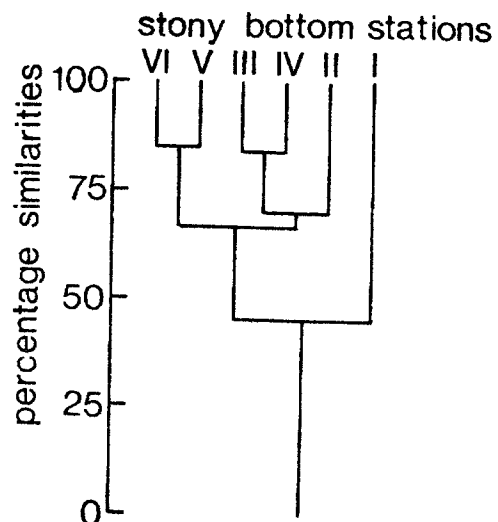| Stony bottom stations	I	II	III	IV	V
VI	47	58	68	70	85
V	51	63	69	72	
IV	46	73	84		
III	37	67			
II	48				

Fig. 3. Dendrogram showing the grouping of samples from stony bottom stations (based on the percentage similarities among samples presented in Table 4).

agrees well with the very nature of the stations. Station I, situated in the outlet of a small helocrene, has a very low water level and the substrate is rather unstable due to a steep down-grade. Stations II, III and IV are all situated in a shaded part of the springbrook with a low water level and many stones protruding through the water surface. Stations V and VI are in the lowermost, exposed part of the springbrook where nearly all stones are submerged. Therefore, it is reasonable to compare these three groups of stations (named 1a = I, 1b = II, III, IV, and 1c = V, VI) separately with other substrate types (Table 5, Fig. 4).

Table 5. Rold Kilde: Percentage similarities among November 1966 samples from all localities (see text for localities)

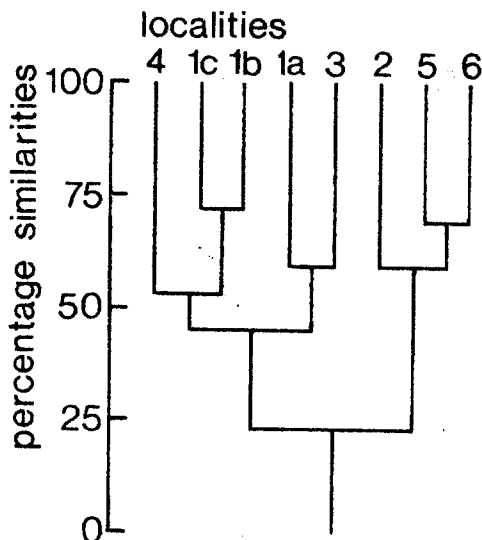| Loca-lities	1a	1b	1c	2	3	4	5
6	31	5	15	51	30	20	69
5	31	5	15	65	33	22	
4	22	48	57	23	44		
3	59	39	53	34			
2	46	16	19				
1c	51	72					
1b	45						

localities

Fig. 4. Dendrogram showing the grouping of all samples (based on percentage similarities among samples presented in Table 5).

It appears from the dendrogram (Fig. 4) that two sets of two substrates each are associated with percentage similarity indexes close to 70, viz. two stony bottom localities (Loc. 1b and 1c) and accumulations of beech leaves (Loc. 6) and emergent mosses (Loc. 5). This last set has low water levels and deposits of particulate organic matter in common.

The next group of similarity indexes lies between 50 and 60 and divides the substrate types into three groups. The first comprises stony bottoms (Loc. 1b and 1c) and submerged mosses (Loc. 4), all characterized by

high current velocity. Further, the moss substrate is composed of a number of smaller tufts attached to stones in the springbrook with areas of stony bottom in between. The second group consists of the uppermost stony bottom locality (Loc. 1a) and submerged vegetation (Loc. 3). Both are characterized by medium to high current velocity. These two major groups in turn show a percentage similarity index of 45 with all five of their localities characterized by high to medium current velocities. By contrast, the third group consists of substrate types with low current velocity and with part of the substrate protruding through the water surface (Loc. 2, 5 and 6).

Movement

A spring area can be conceived of as a mosaic of substrates with different faunal compositions. As the preceeding analysis shows, a number of species are common to several of the substrates, but there are also a number of species which are only, or mainly, found on one substrate type. We were interested in knowing why a species only, or mainly, occurs on a single substrate. Also, does a species occurring on several substrates thrive equally well on all and does it move back and forth between substrates?

To answer these questions we took size measurements of Gammarus pulex L. from various substrate types sampled in November 1966. All specimens were examined and measured under a stereomicroscope and the length of the first free thoracic segment was measured using an eyepiece micrometer (1.0 unit = 0.33 mm).

Jessen (1975), working on Gammarus from the stony bottoms of Stations I and VI in Rold Kilde, found that two generations occur simultaneously, divided at a size of about 1.2 micrometer units. Further, males grow considerably larger than females (Fig. 5). The two generations can easily be distinguished in the histograms of Fig. 6, although it is difficult to separate males from females in these histograms. Therefore, sex was determined for all individuals larger than 1.2 units from two stations (submerged macrophytes, Loc. 3; emergent mosses, Loc. 5 (Fig. 5)).

The histograms from different substrate types differ considerably, particularly with regard to the percentage of each of the two generations present. On all substrates with low current velocity and low water level, the larger generation is underrepresented and, in particular, the large males are missing (Fig. 6). It does not seem reasonable to presume that Gammarus thrives less well on the substrates in question than on other substrates. It seems more probable that individuals migrate to other substrates as they grow up and larger animals only occur at these substrates during propagation. Perhaps the large females alone go into these substrates to leave off their progeny. Jessen (1975) gives evidence that mature animals migrate upstream just before propagation.
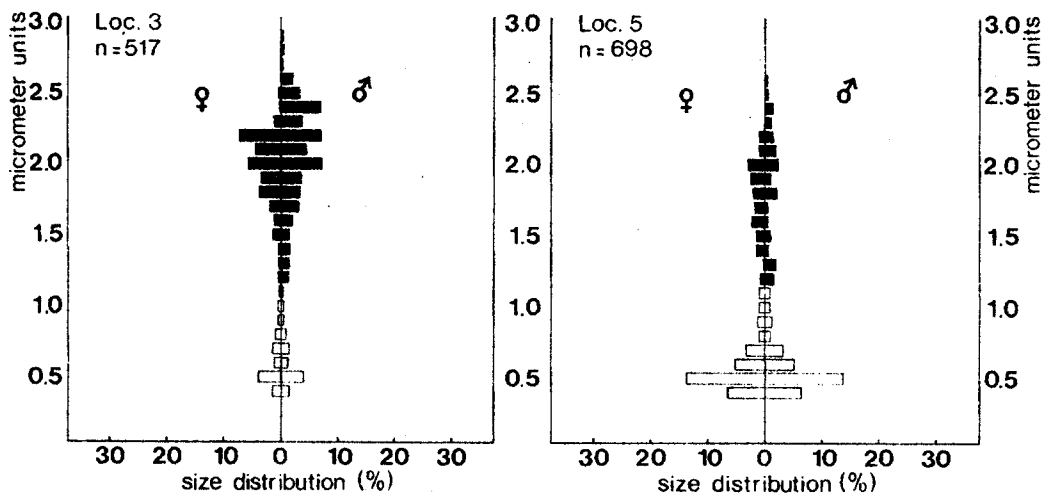
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Fig. 5. *Gammarus pulex* L.: size distribution by percent at localities 3 and 5. Ordinate shows length of first free thoracic segment in micrometer units (1.0 unit equals 0.33 mm). Black bars indicate size classes where males and females could be distinguished.
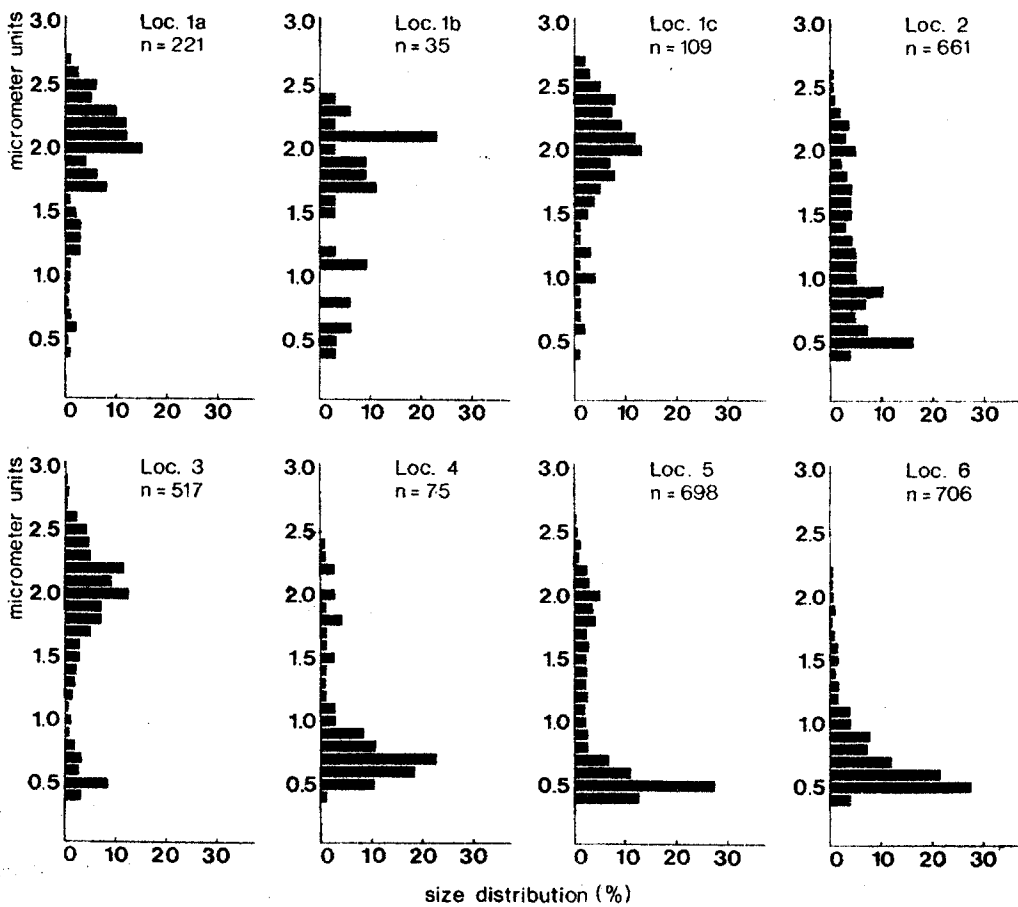

Fig. 6. *Gammarus pulex* L.: size distribution by percent at all sampling localities. Ordinate shows length of first free thoracic segment in micrometer units (1.0 unit equals 0.33 mm).

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Gammarus shows the same type of size distribution when submerged moss substrate is considered. An explanation similar to the above would be in agreement with Thienemann (1912), who regarded the submerged mosses as a "nursery school" for the fauna associated with a stony bottom.

Variation in faunal composition

Samples for the study just reviewed were all taken in the midst of a typically developed substrate. However, along its border a substrate often shows a more or less broad transition zone where the faunal composition may be supposed to differ from the neighbouring faunas. Even where a sharp limit is found between substrates a mixing of the faunas could be expected. In the spring Ravnkilde a study was carried out to see how broad this mixing zone is between the stony bottom and emergent mosses (Lindegaard et al. 1975). The data demonstrated that the faunas are very sharply separated for there was practically no penetration of the moss carpet by species from the stony bottom. Such a finding correlates well with the very low percentage similarity (5) between faunas of the same two substrate types in Rold Kilde. Substrate types with a larger percentage

similarity will presumably show a higher degree of intermingling along a common border, but studies to elucidate this have so far not been carried out.

In the Ravnkilde investigation the study of homogeneity in the moss fauna was emphasized. Some species were characterized as border species (Fig. 7) and others as interior species (Fig. 8), depending on their numerical occurrences in border – and mid-samples, respectively. Variation in current velocity and the amount of detritus deposits were considered responsible for the distributional pattern inside the moss carpet.

Indications of a vertical zonation of the fauna in emergent moss were also found. Four zones can be distinguised: a dry zone above the water surface, a madicolous zone immediately above the water surface, water covered moss below the surface, and, at the bottom, a detritus zone composed of dead moss and detritus. Each zone was characterized by a number of species mainly, or only, found there.

In earlier work, Thorup (1966, 1970) studied homogeinity of the stony bottom substrate in Rold Kilde. Faunal variations were also found on this substrate, but shading and current velocity were thought to be the factors causing these deviations.
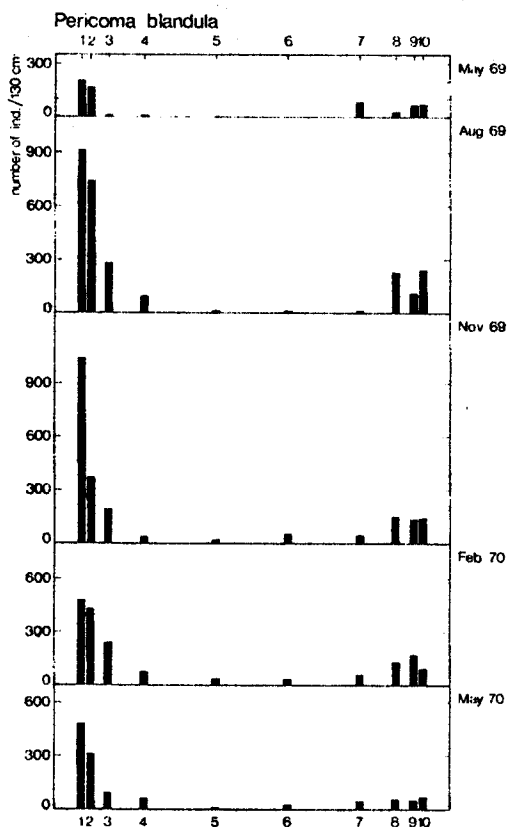

Fig. 7. *Pericoma blandula* Eat., exemplifying species which prefer the border of the moss substrate in the spring Ravnkilde. Numerals 1–10 indicate sampling stations along the transect (see Lindegaard et al. 1975.
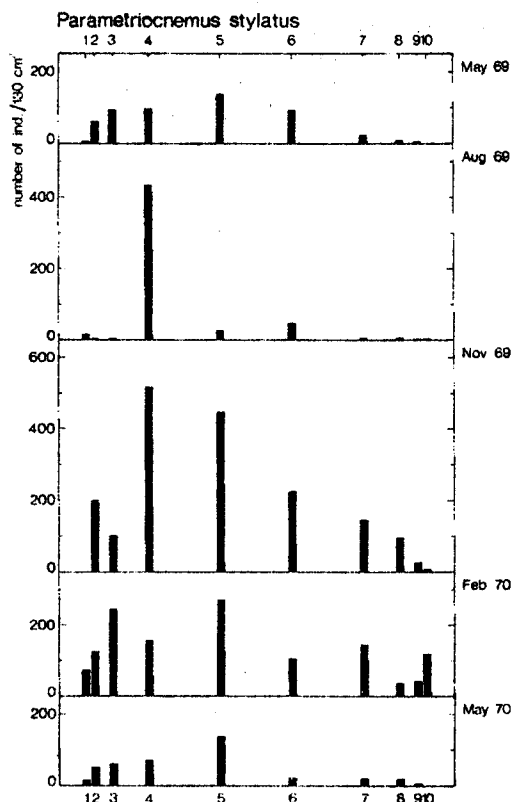

Fig. 8. *Parametriocnemus stylatus* Kief., exemplifying species which prefer the interior of the moss substrate in the spring Ravnkilde. Numerals 1–10 indicate sampling stations along the transect (see Lindegaard et al. 1975.

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Life cycles

Thienemann's (1925) statement that insects from springs all emerge in early summer is not at all confirmed by studies of the life cycles carried out in the springs of Himmerland. Studies by Iversen (1973 b, 1976), Lindegaard et al. (1975), Nielsen (1942, 1950 a, 1950 b) and Thorup (1963, 1974) have revealed that the emergence takes place to some extent throughout the year, although most species do emerge during summer. Many species have a very long flight period often due to more generations (e.g., Simuliidae, Baëtis rhodani Pic.), but in some species one generation may emerge throughout the summer (e.g., Agapetus fuscipes Curt., Potamophylax nigricornis Pic.).

The number of generations per year may also vary. In some Diptera (e.g., Simuliidae) several generations are the rule. Baëtis rhodani Pic. has a summer and a winter generation, whereas most Plecoptera (Nemouridae, Leuctridae, Brachyptera risi Mort.) are found either in winter or in summer. A number of Trichoptera seem to have a one year life cycle, but some take two (Crunoecia irrorata Curt.) or three years (Sericostoma personatum Spence) to mature (Iversen 1973 b, 1976).

In some species the yearly cycle is more or less broken up. Iversen (1976) showed that part of a generation of Parachiona picicornis Pict. has a one year life cycle and the rest a two year life cycle. Nielsen (1950 a) found that, in the large spring Lille Blåkilde, Apatania muliebris McL. has a completely broken year cycle although this does not apply for the same species in Rold Kilde. In Rold Kilde, Iversen (1976) could not determine the life cycle of Beraea maurus Curt. as all instars occurred throughout the year.

Life cycle studies are often based on growth curves showing the variation in size or weight during the year. However, studies on Baëtis rhodani Pic. revealed different growth curves at different stations in the Rold Kilde springbrook (Thorup 1973). Jessen (1975) showed that the differences were due to a selective drift of large individuals from the lowermost stations. Therefore, the interpretation of such curves should obviously be done with care.

At a locality in the uppermost part of the spring where no migration takes place the growth of several species of Trichoptera is retarded or even stopped during winter (Iversen 1973 b, 1976). Earlier studies in Himmerland as well as in other places have demonstrated retardation and halt of growth during winter for species belonging to a variety of invertebrate groups living in springs. However, a number of other species, especially semiannual and multivoltine ones, grow continually during winter.

Thus, a great variety in life cycles can be observed among invertebrates inhabiting springs and only minor adaptations to this biotope's stable ecological conditions have taken place (Thorup 1974). This means that the total food supply can be utilized effectively as there are always animals in all phases of growth.

Since food supply varies with substrate type, also variations in the life cycle pattern may be excepted. Until recently, no comparison had been made between life cycle patterns on different substrates in the same spring. So Lindegaard et al. (1975) attempted the comparison utilizing the moss carpet in the spring Ravnkilde and the mosses in the stream Afon Hirnant (Hynes 1961). They found that long-lasting life cycles dominate the moss carpet fauna of the spring while rapid life cycles were more common in the stream. The observed differences in life cycle pattern can be accounted for by differences in temperature range, current velocity, and food supply.

Suggestions for further work

Up till now the studies on Himmerland springs have concentrated on the biology, life cycle, zoogeography and substrate dependency of individual species composing the fauna. Attempts have been made to determine the interrelationship between substrate and life cycle types.

Hynes (1961) made a model of the sequence of events throughout the year, from which fluctuations in biomass and number of individuals can be estimated. Lindegaard et al. (1975) found that the relative importance of the various groups in this model can differ with locality. It is likely that such differences exist between the faunas of various substrate types, as food supply differs qualitatively and quantitatively with substrate.

Some food supply studies concerning the input and decomposition of allochtonous material have been carried out (Iversen 1973 a, 1976, Iversen and Madsen 1977), but we are in great need of information about production of food in the spring itself. Until now no botanist has been interested in this subject.

A few papers concerning feeding biology have appeared (Bjarnov 1972, Iversen and Thorup 1974), but exact knowledge about the diet of even the most common species is very scarce. Therefore, the understanding of the relationship between substrate type and the life cycle pattern is primarily dependent on further studies of feeding biology and the supply of various food materials. A consequence of the latter, particularly the input of allochtonous material, must be investigations on secondary production of the benthos communities. Such a study is in progress for a dead beech leaves community.

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Jens Thorup
Claus Lindegaard
Freshwater Biological Laboratory
University of Copenhagen
51 Helsingørsgade
DK-3400 Hillerød