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of the reservoir and attains maximum abundance near shore at depths exceeding 2 m. The population is limited in the shallow western section of the reservoir primarily by the effects of wave action, and in the old river channel by reduced oxygen.

The continuous deposit of coarse sediments transported by the Missouri River will undoubtedly reduce the amount of suitable habitat, although at present the extent of such deposits is relatively small.

Oxygen depletion appears to reduce established *Hexagenia* populations. The probability of this occurring will no doubt increase as more extensive accumulations of organic material are deposited by the Missouri River.

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EFFECT OF LIGHT INTENSITY ON THE DRIFT OF STREAM INVERTEBRATES[1]

CHARLES S. HOLT[2] AND THOMAS F. WATERS

Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minnesota

Abstract. Various experiments were conducted in a small Minnesota stream to determine the effect of light intensity on the circadian rhythms in drift of two aquatic invertebrates, the nymph of the mayfly *Baetis vagans* McDunnough and the amphipod *Gammarus pseudolimnaeus* Bousfield. Experiments included 1) artificial light in an exclosure which insured that experimental conditions were applied only to the organisms on the stream bottom area in the exclosure, 2) artificial light in the open stream, and 3) artificially produced darkness in an exclosure. A threshold of light intensity which, decreasing, initiated high drift rates and which, increasing, caused cessation of drift, was about 0.1 ft-c (1 lux) for both species. Continuous artificial light above the threshold level for an entire night period, and also for 4 consecutive days, depressed the normal high nocturnal drift rates in the exclosure to near

daytime levels; on the fifth night in the exclosure, in darkness, drift was much higher than normal. Continuous artificial light for an entire night period on an open stream riffle also greatly depressed nocturnal drift. In another open stream experiment, in which organisms drifted from darkness onto a lighted riffle, some settled to the bottom as evidenced by depressed nocturnal drift rates, while others drifted through the light and off the riffle. The effect of shortened and lengthened "night" periods, produced by artificial light and darkness respectively, was to shift the circadian patterns of drift correspondingly. Rapidly alternating periods (15 min) of light and darkness in the exclosure produced correspondingly alternating drift, with drift rates high in darkness and low in light. When the normal day-night cycle of light was reversed with artificial light and darkness, the phases of the circadian rhythm in drift were also reversed. Observed circadian rhythms in drift appear exogenously controlled; if an endogenous rhythm exists at all, it is very weak and is influenced strongly by environmental light conditions.

INTRODUCTION

Several recent observations of a circadian rhythm in the drift of stream invertebrates have strongly suggested a causal relationship with light intensity. Tanaka (1960) was apparently the first to report such daily changes in drift, especially in mayfly nymphs. Observations of similar rhythms in drift were made elsewhere, apparently correlated with the daily cycle of light intensity, involving in most cases mayflies and amphipods (Waters 1962; Müller 1963a, b; Müller, Kureck and Müller-Haeckel 1963). In Valley Creek, Minnesota (the site of the present study), the drift rates of the mayfly *Baetis vagans* McDunnough and the amphipod *Gammarus pseudolimnaeus* Bousfield (previously reported as *Gammarus limnaeus* Smith) increase markedly at night, and the time of drift increase follows the progression in light changes seasonally (Waters 1962). The high drift in darkness was defined as "behavioral" drift to differentiate it from other drift categories of a passive nature (Waters 1965). Anderson (1965) observed a marked depression of nocturnal drift in bright moonlight, and Elliott (1965) and Müller (1965) reported significant responses in drift to artificially produced changes in light intensity. These observations are thus in agreement with Harker's (1964) suggestion that light is the most important environmental variable affecting the timing of a rhythm.

The objective of studies which we conducted during the summers of 1963 and 1964 was to test experimentally, under field conditions, the relationship between drift and light intensity that has been suggested. Experiments were conducted in Valley Creek, a small, hard-water trout stream located in east-central Minnesota. In the section of the stream in which the tests were conducted, the discharge during the summer months was about 0.14 m³/sec (5 ft³/sec), and midstream current velocity was about 0.5 m/sec (1.6 ft/sec).
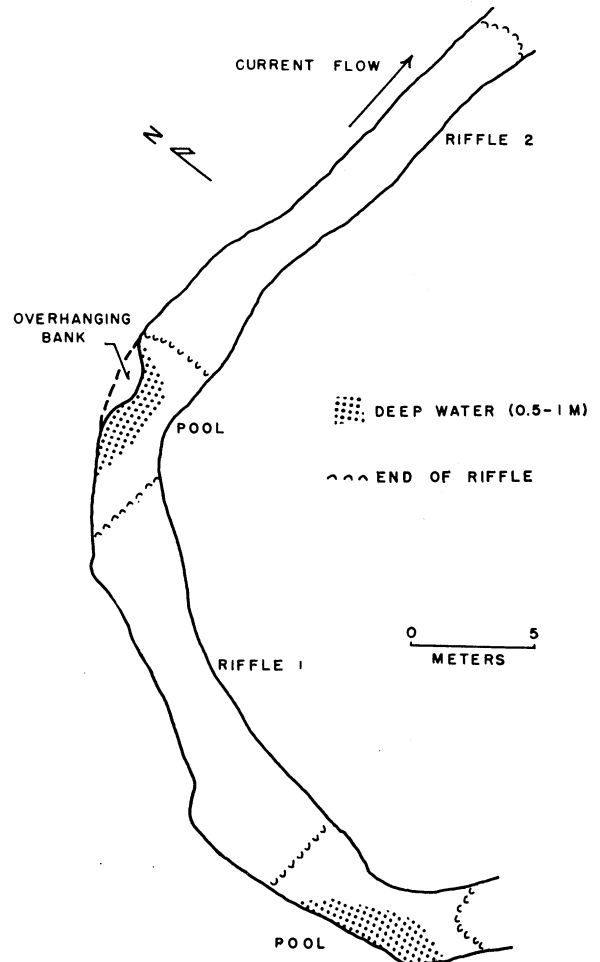
FIG. 1. Map of the study section of Valley Creek, Washington County, Minnesota.

The two test riffles contained sand, coarse gravel, and rubble, and measured about 13 m (45 ft) long and 3 m (10 ft) in mean width (Fig. 1). The invertebrate species composition was simple, the principal macro-invertebrates being the nymphs of the mayfly, *Baetis vagans,* and the amphipod, *Gammarus pseudolimnaeus.* Both of these invertebrates exhibited high behavioral drift rates and were the main subjects of the present study.

METHODS

Drift rates were measured in the open stream with stationary nets measuring 15 cm (6 in.) wide by 30 cm (12 in.) at the mouth opening and about 1 m (3 ft) long. They were constructed of Nitex with a mesh opening of 471 µ, and were supported in position in the stream by iron rods (see Waters 1962). Open-stream drift rates were expressed as grams per hour per drift net.

In certain artificial lighting experiments, an exclosure was used to delineate the experimental area. This was constructed of angle iron and sheet metal, and enclosed two parallel sections of stream bottom, each measuring 2.4 m (8 ft) long by 0.3 m (1 ft) wide, or 0.7 m² (8 ft²) in area (Fig. 2). The two sections were separated by a
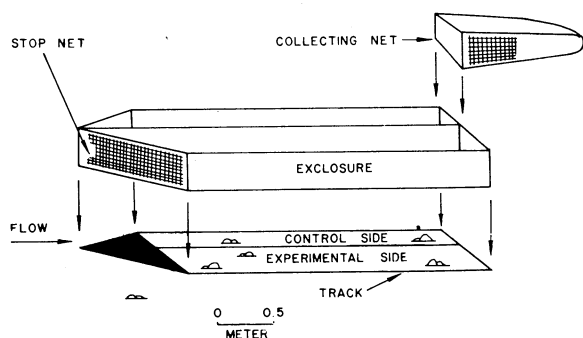

FIG. 2. Schematic drawing of two-section exclosure used in artificial lighting experiments.

center partition. In use, the exclosure was bolted tightly to a permanent companion track on the stream bottom. At the upstream end of the exclosure, a triangular frame held a 253-µ mesh Nitex screen to prevent the entrance of drifting organisms from outside. Drift nets were attached at the downstream end to collect organisms drifting from those areas of stream bottom delineated by the exclosure. This exclosure was located approximately in the center of riffle 1.

A second type of exclosure was used to reduce light intensity in some experiments. This device enclosed an area of 0.18 m² (2 ft²), measuring 1.2 m (4 ft) long by 0.15 m (0.5 ft) wide (Fig. 3). A funneling arrangement channeled stream
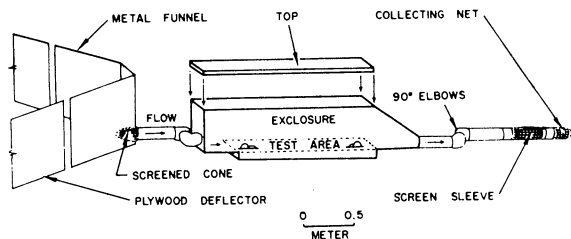

FIG. 3. Schematic drawing of darkening exclosure, showing funneling arrangement and light-shielding elbows.

water into the exclosure through a large-diameter plastic pipe. To prevent light entering the darkening exclosure from the ends, the current flow in the pipes leading to and away from the exclosure was directed through two 90-degree elbows. The upstream opening of the pipe was screened with 253-µ mesh Nitex, and a drift collection net of the same mesh was attached at the rear of the exit pipe. When the light-tight cover was attached to the top, the inside of the exclosure was in darkness (0.0002 ft-c). This exclosure was constructed in one unit and was completely sealed around the bottom. The location was at the upstream end of riffle 2.

Two assumptions were necessary in the exclosure experiments, and these were tested several times during each summer to assure their validity: (1) no drift organisms from outside entered the exclosures, and (2) the drift from both sides of the two-section exclosure was approximately equal under natural conditions.

To test the validity of (1), organisms from inside the exclosure were removed by hand-agitation of the substrate, bottom samples were taken inside the exclosure with a small sampler to determine that the organisms had been removed to negligible levels, the exclosure remained in place overnight when drift was high in the open stream, and then the organisms drifting from the exclosure and in additional bottom samples were measured the next day. When significant quantities entered the exclosure, the leakage was traced to the probable cause and the needed repairs made; then the procedure was repeated. These tests also led to an early decision to change all Nitex screening from 471 µ to 253 µ, the former having permitted the entrance of small early-instar *Baetis* nymphs.

Assumption (2) was tested in the two-section exclosure by comparison of total drift from both sections through a night period under natural conditions. Differences resulting from natural variation were observed, but these were never consistent between the two sections and were small relative to the differences observed in the experiments.

In the two-section exclosure, incandescent lamps were housed in enclosed boxes that fit snugly over either side of the exclosure; experimental light thus applied to one section was completely enclosed and did not enter the other section. Comparison of the drift curves for natural and artificial lighting suggested that the difference in emission was not significant in the organisms' response.

The entire area of the downstream riffle 2 was illuminated in two related tests, for which flood-

lamps were suspended above the stream. When illuminated, the light intensity at the water surface varied from 25 to 170 ft-c.

Water temperatures were identical in both experimental and natural conditions in all experiments.

Light intensity was measured with a Farrand Optical Instrument Company photometer using an IP21 or 931 photomultiplier tube, calibrated by means of neutral density filters, a Kodak No. 106 conversion filter, and a standard lamp provided by the U.S. Bureau of Standards. The purpose of the No. 106 filter was to convert the S–4 response of the photomultiplier tube to a response similar to that of the human eye and permit the light data to be expressed in foot-candles. Light intensity was measured at the water surface in all cases. In the 1963 experiments, light was not accurately measured at intensities greater than 10 ft-c, apparently because of photomultiplier tube fatigue at higher intensities; in 1964, intensities above 10 ft-c were measured with the addition of neutral density filters to avoid tube fatigue.

Samples were preserved in 10% formalin, sorted manually for *Baetis* and *Gammarus*, and weighed by a procedure similar to that of Lindeman (1941): centrifuging to remove excess liquid and weighing on an analytical balance. In all cases, drift rates were expressed in grams per hour.

Experimental Procedures

Early in the study it was observed that a moderate reduction of light during the daytime did not effect an increase in drift. For example, neither a dark cloudy day, artificial shading in the daytime, nor the partial eclipse of the sun on July 20, 1963, produced an increase in drift. It appeared clear that near-darkness was required to elicit a response from the organisms. The following problems were attacked experimentally, employing artificial light and darkness: determination of the threshold light intensities that, decreasing, initiated behavioral drift, and, increasing, caused a cessation; the effect of removal of the phase-setting mechanism, including continuous light through the night periods, both in the exclosure and in the open stream, and the response of organisms drifting from darkness into light; the effects of shortened and lengthened "night" periods; the rapidity of the organisms' response to alternating short periods of light and darkness; and the effect of a complete reversal of the day-night light cycle. Procedural details are given in following specific sections.

Results

Threshold intensity tests

One series of experiments was designed to determine a possible threshold of light intensity that would initiate and stop the high behavioral drift of *Baetis* and *Gammarus*. The procedure was to decrease the intensity of artificial light in the experimental section of the exclosure gradually in small steps. Simultaneously, the reference side remained exposed to natural light conditions. The threshold ranges were 10–0.5 ft-c for *Baetis* and 10–0.1 ft-c for *Gammarus*. These experimentally determined thresholds were similar to those observed in the reference side of the exclosure under natural light conditions, but at a different hour: 10–0.1 ft-c for both species.

Although not determined experimentally, the range of light intensity which, increasing, reduced the drift rates of the two species at dawn was estimated from open-stream drift samples and measurements of natural light intensity. This intensity was 0.1–5 ft-c for both species. Thus, the light threshold levels which initiated and stopped behavioral drift of both species were approximately the same.

Removal of phase-setting mechanism

It was postulated that exposing organisms throughout the night to light above the threshold intensity would inhibit behavioral drift. In a preliminary exclosure experiment extending through one night, the drift of both *Baetis* and *Gammarus* remained near low daytime levels in the experimental section of the exclosure, in which they were exposed to continuous light, while drift in both the reference section of the exclosure and in the open stream increased normally at night.

In another exclosure experiment, organisms were exposed continuously to light in the experimental section of the exclosure for 4 consecutive days. The population of *Baetis* was very low at the time of the experiment, and consequently data only for *Gammarus* were obtained. Drift of *Gammarus* in the reference section was similar to that observed in the open stream, but the continuous lighting of the experimental section produced a marked reduction in behavioral drift of *Gammarus* during the first 4 nights of the test (Fig. 4). On the fifth night, with natural light conditions, the drift rate increased sharply in the experimental section, and the peak drift was approximately twice that observed in the reference section. This suggested that *Gammarus* drifted abnormally on the fifth night to compensate for the reduced drift during the first 4 nights.

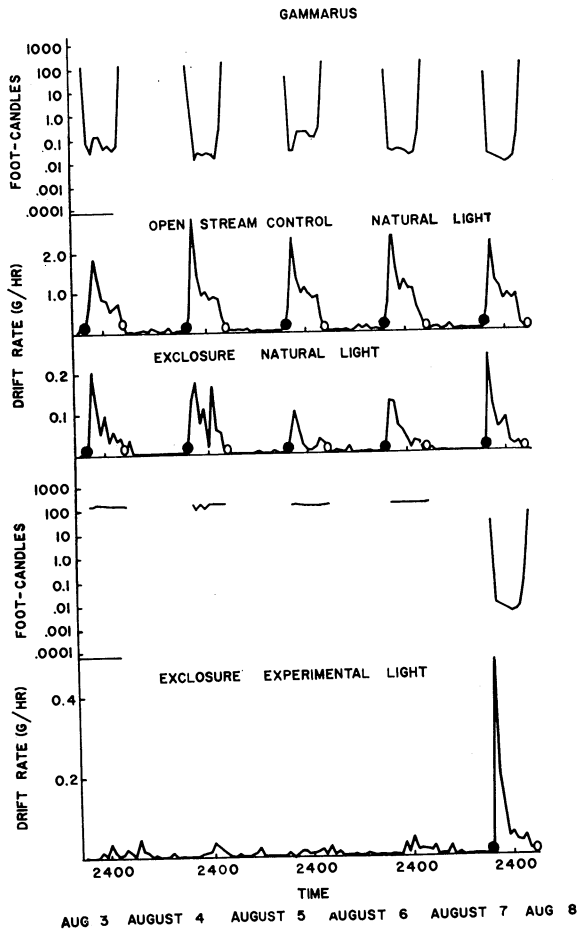In another experiment, the effect of continuous

GAMMARUS

BAETIS

FIG. 4. Extended continuous-lighting test, *Gammarus pseudolimnaeus*, August 3–8, 1964. Natural light in open stream and reference section of exclosure; drift rate per net in open stream and reference and experimental sections of exclosure. Closed circles represent sunset, open circles, sunrise.

FIG. 5. Continuous lighting test in open stream, *Baetis vagans*, August 26–27 and 29–30, 1963. Experimental light intensity 25 to 170 ft-c. Drift rate curves are means of two samples; vertical lines represent range. Closed circles represent sunset, open circles, sunrise.

light on the open stream was observed. Riffles 1 and 2 (see Fig. 1) were used in this test to provide both an experimental and reference area. Stop nets were placed across the entire width of the stream at the upstream end of each riffle, so that sample drift nets at the downstream end of each riffle sampled drifting organisms originating only from their respective riffle.

On the first night of the test, both riffles 1 and 2 were in natural light conditions (i.e., darkness). Stop nets were removed for 2 nights to permit repopulation. During the next night, with stop nets, riffle 2 was lighted and riffle 1 left in darkness as a reference. The pattern of drift was essentially the same for both species from both riffles 1 and 2 during the first night of the test when neither riffle was lighted, but on the night of experimental lighting drift rates in the lighted riffle 2 were much reduced from those observed
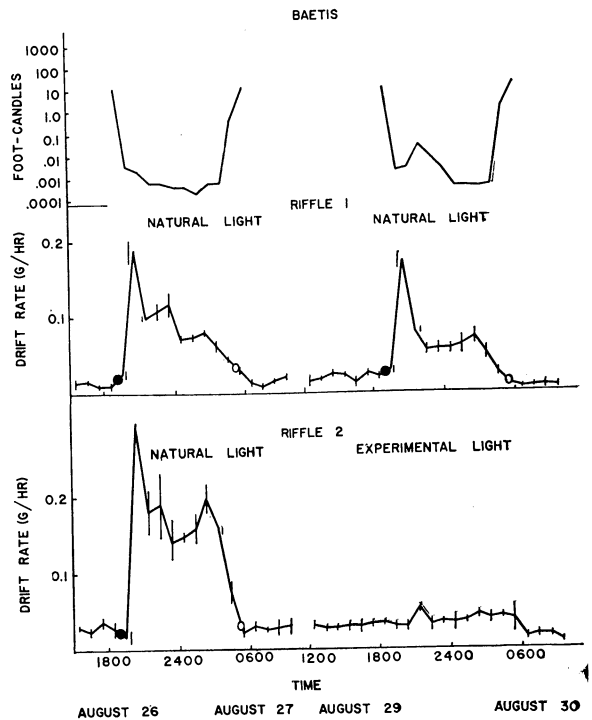
from the same riffle on the previous night, as well as being much less than that from the unlighted reference riffle 1 (Figs. 5 and 6). Approximately 2 hr past sunset the generator failed briefly, and riffle 2 was in darkness for about 3 min. As a consequence both species responded with slightly increased drift rates. This increase was temporary for *Baetis* and more lasting for *Gammarus;* the reason for the difference is unknown.

Another experiment was conducted on riffle 2, attempting to determine the response of organisms drifting from darkness into light. The design of this test was similar to that of the previous one, except that no stop nets were used. During the first night of sampling, both riffles were exposed to natural light conditions (i.e., darkness). On the second night, the upstream riffle 1 remained in darkness, whereas the downstream riffle 2 was lighted artificially. The pattern of drift was essentially the same for both species from both riffles during the first night under natural light conditions, but on the second night, the drift rates in the lighted riffle 2 were reduced (Figs. 7 and 8). The degree of reduction on riffle 2 was not as much as when stop nets were used in the previous experiment, indicating that while some of the organisms drifting into light stopped drifting and
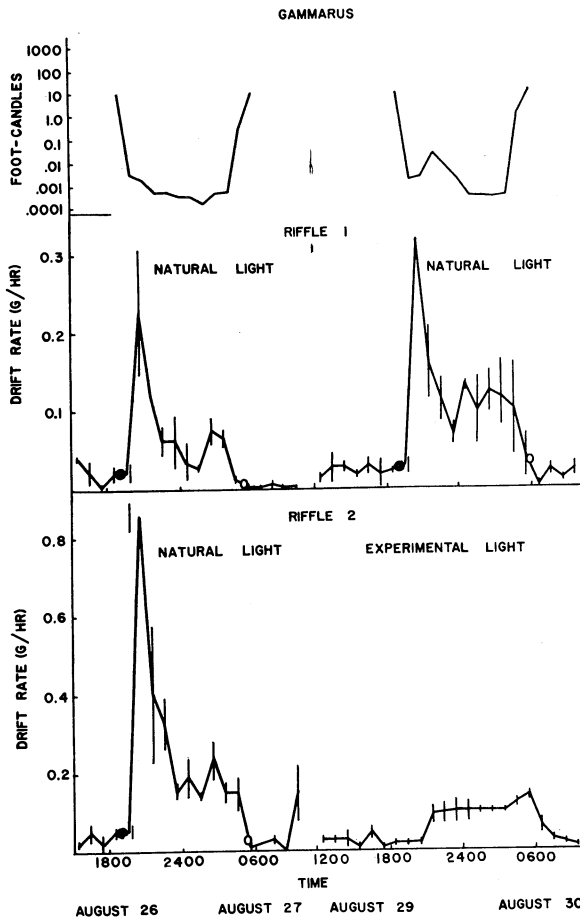
FIG. 6. Continuous lighting test in open stream, *Gammarus pseudolimnaeus*, August 26–27 and 29–30, 1963. Data as in Figure 5.

FIG. 7. Test of *Baetis vagans* drifting from darkness onto lighted riffle, September 9–11, 1963. Data as in Figure 5.

reached the bottom, others apparently were swept through the light and off the riffle.

Changes in length of photoperiod

The length of the "night" period was shortened in one exclosure experiment, in which the time of "sunset" was delayed 2 hr with artificial light and "sunrise" was similarly advanced. In the experimental section, the drift of both species remained low beyond the time of natural sunset and reached a maximum shortly after the time of artificial sunset, whereas the patterns of drift in the reference section and in the open stream were normal. Drift of both species during the artificially shortened night reached considerably higher levels than in the reference section, this perhaps being a compensatory response.

A second experiment involved a lengthened "night" period in the darkening exclosure by attaching the exclosure cover well in advance of the hour immediately following the covering of the exclosure (Figs. 9 and 10). As a reference,
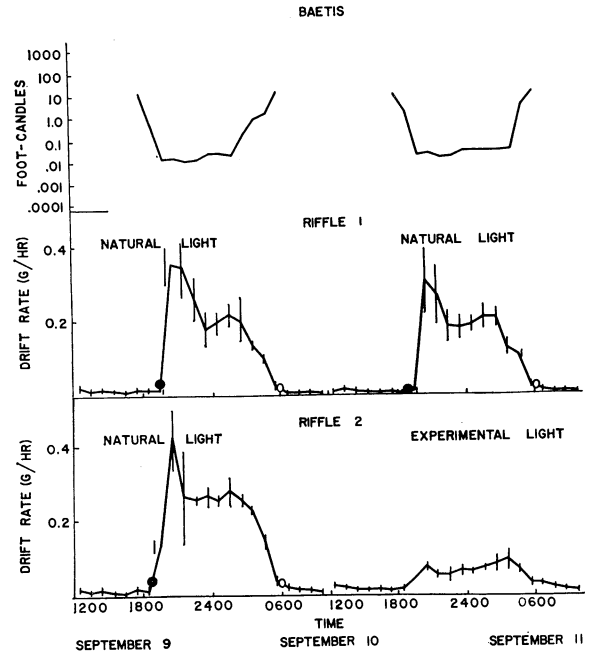
drift rates were measured under natural light conditions in the open stream and from the uncovered exclosure, necessarily on a different date; under these conditions, drift of both species followed the normal pattern with maxima at the normal time.

In a third experiment involving length of photoperiod, the organisms in the two-section exclosure were exposed to 15-min periods of alternating light and darkness. The purpose of this test was to determine whether the response was rapid. Only *Baetis* populations were sufficiently large at the time to provide adequate data. Drift from the experimental section alternated in accordance with the alternation of light, being high in darkness and low in light, while drift in the reference section, under natural light conditions, was normal in pattern (Fig. 11).

Phase reversal

A final experiment in the darkening exclosure tested the effect of complete reversal of the normal day-night cycle of light. At this time, only *Gammarus* populations were dense enough to provide adequate data. The exclosure was illuminated throughout the night by floodlamps suspended over the exclosure. The light intensity at the water surface within the exclosure was 350 ft-c. At approximately dawn the following morning the lamps were turned off and the cover attached, reducing light inside the exclosure to darkness at a time when it normally would be increasing.
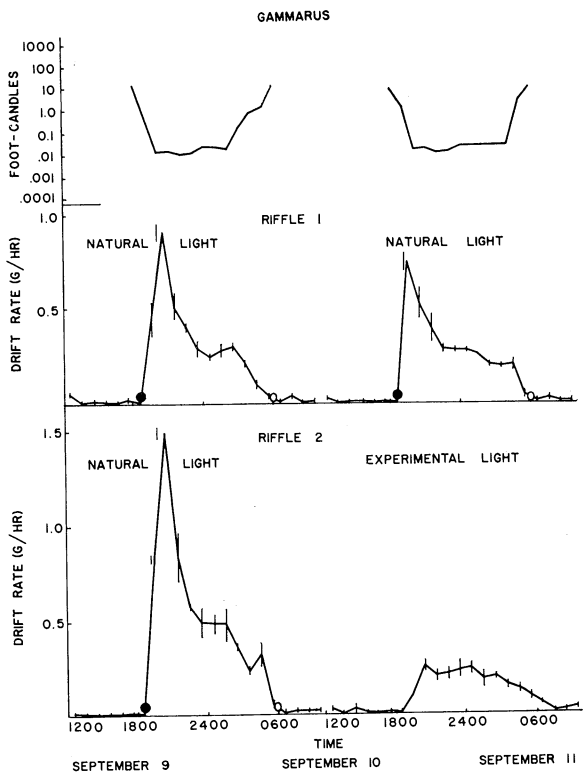
FIG. 8. Test of *Gammarus pseudolimnaeus* drifting from darkness onto lighted riffle, September 9–11, 1963. Data as in Figure 5.

Drift of *Gammarus* in the exclosure was reversed from its normal pattern, in accordance with the reversal of light conditions (Fig. 12). The drift remained low throughout the lighted night, but increased markedly after the exclosure was covered at dawn. The drift remained relatively high throughout the daytime hours, while the exclosure was covered, until the experiment was terminated. A reference test was performed with the uncovered darkening exclosure, in which the circadian drift pattern was normal and similar in both the uncovered exclosure and in the open stream.

DISCUSSION

The conclusion that light intensity was the factor responsible for the observed circadian patterns in drift was supported by all field experiments. Following similar though less extensive experimentation, Müller (1965) and Elliott (1965) both reached the same conclusion. More specific results in the present study were that a rather precise threshold intensity of light acts as a phase-setting mechanism in the drift rhythms, and that an endogenous rhythm, if it exists at all, is very weak and is easily and rapidly modified by changes in light intensity across the threshold.
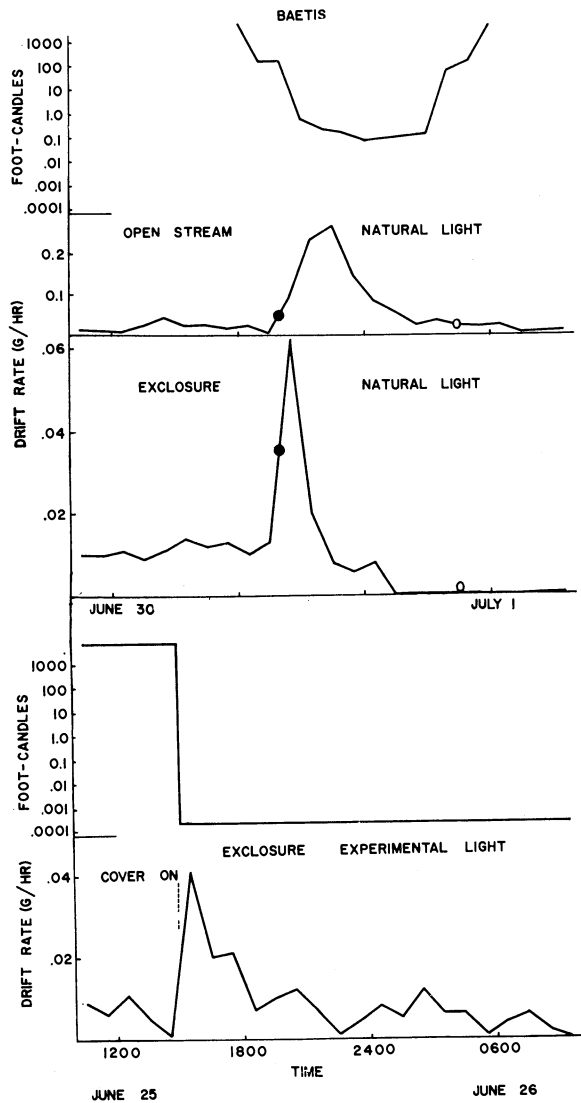

FIG. 9. Lengthened "night" test in darkening exclosure, *Baetis vagans*. Natural light and drift in open stream and in uncovered exclosure, June 30–July 1, 1964; experimental light and drift in exclosure, June 25–26, 1964.

In her recent monograph on diurnal rhythms, Harker (1964) pointed out that a light threshold was often involved in phase setting. A precise estimate of the threshold influencing drift rhythms was attempted in the present study, but for several reasons our estimates can only be expressed as ranges. For example, it was impossible to establish a precise threshold by comparing natural light intensities with drift rate changes, because light intensity changes were more rapid than was the organisms' drift response. Furthermore, it seems certain that, as light intensity approached the threshold value on a natural stream bottom, some organisms (e.g., on the underside of stones)
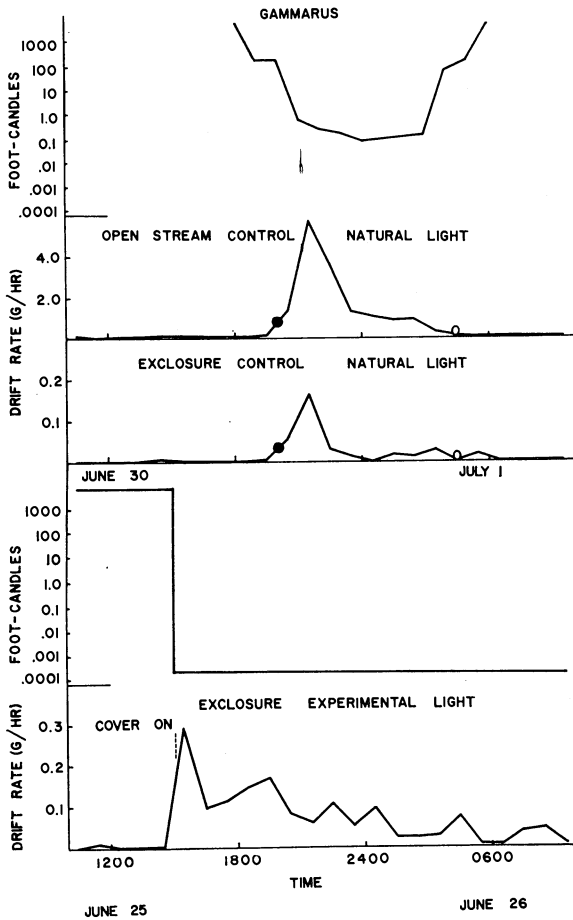
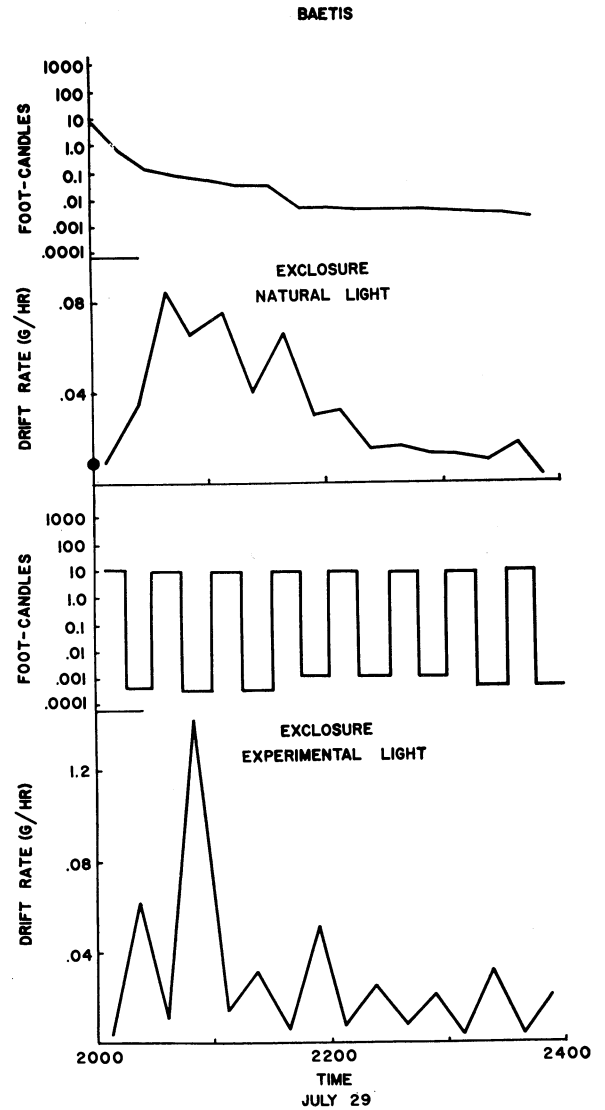FIG. 10. Lengthened "night" test in darkening exclosure, *Gammarus pseudolimnaeus*. Data as in Figure 9.

FIG. 11. Effect of rapidly alternating periods (15 min) of light and darkness on drift of *Baetis vagans*, July 29, 1963. Natural light in reference section of exclosure (closed circle represents time of sunset), artificial light in experimental section, and drift rate in reference and experimental sections.

were in light below the threshold, whereas others (e.g., on top of stones) remained above the threshold. For this reason, it seems likely that the most precise estimate of the water surface threshold intensity would be near the lower end of the ranges observed, about 0.1 ft-c (1 lux). Some of the results indicated an even lower intensity as a threshold. Some data (Waters 1962; Anderson 1965), indicating that moonlight, about 0.01–0.02 ft-c, depresses nocturnal drift, also suggest a lower threshold. The graph of Tanaka (1960), on drift of *Baetis* sp., suggests a threshold in the neighborhood of 1 lux or less. Müller (1965) reported that intensities of 1 and 2 lux significantly reduced the normally high nocturnal drift (2 spp. of *Baetis*). Although Elliott (1965) did not report light intensities with the same precision, it appears from his data that the threshold was well below 1 ft-c (11 lux) (several taxa including, presumably, *Baetis*). Thus the reports so far available agree within an order of magnitude for *Baetis,* with the present study indicating a similar

threshold for *Gammarus pseudolimnaeus*. As perceived with the human eye, an environmental light intensity of 0.1 ft-c would appear to be nearly "dark." Depending somewhat on latitude and season, this intensity occurs about 1 hr after sunset.

All of our results were in agreement that the circadian drift rhythm is labile and quickly modified with artificial changes in light, suggesting that the rhythm may be wholly exogenous. In several experiments involving the removal of the phase-setting mechanism—i.e., continuous light through the night—there appeared nevertheless a slight
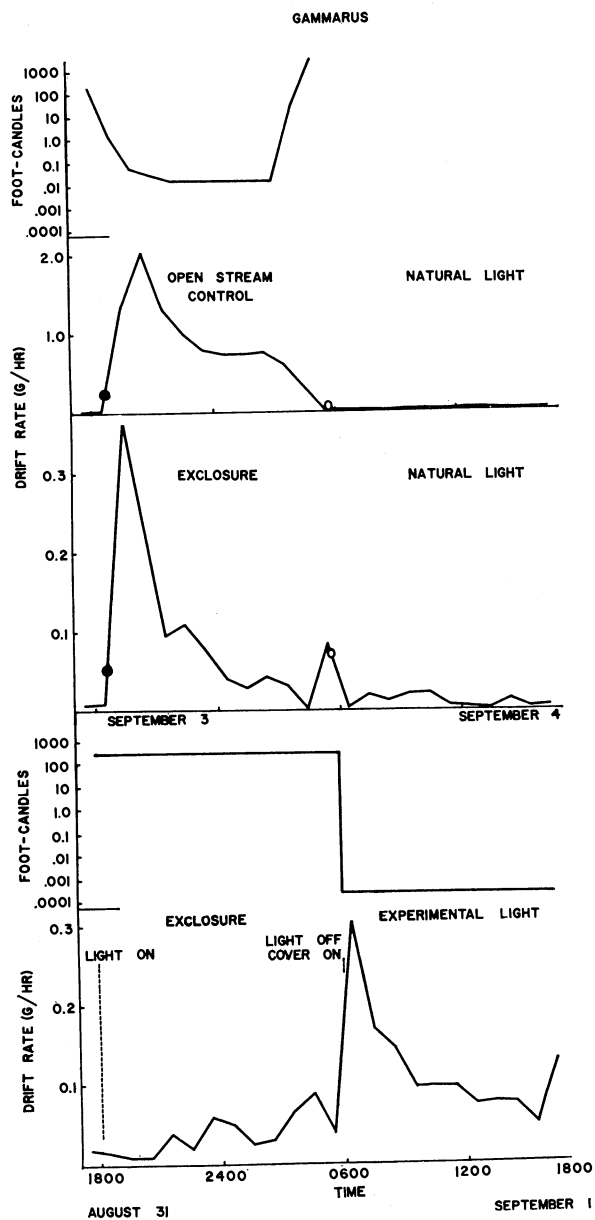
FIG. 12. Phase-reversal test in darkening exclosure, *Gammarus pseudolimnaeus*. Data as in Figure 9. Reference test (natural light), September 3–4, 1964; experiment, August 31–September 1, 1964.

increase in drift at the usual time. At first, this appearance of a normal cycle would suggest the persistence of an endogenous rhythm, although to a reduced degree. However, measurement of drift rate, for the individual organism, is not a matter of degree; it either drifts into the net or it does not. Thus, the more likely postulate must be that there was a variation in the light intensity to which the individuals were exposed. This variation was probably the result of individuals, as suggested previously, being under and in the shade of stones

and other objects, while some were in higher light intensities on upper surfaces. The former would drift in light intensities that, measured at the water surface, were above the threshold, while the latter would not. This same effect may have been shown in the data of Müller (1965) wherein nocturnal drift was reduced but not eliminated by certain artificial light intensities.

Harker (1958) warned of the possible error in concluding the absence of an endogenous rhythm even though it may not be evident in either constant light or darkness; furthermore, she had observed the persistence of a rhythm in activity in mayfly nymphs kept in constant and reversed conditions in the laboratory (Harker 1953). It is difficult to test the effect of constant darkness on drift rate, particularly in field conditions. Using an exclosure in which darkness can be produced, as in the darkening exclosure used in the present study, the experimental stream bottom is necessarily limited to a small area. In constant darkness the population density is rapidly reduced by the nature of the parameter being measured; i.e., by the drifting of the organisms out of the exclosure. Consequently the sample size is soon too small to be useful. Constant light, on the other hand, can readily be tested, as it was in the present study up to 4 days, because the resulting inhibition of behavioral drift does not reduce the population under experimentation. Müller (1965) reported that in the constant light of polar regions *Baetis vernus* did not exhibit an activity rhythm.

We concluded that while some possibility of an endogenous rhythm may exist, it was not evident among a variety of experiments and appeared, if existing at all, to be extremely weak and influenced strongly by environmental light conditions.

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PATTERNS OF PHOTOSYNTHESIS UNDER NATURAL ENVIRONMENTAL CONDITIONS

John D. Hodges[1]

University of Washington, Seattle, Washington

Abstract. Net photosynthesis in six different conifers was studied under various natural environmental conditions. Changes in the pattern of photosynthesis on clear days, especially the midday decrease, are apparently primarily controlled by changes in leaf water potential. In noble fir and Scots pine, water potential probably acts mainly through its influence on stomatal movement. In grand fir, Douglas-fir, hemlock, and Sitka spruce, however, some other mechanism, probably mesophyll resistance to CO_2 diffusion, seems to play a more important role. Both mechanisms probably operate concurrently in all species. Daily variations in leaf water potential seem to occur primarily in response to changes in atmospheric moisture, or, more precisely, vapor pressure gradient from leaf to atmosphere. Variation in carbohydrate content, through its influence on solute concentration, may also influence leaf water potential.

INTRODUCTION

The pattern of assimilation in forest trees differs markedly on days with different local weather conditions and, most often, the highest rates of assimilation occur on cloudy or overcast days (Polster 1950, Pisek and Tranquillini 1954, Gentle 1963, Helms 1963). On overcast days, net photosynthesis normally reaches a peak about midday and then gradually decreases throughout the remainder of the day. On clear days, there is normally a morning peak followed by a marked depression in photosynthesis and a second, lower peak (Rabinowitch 1945, Polster 1950, Stocker 1960). The objective of this research was to study intensively the pattern of net photosynthesis in conifer seedlings of the Pacific Northwest and, if possible, to explain these patterns by measurement of various plant and environmental factors. The research was part of a larger investigation which was also designed to study and compare photosynthetic rates and efficiency of seedlings of west coast conifers under a wide range of natural environmental conditions and to use the informa-

tion in explaining ecological differences between species. Results of the measurements of photosynthetic rates and efficiency will be presented in a subsequent paper.

MATERIALS AND METHODS

Plant material and environment

Seedlings (2–0 stock) of six species—Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Lindley)), western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent), Sitka spruce (*Picea sitchensis* (Bongard)), noble fir (*Abies procera*), and Scots pine (*Pinus silvestris* (L.))—were out-planted in plots along north-south transects extending from deep within a 35- to 40-year-old Douglas-fir stand into an adjacent open area cleared of all vegetation including herbaceous plants. The four most interesting environmental situations were those designated as open (full exposure), outside stand border, inside stand border, and deep inside stand (deep shade). The location designated as "outside stand border" was immediately adjacent to the outer margin of the Douglas-fir stand, while the one designated as "inside stand border" was