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THE MECHANISMS WHICH MAINTAIN POPULATION STABILITY OF SELECTED SPECIES OF EPHEMEROPTERA IN A TEMPERATE STREAM

by

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Abstract

The current exerts a continual force on benthic invertebrates in streams to displace individuals downstream. The mechanisms which compensate for this effect and result in a relatively stable population density were investigated.

Downstream drifting, adult aerial flight patterns and benthic population densities were measured for the eight most common mayfly species found in the Rat River, Manitoba. The study area was a closed system with little possibility of immigration from outside areas of similar habitat type.

In none of the eight species was there any evidence of a colonization cycle such as that described by Muller. An attempt was made to determine whether the adults showed directional tendencies in their flight patterns. There was no significant downstream shift in any of the populations during the aquatic life stages which could be attributed to drifting. There was no indication that this occurred.

The results do support Waters' contention that drifting is a mechanism of reducing intraspecific competition pressures and therefore no mechanism of compensation for drifting need exist. In the three most common species, the proportion of the population in the drift was shown to greatly increase with an increase in the benthic density. The other species apparently never reached their carrying capacity and the proportion of the population in the drift was always low. The overall reduction in the population density due to such causes as to predation is compensated for by a high reproductive rate.

I N D E X

INTRODUCTION

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INTRODUCTION

1) The Stream Community

The stream community is strongly influenced by the effects of current. All benthic invertebrates which are found in streams show some degree of morphological, physiological or behavioural adaptation to it. Many of these adaptations, particularly among species which are found in areas of fast flowing water such as riffles, are for maintaining position in the substrate.

Benthic animals are however found in the water column. Needham (1928) is one of the earliest accounts of observations of significant numbers of benthic invertebrates being carried downstream by the current. He termed this phenomenon 'drifting'. In his conclusions, Needham argued that since most species were adapted to resist the effects of the current, drifting was largely a passive process. During the next two decades, there were several papers published on drifting (Dendy, 1944; Ide, 1942; Lennon, 1941). In each of these, the authors agreed with Needham's conclusions. However, Muller (1954) reported that the density of individuals which he observed in the water column, followed a predictable diel pattern. The greatest densities always occurred at dusk and at dawn and the mean density throughout the night was always greater than that during the day. He concluded that drifting was not merely the result of accidental dislodgement as had been earlier suspected, but was an active process. This paper raised many questions about the population dynamics of stream invertebrates and stimulated further research into drifting and the mechanisms of population stability.

2) Population Shifts and Models of Compensation

Drifting can only result in a downstream movement of individuals.

If there were no mechanism to compensate for drifting then a shift in the population downstream would have to occur and there would be a continual decline in the density of the population along the stream. The rate at which the population would decline would be regulated by the degree to which the population drifted.

Kubicek (1969) estimated that the proportion of the population of invertebrates which is in the drift at any given time may be as high as 4%. However, most estimates which have been made range from 0.01% to 0.5% (Bishop & Hynes, 1969; Ulfstrand, 1968; Elliott, 1967). At first glance, these figures seem small but Waters (1972) has extrapolated these data to obtain estimates of the total daily drift. If the proportion of the population in the drift at any given time averaged 0.01% and the current speed was 1 m/sec., then the ratio of the total daily drift which passed the sampling site to the standing crop in 1 m^2 of substrate would be 8. If the proportion of the population in the drift was 4% rather than 0.01% then this ratio would be 3500. To look at it another way, Ulfstrand (1968) calculated for the Lapland stream on which he was working that in a 24 hr. period 5% of the entire population of benthic invertebrates from an 8 km stretch of the river drifted past his sampling station.

While estimates of the density in the drift are reasonably consistant, the estimates which have been made of the mean distance each individual drifts per day are highly variable. Waters (1965) calculated that Baetis vagans (Ephemeroptera), the average distance drifted per day per individual was at least 38 m. However, Madsen (1968) noted that aquatic insects rarely seemed to drift great distances at one time but rather they made several short drifts, stopping for brief periods each time they came in contact with the substrate. Bishop and Hynes (1969) supported Madsen's observations and concluded that the actual average distance drifted each day per individual was propably very short although some individuals did seem to drift long distances at one time. However, even if the distance that an individual drifted was short, the high proportion of the population which has been shown to drift each day indicates that a rapid downstream shift in the population should occur unless some mechansim of compensation exists; in studies which have been done in the headwaters of streams where a downstream shift in the population would be first evident, the population remains stable (Pearson & Kramer, 1972). This evidence indicates that some mechanism which compensates for drifting must exist.

There have been three hypotheses presented which could explain why population densities remain stable in spite of high drift rates. However, each of these theories is supported only by circumstantial evidence because of the inherent complex of nature of stream communities.

The simplest explanation is that the animals walk back up stream, thus compensating for the distance that they have drifted. Hynes (1970) cites morphological and behavioural characteristics which result in a positive rheotactic response by many species of benthic invertebrates. Other workers (Neave, 1930; Hayden & Clifford, 1974; Elliott, 1971a; Bishop & Hynes, 1969; Hultin, Svenson & Ulfstrand, 1969; Minckley, 1964) have measured upstream movement in a number of species but even the largest estimate only accounts for about 30% of the drift. Also, most species of benthic invertebrates which are found in streams are specific in their environmental requirements, particularly with respect to current speed and substrate size (Hynes, 1970). It is unlikely that an individual would attempt to cross an area which is unsuitable for it. It appears, therefore, that this theory can only partially explain population stability.

Muller (1954) proposed a 'colonization cycle' in which the adults of the aquatic nymphs fly upstream to lay their eggs which compensate for the distance which they drifted during the aquatic stages of their life cycle. There have been a number of papers in which observations of upstream migration flights have been noted (Roos, 1957; Elliott, 1969, 1971b; Lehmann, 1970; Madsen, Bengtsen & Butz, 1973). However, Elliott (1967) found that species of Plecoptera and Emphemeroptera which emerged into exposed areas moved with the wind regardless of which way it was blowing. Bishop and Hynes (1969) observed no continual upstream migration in any of the species with which they were working. Muller's theory is only applicable to insect species which are capable of flying (eg: Ephemeroptera, Plecoptera) but offers no explanation for all of the other taxa (eg: some Coleoptera, Cladocera).

Waters (1961) hypothesized that drifting was a mechanism of reducing population pressures which arose due to overcrowding and it is also ensured that all of the suitable habitat which was available was colonized. When the carrying capacity of a location is reached, any excess individuals drift and these individuals would provide a source for colonization of areas which had a population density less than the carrying capacity. This mechanism would ensure the maximum utilization of the available habitat. Waters hypothesized that no upstream migration was necessary because the adults always produced offspring in excess of the carrying capacity. Dimond (1967) supported Waters' theory when he observed that in an area where the fauna had been eliminated by DDT, re-colonization was rapid but the number of individuals in the drift below this area was low until the benthic density of the area reached what it had been before the introduction of the pesticide. Once this density was reached, the number of animals in the drift dramatically increased. However, if this theory is the main mechanism which ensures population stability in streams, then headwater regions which were subject to disturbances would be slow in recovering because no upstream migration takes place. This however does not seem to be the case (Pearson & Kramer, 1972).

The object of this thesis is to examine the populations of some species of benthic insects under unique environmental circumstances to determine which, if any, of these hypotheses is responsible for maintaining population stability.

METHODS

1) The Study Area

In most streams it is impossible to make valid conclusions about shifts in population densities because the range of each species rarely has well defined boundaries. Habitat zones gradually change from one to another and presumably the species associated with each of these zones would find the transition area suboptimal. Observations on the changes in density in transition areas are always in question since the changes may be due to a natural shift in the population or to a change in the suitability of the habitat. Subtle environmental fluctuations may have a drastic effect on individuals in sub-optimal areas but little or no effect where the habitat is more suitable. The Rat River provides a unique situation which overcomes this problem.

The Rat River arises in the Sandilands region of south-eastern Manitoba. For most of its length it is slow and meandering. The substrate is sand and silt and the stream bed is at grade which is the minimum slope a river can attain since at this point the current is no longer fast enough to cut into the stream bed. The upper part of the stream is in glacial moraine substrate while the lower portion is a glacial lake bed. Where it descends from the morainal uplands to the lake bed across the ancient beach ridges, the Rat River becomes a typical riffle-pool stream. This zone was about 15 km in length until the construction of a dam at St. Malo. The resevoir formed by the dam shortened the zone to 7 km. The drop in elevation in this section of the stream is approximately 50 metres which represents about 50% of the total for the entire river. This portion of the Rat River formed the study area. A schematic representation of the area is shown in Figure 1.

The rapid change in slope as the Rat River reaches the beach ridge area forms a sharp division between the two habitat types. A beaver dam creates a large pond at the upper end of the study area. Immediately below this dam is the first riffle. At the lower end of the study area the transition back to a slow meandering habitat is also well defined because of the dam at St. Malo. This dam causes the river to be at grade for about 8 km upstream from it. Because of the steep slope of the river, the transition from the riffle-pool zone to the zone which is at grade is very abrupt. The point at which this transition takes place is regulated by the height of the St. Malo dam. Since this height is fixed, the point of transition moves very little. The study area therefore has precise and well defined boundaries and there is no transition zone at either the beginning or the end.

Most species of benthic invertebrates which are found in streams are specific in their environmental requirements, particularly with respect to current speed and substrate size (Hynes, 1970). Therefore, the species which are found in the study area, with a few exceptions, will not be found in the areas adjacent to it. For this reason, the study area is essentially a closed system. The only areas of similar habitat from which immigration could occur are below the dam at St. Malo which is about 8 km from the lower end of the study area, and the Rouseau River which is 9 km from the Rat River at its closest point. Because the distances to either of these areas is great, immigration from them into the study area was assumed to be negligable. Since the system is closed, the observations which were made on shifts in benthic density, drift characteristics and adult flight patterns must have been on individuals who had originated within the study area.

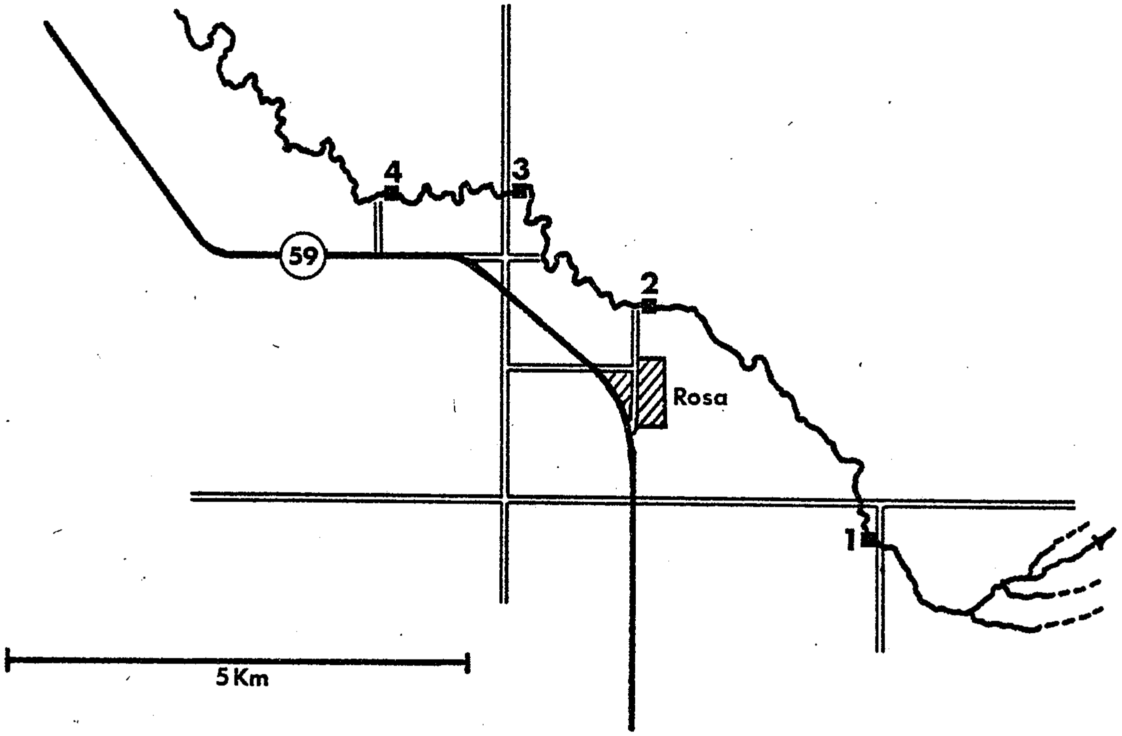

Figure 1: The location of the sampling stations along the study area of Rat River in southeastern Manitoba.

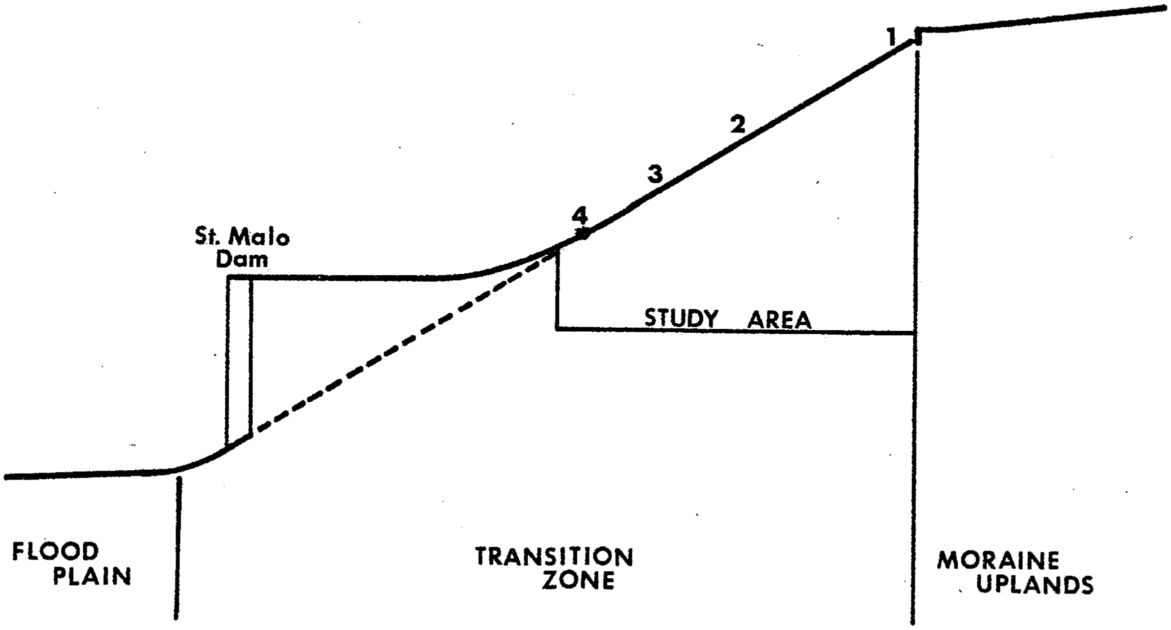

Figure 2: A schematic cross section of the beach ridge area of the Rat River and the location of the study area.

Four sampling sites were established in the study area (Figure 2). Station #1 was in the first riffle immediately below the beaver dam. Station #4 was located in the last permanent riffle before the stream reached the zone which was at grade. During periods of low water, temporary riffles were observed up to 200 metres below this station but throughout most of the summer the stream reached grade immediately after this riffle. An attempt was made to space stations #2 and #3 at equal intervals between stations #1 and #4 but since road access was essential, their location was largely dictated by this factor.

2) Sampling Objectives and Restrictions

In order to reach a conclusion about the mechanisms which ensure population stability in streams based on the proposed models, it is necessary to examine three phases of the life cycle of the aquatic insects. These are: the migration patterns of the flying adults, the drift characteristics of the immature insects and the changes that take place in the benthic density at each station with time. The sampling program was established to examine each of these.

There are over 100 species of benthic invertebrates in the Rat River (de March, 1974). In a study such as this, it would have been impossible to consider all of these species. Therefore, it was decided that one order, the Ephemeroptera, would be examined. This group has several characteristics which made it suitable for the study. Most species are highly selective in their environmental requirements, particularly current speed (Hynes, 1970). They are known to drift in large numbers relative to their benthic density (Waters, 1972) and the nymphs as well as the adults are easily identified to species in most cases.

3) Aerial Migration

An attempt was made to determine if the adult mayflies were flying upstream where reproduction occurred. Madsen, Bengtsen and Butz (1973) had stretched sheets of clear polyethelene which had been sprayed with 'Tanglefoot', a commercial adhesive used to prevent insects from climbing tree trunks, across a stream. By observing the number of insects caught on each side of the plastic, they were able to determine if any upstream migration was taking place. They noted that the insects showed no apparent avoidance behaviour towards the trap. This method was modified for use in this study. Wooden frames, 1 m. square, were covered with clear polyethelene. Each trap was suspended from a metal frame at right angle to the current in the middle of the stream. There was one trap at each station. As the water level fluctuated, the metal frame was adjusted to keep the trap as close to the surface of the stream as possible. The traps were installed on June 19, 1974 while the river was still swollen from the spring runoff. They were changed every ten days to two weeks until August 29. They were changed once more on September 25 and were removed on November 9 after the river had frozen over. The mayflies were removed from each side of the trap by dissolving the Tanglefoot with turpentine. They were then identified and counted and a record was kept as to which side of the trap they had been captured on.

4) Drift Samples

On July 9, 1973 and August 13, 1973, 24 hour drift samples were taken at all stations. The drift traps were metal frames 30 cm. wide and 50 cm. high to which 202 micron nitex screen nets were attached. The nets were constructed so as to reduce the buildup of a pressure wave in front of the opening of the trap as the screening became clogged with silt. They were 1 metre in length and tapered outward for the first 30 cm. before tapering to the collecting cup at the end. The frequency with which the collecting cup had to be changed during the 24 hour sampling period was determined by observing the length of time it took for enough silt to be trapped by the net so that a pressure wave formed in front of the trap. This interval was found to be four hours. The collecting cups were therefore changed every four hours throughout each 24 hr. sampling period. The times at which the cups were changed were so arranged as to ensure that both sunrise and sunset each fell entirely within one sampling interval. As the cup at each trap was changed, the contents were preserved in 10% formalin and the location and time of the sample recorded. After 48 hours in formalin the samples were transferred to a solution of 70% ethyl alcohol.

5) Surber Samples

A standard Surber sampler was used to measure the density of the benthic nymphs. The frame of the sampler was 33 cm. square and therefore each sample had an area of 1/9 of a square metre. The net was of the same design as that used in the drift traps. During each sampling period nine samples were taken at each station. De March (1974) suggested that the substrate preferences of individuals of each species may change with age. To ensure that a bias was not introduced because of this shift in substrate preference, three samples were taken in each of three substrate types at each station. Although somewhat intuitive in nature, these substrate types were: rocks (minimum dimension of 30 mm.), gravel (minimum dimension of 8 mm. and a maximum of 30 mm.) and sand (maximum dimension of 8 mm.).

Sets of samples were taken on July 9, August 13 and September 22, 1973 and July 2, July 22 and September 25, 1974.

The Surber sampler has been criticized when it has been used for comparative studies because its efficiency changes with the current speed, and variations between density estimates often result when different people take the samples. However, these faults can be minimized as follows: All of the samples which were taken during this study were from areas where at least some current was flowing. The net modifications which were described earlier greatly reduced any buildup of a pressure wave in front of the sampler. Fabric skirts were attached between the horizontal and vertical frames, reducing the possibility of losses around the edges of the sampler. To standardize the sampling technique, I personally took all of the samples. Each sample was taken to a depth of 10 cm. and all of the substrate was washed at least twice.

An additional criticism of the Surber sampler is that it only samples the surface layer of the substrate. Coleman and Hynes (1970) have shown that a significant proportion of the population of many species of benthic invertebrates is found deep in the hyporheic zone. However, Williams and Hynes (1974) have noted that few species of Ephemeroptera are found below 30 cm. into the substrate and that the majority of the population of most species is found in the top 20 cm. Furthermore, the Rat River has an underlying clay layer which is seldom more than 20 cm. and often less than 10 cm. below the surface of the substrate. This layer is most certainly impermeable to insects. Therefore, Surber samples taken to a depth of 10 cm. were deemed adequate to estimate the density of mayflies in the Rat River.

Any sampling technique is negatively biased. While this in itself is not critical unless absolute estimates of density are required, the technique must give an accurate estimate of the age distribution and must also have the same relative efficiency under similar circumstances if a valid comparison is to be made between different sampling sites. Both Meeham and Elliott (1974) and Chutter and Noble (1966) conducted tests which showed that the Surber sampler, although not necessarily efficient, gave reliable comparative estimates of the density and age distribution.

6) Sampling During Periods of Drought

From July 27, 1974 until August 22, 1974 there was no water flowing in the Rat River (Water Survey of Canada). Samples were taken at each of the four sampling stations on August 13 to determine if there were any individuals in the substrate. The samples were taken by digging a pit 30 cm. square until the clay layer was reached. At stations #1, #2 and #3 where there was not water at all, the samples were taken along a transect where it was judged that the last pools of water had been. At station #4 where small pools of water were still present, the samples were taken along a transect at the edge of the pool which was closest to the station. All of the substrate material which was removed from the pit was taken to the laboratory where it was washed by hand and the finer material and animals were collected in a 202 micron net. The samples were preserved in 10% formalin for 48 hours and then transferred to a 70% ethyl alcohol solution.

7) Floating and Subsampling

A floatation technique was used on all of the Surber samples and on the samples taken from the dry stream bed to separate the inorganic from the organic material. This process was not only much faster than sorting the samples by hand but was also probably more efficient.

Each of the preserved samples was rinsed in water and allowed to drain. It was then dumped into a tray and a solution of sugar and water was poured over it. The sample was stirred several times to facilitate the separation of the animals from the substrate. As the animals floated to the surface of the solution, they were removed and again preserved in alcohol.

The specific gravity of the sugar and water solution is critical in this process. Flannagan (1973) found that for Ephemeroptera which had been preserved in 70% ethyl alcohol, the best specific gravity was 1.13. He observed that the animals would float for at least 30 minutes in this solution before they became saturated and sank. For the purposes of the samples used in this thesis, the maximum allowable time was set at 20 minutes to ensure that any variation in the specific gravity due to dilution by water trapped in the sample would not affect the relative efficiency of the process. After every third sample, the specific gravity was checked using a hydrometer and sugar was added until it was brought back to 1.13. The minimum observed specific gravity was 1.11 which is still within acceptable limits according to Flannagan (1973).

Anderson (1959) found that a floatation technique was more efficient than sorting the samples by hand, particularly when there was a great deal of inorganic material in the sample as is the case with those from the Rat River. In his work, he found that sorting by hand was only 64%-86% as efficient as sorting by floating. While Flannagan (1973) stated that live animals floated more readily than those preserved in 70% alcohol, Anderson (1959) noted that many species, particularly mayflies, released their grip on the substrate material when preserved. Therefore, in this instance, it probably was better to float the samples after they had been preserved.

The large number of animals in many of the samples made analysis of the whole sample impractical. Therefore, each was subsampled after it had been floated. The device used to subsample was simply a tapered trough which was pivoted in the middle. The sample was put in the deeper end of the splitter and was stirred until it appeared to be homogeneous. In the shallow end of the splitter, a divider split each sample into two equal volumes as the trough was tilted and the sample poured out the open shallow end. Three successive splits were done on each sample. Therefore, the final subsample which was analysed was 1/8 of the original sample. In addition to the Surber samples, the drift samples were also subsampled although they were not floated. The samples taken during the drought were not subsampled because of the low number of animals in them.

In order to estimate the efficiency of the subsampling technique, the mayflies in seven samples were counted. Each sample was then subsampled and the number of mayflies in the subsample counted. A regression analysis which compared the actual number of mayflies in the subsample to the number represented by 1/8 of the original sample, indicated that the subsampling technique was 95.3% efficient.

8) Identification and Measurement

All of the mayflies were identified to species using Burks (1953) as the taxonomic authority. A species list of the mayflies in the Rat River was available from de March (1974).

An estimate of the relative age of each individual was obtained by measuring the pronotum length. The total length of the animal could not be used because of the contortions which occur when they are preserved. Clifford (1970) showed that the pronotum length gave the most reliable estimates of relative total length for the mayfly, <u>Leopophlebia cupida</u>.