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

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ABSTRACT

The study was designed to determine whether either Muller's 'colonization cycle' or Waters' theory of intraspecific competition adequately explained why the population densities of eight species of Ephemeroptera in the Rat River, Manitoba, remained stable in spite of high drift rates. The flight patterns of the adults, the density of nymphs in the substrate and the drift rates were studied over two summer seasons. The results supported Waters' hypothesis that drifting was a mechanism of reducing population densities when the carrying capacity was reached. The proportion of the population in the drift was density dependant and at high drift rates size selective. There was no evidence of a 'colonization cycle' as Muller had proposed.

INTRODUCTION

All benthic invertebrates, which spend at least part of their life cycle in streams, show some degree of adaptation to maintaining their position in the substrate. However, a proportion of each population can always be found in the water column moving downstream or 'drifting'.

Muller (1954) demonstrated that drifting was not simply a passive process but for most species followed predictable cycles and patterns. Later studies (Bishop and Hynes 1969, Ulfstrand 1968, Elliott 1967, Waters 1965) showed that because of drifting, many species should have displayed successive downstream shifts in population density with each generation. However, no such shifts were observed and this led to speculation that there must be some mechanism which compensated for drifting.

Three theories have been proposed to explain why population numbers appear to remain stable in spite of high drift rates: (1) adult insects upon emerging, fly primarily upstream before laying their eggs and thus compensate for the distance that they drifted during the aquatic stages of their life cycle (Muller 1954), (2) drifting is density related and it is a mechanism of reducing intraspecific competition (Waters 1961), (3) individuals simply walk back upstream either on or in the substrate. However, it has been shown by Elliott (1971), Bishop and Hynes (1969), Hultin *et al.* (1969) and Minkley (1964) that walking back upstream can only partially compensate for drifting and it is probably only of importance on a localized scale. Therefore, this study was undertaken to determine whether either of the other two hypotheses adequately explained population stability in streams.

METHODS

As the Rat River in southeastern Manitoba, Canada, descends the beach ridge formations created by glacial Lake Agassiz, a short 7 km zone of riffle-pool type habitat is formed. Both upstream and downstream from this zone the river is slow and meandering. Species which are specifically adapted to a riffle-pool habitat are therefore confined to this one area of the Rat River.

The riffle-pool habitat zone formed the study area. Four permanent stations were established in riffles. Station 1 was at the beginning of the zone, Station 4 at the end and Stations 2 and 3 spaced approximately equidistant between 1 and 4.

The study was restricted to the eight most abundant species of Ephemeroptera that were found exclusively in the study area: *Baetis hageni* Eaton, *Baetis intercalaris* McDunnough, *Pseudocloeon myrsum* Borks, *Paraleptophlebia praepidita* (Eaton), *Ephoron album* (Say), *Stenacron interpunctatum canadense* (Walker), *Stenonema nepotellum* (McDunnough) and *Heptagenia maculipennis* Walsh.

To adequately evaluate Muller's and Waters' hypotheses, three aspects of mayfly ecology were studied: (1) the flight patterns of the adults, (2) the relative change in benthic density among the stations with time, (3) the proportion of the population that was drifting compared to the benthic standing crop.

Traps similar to those in Madsen *et al.* (1973) were used to determine whether there was a directional migration to the flight patterns of the adults (subimagos and imagos). Each trap consisted of a vertical wooden frame, 1 m^2, that was covered with clear polyethelene film and sprayed with Tanglefoot^{R}. One trap was set up at each station and the frames were changed at approximately 10 day intervals throughout the 1974 sampling season. The adult mayflies that had flown into the traps, and adhered to the plastic, were removed by dissolving the Tanglefoot^{R} with turpentine, then identified and counted. To determine whether a migration was taking place, a series of Chi-squared analyses were calculated comparing the number of individuals on either side of the traps. A separate analysis was done for males and females of each species caught in the traps.

Estimates of the benthic standing crop were obtained using a 0.11 m^2 surber sampler with a 202 μm net. Nine samples were taken at each station on July 9, August 13 and September 22, 1973 and July 2, July 22 and September 25, 1974. The nine samples were allocated equally among three substrate types: rocks, gravel and sand. Each sample was floated following the procedures recommended by Flannagan (1973) and subsampled using a volume type splitter (Gyselman 1976). Each sample was successively split three times so that the 'working subsample' was 1/8 the volume of the original sample. A regression analysis of the predicted number of individuals of each species in the subsample to the actual number showed that the technique was 95.3% efficient. The mayflies from the working subsamples were identified and the pronotum length of each individual was measured using an ocular micrometer. For each species, the range of pronotum lengths was arbitrarily divided into eight length groups. These groups were used as a measure of relative age with group 1 being the youngest and group 8 the oldest.

A four-way factorial analysis of variance of the benthic density data was calculated for each species in each year to determine the effects of sampling period, station, substrate type and age (pronotum length group). As with most age distribution data, the variance among the replicates within the period-station-substrate combinations for each species was found not to be homogeneous and a log (X+1) transformation of the data was used.

During the first two sampling periods of 1973, drift samples were taken over a 24 hour period at each station. The samplers were 33 cm wide with 202 μm nets and sampled the whole water column. There were two samplers at each station and each was emptied every-four hours. The drift samples were subsampled using the same technique as that used for the Surber samples. The mayflies from each working subsample were identified and the pronotum of each was measured. There was sufficient data on *Baetis hageni*, *Baetis intercalaris* and *Pseudocloeon myrsum* to carry out analyses on the relationship between the benthic density and the number of individuals in the drift. A curvilinear regression was done for each species to determine whether the number of individuals in the drift was linearly related to the benthic density. A second degree polynomial was proposed as an alternative model. In addition, a series of Student's *t*-tests were done to compare the mean pronotum length of the benthic populations with that of the individuals caught in the drift.

RESULTS

Aerial Migration

Only 5 species, *Ephoron album, Stenacron i. canadense, Stenonema nepoltellum, Heptagenia maculipennis* and *Pseudocloeon myrsum*, were caught in the aerial migration traps. In none of the Chi-squared analyses was there a significant different ($P < 0.05$) in the number of individuals caught on either side of the traps.

The Relationship of Density and Age Between the Drift and the Benthic Population

Four species were caught in significant numbers in the two sets of drift samples: *Baetis hageni, Baetis intercalaris, Pseudocloeon myrsum* and *Paraleptophlebia praepidita. Ephoron album, Heptagenia maculipennis,* and *Stenonema nepotellum* were not found in any of the drift samples and only five individuals of *Stenonema i. canadense* were caught.

The probability of Type I error in the curvilinear regressions was less than 0.01 for *P. myrsum* and *B. intercalaris* and less than 0.05 for *B. hageni*. Therefore, in each case the second degree polynomial is a better model of the data than is the linear equation.

The results of the Student's *t* analyses are summarized in Table 1.

Benthic Densities and Age Structures

A four-way factorial analysis of variance generates four main factor effects and 11 interaction effects. However, only the period/station/age interaction which measures the change in age structure differences among the stations throughout the sampling season is important in this study. The period/station/age interaction was significant for *Baetis hageni* in 1973, *Baetis intercalaris* in 1973, *Pseudocloeon myrsum* in 1974, *Paraleptophlebia praepidita* in 1974, and *Stenacron i. canadense* in 1974.

The drought in August, 1974 that caused the Rat River to dry up was the obvious cause of the significant period/station/age interaction for *P. praepidita* and *S. i. canadense*. Both of these species

Table 1. A comparison of the mean pronotum length of individuals caught in the drift and the benthic population.

			SURBER		DRIFT		
	DATE	STATION	$\overline{X}$	N	$\overline{X}$	N	t
Baetis hageni	July 9 1973	1	0.65	5	0.82	5	2.50
		2	0.67	17	0.60	9	1.08
		3	0.67	37	0.66	12	0.60
		4	0.66	43	0.66	6	1.82
	August 13 1973	1	0.64	266	0.75	201	172.21**
		2	0.58	117	0.64	32	34.19**
		3	0.64	105	0.65	57	2.55*
		4	0.52	22	0.61	16	13.07**
Baetis intercalaris	July 9 1973	1	0.84	70	0.66	5	9.15**
		2	0.88	76	0.61	7	12.50**
		3	0.72	87	0.99	3	24.90**
		4	0.87	189	0.80	9	16.12**
	August 13 1973	1	0.94	199	0.75	43	106.38**
		2	0.88	36	0.78	2	3.56**
		3	0.96	59	0.80	7	28.93**
		4	0.91	41	0.87	7	6.99**
Pseudocloeon myrsum	July 9 1973	1	0.69	21	0.80	3	15.65**
		2	-	--	-	-	-
		3	-	-	-	-	-
		4	0.65	21	0.73	6	5.69**
	August 13 1973	1	0.79	59	0.85	117	16.34**
		2	-	-	-	-	-
		3	-	-	-	-	-
		4	0.62	6	0.63	6	0.16

$\overline{X}$ = Mean Pronotum Length
N = Total Number of Animals Caught by the Sampling Method
* = $P < 0.05$
** = $P < 0.01$

were common in all of the Surber samples taken in 1973 including those taken on September 22. They were also abundant in the samples taken on July 2 and July 22, 1974 but were absent from those taken after the drought on September 25, 1974.

The significant period/station/age interaction for *B. hageni* in 1973 appears to be the result of differential hatching and development of the nymphs (Fig. 1). There is an increase in the density of young individuals at station 1 on August 13 but the corresponding increase does not occur at Stations 2 and 3 until September 22. This was a feature of the 1973 sampling season only and it was not repeated in 1974.

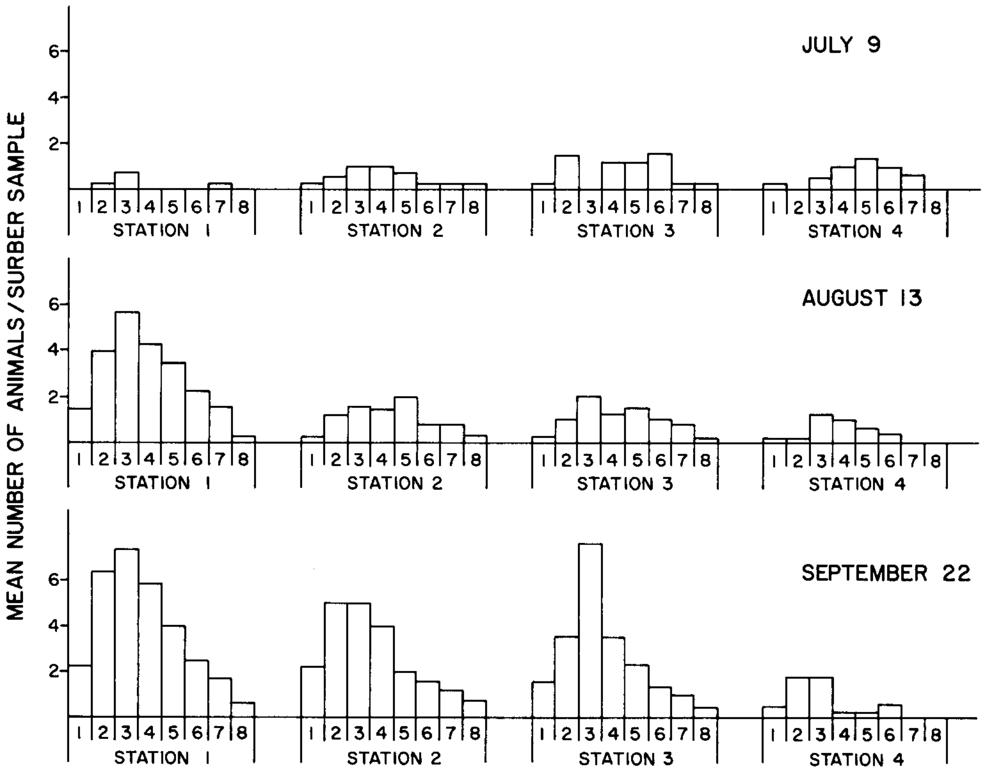

Figure 1. The mean density of *Baetis hageni* in each age cohort at each station during 1973.

There is a significant decline in density at station 4 over the sampling season of both *P. myrsum* in 1974 (Fig. 2) and *B. intercalaris* in 1973 (Fig. 3). While there is no explanation for these declines, they do not appear to be the result of an upstream shift in the population. In neither case was the decline repeated during the other sampling season.

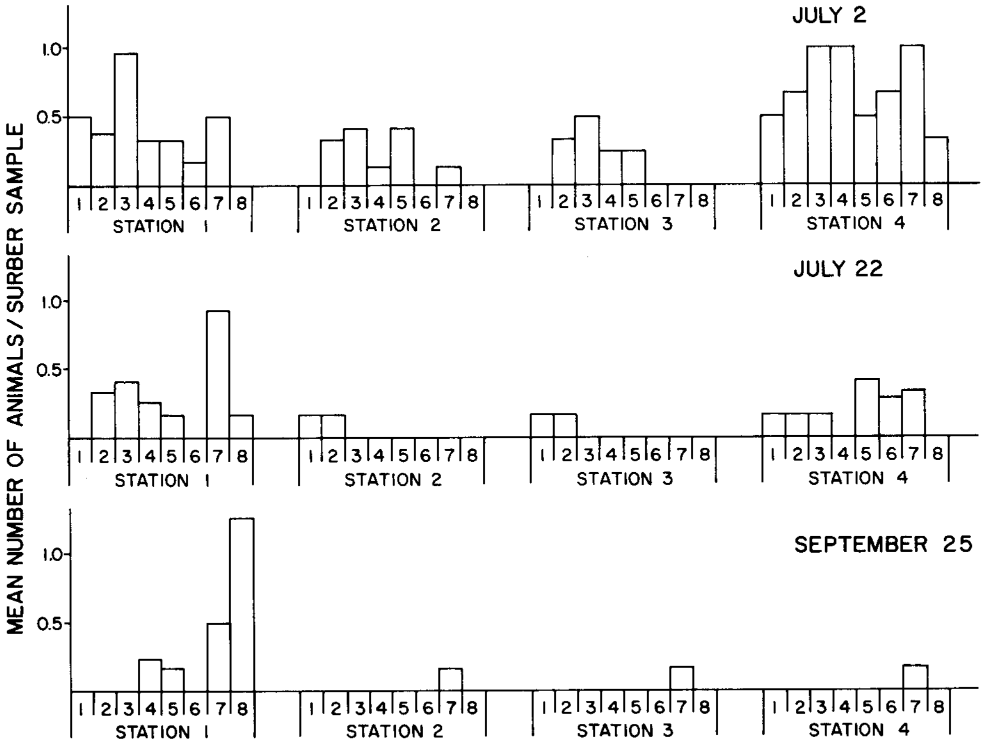

Figure 2. The mean density of *Pseudocloeon myrsum* in each age cohort at each station during 1974.

It is important to note that there is no evidence of either an upstream or downstream shift in the population over the sampling season in any of the cases where the period/station/age interaction was significant.

DISCUSSION

The results of this study do not support Müller's theory of a 'colonization cycle'. The analyses of the data from the aerial migration traps show that there was no upstream flight by the adults of the five species caught. Furthermore, the factorial analyses of the benthic density data indicate that the relative density among the stations remains stable throughout the summer for 11 of the 16 species/year groups. Of the five species/year groups that did have a significant period/station/age interaction, two were caused by the drought in August, 1974 and an examination of the age distribution histograms for the other three shows no indication of an upstream or a downstream shift in the population.

Waters' (1961) hypothesis is supported by some of the data from this study. The curvilinear regressions show that for *Baetis hageni*, *Baetis intercalaris* and *Pseudocloeon myrsum* the proportion of the population in the drift increases as the benthic density increases. This idea fits Waters' model well. He states (Waters

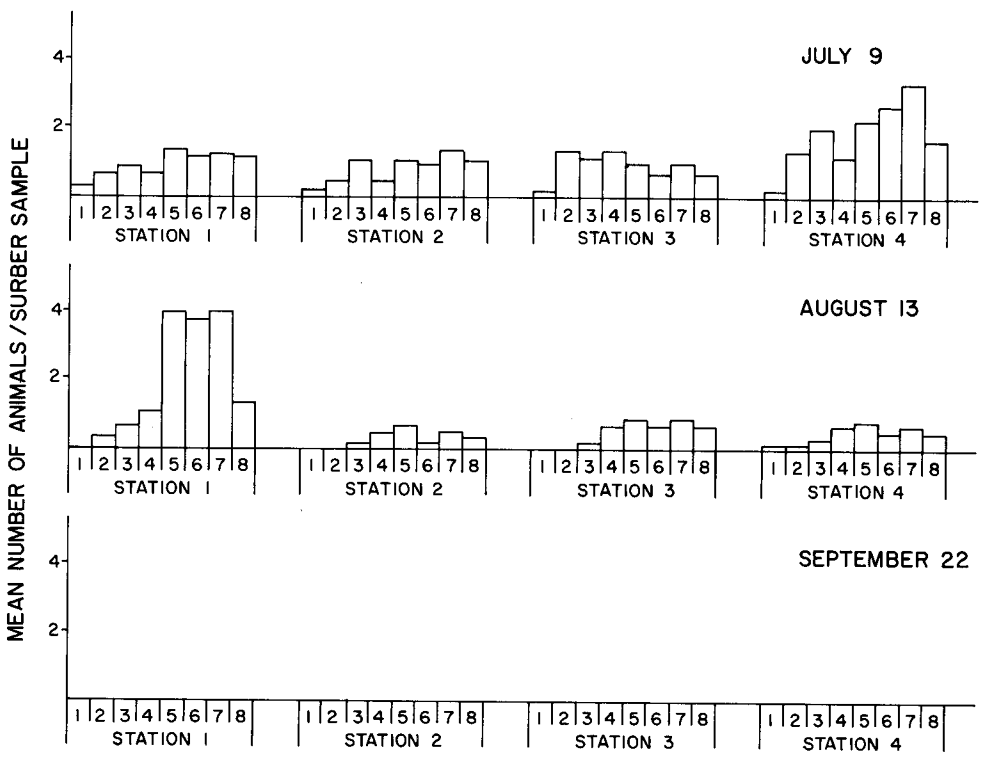

Figure 3. The mean density of *Baetis intercalaris* in each age cohort at each station during 1973.

1972) that the observed drift is a combination of 'constant drift' which is the result of involuntary dislodgement of individuals by the current and 'behavioural drift' which is made up of individuals who voluntarily enter the current because of population pressures. Apparently, the densities of *E. album, P. praepidita, S. i. canadense, S. nepotellum* and *H. maculipennis* were below their carrying capacities because they were rare in the drift although they were abundant in the sediments. Presumably there was very little behavioural drift. However, for *B. hageni* and *B. intercalaris*, the two most abundant species of mayflies in the Rat River, and for *P. myrsum*, the proportion of the population in the drift increased with the benthic desnity. This suggests that these species must have been near their carrying capacities. The high drift rate for these species was apparently due to behavioural drifting.

If the high drift rates for *B. hageni, B. intercalaris* and *P. myrsum* were the result of behavioural drift and if behavioural drift is caused by intraspecific competition, then there may have been a size selection for those individuals who were drifting. The Student's t analyses show that this is the case when the benthic density was relatively high (Table 1). The pronotum length was significantly greater for the *B. hageni* and *P. myrsum* in the drift and significantly less for the *B. intercalaris* with the exception of Station 3 on July 9, 1973. However, when the benthic density was relatively low there was no significant differences in size.

In summary, the benthic populations of the mayfly species used in this study seem to remain relatively stable over the summer months. As Waters (1961) had postulated, the proportion of the population in the drift is low as long as the benthic density is low. However, as the benthic density increases and presumably the carrying capacity is reached, the proportion of the population in the drift greatly increases. The fact that there was a size selection process taking place when the drift rate was high suggests some kind of intraspecific competition. There was no evidence of a 'colonization cycle' as Muller (1954) had proposed.

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RESUME

L'étude avait pour but de vérifier si le 'cycle de colonisation' proposé par Muller ou la théorie de la 'concurrence entre les espèces' soutenue par Waters expliquait adéquatement pourquoi la densité de la population de huit espèces d'éphéméroptères dans la Rat River (Manitoba) demeurait stable en dépit de taux élevés de déplacement. On observa deux étés durant les habitudes de vol des adultes, la densité des nymphes dans le substrat ainsi qui les taux de déplacement des éphéméroptères. Les résultats corroborent l'hypothèse de Waters selon laquelle le déplacement constitue un mécanisme de réduction de la densité des populations quand la capacité de charge est atteinte. Les mouvements de la population sont proportionnels à sa densité alors que les grands déplacements sont affaire de sélection liée à leur taille. Rien ne permet de conclure à un 'cycle de colonisation' tel quie le propose Muller.

ZUSSAMENFASSUNG

Mit der vorliegenden Arbeit sollte entschieden werden, ob Müllers 'Kolonisationszyklus' oder Waters 'Theorie der intraspezifischen Konkurrenz' hinreichen erklären, warum die Populationsdensitat acht verschiedener Ephemeropterenarten im Rat River (Manitoba) trotz hoher Driftraten stabil bleiben. Die flugpattern der voll ausgewachsenen Tiere, die Dënsitat der Nymphen im Substrat und die Driftraten wurden zwei Sommer hindurch beobachtet. Die Ergebnisse bestätigten Waters Hypothese, daß das Driften ein Mechanismus zur Reduzierung der Populationsdensität ist, sobald die Tragkapazität erreicht wurde. Die Proportion der Population beim Driften war densitätsabhängig und bei hohen Driftraten größenselektiv. Es gab keinen sicheren Beweis eines 'Kolonisationszyklus', wie ihn Müller vermutet hatte.

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