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Endogenous activity as a factor in Invertebrate Drift

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With 10 figures in the text

The occurrence of downstream drift in the lotic habitat and its periodicity in relation to light has been well established (WATERS 1961 and MÜLLER 1963 a, b, 1965 a, b), although the reasons for the regular fluctuations of the number of animals found in drift during a 24-hour period have yet to be fully explained. MÜLLER (1965 a) has shown that these fluctuations are due to the onset and duration of darkness and he has suggested (1963 a, b) that drift is a reflection of the diurnal rhythmicity of freshwater invertebrates. Rhythmicity has been studied in some freshwater insects (HARKER 1953 and LEHMAN 1964), but no direct comparison between the endogenous activity of any animal and the numbers found in drift has yet been made. Therefore it was decided to examine this relationship by analysing the activity patterns of three insect larvae and to attempt to relate this to their occurrence in drift.

The three insects used, *Simulium* (Diptera), *Isoperla* (Plecoptera) and *Ephemerella* (Ephemoptera), were chosen because they could be obtained in sufficiently large numbers. The activity experiments were carried out using a technique similar to that employed by HARKER (1953). Ten animals of the same species in each case were placed in a perspex dish (30×10×7.5 cm) six hours before the start of the experiment. Fine gravel was used as a substrate and this was covered by 6 cm of water. During the experiment, which lasted 24 hours, observations on the number of animals active was made every 30 seconds during a 15-minute period in each hour. After each 15-minute period the water was aerated for a further 15 minutes and then the animals were left for 30 minutes to eradicate any disturbance due to aeration. For each species four experiments were carried out under the same light conditions and the results of the four readings in each hour summed. The resultant mean expressed the activity level of the different species for a standard 15-minute period in each hour. Three different light conditions were used: normal light conditions produced by placing the experiment near a window in the laboratory; continuous darkness in a constant temperature room; and continuous illumination using a 25 watt bulb mounted sufficiently far above the experiment to eliminate any heating effect. During the periods of darkness, observations were carried out by illuminating the animals with a dim red light. A water bath surrounded the dish so that all the experiments were done under the same temperature conditions. Thus for each species, a series of twelve, 24-hour experiments on activity were carried out.

In order to relate the level of drift to any endogenous activity patterns in freshwater insects, drift samples were taken in two different series. One series involved sampling from a Dartmoor stream in south-west England using modified high-speed plankton nets (ELLIOTT 1965). Experiments were started an hour before sunset, and the nets changed at hourly intervals until an hour after sunrise next day. To obtain some indication of the effect of different durations of darkness, samples were taken in summer, autumn and winter. All samples were taken on nights when there was no moon and only light cloud cover. Although these observations gave a general indication of the variations in drift, the actual number of individual species was low. Thus it was not possible to make an accurate direct comparison between activity and drift for any one species.

A second series of experiments was therefore carried out in the laboratory using a model stream. This consisted of a perspex tank (see fig. 10) containing gravel and water, the water being continually circulated through the tank at a constant rate of 300 litres per hour by an electric pump. Samples of animals in the water column were obtained at hourly intervals from a net mounted in a reservoir at one end of the tank. Approximately 150—200 animals of the same species were used in one experiment. For each species the effect of summer, autumn and winter periods of darkness upon drift was examined. Experiments in which *Simulium* and *Ephemerella* were kept in the dark for periods of 24-hours were also carried out. This was done to further elucidate the relationship between activity and drift. After any restocking of the tank due to replacement of animals after an experiment, mortalities or change of species, the animals were left to settle under the light conditions to be used for 24 hours. This settlement period was also used if the light conditions were to be changed. From this study on individual species it was possible to make a reasonable comparison with the results on activity.

Results

The results are initially described for each species before any general conclusion is drawn, because there is some deviation between the results for the three species observed.

Isoperla:

The results of the activity experiments for *Isoperla* are shown in Figure 1. On comparing the activity patterns under normal conditions and constant darkness, one finds that the peaks of activity occur at the same time in both experiments. However there is no correlation between these results and those from animals under continuous illumination. The phenomenon of light altering activity patterns has already been found by LEHMAN (1964) and CHIBA (1964). In order to investigate this effect, four batches of ten animals were kept in complete darkness for six hours. They were then illuminated and their activity observed for a further six hours. From Figure 2 it can be seen that there is a decrease in activity with time. I suggest that this is a reflection of an orthokinetic reaction to light which then masks any underlying activity pattern. On comparing these results for activity with drift experiments on *Isoperla* in the tank (Figure 3), one finds that the activity peak at 4.00 hours G.M.T. coincides with a peak in drift. In the winter drift experiment (Figure 3) one finds a peak at 22.00 hours which is comparable to a peak found at the same time in the activity experiments.

Ephemerella:

In the activity experiments on this species (Figure 4) there is not such a clear correlation of activity under different light conditions. However on

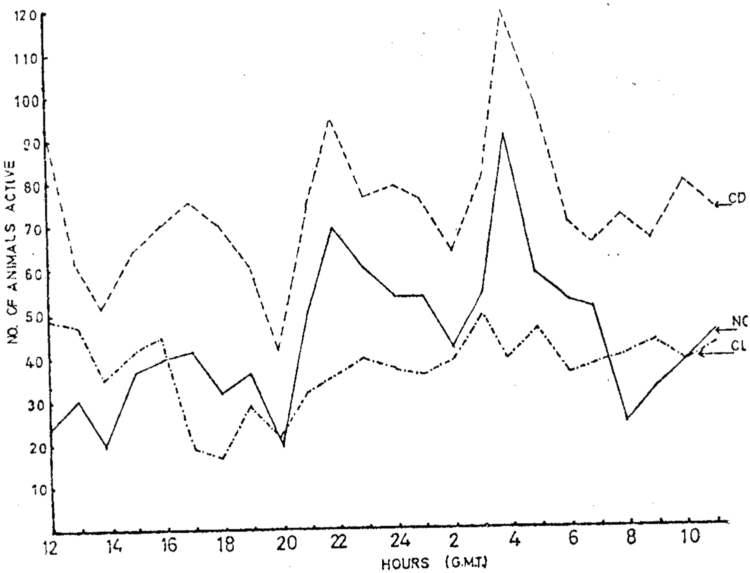


Fig. 1. Activity pattern of *Isoperla* under different light conditions. NC = normal conditions; CD = continuous darkness; CL = continuous illumination.

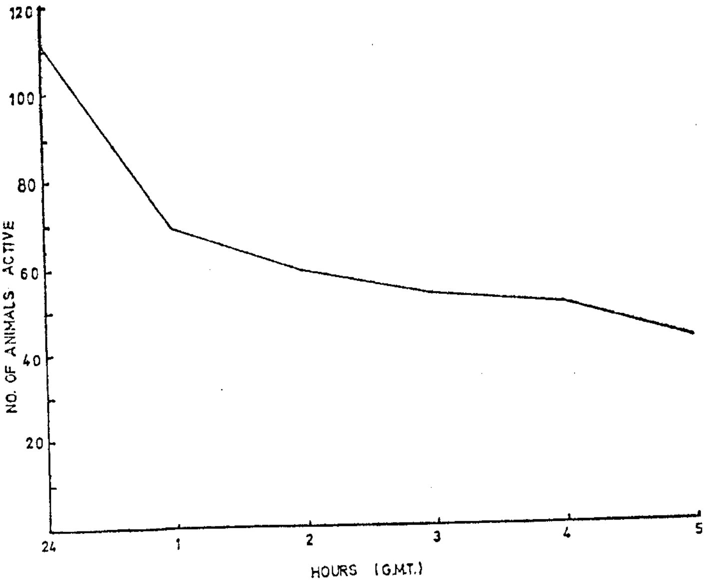


Fig. 2. Activity of *Isoperla* under continual illumination.

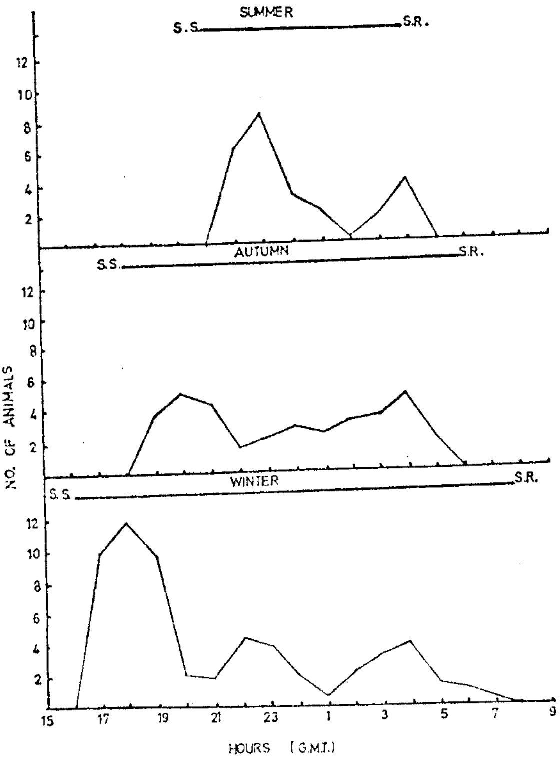


Fig. 3. Laboratory drift experiments using *Isoperla* under different seasonal light conditions. SS = sunset; SR = sunrise.

comparing the daylight part of the normal condition experiment with the tank experiment under 24-hour periods of darkness (Figure 5) one finds peaks in both occurring at the same time. Moreover the peak at 3.00 hours G.M.T., which occurs in both these experiments, is also found in the tank experiments on seasonal light conditions (Figure 6). As in *Isoperla* a peak at 22.00 hours occurs in the winter drift experiment (Figure 6). It is believed that the activity experiment results were modified not only by light but also by a lack of current. For it was found that upon reducing the current in the tank there was a resultant decrease in animal activity.

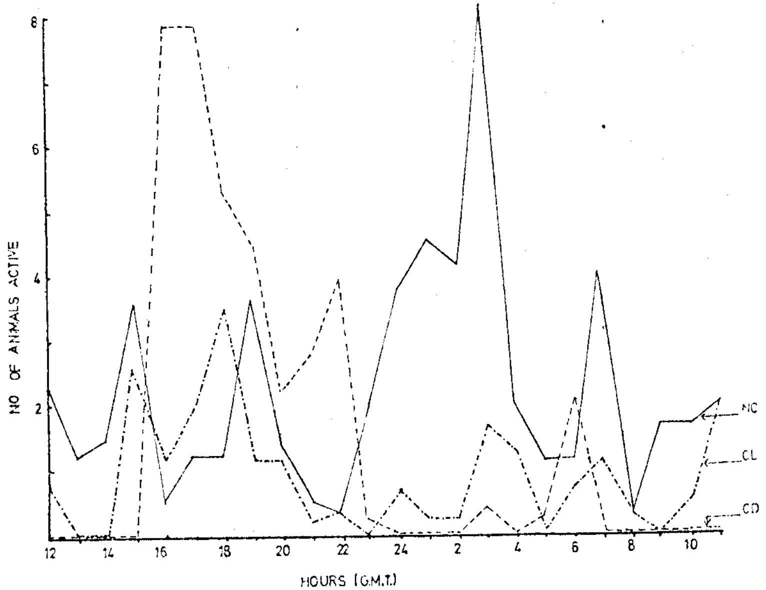


Fig. 4. Activity patterns of *Ephemerella* under different light conditions (for further explanation see Fig. 1).

Simulium:

Again for *Simulium* there seems to be little correlation between activity under different light conditions (Figure 7). However a relationship can be seen between the time of peaks in the continual illumination experiment and the tank experiment under continuous darkness (Figure 5). Two of these peaks, at 23.00 and 3.00 hours G.T.M., again appear in the results of the tank experiments on drift under autumn and winter light conditions. It seems likely that the divergence found between activity experiments was due to darkness causing such an exogenous increase in activity as to mask any underlying rhythm. This exogenous increase appears to be a short term effect, as it was not evident in the tank experiments under continuous darkness. For in these experiments the animals were left for a full day in

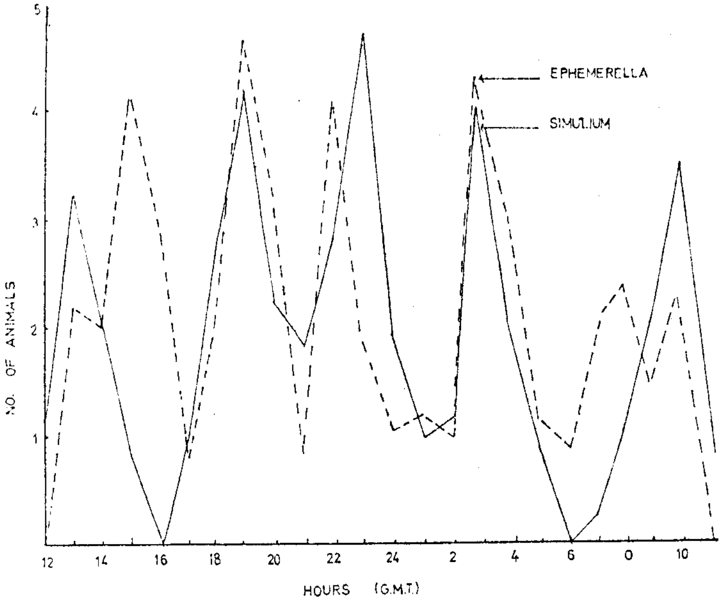


Fig. 5. Laboratory tank experiments using *Ephemerella* and *Simulium* under complete darkness.

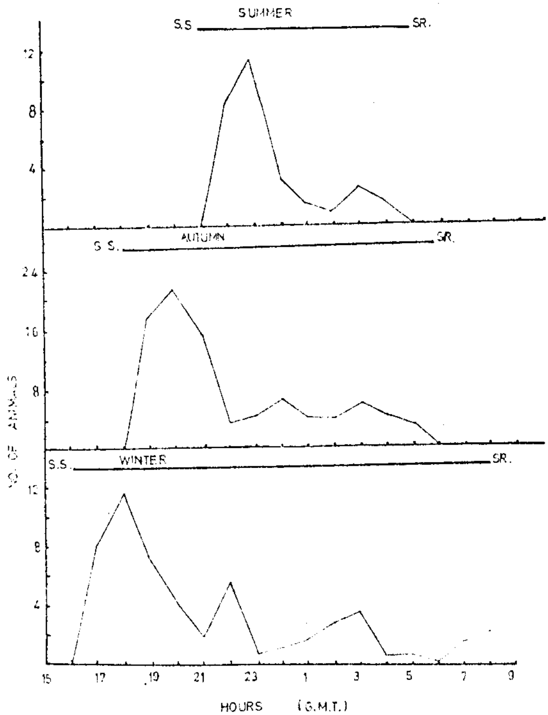


Fig. 6. Laboratory drift experiments using *Ephemerella* under different seasonal light conditions (for further explanation see Fig. 3).

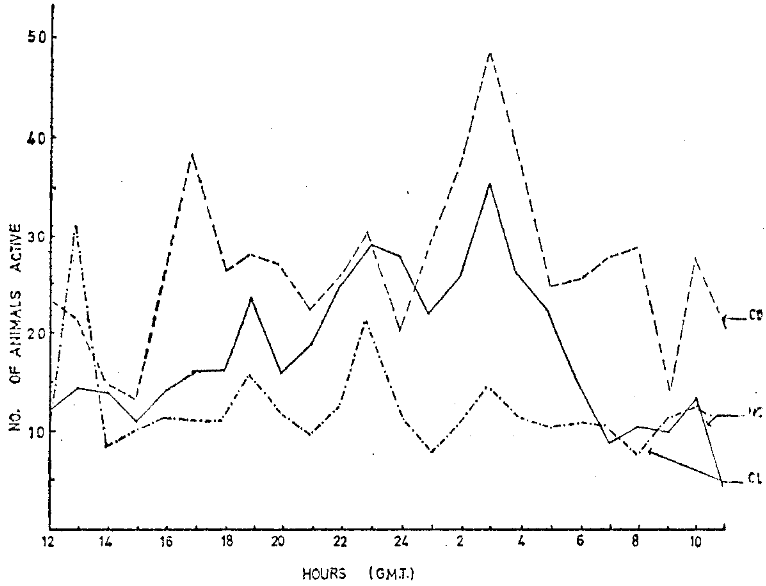


Fig. 7. Activity patterns of *Simulium* under different light conditions (for further explanation see Fig. 1).

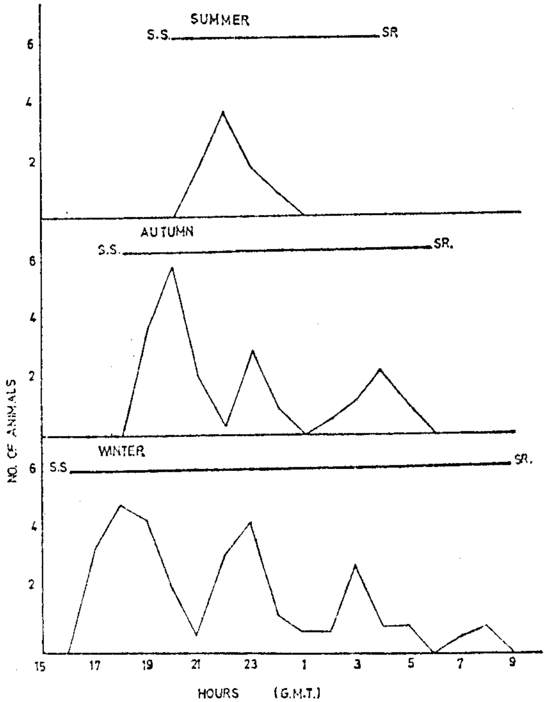


Fig. 8. Laboratory drift experiments using *Simulium* under different seasonal light conditions (for further explanation see Fig. 3).

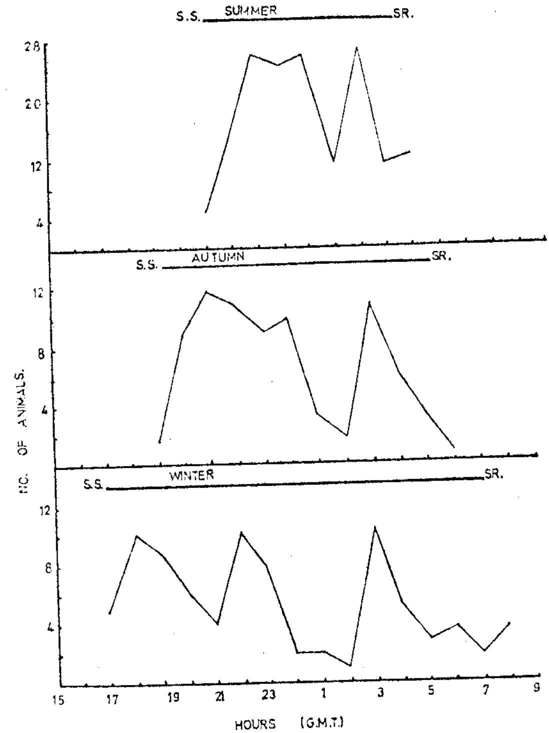
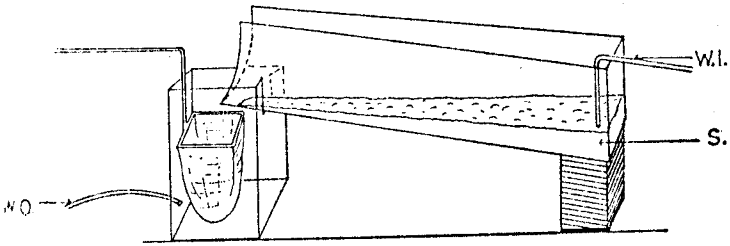


Fig. 9. Drift samples from a Dartmoor stream during different seasons.
SS = approx. time of sunset; SR = approx. time of sunrise.



10. The model stream. (S = substrate, W. I. = water in, W. O. = water out.)
Scale of diagram = I/5 normal size.

before sampling commenced. Also in the activity experiments normal conditions and constant illumination there is a correlation be- the time of peaks even though there is an obvious general increase in during darkness.

The results of the field samples of drift are shown in Figure 9.

Conclusion

Examination of activity under various light conditions did not give an entirely conclusive picture of endogenous activity patterns. For in all three animals endogenous variations were often masked by exogenous increases in activity caused by changing light conditions. However certain regular variations of activity were found that were reflected in the occurrence of peaks in the laboratory drift experiments. From Figure 9, one can see that the peaks mentioned at 22.00 hours and 3.00 hours G.M.T. again appear in the drift samples taken in the field. It is therefore concluded that the regular occurrence of peaks in the later part of the night is a reflection of an endogenous activity pattern.

Discussion

Although the nocturnal increase in drift is a reflection of a higher level of animal activity, it is not believed that this is due to any diurnal rhythmicity. For in these experiments no endogenous increase in activity was found that corresponded to the time of sunset. It is therefore suggested that during the day light depresses the level of animal activity. At night, the onset of darkness causes an increase in activity which results in a higher level of drift. This variation in activity is therefore entirely exogenous. However during darkness the overall level of activity is increased and thus the endogenous activity patterns are amplified to a level sufficient enough to also be reflected in drift. These variations are only obvious after the baseline of activity has stabilished 3—6 hours after sunset, for during the first few hours after sunset any endogenous variations are masked by an exogenous increase in activity due to the onset of darkness. This exogenous increase appears as the first nocturnal peak in drift. Such a hypothesis is further substantiated by the results obtained for drift under constant conditions of illumination. Samples of drift taken in underground streams (Müller and Kureck 1963) showed a nocturnal increase which directly reflected a diurnal rhythm. In this case there is no exogenous masking of the rhythm due to changes of illumination. Sampling under continuous light in polar regions (Müller 1965 b) showed that there was no nocturnal increase in drift. I suggest that this was due to the continuous presence of light which depresed activity to a level below which any endogenous variations could be reflected in drift.

Therefore I propose that under normal conditions of illumination the variation in drift is due to both exogenous and endogenous changes of activity.

Summary

The increase of downstream drift at night has been well established. It has been suggested that this variation is a reflection of a diurnal rhythmicity. Therefore it was decided to investigate the activity patterns of a number of invertebrate larvae and compare this with their occurrence in drift. The insect larvae investigated were *Simulium* (Diptera), *Ephemerella* (Ephemoptera) and *Isoperla* (Plecoptera). Their activity was observed under different light conditions. The results were compared with drift experiments in the laboratory and the field.

From this comparison it was concluded that endogenous variations of activity were reflected in the occurrence of peaks in drift during the later part of the night. However there was found to be no evidence of any diurnal rhythmicity. The exogenous effect of light and dark on activity was discussed. It was concluded that fluctuations in drift are due to both exogenous and endogenous variations of activity.

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Zusammenfassung

Eine Zunahme der stromabwärts gerichteten Drift in der Nacht ist eindeutig festgestellt worden. Es wurde vermutet, daß der zwischen Tag und Nacht vorliegende Unterschied auf einen Tagesrhythmus zurückzuführen sei. Wir untersuchten daher das Aktivitätsmuster einer Reihe von Invertebraten-Larven und stellten Vergleiche mit ihrem Auftreten in der Drift an. Die untersuchten Insekten-Larven waren *Simulium* (Diptera), *Ephemerella* (Ephemoptera) und *Isoperla* (Plecoptera). Ihre Aktivität wurde unter verschiedenen Lichtbedingungen geprüft. Die Resultate wurden mit den im Laboratorium und im Freiland durchgeführten Drift-Experimenten verglichen.

Aus diesem Vergleich wurde geschlossen, daß sich endogene Aktivitätsvariationen in dem Auftreten von Driftmaxima während der zweiten Nachthälfte widerspiegeln. Jedoch wurde keinerlei Beweis für einen Tagesrhythmus gefunden. Der exogene Einfluß von Licht und Dunkel auf die Aktivität wird bsprochen. Es wird angenommen, daß sowohl exogene als auch endogene Aktivitätsvariationen für die Drift-Fluktuationen verantwortlich zu machen sind.

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