Some Effects of Heated Water on the Drift of Two Species of Stream Invertebrates¹

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ABSTRACT

Experiments were conducted on the effect of water temperature on the drift of the amphipod, Gammarus pseudolimnaeus Bousfield, and the stream mayfly, Baetis vagans McDunnough, using a water heater to produce various temperature regimes in exclosure channels in a natural stream. Under a constant temperature, the diel drift patterns of both species were unchanged relative to patterns exhibited under natural stream temperatures, indicating that water temperature was not effective in determining the length of the period, the beginning and ending of high nocturnal drift, nor the general shape of the diel pattern. In experiments involving a constant differential from natural stream temperatures, B. vagans exhibited higher nocturnal drift with higher differentials, while the drift of G. pseudolimnaeus was unaffected. Apparently water temperature affects the amplitude of drift within the diel periodicity for some species but not for others.

INTRODUCTION

An important problem in freshwater ecology is that of changing environments and the resultant effects on organism behavior, particularly in the case of fishes and their invertebrate food organisms. Rapidly increasing in importance is the effect of elevated water temperatures as a consequence of thermal discharges. It is widely accepted that temperature may exert a strong influence upon the magnitude of response to a stimulus, so that natural ecological effects may well be magnified to disruptive levels by unusually high temperatures.

In streams, the effect of normal downstream drift has received much recent attention as an important element in invertebrate population dynamics. The phenomenon of a diel periodicity in invertebrate drift, with highest drift rates at night in the case of night-active species, has been well documented, involving extremely large quantities in some streams and species. The possibility that the effect of this factor may be further increased by higher water temperatures suggests that significant, perhaps catastrophic, changes in the invertebrate community may result.

It is likely that most drift periodicities

are the result of circadian activity rhythms entrained in an "on-off' fashion by light intensity. The free-running periods of most circadian rhythms appear to be independent, or nearly so, of temperature (Pittendrigh, 1960; Sweeney and Hastings, 1960). On the other hand, temperature may modify the amplitude of activity within the rhythm, or, in some cases, may itself act as the entraining agent (Sweeney and Hastings, 1960).

The relation between the temperature of stream waters and invertebrate drift has been postulated in two ways. When drift periodicities were first observed, and before experiments with artificial light had been conducted, there appeared the possibility that water temperature, decreasing in the evening when drift was increasing, and increasing in early daytime when drift returned to low levels, was acting as the entraining agent. Subsequent experiments with artificial light and darkness clearly indicated that light acted as the entraining agent for these night-active forms (Elliott, 1965; Müller, 1966; Holt and Waters, 1967). However, several day-active periodicities have been reported recently, and in one of these the entraining agent was indicated to be water temperature (Waters, 1968).

The second postulate was that water temperature had a positive effect on the amplitude of the drift within the periodicity, the period of which was set by light. Measuring the drift on days with different stream temperatures, Müller (1963) has reported a correlation be-

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FIGURE 1.—Two-channel exclosure used in temperature experiments.

tween the amplitude of drift for the amphipod *Gammarus pulex* and water temperature.

The present study was designed to test the above two postulates with an experimental approach: artificially manipulating daily temperature regimes in a portion of a natural stream. The experiments were carried out on a riffle in Valley Creek, Minnesota, in an area where previous observations and experiments had been conducted on invertebrate drift (Waters, 1962; Holt and Waters, 1967). Subjects of the experiments were the two macroinvertebrates dominant in this stream, the amphipod Gammarus pseudolimnaeus Bousfield and the mayfly Baetis vagans McDunnough, both of which were known to exhibit night-active periodicities that often included high drift rates.

METHODS AND MATERIALS

Exclosure and Heating Apparatus

All heating experiments were conducted in a two-channel exclosure placed in a stream riffle (Figure 1). The inside dimension of each channel was 15 cm (6 inches) wide by 10 m (32 ft) long. One channel served as the experimental area to which was applied various temperature regimes and the other as a reference through which natural stream water flowed. The bottom of each channel consisted of natural stream substrate materials—stones, gravel, and sand—but was sealed off from the surrounding stream bottom. A stop cone of 253 μ -mesh Nitex at the upstream end of



FIGURE 2.—Schematic drawing of heating and recirculating apparatus.

the exclosure prevented the entrance of organisms from outside the exclosure, but was removed to allow natural invertebrate drift to flow through the exclosure and recolonize the exclosure between experiments. A metal discharge box was placed at the upstream end of the experimental channel during an experiment, from which recirculated and heated water exited through a large number of small holes in the downstream face. Natural stream water, filtered through the stop cone, flowed through the reference channel. Turbulence screens, of 253 μ -mesh Nitex, were placed next in the path of flow on a splash apron to reduce turbulence and prevent erosion at the head of the channels. Current velocity was maintained in both channels at about 0.3 m/sec (1 ft/sec). At the downstream end of each channel a sample net was placed to collect organisms drifting out of the channel. Behind the sample net in the experimental channel a pick-up box was sunk into the stream bottom from which water was pumped to the heat source.

The heating and recirculating apparatus consisted of a gasoline engine-driven pump, a bottled-gas-fueled water heater, a reservoir tank with by-pass, and a mixing barrel in which heated and cold water were mixed (Figure 2). During an experiment, water was pumped from the pick-up box, some diverted through the water heater and some directly to the mixing barrel, and then to the discharge box at the upstream end of the exclosure. Discharge in the experimental channel was

controlled by a valve in the intake side of the pump. (An original valve in the discharge outlet of the pump produced slightly higher temperatures due to water pressure in the pump; placing the valve in the intake side removed this problem.) The reservoir tank permitted the storage of a large supply of hot water in the event of pump break-down or for producing rapid changes in temperature; it was rarely used. Temperature control was achieved by adjustment of flow in the two lines leading to the mixing barrel. Thermistor sensors were placed at various points in the entire flowing system and in the substrate to monitor temperature at desired points. Upon original placement, the exclosure was tested for leakage of organisms from outside the exclosure. Prior to each series of experiments the difference in drift between the two channels was measured with natural stream water flowing through both channels (Natural); similar tests were made with recirculated water, but no heat applied, in the experimental section (Recirculation).

Experimental Procedures

Preliminary observations and equipment development were conducted in the summers of 1964 and 1965, and final experiments were conducted from the spring of 1966 through the winter of 1966–1967.

Tests with constant temperature were run on August 9-10, 1966. The temperature to be held constant was near the normal maximum for that day, there being no provision for cooling. Temperature in the experimental channel was maintained at this constant level (15 C) by continuously adjusting the relative proportions of heated and natural water entering the mixing barrel, according to temperatures monitored at various points in the system.

Experiments with a constant differential from natural temperature were conducted as a series of daily tests as follows: Natural (natural stream water through both channels), Recirculation (no heat applied), and various constant differentials from 0.5 to 8.3 C higher than reference channel. Between each two successive tests the stop cone was removed for recolonization for one or more days. The recolonization time varied from only one day



FIGURE 3.—Drift of *Baetis vagans* and *Gammarus* pseudolimnaeus under constant temperature (15 C) in experimental channel (dashed line) and natural temperature in reference channel (solid line). Closed circles represent time of sunset; open circles, sunrise.

during the summer when drift rates were high, to a week or more under the low drift conditions of winter. Four series were conducted: May 1966, July 1966, August-September 1966, and December-January 1966-1967. The winter series consumed the longest time, because drift was low, and longer recolonization times were required.

RESULTS AND DISCUSSION

Constant Temperature

Both G. pseudolimnaeus and B. vagans exhibited normal diel periodicities in drift under conditions of constant temperature (Figure 3). Neither the length of the period, beginning and ending points of the high nocturnal drift, nor the general shape of the diel pattern appeared to be any different from that exhibited in the reference channel where the organisms were subjected to the normal daily fluctuation in water temperature. The diel pattern appeared related to changes in light intensity at sunset and sunrise, as in natural temperatures. In a Recirculation test on August 4, 1966, the shapes of the curves were virtually identical to those in Figure 3.

These results confirm the experimental results of Elliott (1965), Müller (1966), Holt and Waters (1967), and Bishop (1969), which indicated light as the external factor setting the diel pattern. These results do not exclude the possibility that water temperature may affect the amplitude of the periodicity, nor even the shape of the pattern with other species, nor that temperature itself may act as the phase-setter for some species as in the case of the day-active trichopteran reported by Waters (1968). It seems probable, however, with most night-active periodicities showing a close correlation with light, similar to those exhibited by *B. vagans* and *G. pseudo*. limnaeus, that the shape of the diel pattern is not affected by natural water temperature fluctuations. Bishop (1969), as a result of intensive laboratory experiments with artificial light, arrived at a similar conclusion.

Constant Differentials

Experimental temperatures, held at constant differentials from natural stream temperatures, produced different effects between the two species. In general, *B. vagans* responded with successively higher amplitudes in drift with successively greater temperature differentials, while no apparent response of any kind was elicited from *G. pseudolimnaeus*.

Baetis vagans

The first series of experiments was conducted from May 1 to May 29, 1966, and included Natural, Recirculation, 1.1 C, 2.8 C, 5.6 C, and 8.3 C differentials. This was a period of considerable change in drift rate, emergence, hatching, mean size of nymphs, and natural stream temperature. These changes apparently complicated the results of the experiments, since some were run with large mature nymphs and some with small newly-hatched nymphs, some with high drift, others low drift, and so forth. While the results as a whole indicated some greater drift with warmed water, they were neither conclusive nor consistent.

The July series was conducted from July 5

through July 29, 1966, a period when the *Baetis* nymphs were of a consistently small mean size (about 0.5 mg) and natural drift rates were relatively high (peak drift in the reference channel about 0.5 to 1 g/hr, or 1,000 to 2,000 individuals/hr in most experiments). Temperatures in the reference channel and open stream ranged daily from about 12 C to 16 C. The series included Natural, Recirculation, 0.5 C, 1.1 C, 2.2 C, 3.3 C, 4.5 C, 5.6 C, and 8.3 C differentials. While the drift was approximately equal from both channels in the Natural and Recirculation tests, drift rates from the experimental channel were successively higher at the greater differentials, the drift being about 4-fold greater in the experimental channel at the hour of maximum drift in the 8.3 C differential test (Figure 4). The higher nocturnal drift appeared also to reach a peak earlier in the experimental channel than in the reference side in several experiments. A high second peak in the experimental drift, at 1.1 C differential, was due to a temporary equipment disturbance.

The third series was conducted from August 20 to September 7, 1966, a period in which the nymphs were still relatively small and natural drift rates consistent. The mean size of the nymphs was about 1 mg, and reference peak drift was about 0.5 g, or 500 individuals, per hour in most experiments. Natural stream temperature fluctuated daily from about 10 C to 14 C.

The series included Natural, Recirculation, 0.5 C, 1.1 C, 2.8 C, 5.6 C, and 8.3 C differentials. As in the July series, *Baetis vagans* responded to the experimental heating with successively higher drift at the larger differentials (Figure 5). Again, the maximum drift in the experimental channel was about 4 times the reference drift at the 8.3 C differential. Drift from the experimental channel ranged up to about 2.5 g, or 2,500 individuals, per hour.

The winter series (December 23-January 30) was extended because of low rates of exclosure colonization, and included only Natural, Recirculation, and selected differential experiments. Open stream and reference drift rates were very low, and natural temperatures fluctuated daily from about 1 C to 5 C. The results were inconsistent, but did include



FIGURE 4.—Drift of *Baetis vagans* in constant differential temperature experiments, July 5 to July 29, 1966. Dashed line, experimental; solid line, reference. Explanation of experiments in text.

some responses of *B. vagans* even greater than those during the summer.

In the above series of experiments that were run under essentially consistent environmental



FIGURE 5.—Drift of *Baetis vagans* in constant differential temperature experiments, August 20 to September 7, 1966. Dashed line, experimental; solid line, reference. Explanation of experiments in text.

and drift conditions (i.e. July and August-September experiments), *B. vagans* clearly responded to elevated temperatures with higher drift. This response was significant, however, only during the night when the drift was naturally high; that is, the elevated temperatures did not result in higher drift rates during the daytime, an effect which may be important in the control of heated water effluents.

Standing crop estimates were made in the exclosure areas only at the end of an experimental series, in order to avoid disturbance of the populations. But those made in the reference channels, as well as those made in the open stream in similar bottom types, indicated standing crops about 2 g/m^2 . With less than 2 m^2 area inside an experimental channel, it would appear that the higher drift of certain



FIGURE 6.-Drift of Gammarus pseudolimnaeus in constant differential temperature experiments, August 20 to September 7, 1966. Dashed line, experimental; solid line, reference. Explanation of experiments in text.

experimental temperatures would effect a serious reduction or even approach complete depletion of the standing crop of this species.

Gammarus pseudolimnaeus

The natural drift of G. pseudolimnaeus, as well as its standing crop, was too low during both the May and July series of heating experiments to provide sufficient populations for experimentation. The stream had suffered several serious floods in the previous year, including recent destructive snow-melt floods, and recovery of this species was much retarded relative to B. vagans. By the time of the August-September experiments, however, G. pseudolimnaeus density had increased to satisfactory levels, apparently as the result of spring reproduction. In this series, G. pseudolimnaeus drift from the experimental channel

was normally somewhat lower than in the reference channel, as indicated in the Natural and Recirculation tests, and it retained approximately the same relation to the reference drift throughout the entire series of temperature differentials, without responding to the higher temperatures (Figure 6). In the December-January experiments also, G. pseudolimnaeus failed to respond to the higher temperatures although density was moderate $(3 \text{ to } 5 \text{ g/m}^2)$.

Sampling the organisms resident in the exclosure channels at the termination of the experiments revealed that the Gammarus did not burrow into the substrate to escape the heated water, as was suspected. Less than 1% of the Gammarus were below 5 cm depth in the substrate, at which point the temperature was higher than in the reference channel and the open stream at the same depth. Over 90% were within 2.5 cm depth in the substrate, where the substrate temperature, while lower than the heated water above, was about 4 C higher than in the reference channel and open stream substrate at that depth. The G. pseudolimnaeus, therefore, were known to have been subjected to the higher temperatures.

These results for G. pseudolimnaeus conflict with those of Müller (1963) for G. pulex. No explanation of the difference appears to be available, even though Müller's data were the result of empirical observations and these in the present study were experimental, except that it may be due to species difference.

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