

## Phenology of spawning for the Common Frog (*Rana temporaria* L.) in Finland from 1846 to 1986

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The onset and changes in the timing of spawning of the common frog (*Rana temporaria* L.) in Finland was studied through the 3888 records received through enquiries carried out by the Finnish scientific society “Finska Vetenskaps Societeten-Suomen Tiedeseura” in each year over the period 1846–1986. Spawning begins at the end of April in southwestern Finland and gradually proceeds towards northeastern parts of central Finland and from there to the north. The mean date of the first spawning of the year is 18 April. The maximum delay between the mean dates of all the records of spawning from the southernmost (lat. 60°N) and northernmost (lat. 70°N) 100×100 km Finnish uniform grid squares is 35 days.

The mean date of spawning correlates well with mean air temperatures (April in southern, and May in northern, Finland) and with the dates when the ground was no more permanently snow covered. A long-term shift towards earlier spawning (2–13 days depending on the indice used and the area studied) during the observation period of about 150 years can be seen after smoothing the means of 10-year periods with a 50-year moving average. This long-term change is in accordance with the changes observed in spring temperatures in Finland during the same period. The “greenhouse effect” causing a worldwide increase in the mean air temperatures probably influences the onset of spawning in amphibian populations and accordingly its impacts should be monitored in this respect in other areas as well.

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### 1. Introduction

In Scandinavia the common frog (*Rana temporaria*) lives at the northern limit of its range (see e.g. Terhivuo 1981). In Finland Koskela (1973), Koskela & Pasanen (1974, 1975), Pasanen & Koskela (1974) and Harri & Koskela (1977) have studied ecophysiological aspects of the growth and breeding of the species and showed among other things that in laboratory conditions frogs from different parts of Finland emerge and start spawning according to an endogenous rhythm that is locally adapted. Outdoors these phases are, however, modified by environmental factors. Spawning takes place later in higher than in lower latitudes (e.g. Juszczuk 1959, Savage

1961, Koskela & Pasanen 1975) and the same is true for altitude (e.g. Beattie 1985).

If the climate and the topography of an area vary, one may expect differences in the timing of spawning between the common frog populations there. As long series of meteorological observations, as well as observations on the onset of spawning among populations of the common frog in different parts of the country are available the impact of climatic factors can be studied in the present study area.

In the present study I describe a pattern for the chronology of the onset of spawning for the common frog in Finland and I also analyze the relationship between the temperature and the timing of spawning and the long-term changes in them during a period of about 150 years.

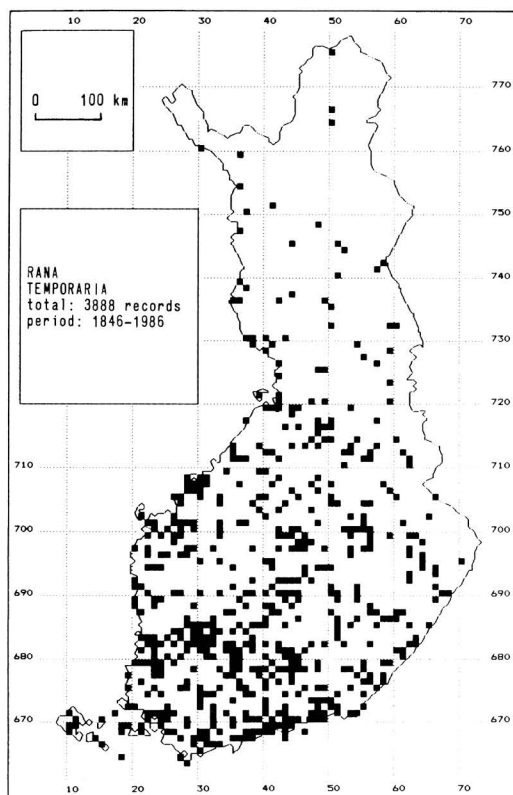


Fig. 1. Distribution of the 3888 records referring to the timing of spawning for the common frog (*Rana temporaria*) in Finland during 1846–1986. The records are given as 10×10 km squares of the Finnish uniform grid (27°E) system (see Heikinheimo & Raatikainen 1971). For the total number of records in the 100×100 km squares see Fig. 3.

## 2. Material and methods

In the early decades of the 19th century the Finnish scientific society "Finska Vetenskaps Societeten — Suomen Tiedeseura" established a programme for recording meteorological data from different parts of the country. Since 1846 phenological observations have also been asked for in the questionnaires annually sent to the contributors. One of the questions refers to the onset of spawning in the common frog (*Rana temporaria*). In the present study the 3888 records coming from different parts of Finland and referring to the years 1846 to 1986 are taken into account. I have located these records to the 10×10 km squares of the Finnish uniform grid 27°E system (see Heikinheimo & Raatikainen 1971), as shown in Fig. 1. For the total numbers of records in the 100×100 km grid squares see Fig. 3 (upper figures) and for the numbers of the records in successive ten-year periods see Table 1.

Another study material comprises 8952 observations referring to 1332 10×10 km grid squares (Fig. 2). These were received from schoolchildren aged 13–16 years voluntarily re-

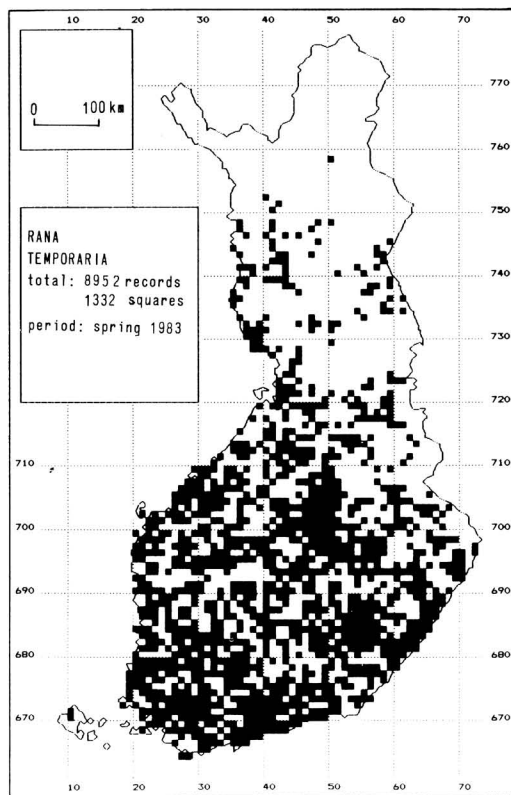


Fig. 2. Distribution of the observations referring to the spawning of the common frog (*Rana temporaria*) in Finland during the spring of 1983. For further explanation see the text and Fig. 7.

sponding to a questionnaire sent to schools in connection with a campaign called "Tarkkaile luontoa" (= "Observe nature") in the spring of 1983. This campaign was organized by Suomen Luonnonsuojeluliitto, Luonto-Liitto, Lintutieteellisten Yhdistysten Liitto, Natur och Miljö and Natur och Ungdom. The numbers of these records in the 100×100 km grid squares are given in Fig. 7 (lower figures).

All the records in the two data sets were subjected to a computer data base analysis. The following indices were used to estimate the timing of spawning:

- 1) the first spawning of the year refers to the earliest date of all the records in the same year from a given area unit, such as a 100×100 km grid square or a zone made of such squares, 2) the mean date of these records is counted for a given time span, such as a ten-year period, and this is referred to as the mean date of the records for the first spawning of the year, 3) the mean and 4) the median dates of spawning are counted for all the records made within an area unit during a given period.

The climatological data were received from the archives of Ilmatieteen Laitos (the Finnish Meteorological Institute) in Helsinki and from the annual reports published by this institute. The meteorological stations mentioned in the text are indicated in Fig. 4.

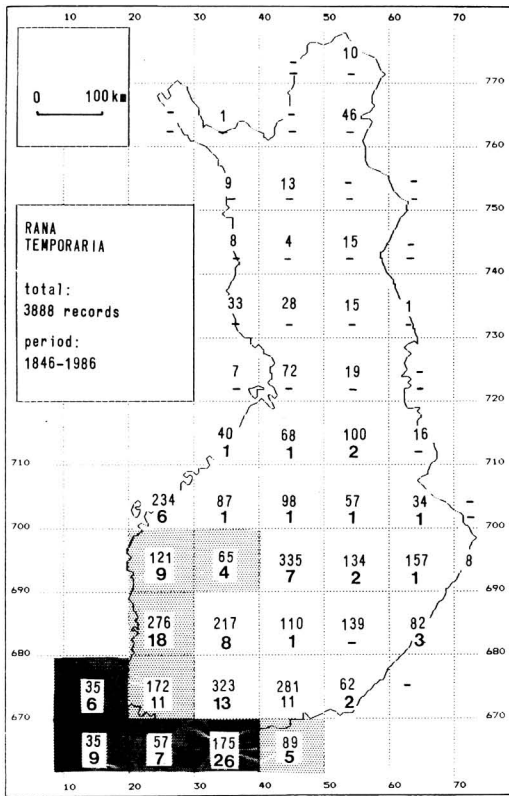


Fig. 3. Total number of records (upper figures) of the spawning of the common frog (*Rana temporaria*) and the number of times (lower figures, relative frequency indicated by hatching) when the first spawning of the year was recorded in the 100×100 km squares of the uniform grid (27°E) system in Finland during 1845–1986.

### 3. Results

#### 3.1. The geographical pattern for the chronological onset of spawning

Fig. 3 (lower figures) shows that most of the records of the first spawning of the year are confined to the coastal areas of southern Finland and to the Åland archipelago, SW Finland. The mean date of all these records is 18 April ( $SD=10.6$ ,  $SE=0.9$  days) and the corresponding median date is 19 April.

In 121 (85%) years out of the 141 year-long study period the first spawning of the year occurred in April. In eighteen (13%) years it took place in May and in 1881, 1887 and 1903 the common frog was reported to start spawning in March. In the latter three years the records chronologically next to them were made, however, much later, i.e., 1.5–3.0 weeks later.

Fig. 3 and Table 1 show that the records in the study material of the years 1846–1986 are not uniformly distributed over the country, either geographically or in time. To work out the areas where the onset of spawning takes place fairly simultaneously, I calculated the onset of spawning separately for each 100×100 km grid square. Because the first spawning of the year is affected by the total number of records in the square, i.e., the more records made, the earlier the date of the first spawning of the year expected, I adopted the mean and the median dates of all the records in the square to indicate the squares that are similar to each other in these respects.

Table 1. Numbers of records referring to the spawning of the common frog (*Rana temporaria*) in Finland in periods of ten years in the five zones (A–E) corresponding to those in Fig. 4. Brackets show the periods pooled for the diagrams in Figs. 8, 9 and 10.

Period	Numbers of records in zones A–E					Total <i>n</i>	%
	A	B	C	D	E		
1846–1855	74	36	27	12	26	175	4.5
1856–1865	24	17	28	7	5	81	2.1
1866–1875	8	17	6	1	15	47	1.2
1876–1885	81	114	24	7	11	237	6.1
1886–1895	118	181	83	15	29	426	11.0
1896–1905	112	137	72	21	29	371	9.5
1906–1915	101	114	83	24	20	342	8.8
1916–1925	66	82	89	7	12	256	6.6
1926–1935	62	98	84	3	4	251	6.5
1936–1945	62	141	89	2	1	295	7.6
1946–1955	49	105	93	1	7	255	6.6
1956–1965	34	80	99	–	5	218	5.6
1966–1975	47	148	147	19	10	371	9.5
1976–1986	48	322	161	23	9	563	14.5
Total <i>n</i>	886	1592	1085	142	183	3888	
%	22.8	41.0	27.9	3.7	4.7	100	

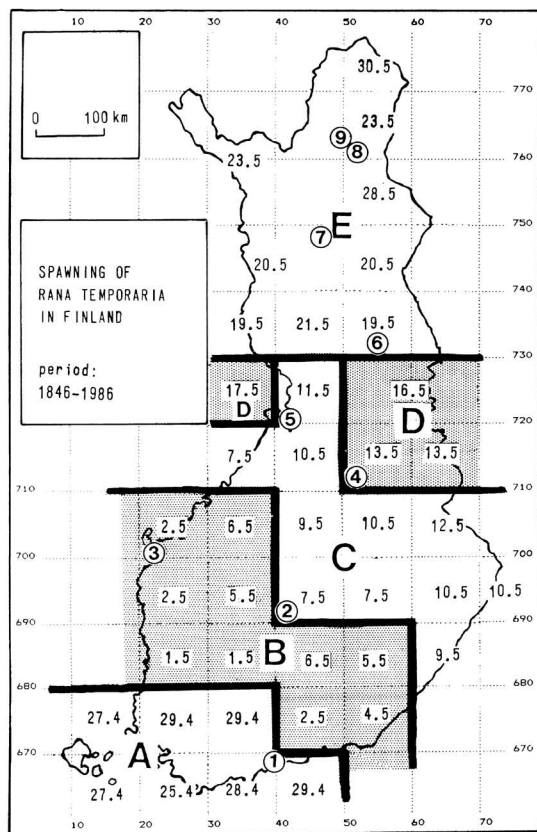


Fig. 4. Mean dates (figures with white background) for the observations referring to the spawning of the common frog (*Rana temporaria*) in the 100×100 km squares of the Finnish grid 27°E system during 1846–1986. The squares are united on the basis of their mean date of spawning into zones A–E representing chronological six-days periods (25.4–30.4, etc.) for the timing of spawning. The meteorological stations (figures in open circles) mentioned in the text are as follows: 1= Helsinki, 2= Jyväskylä, 3= Vaasa, 4= Kajaani, 5= Oulu, 6= Kuusamo, 7= Sodankylä, 8= Ivalo and 9= Inari.

In Fig. 4 I have grouped the 100×100 km squares on the bases of their mean dates of spawning as follows: those squares with a mean date of 25.4–30.4. (six-day period) constitute zone A, those of mean date 1.5–6.5. form zone B, those of mean date 7.5–12.5. are in zone C, those of mean date 13.5–18.5. in zone D and squares with mean dates later than 18.5. are in zone E. I also used another grouping, viz., three-day periods, but as the mean dates of the squares in Fig. 4 show, such three-day patterns run parallel to the six-day patterns, showing that the two groupings are basically alike.

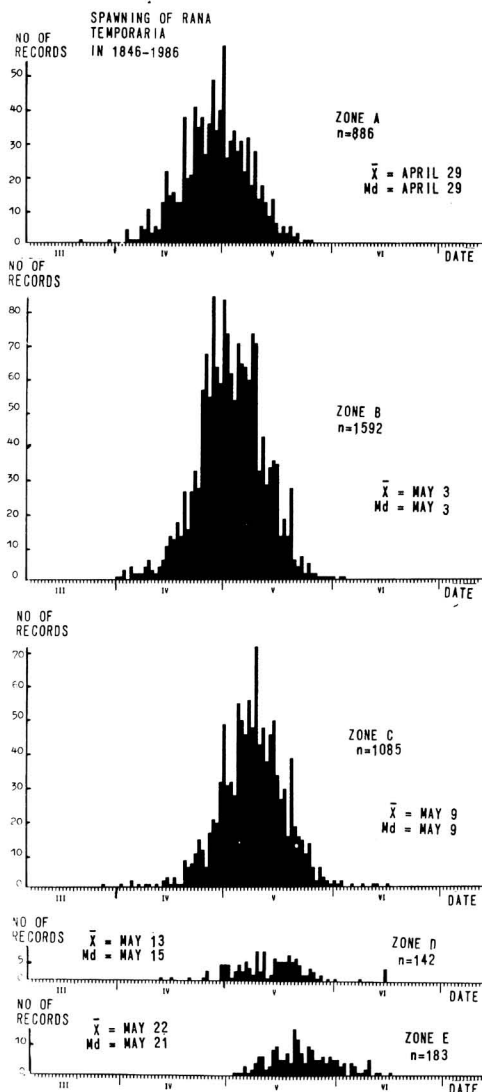


Fig. 5. Frequency distributions of the records indicating the spawning of the common frog (*Rana temporaria*) in Finland during 1846–1986 in the zones A–E corresponding to those in Fig. 4. Symbols:  $\bar{x}$  = mean date and Md = median of all the records in the zone.

According to Fig. 4, the chronological onset of spawning proceeds from southwestern Finland to the southeastern parts of central Finland and from there the zones turn towards the north. The zones do not run parallel to the latitudes indicating a difference between eastern and western parts of the country.

Fig. 5 indicates that there is a wide range in the dates of the records within the zones and a wide

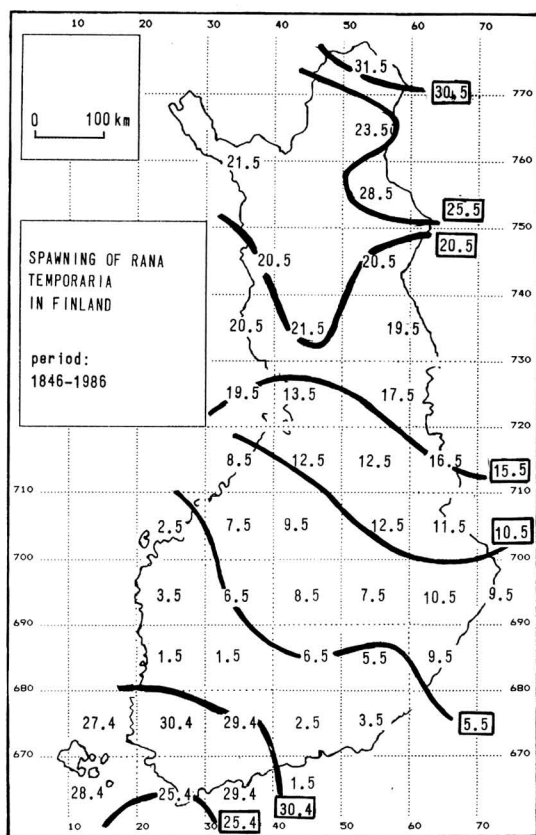


Fig. 6. Isochrones for five-day periods indicating the timing of spawning for the common frog (*Rana temporaria*) in Finland according to the means for the records of the first spawning of the year in each 100×100 km grid square. For further explanation see the text.

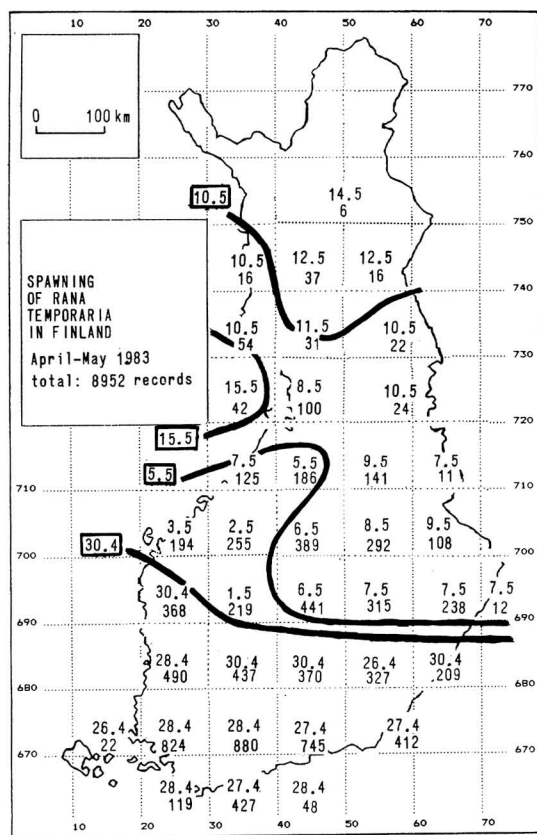


Fig. 7. Isochrones for five-day periods (25.–29.4, etc.) showing the onset of spawning for the common frog (*Rana temporaria*) in Finland in the spring of 1983 according to the median dates in the 100×100 km squares. Upper figures show the median date and lower ones the total number of records in the squares. The material is based on an enquiry undertaken in schools (see the text).

overlap between the zones. Considering the mean and the median dates of spawning for zone A and those in zone E, the difference is about 3 weeks, but the maximum difference between the southernmost and northernmost 100×100 km squares is greater than that, namely 35 days (Fig. 4).

Fig. 6 shows the isochrones drawn on the bases of the median dates for all the records in the 100×100 km squares during 1846–1886. This is a more “natural pattern” than that in Fig. 4 for demonstrating a phenomenon taking place without discontinuities. In order to make a different type of grouping than that appearing in Fig. 4, I adopted five-day periods to unite the squares. Because linear correlation between

the mean (Fig. 4) and the median dates (Fig. 6) of the same squares is highly significant the patterns in the two figures are actually very similar to each other ( $r=0.994$ ,  $P<0.001$ ,  $df=39$ ).

To study variation in the chronological patterns shown in Figs. 4 and 6, I calculated the median dates for the records collected in the spring of 1983 within the 100×100 km squares and drew the isochrones corresponding to those shown in Fig. 6. Fig. 7 shows that in 1983 the maximum delay between the squares in southern and northern parts of the country is only 18 days, indicating that the chronological pattern was highly modified then. Accordingly, annual variation can be great in this respect.

Table 2. Correlation between the date for the disappearance of snow ( $x$ , 1 January = 1, etc.) from open fields and the mean date ( $y$ ) of the records of the year for the spawning of the common frog (*Rana temporaria*) in zones A–E (see Fig. 4). The locations of the meteorological stations are indicated in Fig. 4. Due to the lack of data many years within each period are not taken into account.

Zone	Period	Linear regression	$r$	$P$	$df$	Meteorological station(s)
A	1893–1986	$y = 0.331x + 83.90$	0.457	<0.001	85	Helsinki
B	1911–1986	$y = 0.331x + 87.59$	0.612	<0.001	60	Vaasa
C	1916–1986	$y = 0.360x + 87.10$	0.524	<0.001	53	Jyväskylä
D	1911–1986	$y = 0.546x + 65.90$	0.601	<0.001	27	Kajaani
E	1911–1986	$y = 0.765x + 36.78$	0.627	<0.001	30	Sodankylä, Kuusamo, Ivalo

### 3.2. Spring temperatures and snow cover related to the timing of spawning

The influence of the temperature conditions prior to spawning is hard to assess because the depth of snow varies from year to year in different parts of the country and because there is no information of the period when the overwintering frogs can respond to the temperature changes in their surroundings. In order to correlate the mean temperature to the timing of spawning, I assumed that in zone A (Fig. 4) the mean air temperature of April may be important in this respect but that in zone E, where the ground is still snow-covered in that month the mean air temperature of May could be more important than that of April. The mean air temperatures of April are according to the measurements made in the meteorological station in Helsinki and they correlate highly significantly with the mean date of the records for the spawning in zone A. The two factors can be correlated over a period of 135 years ( $r = -0.698$ ,  $P < 0.001$ ,  $df = 133$ ). In zone E the meteorological data of May come from Inari and the corresponding correlation is based on data sets spanning 41 years. Again, the correlation is statistically highly significant ( $r = -0.638$ ,  $P < 0.001$ ,  $df = 39$ ). I conclude that temperature plays a role in modifying the timing of spawning of the common frog in Finland. On the other hand, the snow cover varies both annually and in different parts of the country, so that in the normal period (1931–60) the mean depth of snow in zone E is between 50 and 75 cm, but in zone A about 25 cm (Lavila 1975). As the amounts of heat needed to melt such dissimilar layers serving to insulate the underlying overwintering frogs cannot be equal, the changes in the temperatures taking place in different parts of the country at the same time probably also have an unequal impact upon the frogs. The period when frogs can respond to this factor is, however, difficult to assess. From this point

of view some other index not based on the changes or on any sum of temperatures from a given period might be more appropriate to relate the impacts of the temperatures in general upon the timing of spawning. This is why I have adopted the date when the ground was no longer permanently snow-covered and calculated linear correlation between it and the mean date of spawning in the five zones of Fig. 4. Table 2 shows that the correlation is highly significant in all the five zones, suggesting that the temperature relations as indicated by the disappearance of snow annually have a modifying influence on the timing of spawning for the common frog in Finland.

### 3.3. Changes in the timing of spawning during 1846–1986

Heino (1978) writes that “the worldwide increase in temperatures from the 19th century up until the middle of the present century and subsequent drop are clearly in evidence in Finland”. He concludes that “The improvement in the climate which began in the 19th century was pronounced in all the cases of the spring temperatures, amounting to a rise of the order of 2°C by the 1930s, after which spring temperatures have remained on average unchanged, or even risen very slightly, if one is to take into account the most recent years”.

Because the mean spring (March–May) temperatures have changed during the past some 150 years one may well ask whether these changes have also influenced the timing of spawning of the common frog populations in Finland. To study this I pooled the records according to the periods of ten-years, starting from 1846–1855 in zones A–E, as shown in Table 1. To show possible long-term shifts I calculated the moving averages over five successive periods in the diagrams showing the means for ten-year periods

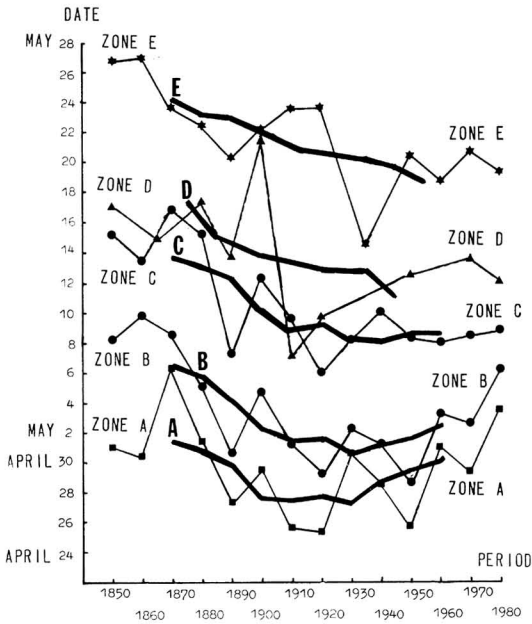


Fig. 8. Changes in the timing of spawning for the common frog (*Rana temporaria*) in Finland as indicated by the diagrams (thin lines) for the mean dates of the records in the ten-year periods indicated in Table 1 (1850=1846–1855, etc.). The zones (A–E) correspond to those in Fig. 4. Long-term shifts are indicated by the moving averages (bold lines, zones A–E) each calculated over five means of successive ten-year periods. See also the text.

(Fig. 8). The moving averages were obtained by first calculating the average over the means of the first five ten-year periods of the zone. Then the first mean was replaced with the mean of the 6th ten-year period in the same zone, and so on. I also worked out the corresponding diagrams and moving averages for the zones on the basis of the records for the first spawning of the year (Fig. 9). Fig. 10 demonstrates the mean temperatures of April and May in successive ten-year periods in Helsinki (zone A, see Fig. 4) and in Oulu (zone C) and the moving averages each calculated over five mean dates of spawning of the ten-year periods. Figs. 8–10 indicate that long-term changes have taken place in the timing of spawning of the common frog in Finland and these seem to correlate with the corresponding changes in the spring temperatures. In southern parts of the country the moving averages culminate, however, in about the 1930s or 1940s, while elsewhere the onset of spawning seems to have become more or less earlier all the time (Figs. 8–9). In Fig. 8 the range of the

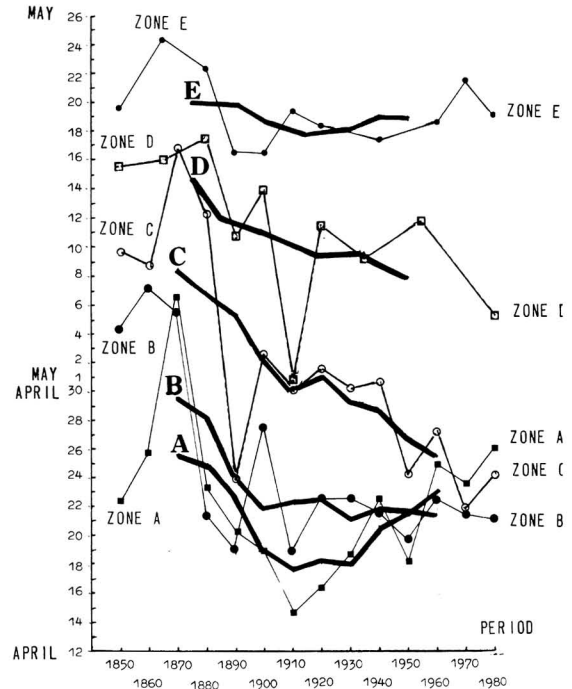


Fig. 9. Changes in the timing of spawning for the common frog (*Rana temporaria*) in Finland as indicated by the diagrams (thin lines) for the means of the first spawning of the year within zones A–E (see Fig. 4.) in the periods of ten years shown in Table 1 (1850=1846–1855, etc.). Long-term shifts are indicated by the moving averages (bold lines, zones A–E) each counted over five means of successive ten-year periods. See also the text.

moving averages is 4.0–6.5 days in the five zones, while in Fig. 9 the corresponding range is 2.0–13.0 days.

## 4. Discussion

### 4.1. Quality of observations

The calling of male frogs was taken as an indication of the onset of spawning at breeding sites, but in many records the presence of eggs was also indicated. Most observations may in fact not refer to the very first date for either the calling of males or oviposition. It is worth recalling that males can keep calling for some time after all the females have deposited their eggs. The records concerning that period are naturally too late to indicate the timing of spawning.



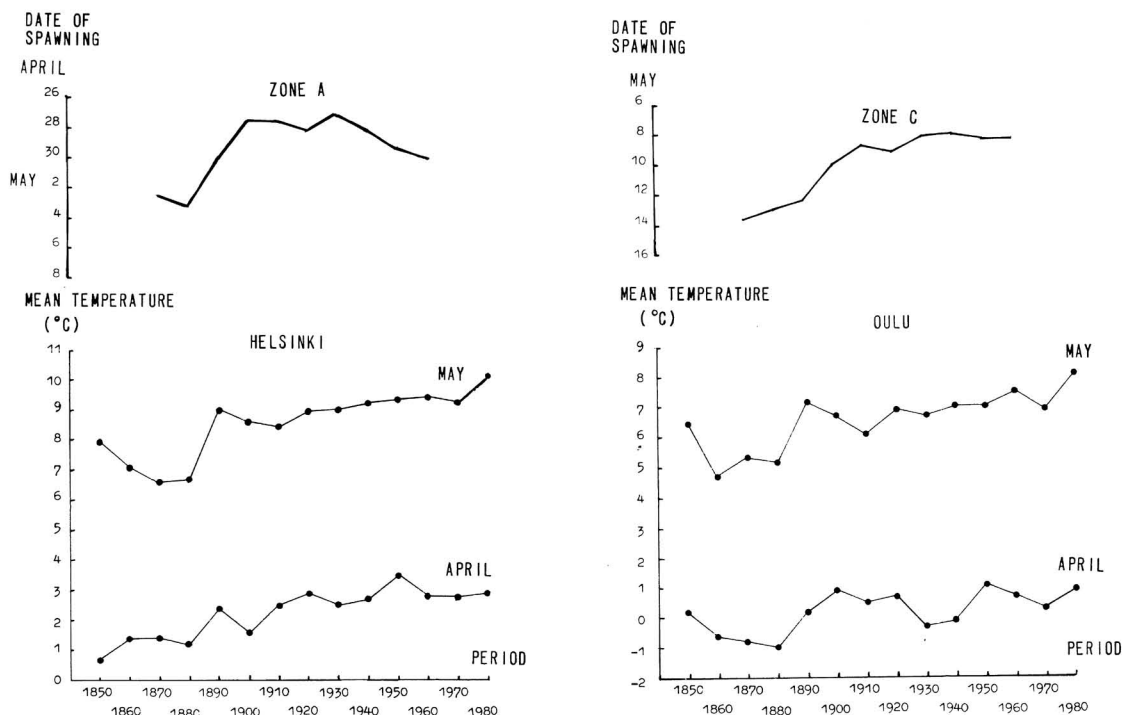


Fig. 10. The mean air temperatures of April and May in Helsinki (zone A, Fig. 4) and Oulu (zone C) in periods of ten years and the moving averages for the mean date of spawning in the common frog (*Rana temporaria*). Each moving average is counted over five successive ten-year periods. The periods are like those in Figs. 8 and 9.

In the study material for the spring of 1983 there are several records indicating the onset of spawning in periods when the air temperature was continuously below zero, as well as those records that are so late, i.e. refer to the second half of May in southern parts of Finland, that I consider them to be more or less dubious. However, in adopting the median to indicate the timing of spawning, these records have a negative effect on each other and this explains why I have used all the records for the analysis indicated in Fig. 7.

The efficiency of the contributors in making observations in the field can also vary annually, but this is a difficult factor to assess.

Some records indicating late dates of spawning may in fact refer to the common toad (*Bufo bufo*), which begins to breed in Finland about two or three weeks later than frogs. Were the number of such records high, the frequency distributions of the observations should show two peaks or at least they should be negatively skewed. This was, however, not observed in any of the zones (Fig. 5).

Another inaccuracy which could not be avoided in the present study is that some of the records evidently refer to the moor frog (*Rana arvalis*). It may be worth recalling that it was only four years prior to the beginning of the study period when S. Nilsson, who 'discovered' the moor frog, described it in Sweden as being new to science (cf. Gislén & Kauri 1959). Not until the past few decades have a considerable number of records of this species in Finland been made (Terhivuo 1981). The two *Rana* species, however, have much the same range and they spawn in the same waterbodies at about the same time in the study area. I assume that this inaccuracy in observations has caused little systematic bias to the indices of the timing of spawning because there is no reason to assume that the records of the moor frog are confined to some definite areas or periods.

The indices adopted, namely the first spawning of the year and the mean (also median) date of spawning, are unequally affected by the quality and the total numbers of records. For instance, if the date of the



first spawning of the year is more or less dubious (but hard to assess in that respect) the other records cannot "correct" it. One can also expect that the more records that come from the same square the earlier the date that can be expected for the first spawning of the year. By adopting the mean and the median dates some of these discrepancies can be avoided, but the latter two indices always show a delay to the corresponding mean of the records for the first spawning of the year. This delay in zone A is seven days (both the mean and median considered), in B nine, in C eight, in D three (mean) to four (median), and in E four (median) to five (mean) days.

#### 4.2. Endogenous factors related to the timing of spawning

Laboratory experiments with the common frog kept under identical conditions show that spermatogenesis and ovulation are governed by an endogenous rhythm that is locally adapted (Juszczyk 1959, Juszczyk & Zamachowski 1965, Van Oordt 1960, Koskela & Pasanen 1975, Harri & Koskela 1977). For instance, at lat. 64°N in Finland the common frog ovulates in the second half of April, but oviposition takes place about two weeks later (Koskela & Pasanen 1975). One can state that in the primary sense the onset of spawning is governed by an endogenous rhythm, but the present study material shows that extrinsic factors have a highly modifying effect on the timing of spawning.

#### 4.3. Extrinsic factors related to the timing of spawning

Koskela & Pasanen (1974) concluded that adults of the common frog start to emerge from their wintering sites in spring after the breaking up of the ice, when the mean air temperature by day reaches the level of +5°C. In lat. 64°N oviposition takes place about one week later than emergence (Koskela & Pasanen 1975). Considering the curves indicating the normal date for the beginning of the growing period in 1931–60, i.e. the date when the daily mean air temperature rises above +6°C in Finland (see e.g. Johannesen 1970, p. 54) or that (+5°C) for the period of 1921–50 (Kolkki 1960, map 5:9) the beginning of the growing period in coastal parts of the southern Finnish mainland and in the Åland archipelago in SW Finland takes place about 5–10 days later than in the nearby areas of the inner parts of the mainland. Probably the joint impact of different environmental

(topography, position, latitude) and climatic (continentality, depth of snow cover) factors contribute to the variation so that any definite level of the daily mean air temperature may not alone indicate the onset of spawning.

Beattie (1985) proposed a theory that the common frog in northern England becomes sensitive to environmental temperatures at about the middle of February and emerges in the spring after experiencing a temperature-sum of 106 degree(C)-days. The onset of sensitivity in this respect may be governed by an endogenous rhythm that can be locally adapted. In Finland snow cover modifies the impact of the sum of temperatures as well. For instance, the snow cover is thinnest and also disappears first and thus allows an earlier onset of spawning, in the areas that are hatched in Fig. 3 (compare to e.g. Kalliola 1951, Lavila 1975) than e.g. in areas where the beginning of the growing period takes place first. Air temperatures can be higher in the inner parts of the Finnish mainland where the sea has no ameliorating influence upon them. Despite this, spawning starts in most years in the hatched area of Fig. 3.

In Finland a stiff night frost may cover the spawning sites with ice so thick that despite rather high air temperatures in the daytime, spawning sites may remain covered. Such frosts also slow down the rate of the disappearance of snow. On the other hand, periods of stiff frost can occur after the disappearance of snow and in such springs the date of the disappearance of snow is not in accordance to the onset of spawning.

My observations in the field indicate that on windy days spawning may be suppressed, especially if the air temperature is not much above zero. Koskela & Pasanen (1974) demonstrated that during rainy periods the emergence of frogs from wintering sites may take place at rather low temperatures and this may enhance an early onset of spawning. On the other hand, rainfall is at its minimum in Finland in springtime and accordingly the number of rainy days is low then, too. Windy and rainy days may influence the onset of spawning in some years but they hardly play any major role in the timing of spawning or in the synchronization of the endogenous rhythm in general.

The eastern parts of Finland are in general more elevated and the climate there is more continental and the snow cover thicker than in western parts of the country at the same latitude (Lavila 1975, Abrahamson et al. 1977). This appears to explain why the zones (Fig. 4) or the isochrones (Fig. 6) are not parallel to the latitudes.

In the spring of 1983 the onset of spawning took place in less than three weeks, i.e. very quickly in different parts of the country. This is in accordance with the early disappearance of snow (3 April) that took place in 1983 in Helsinki when the mean date for melting in 1893–1986 is 16 April. In Kajaani (see Fig. 4) the snow disappeared in the same year from open fields on 24 April, whereas the mean date in 1911–1986 is 1 May.

#### 4.4. Comparison of the chronological pattern with the data in other references

Moberg (1857) reported the following mean dates of spawning for the period prior to 1850. 23 April (Åland area, squares 660:10 and 670:10 in zone A) 26 April (Turku area, 660:20 and 670:20/A), 25 April (W-Uusimaa, 660:20 and 660:30/A), 3 May (S-Häme, 670:30/B), 15 May (Kuopio area, 690:40 and 700:40/C), 18 May (Hailuoto-Oulu area, 720:30 and 720:40/C), 22 May (Kuusamo-Rovaniemi area 730:50 and 730:40/E) and 7 June (Utsjoki, 770:50/E). Moreover, Koskela & Pasanen (1975) indicates 9 May as being the mean date for the onset of spawning in Haapavesi (710:40/C) in 1968–73.

Comparing these dates to those in the corresponding squares in Fig. 4, the mean of the differences is 3.6 days (the sign of the differences ignored). In nine of the squares the corresponding dates are later, in five they are earlier and in one the date is the same as those in Fig. 4. In the case of an area comprising two squares I considered the average of the mean dates of the squares in the comparison. Considering the variation in the dates for the onset of spawning within the zones, I conclude that the data in earlier references are in accordance with those in Fig. 4.

In Krakow (lat. 50°N) spawning takes place in the 2nd half of March (Juszczyk 1959) and in Haapavesi, Finland (lat. 64°N) in the 1st half of May (Koskela & Pasanen 1975), indicating a difference of about six weeks, i.e. three days/degree of latitude. For Finland (lat. 60°N–70°N) the earliest and latest mean dates in

Fig. 4 show a mean difference of 3.5 days/one degree of a latitude.

#### 4.5. Long-term changes in the climate related to the timing of spawning

The improvement in the climate since the beginning of the 19th century is evidenced both in Scandinavia (Johannesen 1970) and on a global scale (e.g. Wigley 1986). During this time span great changes both in the geographical ranges and in the abundances of many plant and animal species have taken place in Finland (see e.g. Kalela 1952, Erkamo 1978). Today the carbon dioxide concentration of the atmosphere is increasing due to the activities of man. "The greenhouse effect" is as being responsible for a rise in the mean annual temperature by about 0.5–1.5°C by the beginning of the 2000s (Wigley 1986). According to Figs. 8–10 the timing of spawning for the common frog has changed during the past 150 years or so and these changes correlate to those observed in the spring temperature relations as noted by the disappearance of snow. Because the improvement of the climate seems to be continuing, I consider that records on the timing of spawning in different amphibian species should be made continuously, so that in the future they will provide valuable material for comparative purposes in this respect.

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## References

- Abrahamsen, J., Dahl, E., Jacobsen, N. K., Kalliola, R., Pålsson, L. & Wilborg, L. 1977: Naturgeografisk regionindelning av Norden. — NU (B): 34:1–137.
- Beattie, R. C. 1985: The date of spawning in populations of the Common Frog (*Rana temporaria*) from different altitudes in northern England. — J. Zool. Soc. London (A) 205:137–154.
- Erkamo, V. 1978: Phytobiological consequences of climatic changes in Finland during recent decades. — Fennia 150:15–24.

- Gislén, T. & Kauri, H. 1959: Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. — *Acta Vertebratica* 1(3):197–397.
- Harri, M. N. E. & Koskela, P. 1977: Terms of spawning in southern and northern Finnish populations of the Common Frog, *Rana temporaria* L. under laboratory conditions. — *Aquilo* (Ser. Zool.) 17:49–51.
- Heikinheimo, O. & Raatikainen, M. 1971: The recording of localities of biological finds in Finland. — *Ann. Entomol. Fennici* 37(1a):9–12.
- Heino, R. 1978: Climatic changes in Finland during the last hundred years. — *Fennia* 150:3–13.
- Johannesen, T. W. 1970: The climate of Scandinavia. — In: Wallén, C. C. (ed.), *Climates of northern and western Europe*. — *World Surv. Climatol.* 5:23–79.
- Juszczyk, W. 1959: The development of the reproductive organs of the female Common Frog (*Rana temporaria* L.) in the yearly cycle. — *Ann. UMCS, Lublin* 14:169–231.
- Juszczyk, W. & Zamachowski, W. 1965: Terms of ovulation and oviposition of the Grass Frog (*Rana temporaria* L.) in conditions of artificial and prolonged hibernation. — *Acta Biol. Cracov.* (Ser. Zool.) 8:211–223.
- Kalela, O. 1952: Changes in the geographic distribution of Finnish birds and mammals in relation to recent changes in climate. — *Fennia* 75:38–51.
- Kalliola, R. 1951: Suomen luonto vuodenaikojen vaihteluissa. — 388 pp. Porvoo, WSOY.
- Kolkki, O. 1960: Climate II, maps 1–9. — In: Aario, L. (ed.), *Suomen Kartasto*. Otava, Helsinki.
- Koskela, P. 1973: Duration of the larval stage, growth and migration in *Rana temporaria* L. in two ponds in northern Finland in relation to environmental factors. — *Ann. Zool. Fennici* 10:414–418.
- Koskela, P. & Pasanen, S. 1974: The wintering of the Common Frog, *Rana temporaria* L., in northern Finland. — *Aquilo* (Ser. Zool.) 15:1–17.
- Koskela, P. & Pasanen, S. 1975: The reproductive biology of the female Common Frog, *Rana temporaria* L., in northern Finland. — *Aquilo* (Ser. Zool.) 16:1–12.
- Lavila, T. O. 1975: Die Schneehöhe in Finnland, Norwegen und Schweden, gegliedert nach Regionen und Monaten in der Normalperiode 1931–1960. — *Nordia* 1975(2):1–70.
- Moberg, A. 1857: Om de ifrån år 1750 till år 1850 i Finland gjorda naturhistoriska daganteckningar och deras betydelse i klimatologiskt hänseende. — *Bidr. Finlands Naturkännedom, Etnokgr. Stat.* 2:87–113.
- Pasanen, S. & Koskela, P. 1974: Seasonal and age variation in the metabolism of the Common Frog, *Rana temporaria* L. in northern Finland. — *Comp. Biochem. Physiol.* 47(A):635–654.
- Savage, R. M. 1961: The ecology and life history of the Common Frog (*Rana temporaria temporaria*). — 221 pp. Pitman, London.
- Terhivuo, J. 1981: Provisional atlas and population status of the Finnish amphibian and reptile species with reference to their ranges in northern Europe. — *Ann. Zool. Fennici* 18:139–164.
- Van Oordt, P. B. J. 1960: The influence of internal and external factors in the regulation of the spermatogenic cycle in Amphibia. — *Symp. Zool. Soc. London* 2:29–52.
- Wigley, T. M. L. 1986: Testimony to the U. S. Senate on the greenhouse effect. — *Climate Monitor* 15:69–77.

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