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Causes and effects of short emergence periods in insects

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With 1 figure in the text

The adults of many species of Plecoptera, Ephemeroptera, Odonata and Diptera are found only during a comparatively small part of the season that appears suitable for them. I am starting with the assumption that these short emergence periods are maintained by selection; though not strictly analogous, they may be compared with the encystment periods of the ciliate *Strombidium oculatum* observed by Fauré-Fremiet (1948). It is a planktonic form inhabiting rock-pools, and at intervals it settles on a hard surface and encysts for a short period. The whole process is so timed that the ciliates are encysted while their pool is under the sea at high water and active while the tide is out. In captivity, where there are no tides, the intervals between encystments gradually become more and more variable in length. It, therefore, seems likely that the regularity in nature is maintained by the elimination of those whose rhythm does not keep time with that of the sea.

A life history may of course be adapted to conditions that have changed, as Anker Nielsen (1951) described to the congress in Belgium six years ago. The caddis fly *Apatidea muliebris,* believed to be a glacial relict, has a short flight season in late spring, grows rapidly in summer, and then lies quiescent throughout the winter — a life cycle which, as Anker Nielsen points out, is suited to high latitudes where the summer is short, but seems inappropriate in the cold springs in Denmark where he studied it. In other springs, closely related species, which are thought to be mutants of the original relict, have a life cycle better fitted to their surroundings and are on the wing all summer and active in the larval stage in winter.

What causes these short emergence periods? There seem to be four possibilities:

1. Various people have seen advantage in the ease with which the sexes find one another but no-one, to my knowledge, has proved it. Obviously, if a population is too scattered in time and space, not every female will find a mate, which is undesirable, but one objection to the idea is that there are examples of two apparently similar species of which one emerges in a mass within a small compass of time and the other in driblets throughout the summer. *Rhithrogena semicolorata* and *Ecdyonurus torrentis* are examples taken from the writer's recent studies.

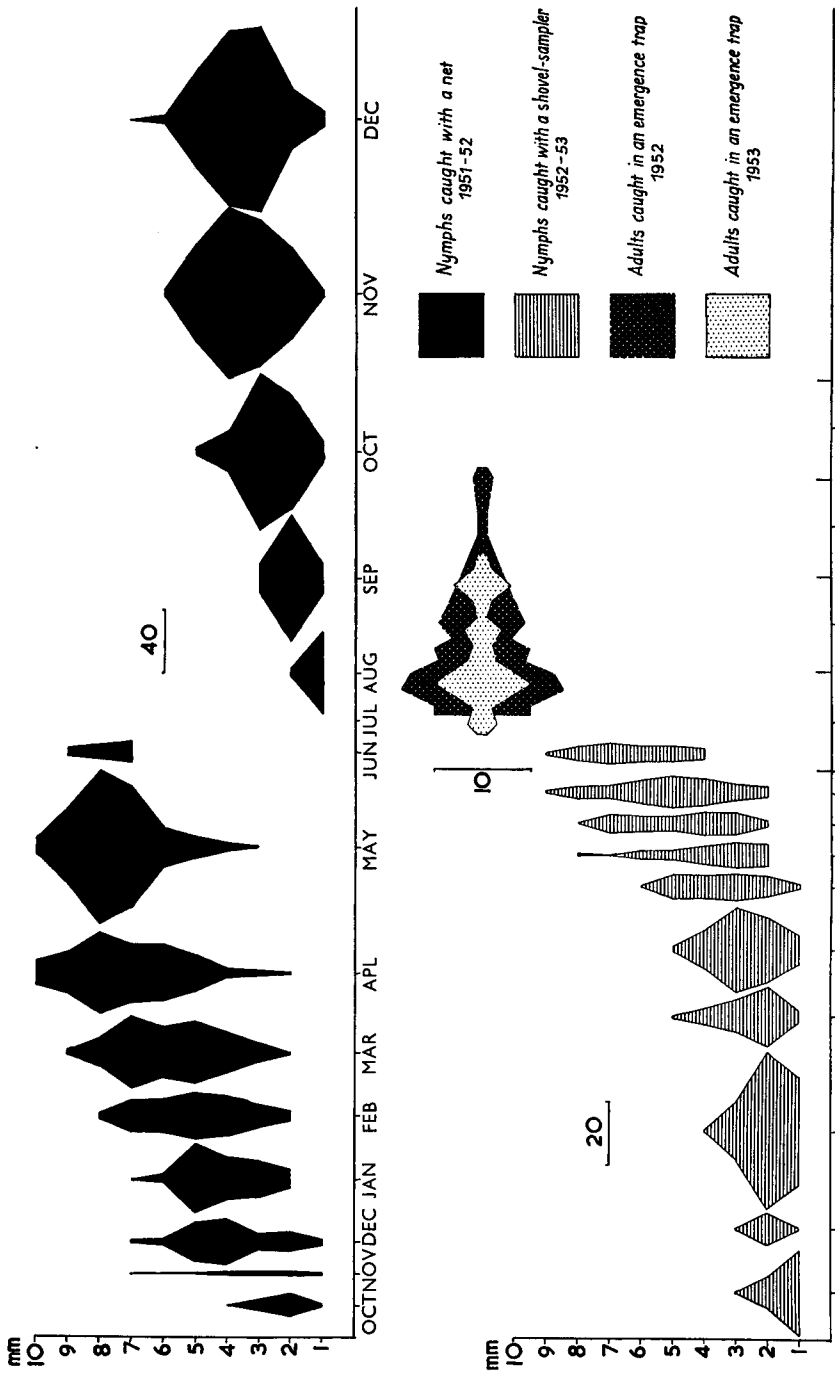

Fig. 1. *Rhithrogena semicolorata*. Numbers of nymphs caught each month in a net (above) and a shovel sampler (below). The histograms show absolute numbers caught arranged in millimetre size groups. The horizontal figure shows numbers of adults caught in an emergence trap in two successive years.

2. Temperature. Probably the best known exposition of this theory is that of IDE (1935), who believes that certain species tide over the summer in the egg, and are killed by a lethally high temperature if they are too late turning into adults or too early hatching from the egg.

The evidence certainly suggests that temperature is concerned but PLESKOT (1953) believes that it acts indirectly, not directly, which brings us to the third point:

3. Oxygen. *Habroleptoides modesta,* a stream-dwelling Ephemeropteron, emerges early in the year, earlier in warmer streams and warmer seasons. The eggs hatch after two weeks and the nymphs grow throughout the summer. Clearly the water is not too warm for them. PLESKOT postulates that there is a critical period just before emergence when oxygen requirements are particularly high and when the transfer of oxygen from the water to the tissues of a nymph is difficult. Above a certain temperature, even though saturated, water does not contain enough oxygen for the needs of a nymph in this condition, which must therefore emerge before this temperature is reached.

4. Competition. In certain genera of Ephemeroptera (IDE 1935) and Plecoptera (ILLIES 1952), there is a succession of species throughout the summer. Possibly competition prevents any species extending its emergence period.

Turning now from cause to effect, a second assumption is that it is undesirable, at least in herbivores, to have all the young make their debut together, because there may not be enough food to go round. If some of the eggs hatch now and some later when the nymphs from the first batch have grown bigger and have changed their food, the resources of the environment, it may be supposed, can be exploited more fully. Some species, possibly quite a lot of species, that have a short emergence period do apparently achieve this, a point I should like to illustrate by reference to my own work on *Rhithrogena semicolorata* (MACAN 1957). The adults, horizontal kite on the figure, are on the wing from mid-May till mid-July or later, though abundant only during a shorter period that is not much more than a month. The first nymphs were found in August. Thereafter there was a steady growth, for the biggest nymph is bigger in nearly every month, but small nymphs persisted, and tiny nymphs 1 to 2 mm long were found in every month up to January, a period of six months. The most likely explanation, though definite proof still has to be obtained, is that there is big variation in the duration of the egg stage. There are two rather important corollaries. First, the standard method of calculating growth by taking samples at intervals, averaging the lengths of all the specimens, and subtracting each average from the one that follows, is invalid; if part of the population is still in the egg stage on the first occasion, it will depress the average on the subsequent one.

Secondly it may add a big error to production studies. These generally ignore the individuality of species and sometimes yield unexpected results as when ALLEN (1951) found that *Salmo trutta* apparently ate seventeen times more than there

was present for it to eat. ALLEN's detailed analysis of a trout population, perhaps one of the most thorough studies of the population of an aquatic organism ever completed, provides useful data for illustrating the point that I wish to make here. He found that, of 1000 fry at the beginning of the season, only 15 were still alive six months later (ALLEN 1952, fig. 6). The surviving 15 weighed 1³/₄ lb and he reckoned that the total weight of fish flesh produced by the others before they died was 3³/₄ lb. Incidentally, after three years there was only a single survivor of the original thousand and by that time a total of 10 lb of fish flesh had been produced. During the first six months, therefore, a considerable amount of the total production takes place; the same is probably true of many invertebrates and yet it is the tiny stages that many methods fail to catch (cf. JONASSON, p. 860). However, this is a slight digression. Of ALLEN's original 1000 specimens, 985 perished during the first six months, many doubtless having been eaten. ALLEN could base calculations on this figure because he knew that all eggs had hatched at the time of the first sampling. Had this not been the case, the figure of 985 would have been too low; it might have been much too low. If the hatching of the egg is spread over a period of six months, as that of *Rhithrogena semicolorata* appears to be, an enormous error could be introduced into productivity calculations by anybody unaware of the phenomenon.

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Discussion

JOHNSON: From experience in an equatorial climate I feel that other factors than those mentioned probably affect the occurrence of restricted emergence periods. In Malaya there are insufficient variations in temperature and oxygen content to explain such periods; nevertheless they still occur in a limited number of species. There is a possibility that these are associated with periods of water-dilution by heavy rains and flooding.

LE CREN: Can you suggest any physiological mechanism that would give rise to the large variation in time between egg laying and hatching?

MACAN: The only relevant piece of work that I can think of is by GROS (1923) in *Ann. biol. lacustre* **12**, 49—74. He noticed that eggs of *Ecdyonurus forcipula* which fell to the bottom of an aquarium hatched in 15 days, whereas those that lodged in the axils of *Fontinalis* leaves took 46 days to hatch. He suggests that the amount of light falling on the egg may affect its rate of development.

HYNES: I have some figures which show that in the stonefly *Leuctra inermis* there is a steady decline in numbers during the winter, although this is the period of recruitment from hatching eggs.

CASPERS: In small ponds near Hamburg we found that the fauna was reduced in winter, chiefly owing to oxygen lack under ice. Have you observed anything similar in running water?

MACAN: No. Our streams never freeze over.

BROOK: Could you elaborate on your comments about the change of food at some stage in the life history of these insect larvae?

MACAN: It is pure supposition on my part that there is any change, but I do think it is likely that, when 5 mm long, a nymph can eat things that were too big for it when it was 1 mm long.

MORGAN: Following Dr. BROOK's remarks, I think that the difference in feeding behaviour between large and small larvae may be important in carnivorous forms and in herbivores which feed on macrophytic material. Work which Dr. BROOK and I have carried out on *Leptocerus aterrimus* indicates that, in forms which feed on algae, larger and smaller larvae may feed on the same food at the same time.

With regard to the prolonged hatching period of the eggs of *Rhithrogena semicolorata*, I have also found very small nymphs of *Caenis horaria* from August to approximately April although the emergence period of adults is restricted to June and July.