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Circadian rhythms of locomotor activity in aquatic organisms in the subarctic summer

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Eight years investigations of diurnal and seasonal rhythmic behaviour in fishes, insect larvae, emerging of aquatic insects and flying activity of insects at Messaure Biological Station (66°42'N, 20°25'E) have shown that the locomotor activity of evertebrates and fishes living in running water are not synchronized with the 24 hour light dark-cycle during a period around midsummer. These organisms may have a desynchronized or an arhythmic activity spread over the whole 24 hour period or an organized activity — endogenous, free-running circadian rhythm. Desynchronization and free-running circadian periodicity under natural conditions have been found only in organisms living in water or soilnear habitats, with reduced amplitude of water temperature and light intensity. On the other hand all periodical phenomenon of air living organisms investigated, such as emerging and flying, of water insects, are synchronized with 24 hour cycle even under midsummer conditions.

I. Introduction

In nearly all organisms the daily light-dark cycle determines the alternation of activity and rest. This basic property of the daily periodicity in plants and animals has been demonstrated in numerous experiments (Cloudsley-Thompson 1961, Aschoff 1962, Remmert 1965 b, Bünning 1967). In the arctic and antarctic regions extreme light conditions are met with around the winter and summer solstices. These times of the year are characterized by a reduction of the zeitgeber strength for both day-active and night-active organisms. The effect of the zeitgeber on circadian rhythms disappears more rapidly with an extreme reduction of the duration of darkness, than with an extreme reduction of the duration of light (Bruce 1960, Aschoff 1963). This explains why in the subarctic regions desynchronization has been found more often in summer than in winter.

The literature on circadian periodicity in the subarctic summer is controversial. Remmert (1965 a) conclused from his studies in northern Norway and Spitzbergen, that all animals studied are capable of perceiving the 24-hour rhythm in the environmental conditions, and thereby of synchronizing their endogenous clock with the earth's rotation. Contradictory results are reported by other authors. Erkinaro (1969 b) has shown a free-running circadian rhythm in a wood mouse (*Apodemus flavicollis*), persisting for 76 days in summer at a locality 100 kms south of the arctic circle. In Messaure, 20 kms north of the arctic circle, free-running circadian rhythms in midsummer were demonstrated in four species of fishes: Minnow (*Phoxinus phoxinus*, Müller 1968), Brook trout (*Salmo trutta*, Müller 1969), Sculpin (*Cottus poecilopus*, Müller 1970 a) and Speckled trout (*Salvelinus fontinalis*, Eriksson 1972). Aschoff (1967) has stated that circadian rhytms are never free-running under natural conditions unless in very special circumstances. The latter are probably realized in the subpolar regions of the earth.

According to the observations hitherto made in aquatic animals, the freeruns observed can be considered exceptions rather than a general rule. In fishes, free-running circadian rhythms have occured so far only during prolonged periods of bright weather in midsummer. In Alaska, Swade & Pittendrigh (1967) observed free-running rhythms in *Clethrionomys rutilus*, and reported further: "When the amplitude of the light cycle was insufficient to entrain an animal, "oscillatory freeruns" were frequently observed, i.e., as an organism's rhythm free-run across the light cycle, its period changed systematically."

On other hand, most species native to the subarctic region show aperiodic patterns around the summer solstice. This was demonstrated first by Peiponen (1962) in the vole *Clethrionomys rufocanus* in Kilpisjärvi (northern Finland, 69°N,21°E). Animals of this species had no systematic alternation of activity and rest from the start of the experiments (Mid-June) untill the beginning of August, when the daily periodicity returned with activity concentrated in the lengthening night.

The present study reviews the responses of the daily periodicity to subarctic summer conditions as found in a number of aquatic organisms in Swedish Lapland.

II. Investigation area and methods

The experiments reported were carried out in the Kaltisjokk, a woodland stream (»jokk») near Messaure (66°42'N,20°25'E), and in the Messaure Biological Station in Swedish Lapland.

The methods used in the assay of biological rhythms have been described previously in the following publications: Müller (1965, 1966 1970 c): locomotor activity of invertebrates in fresh water currents; Kureck (1969), Thomas (1970): Eclosion rhythms of water insects; Müller & Ulfstrand (1970): Flight activity of water insects; Müller & Schreiber (1967): Locomotor activity of fishes.

III. Abiotic factors in the subarctic region

1. Environmental parameters measured

Some of the major abiotic environmental parameters were continuously recorded with help of the following equipment:.

a. Water temperature: Lambrecht Fernthermograph
b. Air temperature: Lambrecht Meteorograph
c. Solar irradiation: Kipp Solarimeter, with integrator. The sensor of the solarimeter was mounted on the roof of the laboratory building and kept snow-free by a ventilator (2500 r/min), producing an air current over the surface of the sensor.
d. Daily times of 5 lux light intensity: ART

twilight relais, connected to an Esterline — Angus event recorder.

e. Measurements of light intensity: Lange Standard II Lux-meter with selenium photocell.

2. The daily course of water and air temperature

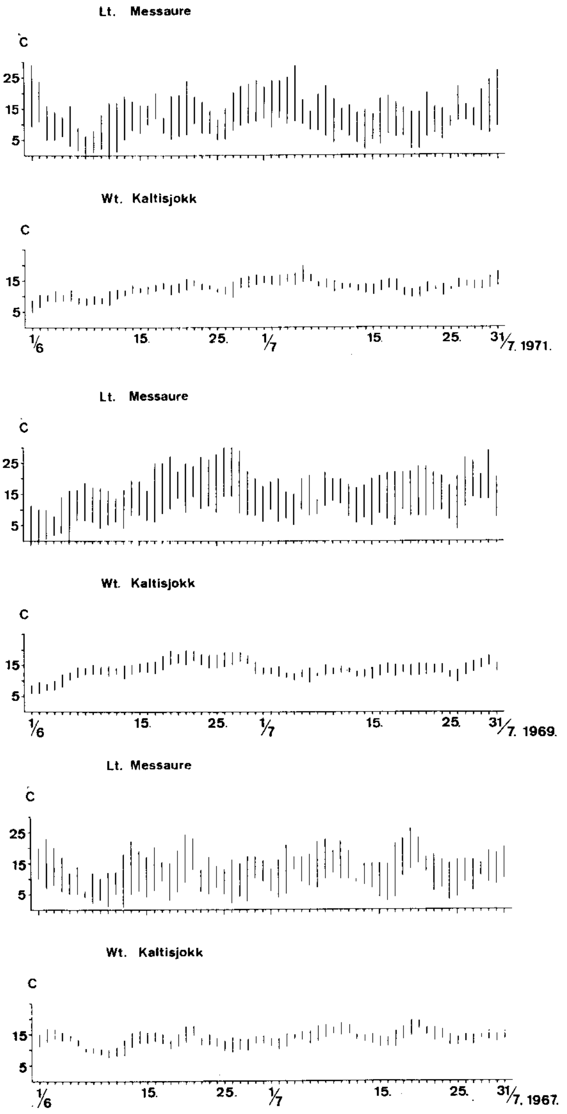
Figs. 1,2 and 3 show the daily maxima and minima of the air temperatures and Kaltisjokk water temperatures recorded from June 1 to July 31 in 1967, 1969 and 1971. As is to be expected, the daily amplitudes of air temperature (maximum amplitude 22°) are considerably higher than those of water temperature (maximum amplitude 6°C).

3. Solar irradiation

The caloric values of solar irradiation were integrated over 1-hour intervals and printed out by an Elmeg count-printer. Fig. 4 shows the monthly averages (cal/cm²/day) for one year. It is clear that arround the winter solstice no measurable solar irradiation occurs in Messaure.

4. Time of the 5-lux light intensity

In the majority of the organisms we studied, onset and end of the daily activity periods usually coincide with light intensities in the region of 1 to 10 lux. Therefore, we recorded the times of day when light intensity passed the 5-lux threshold. This produces a better reference point for the light-dark cycle than a fixed solar altitude (e.g., sunset or sunrise), due to the long twilights in the subarctic. The records obtained during seven years are in good agreement with each other. Light intensity remains larger than 5 lux throughout day and night from May 16—20



Figs. 1—3. Daily ranges of air temperature (Lt Messaure) and water temperature (Wt Kaltisjokk) in June and July of the years 1967, 1969 and 1971, respectively.

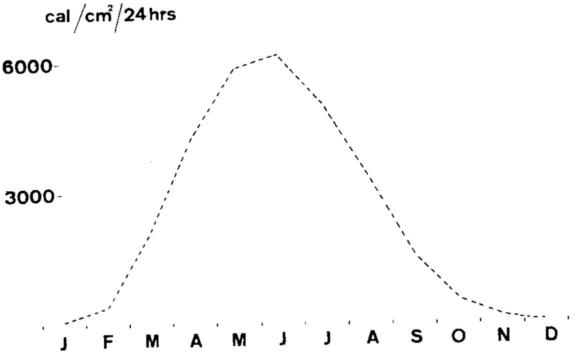


Fig. 4. Monthly mean values of the solar irradiation (cal/cm²/24 hrs) in Messaure in the period from May 1, 1972 until April 30, 1973.

until July 16—20. Thus, there is an average period of 60 days (35 days before and 25 days after the summer solstice) during which the daily minimum intensity is higher than 5 lux. Fig. 5 shows the daily times at which the 5 lux threshold was passed in the course of the year 1972.

5. The daily course of light intensity

Examples of the daily course of light intensity in Messaure are shown in Fig. 6 A (Midwinter) and Fig. 6B (Midsummer). The recordings were made from a selenium photocell at the south side of the Laboratory. The maximum light intensity recorded in daytime was about 600 lux in midwinter and between 60.000 and 70.000 lux in midsummer. The minimum midnight light intensity was below the measurable range in midwinter and in the order of 500—600 lux in midsummer.

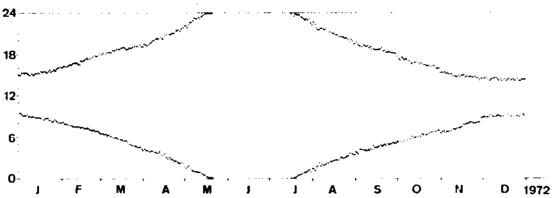


Fig. 5. Daily times of crossing of the 5 lux light intensity treshold in the laboratory at Messaure, as a function of time of year.

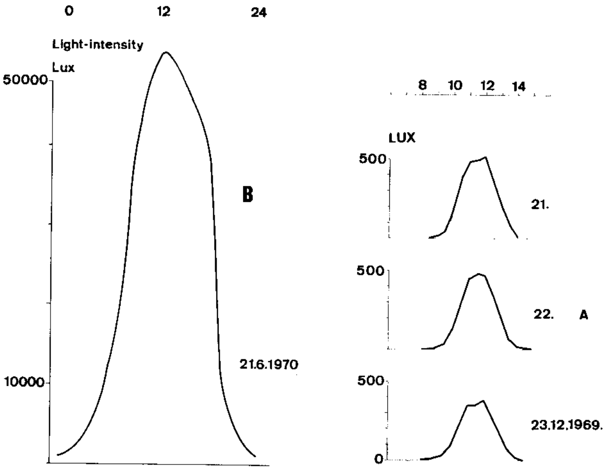


Fig. 6. Daily records of outside light intensity under midwinter (December 21—23, 1969) (A) and under midsummer conditions (B) (June 21/22, 1970) at Messaure.

IV. Results

1. Locomotor activity of insect larvae

Several authors (Tanaka 1960, Waters 1962, Müller 1963, Levanidova & Levandov 1965, Elliott 1965), working in different parts of the world, have demonstrated that the daily periodicity in the organic drift of invertebrates in streams is the result of the animals' daily rhythm of locomotor activity. Waters (1972) has given a comprehensive account of these phenomena.

The significance of the geographical position for the synchronization of the activity of insect larvae by the light-dark cycle, was first noted in experiments which we carried out at different latitudes in the summer 1963 (Müller 1966). The organic drift of the mayflie *Baetis rhodani* was simultaneously measured in central Europe (51°N), central Sweden (60°N) and northern Sweden (67°N). The results of these experiments are summarized in Fig. 7. It is readily apparent, that the pronounced daily periodicity occuring at lower latitudes is absent in the subarctic summer. Obviously, neither the daily light-dark cycle (amplitude c. 2 log units) nor the daily fluctuations in water temperature (amplitude in this experiment 5°C) is strong enough to synchronize the larvae to a 24 hr periodicity.

Continuous measurements of organic drift of the larvae of several species of insects in the Kaltisjokk were made 1965—66 during one yearly cycle. In the larvae of stoneflies (Plecoptera), mayflies (Ephemeroptera) and blackflies (Simuloidea) no daily periodicity was found in the time between June 10 and July 10 (Müller 1970 b,c). A weak periodicity has been demonstrated in the drift of mayflie larvae at 64°N in the river Rickleå, north of Umeå in northern Sweden (Södergren 1963).

The results obtained in the Kaltisjokk were confirmed by continuous records of activity of stonefly larvae *(Dinocras cephalotes)* in the laboratory. The animals were kept in a ring-shaped tank in a continuous water current, and their activity recorded by a red-light photocell detector (for method, see Müller & Benedetto 1970). In the period between June 16—18 and July 10 these larvae had arhythmic activity patterns (Fig. 8). During the remaining part of the year they were night-active and clearly synchronized (Müller & Thomas 1972).

2. Emergence activity of stream insects

Thomas (1970) has collected the "surface-drift" (Hunt 1965, Tobias & Thomas 1967) in the Kaltisjokk by means of an automatic sampler. He recorded the emergence activity of a great number of insect species, between May and October 1967. Fig. 9 shows the daily periodicity of emergence of three species of Ephemeroptera, emergence around midsummer: *Heptagenia sulphurea, Baetis pumilis*

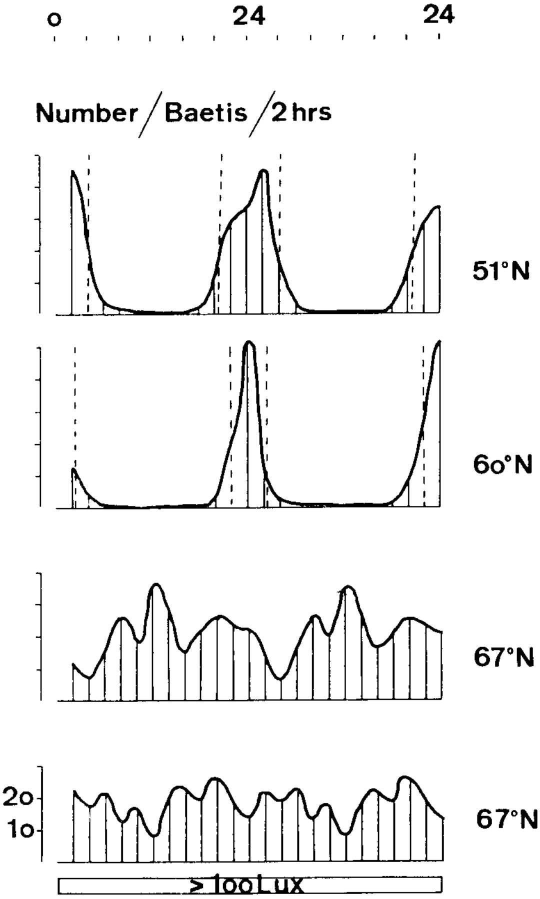


Fig. 7. Number of larvae of *Baetis rhodani* sampled in stream drift at different latitudes between June 20 and June 24, 1963. On the ordinate numbers per interval of two hours, averaged over two sampling days, are plotted. Localities from top to bottom: Breitenbach 50°40'N,9°40'E, stream near Lindesberg/Sweden 59°40'N,15°10'E, and left and right bank of the stream Tjatjesjokk, near Kvikkjokk (Swedish Lapland) 67°10'N,17°50'E.

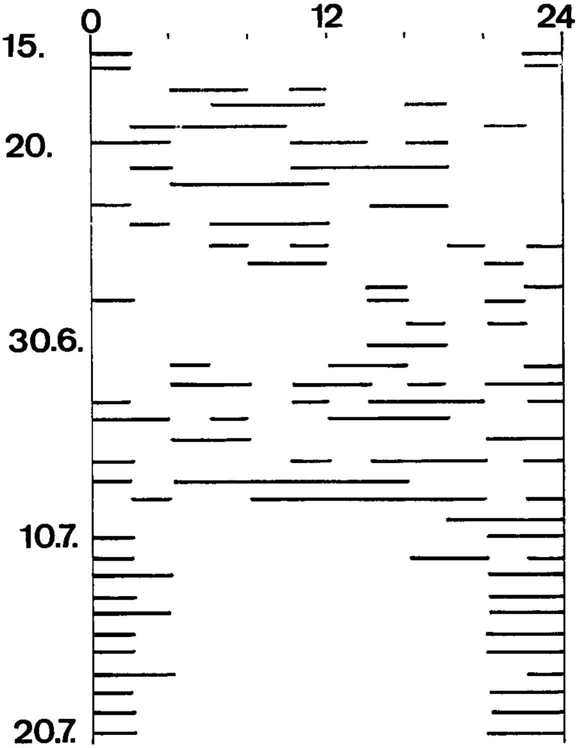


Fig. 8. Locomotor activity of a stoneflie larva, *Dinocras cephalotes*, in Messaure from June 15 until July 20, 1971.

and *Baetis macani.* Apparently, the process of emergence is even in midsummer synchronized with the daily cycle. Also in Plecoptera (Fig. 10), Trichoptera (Fig. 11) and in Simuloidea (Kureck 1969, 1972) there is a conspicuous species-specific daily periodicity of emergence.

3. Flight activity of stream insects

The daily periodicity in the number of flying imagines of water insects was analysed with automatic traps, taking 2-hourly samples with help of a ventilator, and without light attraction (method described by Müller & Ulfstrand 1970).

The stoneflie *Leuctra hippopus* has a pronounced daily maximum flight activity at c. 16:00 h (Fig. 12), coinciding with the emergence maximum (Fig. 10). Two trichopteran species studied, *Philopotamus montanus and Polycentropus flavomaculatus,* were caught in flight between 8:00 and 22:00. In *Plectrocnemia conspersa* flight activity is

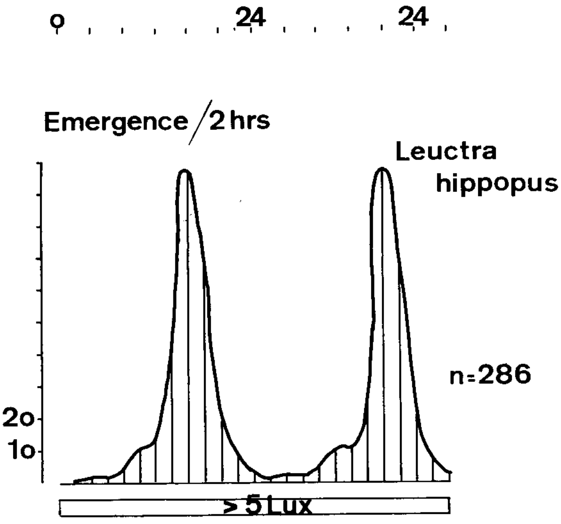


Fig. 10. Daily distribution of the number of emerging stoneflies, *Leuctra hippopus* in the Kaltisjokk, June 10—18, 1967. Redrawn from Thomas (1970).

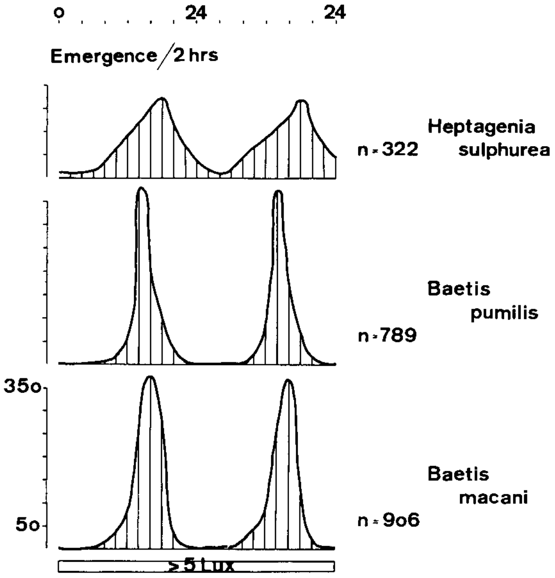


Fig. 9. Daily distribution of the number of emerging Ephemeroptera in the Kaltisjokk: *Heptagenia sulphurea:* June 20—25, 1967, *Baetis pumilis:* June 16—25, 1967, *Baetis macani:* July 1—10, 1967. Redrawn from Thomas (1970).

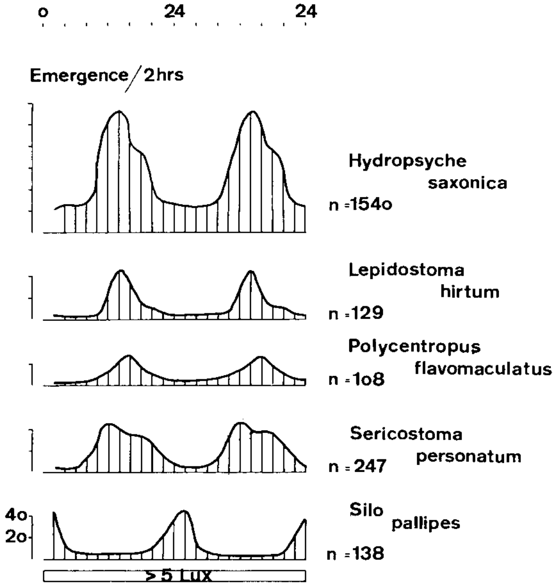


Fig. 11. Daily distribution of the number of emerging Trichoptera of five species: *Hydropsyche saxonica* (June 21—26, 1967), *Lepidostoma hirtum* (June 27—July 12, 1967), *Polycentropus flavomaculatus* (June 23—July 20, 1967), *Sericostoma personatum* (July 8—13, 1967) and *Silo pallipes* (July 4—8, 1967). Redrawn from Thomas 1970.

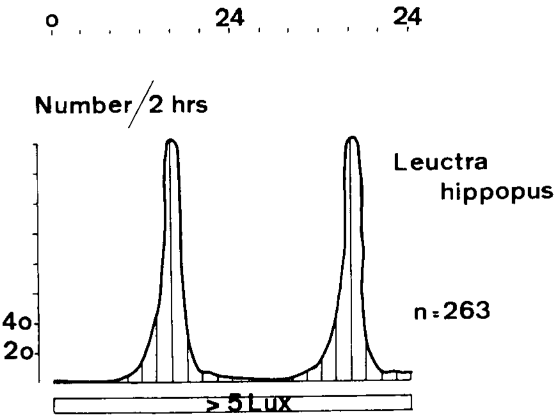


Fig. 12. Daily distribution of the number of flying *Leuctra hippopus* (Plecoptera) caught with a suction trap, May 25—June 6, 1969.

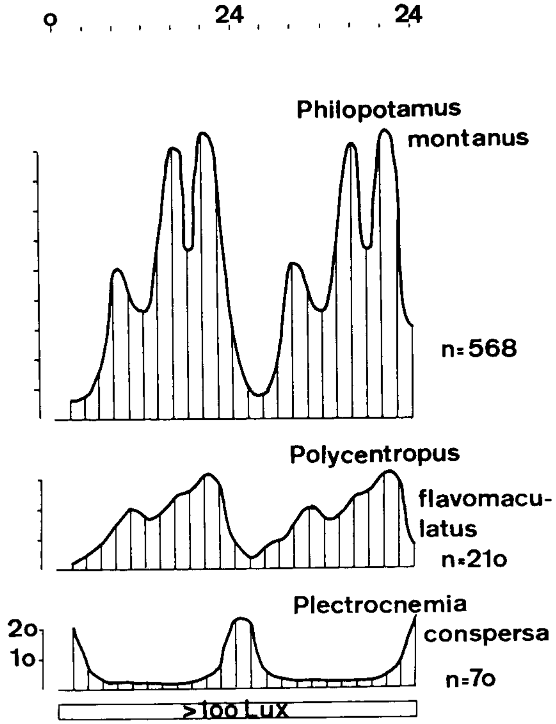


Fig 13. Daily distribution of the numbers of three species of Trichoptera caught with a suction trap near the Kaltisjokk: *Philopotamus montanus* (June 16—24, 1969), *Polycentropus flavomaculatus* (June 26—July 5, 1969) and *Plectrocnemia conspersa* (June 29—July 10, 1969).

concentrated in the night. According to our observations, these daily flight periods comprise different types of activity. Trichopterans caught in the traps before noon are quite often newly hatched animals. The evening catches are apparently connected with copulation flights.

Pericoma stammeri (Psychodidae) occuring in huge numbers around midsummer, was caught in the traps mainly in the evening (Fig. 14).

Two species representing the Sialidae, *Sialis morio* and *Sialis sordida* (Kaiser & Müller 1971) which were caught with the same traps in Finnish Lapland (Utsjoki 69°45'N,27°E) have their maximum flight activity around noon (Fig. 15).

The results of our studies on the flight activity of insects in the subarctic are in good agreement with studies by Nuorteva (1965 a, b, 1966) and Nuorteva & Hackmann (1970) on dipterans in northern Finland, by Syrjämäki (1969) on dipterans in Spitsbergen and by Mendl (1971) on Limoniidae in Messaure.

4. Activity patterns of day-active fishes

In the foregoing sections it was demonstrated that the different ontogenetic stages of water insects respond differently to the subarctic summer conditions. Also among fishes, differ-

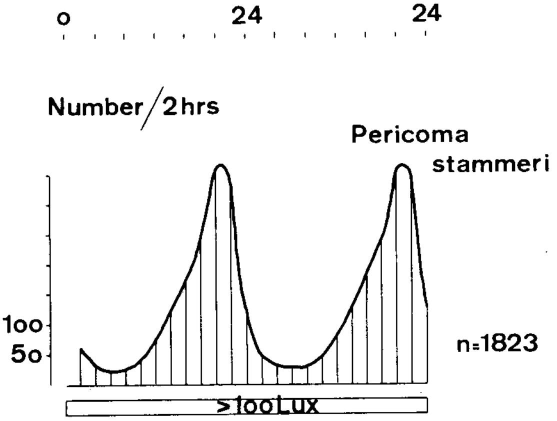


Fig. 14. Daily distribution of the number of flying *Pericoma stammeri* (Psychodidae) caught with a suction trap near Kaltisjokk (June 21—30, 1969).

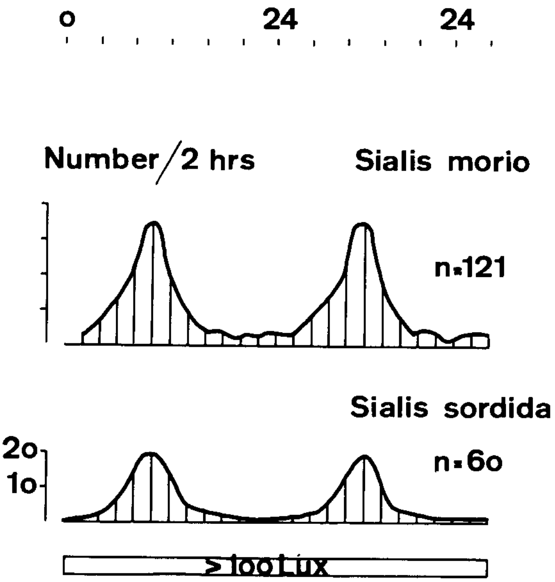


Fig. 15. Daily distribution of the number of flying Sialidae caught with suction trap near the west bank of the stream Utsjoki in northern Finland (69°45'N, 27°1'E).

ent responses to the reduced strength of the zeitgeber were found.

The cyprinid *Barbus partipentazona,* native to the indomalaysian tropics, was always synchronized to the natural light-dark cycle in Messaure, when kept in constant water temperature of 25°C (Figala & Müller 1972). Species native to the subarctic waters in Lapland had a less pronounced daily activity rhythm.

Coregonus lavaretus, a coregonid species with wide distribution in the waters of northern Europe, shows most clearly the effect of the reduced zeitgeber amplitude in midsummer. Fig. 16 contains the monthly averages over 1-hour intervals of lightbeam interruptions by one solitary fish in Messaure. In midwinter, the animal was day-active. From January onwards, the total amount of activity steadily increased, and in May the major portion of the activity was shifted into the night. With further increase of total activity in June, the daily periodicity in its distribution disappeared. The month July showed a slight tendence towards resynchronization, and from the end of July onwards the fish stayed synchronized. The occurence of activity in another specimen of the same species and age (2 years) is shown over a whole year (Fig. 17). The activity of this fish was synchronized with the light-dark cycle until May 10, i.e. shortly before the time when the 5-lux threshold is no

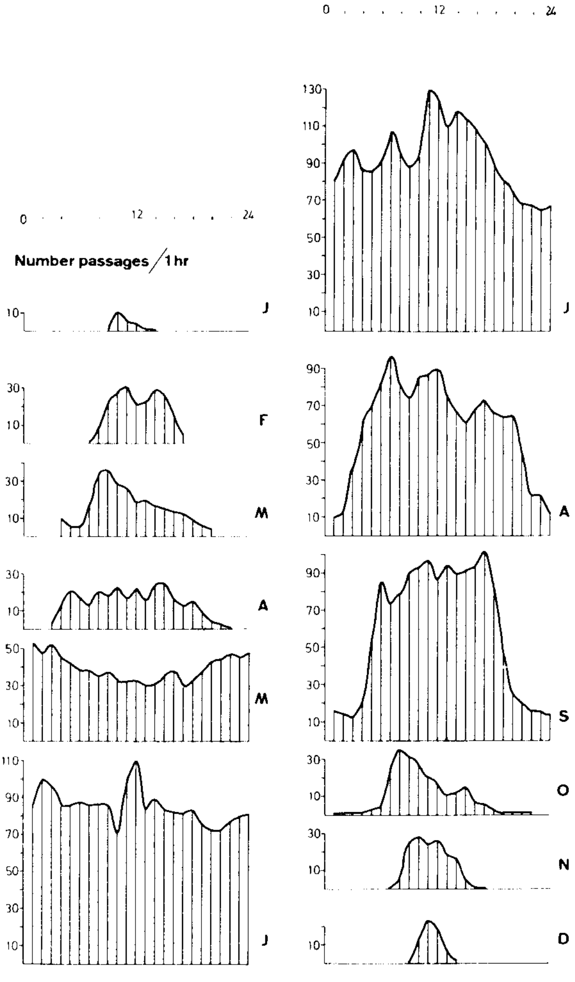


Fig. 16. Daily distribution of activity (mean number of passages per hour) of one specimen of *Coregonus lavaretus* kept in Messaure. Results from 352 days of undisturbed records of light-beam interruptions in 1971.

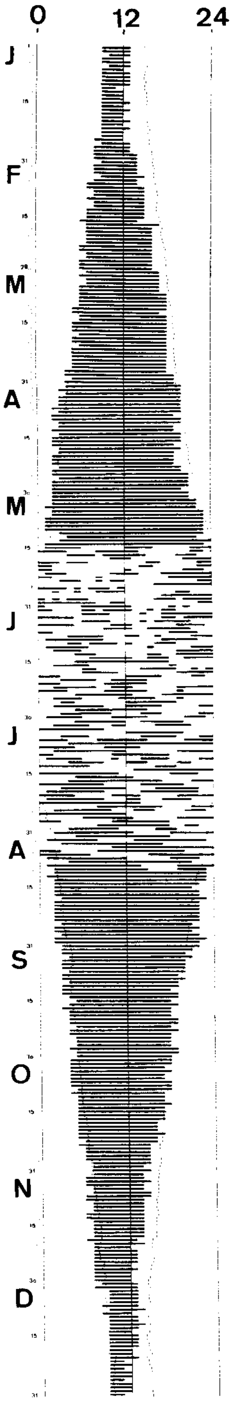


Fig. 17. Seasonal change of activity in a specimen of *Coregonus lavaretus* in Messaure in the course of 1971. For every day, the hours in which the number of recorded passages was above the daily average are marked with a horizontal black bar.

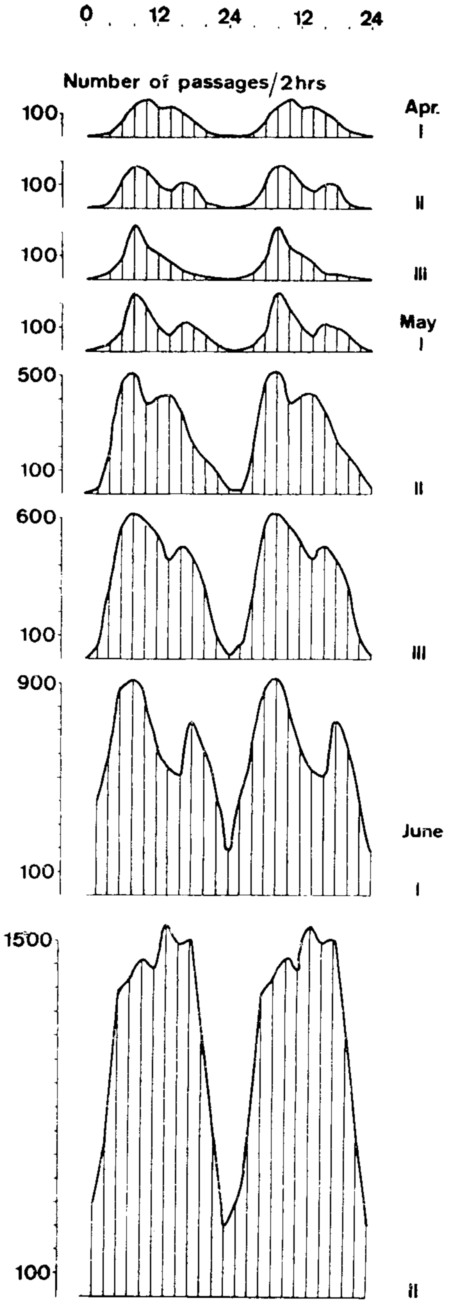


Fig. 18. Daily distribution of photocell passages in a specimen of *Coregonus lavaretus,* kept in Messaure from April 1, to June 20, 1972 in reduced natural daylight. Twohourly averages over period of 10 days are shown on the ordinate.

longer crossed during the night (May 16). From May 10 until August 5, we see an irregular distribution of activity. From August 5 onwards, the activity was again clearly synchronized.

Both specimens were studied in tanks placed close to the south-west windows of the laboratory. The maximum and minimum light intensities measured there in June were 20.000 and 200—300 lux, respectively. A third specimen of *Coregonus lavaretus* was studied in a tank placed further from the windows, where maximum and minimum intensities in June were 200 and 5 lux, respectively. The activity of this specimen was recorded from April 1 until June 20, and appear to be fully synchronized with the light-dark cycle until the summer solstice (Fig 18).

In Fig. 17 we can distinguish, in the second half of June and with returning synchronization in the second half of July, components in the activity which gradually shift towards the right, from the morning into the afternoon. For another specimen, the daily distribution of activity in such period with

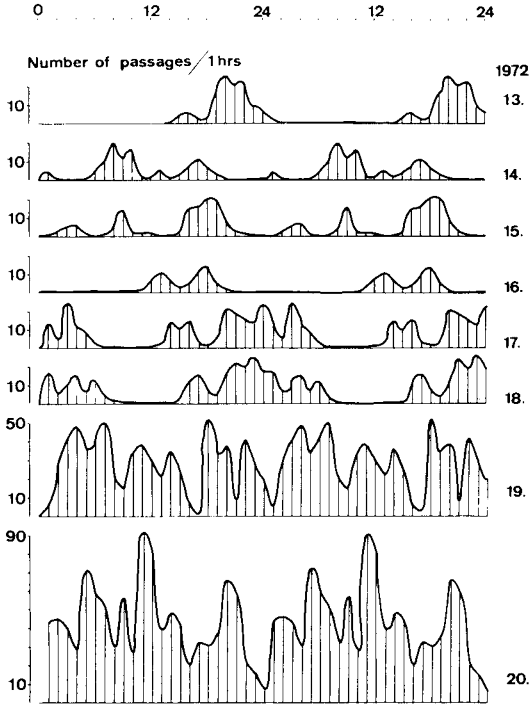


Fig. 19. Daily distribution of photocell passages per hour in a single specimen of *Coregonus lavaretus* in Messaure. June 13—20, 1972.

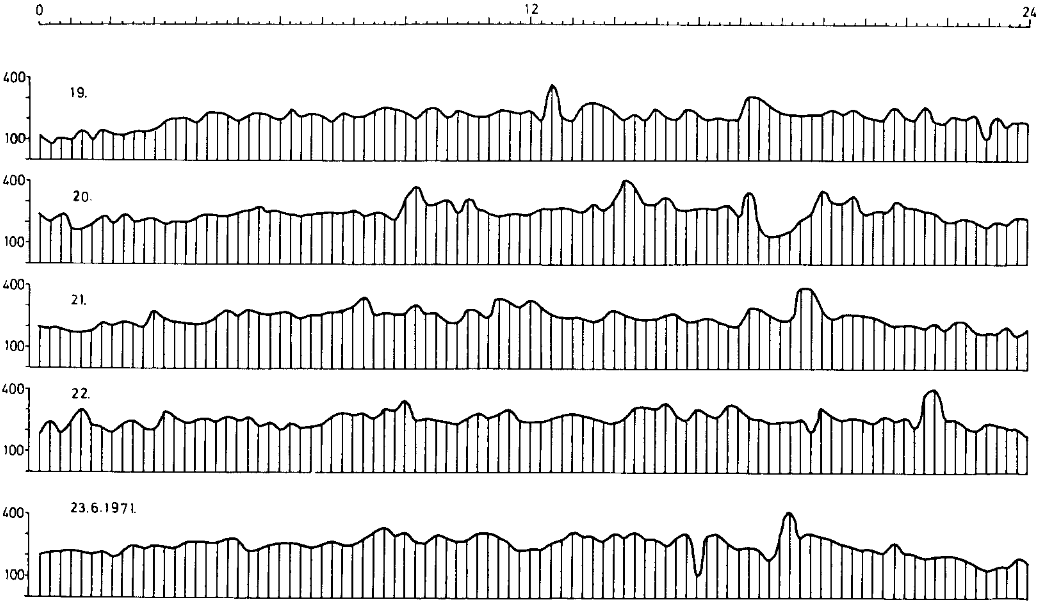


Fig. 20. Daily distribution of photocell passages per $1/4$ hour in a school of 100 *Coregonus lavaretus* in Messaure. June 19—23, 1971.

temporary freerun (June 14—20) is plotted in Fig. 19. Continuous free-running circadian rhythms producing phase shifts over more than 360°, as reported for minnows *(Phoxinus phoxinus,* Müller 1968) and speckled trout *(Salvelinus fontinalis,* Eriksson 1972) have not yet been detected in *Coregonus lavaretus.*

A school of 100 specimens of *Coregonus lavaretus* of the same age as the individuals studied solitarily was better synchronized by the zeitgeber. On June 9, 1972 this school still had a minimum of almost zero lightbeam interruptions around midnight. June 15—28 activity was arhythmically distributed over the 24 hours of the day. The number of interruptions per 15 min intervals in the period June 19—23 is shown in Fig. 20.

Similar arhythmicity in midsummer as in *C.lavaretus* is found in the minnow *(Phoxinus phoxinus),* as demonstrated by the activity distributions of a solitary specimen in March, June, September and December 1968 (Fig. 21).

5. **Activity patterns of night-active fishes**

All fish species that were studied so far in the subarctic and that are night-active in summer have the habit of shifting the phase of their activity over 180° relative to the zeitgeber two times per year. This means that they become day-active for a longer or shorter period in winter. This highly interesting phenomen has now been demonstrated in *Cottus poecilopus* and *Cottus gobio* (Andreasson & Müller 1969, Müller 1970 a, Andreasson 1972), *Myoxocephalus quadricornis* (Westin 1971) and *Lota lota* (Müller 1970 d). Evidently, these species of fishes have the potential of being either day-active or night-active, depending on seasonal variations in daylength, light intensity (Müller 1970 d) and other environmental factors. The activity patterns of the burbot *(Lota lota),* of which a large body of experimental data has accumulated will be discussed as an example.

The activity of one burbot, caught as a three-year old fish in the Kaltisjokk in the autumn of 1968 has been continuously recorded over three years. Fig. 22, 23 and 24 present the data from the summer half year of 1969, 1970 and 1971, respectively. It is seen that every year around May 10 the activity of the fish started to shift gradually from the early night into the afternoon. In each of the three years, periods with adverse weather conditions and reduced light inten-

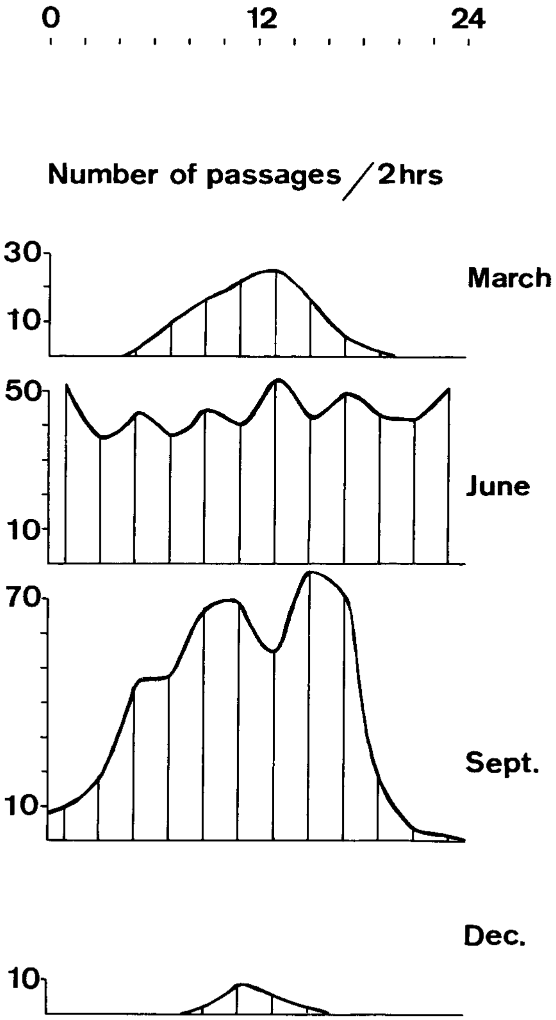


Fig. 21. Daily distribution of photocell passages per 2 hours in a single minnow (*Phoxinus phoxinus*) kept in Messaure. Monthly averages are shown for March, June, September and December 1968.

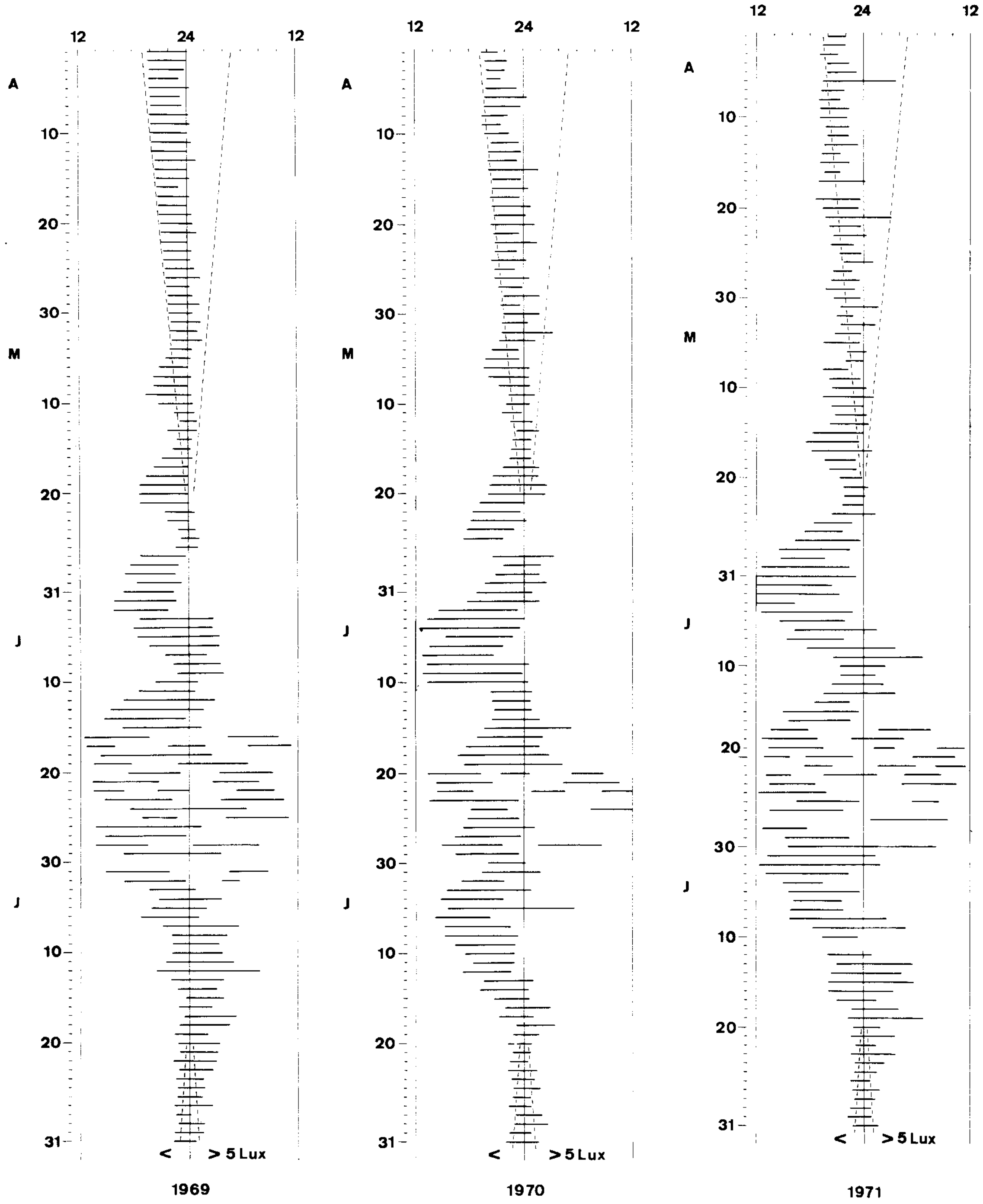


Fig. 22—24. Daily activity periods of a burbot (*Lota lota*) in three subsequent summers. The specimen was kept in a circular tank in Messaure for over three years.

sities resulted in backward shifts of the activity into the night. Around the summer solstice, between June 10 and June 30, the activity was always irregulary distributed over the 24 hours. Around the middle of July, the fish always resumed night-active pattern, in apparent synchronization with the light-dark cycle. The temporary advancing phase shifts in May 1969 and the loss of synchronization in June 1969 are shown in more detail in Figs. 25 and 26. In both cases the activity rhythm temporarily had a circadian period less than 24 hours.

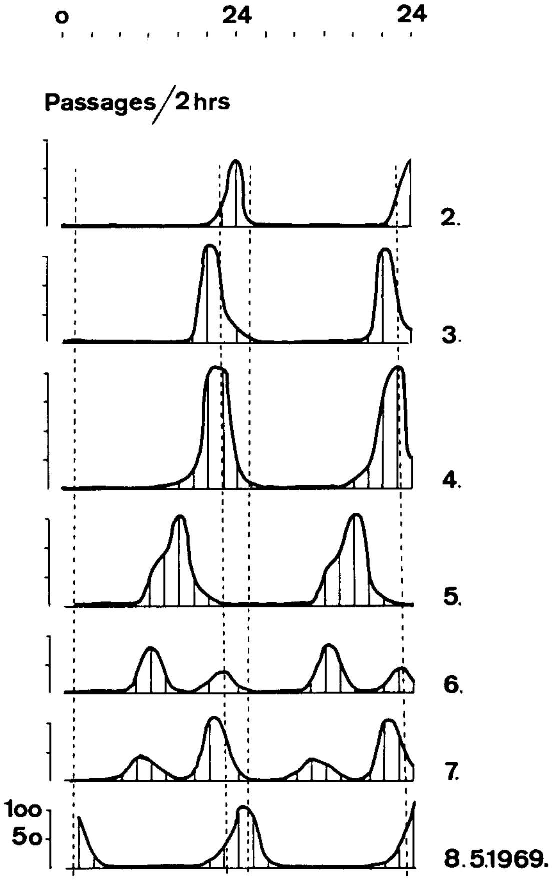


Fig. 25. Daily distribution of photocell passages per 2 hours in a single burbot, *Lota lota*, in Messaure. May 2—8, 1969. Dashed vertical lines connect the morning and evening times at which the 5 lux threshold was crossed.

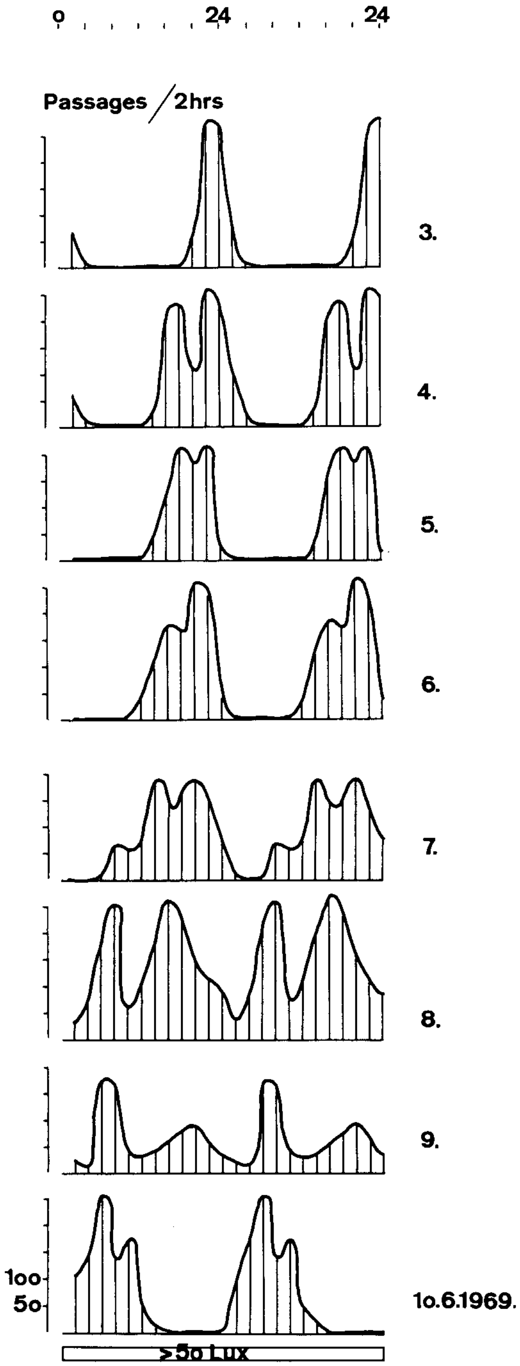


Fig. 26. Daily distribution of photocell passages per 2 hours in a single burbot, *Lota lota*, in Messaure. June 3—10, 1969.

Fig. 27 shows the daily activity distribution of a 4 -year old burbot in Messaure in the summer half year of 1972. In this animal advancing shifts of the activity started already in the end of April. However, the activity peak remained present in the midnight hours, except on the days around the summer solstice. Evidently, from the middle of July onwards also this animal was again synchronized and night-active. Fig. 27 demonstrates most clearly that the fish's activity was not fixed to a constant phase position during 56 days in the subarctic summer. The clear phase relationships in the beginning and end of the period of observation are in contrast with the arhythmicity in midsummer. It should be noted that the period of arhythmicity was not symmetric around the summer solstice. Loss of entrainment started 7 weeks before June 21, and entrainment was reestablished 4 weeks after June 21.

All burbots studied, both simultaneously and in different years, showed this general picture of arhythmic activity in midsummer. Solem (1973), studying juvenile burbot, has confirmed our results in experiments near Trondheim, Norway 63°N. Also at this lower latitude burbots were arhythmic during the summer months, with a minimum midnight intensity of 20 lux. Solem's animals were not sychronized by the natural light-dark cycle until the end of August.

V. Discussion

The contrasting opinions on the responses of animals to midsummer conditions mentioned in the introduction can now be reconsidered on the basis of long-term observations and activity records in a wide array of organisms.

The meteorological measurements made demonstrate the persistence of daily fluctuations in abiotic parameters around the summer solstice in the subarctic region. Yet it is open to question if these fluctuations are of large enough amplitude to be perceived by

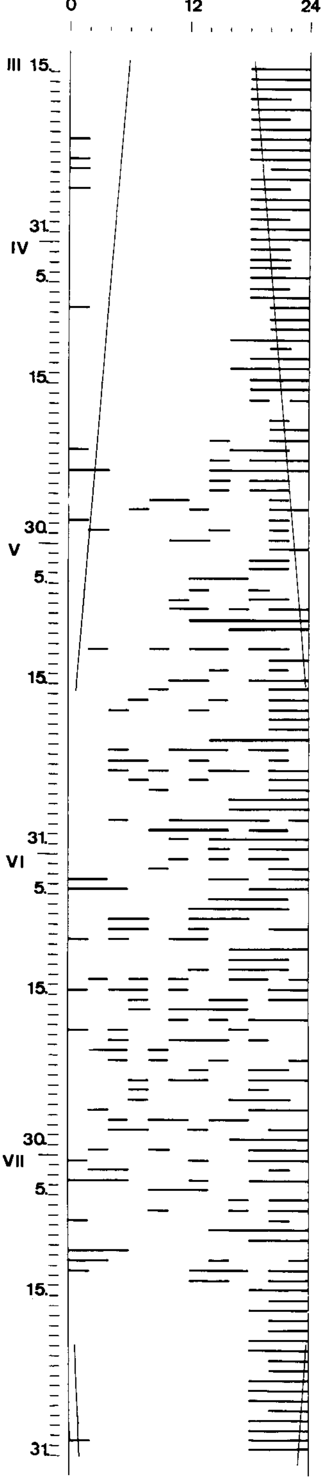


Fig. 27. The periodicity of activity in a single 4-year old burbot, *Lota lota*, in Messaure, from March 15 to July 31, 1969. Vertical lines: times of 5 lux light intensity. Horizontal bars mark the hours during which the number of passages was above the daily averages.

the organisms and to synchronize their circadian rhytms. It is known that a minimum strength of a zeitgeber is required to produce stable entrainment (Hoffmann 1969). For the daily light-dark cycle, zeigeber strength is dependent on (1) the amplitude of light intensity fluctuations, (2) the ratio of the duration of light and darkness and (3) the duration of twilights. All three parameters attain extreme values in the subarctic summer, with small daily amplitudes of light intensity, extremely long days and long twilights. All three tend to reduce zeitgeber strength toward midsummer, although Wever (1967) proposed that zeitgeber strength is greater with longer twilights. Sensitivity to the zeitgeber may, however, vary greatly among different species and among different development stages within a species.

There is one general impression emerging from the results reported here: Summer aperiodicity was found only among aquatic organisms, i.e., insect larvae and fishes, whereas all aerial insects were evidently either nocturnal or diurnal troughout midsummer. Thus, while larvae of mayflies (Ephemeroptera) and of the stoneflies (Plecoptera) *Dinocras cephalotes* and *Diura nanseni* had aperiodic activity over a period of four weeks, adults of the same species were clearly day-active.

It is unlikely that the aperiodicity found is due to low sensitivity of the methods of assay, as the studies on aquatic animals included such diverse methods as counting interruptions of light-beams in aquaria and automatic drift sampling in streams. The possibility can be completely excluded that more refined techniques would reveal slight daily periodicities in the activity of aquatic animals in the subarctic midsummer. But these would certainly turn out to be of much smaller amplitude than at other times of the year. On the other hand, unequivocal proof of the absence of synchronization is given in some cases by free-running rhythms with a period deviating consistently from 24 hours. Such evidence is available for the fishes *Phoxinus phoxinus* (Müller 1968) and *Salvelinus fontinalis* (Eriksson 1972), as well as for wood mice, *Apodemus flavicollis* (Erkinaro 1969 a, b).

That synchronization of the circadian rhythm fails in small rodents in the subarctic summer is further indicated by arhythmic activity in the voles *Clethrionomys rufocanus* and *C. rutilus* at 69°N, reported by Peiponen (1970). On the other hand, in a number of bird species at high latitudes, both in captivity (Palmgren 1944, Peiponen 1970, Daan 1973, Daan et al. 1973) and in nature (Palmgren 1935, Franz 1949) a clear daily activity rhythm was found. The difference between birds and aquatic animals in this respect may be related to lower sensitivity of the latter group to the light-dark zeitgeber.

In poikilotherms, apart from the light-dark cycle also the daily temperature fluctuations can play a role as a powerfull zeitgeber to entrain the circadian rhythm. The daily amplitude of temperature is much larger in air than in water. This difference may account for the difference in periodicity between aquatic and aerial insects mentioned above. Thus, some of the differences in midsummer rhythmicity found among species and developmental stages probably related to differences in habitat (aquatic versus aerial insects), and other to different sensitivity to the same zeitgeber-amplitude (mammals versus birds).

In the latter category, also systematic differences between animals native to the subarctic region and to lower latitudes belong. Among the fish species studied in Messaure, the cyprinid *Barbus partipentazona,* native to the indomalaysian tropics, was clearly day-active troughout midsummer (Figala & Müller 1972). Also *Salvelinus namaycush* a trout species living in North-America south of 50°N, and recently introduced in Scandinavian lakes, retained slightly more day- than night-active in summer. In contrast, all fishes of Lapland origin were either aperiodic or showed a free-running circadian activity rhythm.

This reminds of observation by Swade & Pittendrigh (1967) that in Point Barrow, Alaska (71°N) small rodents imported from lower latitudes (*Ammospermiphilus leucurus, Peromyscus leucopus)* were better synchronized than the local species. Similarly, tropical tree shrews (*Tupaia belangeri)* and temperate zone golden hamsters (*Mesocricetus auratus)* and flying squirrels *(Glaucomys volans)* remained synchronized at the arctic circle in midsummer (Aschoff et al. 1970, Daan 1973, Daan et al. 1973), while local voles and mice were aperiodic or free-running (Peiponen 1962, Erkinaro 1969 a, b).

In this connection, the hypothesis can be advanced that photoperiodic conditions at lower latitudes have led to the evolution of a more strongly developed circadian system than at high latitudes. It can be speculated that the temporal structure of behaviour in *Salvelinus namaycush* is involved in its unsuccessfull introduction into the waters of northern Scandinavia (Gönczi & Gad 1972).

Indeed, aperiodicity in midsummer may be of positive selective advantage in animals of the subarctic region. The summer period of organic growth is short, and it must be of great importance to the animal world to exploit all feeding opportunities at this time of the year. In streams, a bloom of algae presents a continuous food source for aquatic insect larvae throughout the day (Müller-Haeckel 1966, 1967, 1969, 1970, 1973 a, b). Feeding activity of these larvae, as reflected by their occurrence in the drift, is accordingly continuous or aperiodic, and so is the locomotor activity of fishes which in nature feed on the insects. In contrast, for the adult aerial insects, confronted with daily fluctuations in air temperature and relative humidity, it may be of positive survival value to retain a strong daily rhythmicity. At this stage of life, reproductive success is of more importance than efficient feeding, and probably requires good synchronization of the activity of males and females, both to each other and to the daily fluctuations in the abiotic environment.

It seems that life in habitats at high latitudes, with their characteristic temporal structure of the environment, would place a selective premium on a high flexibility of an organism's circadian system.

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