On The Taxonomy And Biology Of Ephemeroptera (Mayflies) Of Meghalaya State, India

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THESIS SUBMITTED IN FULFILMENT OF THE DEGREE OF DOCTOR OF PHILOSOPHY (SCIENCE) IN ZOOLOGY AT THE NORTH EASTERN HILL UNIVERSITY, SHILLONG

1980

CERTIFICATE

I herewith forward the thesis entitled "On the taxonomy and biology of Ephemeroptera (mayflies) of Meghalaya state, India," submitted by Shri Abhik Gupta for consideration of North Eastern Hill University for award of the degree of doctor of Philosophy in Zoology to him. The research work presented in this thesis was carried out by Mr. Abhik Gupta under my supervision. I certify that this work has not been submitted to any other institution for any degree of diploma.

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ACKNOWLEDGEMENTS

I wish to express my grateful thanks to Dr. R. G. Michael, Professor, Department of Zoology, North Eastern Hill University, Shillong for his unfailing guidance and valuable advice during the entire period of study. My thanks go to Dr. J. R. B. Alfred, Reader, Department of Zoology, NEHU for his sincere help in various matters and also to the other faculty members for their kind cooperation. I am grateful to Dr. I. Muller-Liebenau, Max-Planck-Institut fur Limnologie, Plon, DBR, for kindly confirming the identification of Baetidae specimens, and to Dr. W. L. Peters and Mr. Michael D. Hubbard, A. & M. University, Florida, U.S.A. for their valuable suggestions and also for providing literature pertinent to the present problem. My thanks go to Mr. S. Roy Choudhury, Artist, Department of Zoology for his help in making the illustrations, to Mr. S. Ghosh, Department of Economics, North Eastern Hill University for statistical analysis.

Last but by no means least, I thank all my research colleagues in the Department of Zoology, NEHU for the help and cooperation they have never failed to extend.

PREFACE

Popular conceptions on the ephemeral lifespan of mayflies have inspired philosophers to ponder over the transient nature of life itself. These fragile creatures, which are considered as art pieces of Nature, have found their place in several folklores and the poetic expression of many a poet. From a practical view point, however, mayflies may be most attractive as food on items to trouts, birds and spiders and in recent years their importance as detritus processors and biological indicators of pollution has attracted many ecologists and students of Ephemeroptera to study this group of insects with interest. Even to a conventional zoologist, this group appears to be important because of the possession of an unique subimago stage in the life history and adults which do not feed, having degenerated mouthparts. Functionally, the role played by the nymphs of Ephemeroptera and a few other group of freshwater macro-invertebrates in the ecosystem are increasingly realized as converters of reduced carbon compounds coming in as allochthonous inputs, supplemented further by instream autochthonous fixation, which are known to be temporarily stored in their tissues and ultimately transformed as carbon-dioxide (Cummins 1973).

Early studies on mayflies revolved mostly around their Taxonomy in a given geographical region. Without minimizing the importance of such studies, it can be said that taxonomic studies with a global perspective as well as knowledge of mayfly ecology, particularly in relation to nymphal stages are gathering momentum in recent years (Edmunds 1973a). The accumulated data from thise investigations are now quite satisfactory in Europe and North America as seen in recent reviews by Cummins (1973), Hynes (1970) and Macan (1974). In contrast, available information on mayfly taxonomy as well as ecology is very less from Asian countries, and India is no exception. This lacuna is probably due to the paucity of knowledge on the taxonomy, absence of revisionary studies and keys for the Indian species (Hubbard and Peters 1978a). However, the development of stream ecosystem theory in recent years, which involves ecological studies on mayflies too, cannot possibly wait for all monographs to be completed (Cummins 1973). Moreover, it is felt that by the time these taxa are worked out, our aquatic habitats will be so much under stress from urban and industrial pollution that may totally alter their fauna. Many interesting species of mayflies in Europe and America are now facing such extinction (Edmunds 1973a) and parallel information is yet to be obtained for tropical countries like India. Apart from these biological interests, our streams and lakes are to be maintained in a healthy condition in view of their importance for the increasing demand of water as a multipurpose resource, which in turn makes detailed ecological studies a necessity.

The hill regions of North East India with their swift flowing streams offer an excellent scope for studies on mayflies. The traditional practices of shifting cultivation termed 'Jhum' which increases denudation and soil erosion are part of the stresses to which the fauna are subjected both in terrestrial and aquatic habitats in this region. In view of these imminent problems, the present study has been undertaken to work out the taxonomy of major ephemerid species in a few aquatic environments of central Shillong plateau in Meghalaya, as well as to throw some light on various basic aspects of their ecology like seasonality, population studies, food habits and drift. Such detailed investigations on the taxonomy and ecology of a selected number of species as model studies for the essential understanding of the group in the entire region are suggested by a number of leading workers in this field (Edmunds and Allen 1966; Edmunds 1973a). It is hoped that studies of this nature will provide some baseline information on the mayflies and as well on the general ecological principles of running water ecosystems in this region.

Thus the present study deals with the measurement of climatic and physicochemical parameters of the environment, taxonomic survey of the area and detailed biological studies on a selected number of species with special reference to population ecology, food habits and feeding propensities as well as studies on the drift. Some information is also added on a few other major groups of macro-invertebrates associated with mayflies.

REVIEW OF LITERATURE

Information on Indian Ephemeroptera has so far remained very scanty, comprising isolated taxonomic studies, mostly on imaginal stages only as reviewed by Hubbard and Peters (1978a). Apart from the above, some adaptational and other ecological aspects were treated by Hora (1923, '29, '30). On the other hand, information from temperate countries, particularly continental Europe, British Isles and North America are quite extensive. A brief review of such investigations is presented here.

Many earlier taxonomic studies comprising description of new genera and species, Synopsis, catalogues and keys from Europe and America were reviewed in the first comprehensive text book on Ephemeroptera by Needham et al. (1935). Another notable work was the reclassification of Ephemeroptera with new familial arrangements (Edmunds Jr. and Traver 1954). Certain species of the genera Baetis, Heptagenia, Rhithrogena and Ephemera were described alongwith a key to the family Caenidae in Britain (Macan 1955, '57, '58a,b). New forms of Leptophlebiidae, Ephemerellidae, Baetidae, Heptageniidae and Ephemeridae were described from China, Africa and Madagascar (Allen and Edmunds Jr. 1963; Allen 1965); Gillies 1957; Peters 1963, '64a,b), while a key to the families and sub-families of ephemeroptera was published including comments on its classification in relation to the evolutionary status of nymphal and adult stages (Edmunds, Allen and Peters 1963; Edmunds 1964). Further, records and descriptions of new genera and species from Seychelles and South Asia were made (Peters and Edmunds 1966; Peters 1967) and in another study the importance of the nymphs in the study of Ephemeroptera was stressed

(Edmunds and Allen 1966). A study on the phylogeny and relationship and subsequently a revision of 29 genera and 4 subenera of the Eastern Hemisphere Leptophlebiidae were published (Peters and Edmunds 1968, '70) and several new genera and species belonging to a number of families were described from various parts of the world like Brazil, South Africa and continental Europe (Peters 1969; Jacob 1969; Mathew 1969). Yet another notable contribution was a revision of the European species of the genus Baetis Leach by Müller-Liebenau (1969). Investigations on the phylogeny of certain families were made (Demoulin 1968a,b, '69). A key to the nymphs of the British species of Ephemeroptera and a key to genera of Wisconsin Ephemeroptera were published (Macan 1970; Hilsenhoff 1970). New species of mayflies from Europe and South Asia were described (Sowa 1970; Tsui and Peters 1970). An attempt was made to provide a sperm quide morphology to Ephemeropteran eggs by Koss and Edmunds Jr. (1970). A revision of West Indian Leptophelebiidae (Peters 1971) and a key to the adults of the British species of Ephemeroptera were published (Kimmins 1972). Around this period additional information on new species, generic and familial revisions and distributional studies were given by a number of workers from different parts of Europe, North and South America (Edmunds Jr. 1971; Pescador and Peters 1971; Sowa 1971a, b; Traver 1971; Peters 1972). A considerable attention was paid to the mayfly fauna of Asia and Africa and a number of such studies involved taxonomic revisions, laying down keys, new specific and generic descriptions (Allen 1971; Ali 1971; Puthz 1972; Peters and Edmunds 1972; Peters and Tsui 1972a,b). Further descriptions of new species and genera, generic revisions and zoogeographic aspects in Ephemeridae, Tricorythidae and Ephemerellidae, mainly from Asia and Africa, were published through a number of papers (Allen 1973, '75; McCafferty 1973a,b, McCafferty and Edmunds Jr. 1973). New species of Baetis and Baetodes from Mexico and Ecuador (Mayo 1973a,b) and species of Baetis from Finland and Norway as well as new Baetid genus from Georgia were described and illustrated (Müller-Liebenau 1974). Taxonomic changes and reinstatement, Biosystematics, enumeration and use of newer morphological characters of a number of genera under the family Baetidae were outlined (Müller-Liebenau 1973; Edmunds Jr. 1974; McCafferty and Provonsha 1975; KefferMuller and Sowa 1975). Around the same period, investigations on generic composition along with descriptions of many new species and genera as well as taxonomic revisions and clarifications on synonymy and homonymy of various families from U.S.S.R., U.S.A. and different parts of Europe were also carried out (~~Sch~~ Tschernova 1974; Sinichenkova 1973a, b; Sowa 1973a,b; Puthz 1975; Jensen and Edmunds Jr. 1973; Edmunds Jr. and Jensen 1974; Hubbard 1974; Flowers and Hilsenhoff 1975). Generic and field keys, annotated Checklists and distribution and Survey data on mayflies were presented from various countries like British Isles, U.S.A. and South America (Brittain 1974; Hilsenhoff 1975). Aspects of classification, biogeography, homonymy and nomenclatural and morphological analyses of mayflies as a whole as well as those of particular familial/generic groups were discussed (Edmunds Jr. 1973b, '75; Riek 1973; Sowa 1975). Species descriptions, phylogenetic relationship and distribution of the mayfly family Leptophlebiidae were studied from Portugal and United States (Peters and Daterra 1973; Berner 1975) and the importance of eggs in the phylogenetic studies of the order was stressed (Koss and Edmunds Jr. 1974). New Heptageniidae from USSR (Baikova 1977) and these belonging to Palingeniidae, Ephemerellidae, Caenidae and Baetidae from Asia and Africa (McCafferty and Edmunds Jr. 1976a; Allen and Edmunds Jr. 1976; Gillies 1977; Müller-Liebenau 1978) were described. Nomenclatural notes, keys, revisionary works at generic and familial levels and distributional and zoogeographic data were brought forth through a number of studies from different parts of thw ≠ world (Allen and Brusca 1978; Berner 1977; Hubbard 1976; Hubbard and Edmunds Jr.1977; McCafferty and Edmunds Jr.1976b; Sinichenkova 1976; Tshernova 1976). Taxonomic surveys in different countries like Mexico and U.S.S.R. revealed a number of new distributional records and species (Allen and De Cohen 1977; Kustareva 1976). The total number of world genera and species of mayflies was published (Hubbard and Peters 1976). Intraspecific variations were observed in the mayfly Potamanthus myops (Lord and Meier 1977). Catalogues of the ephemerid fauna of Philippines (Hubbard and Pescador 1978) and those of Indian Sub-region (Hubbard and Peters 1978a) were other notable contributions among a number of other taxonomic studies in the past two years (Kustareva 1978; Fiance 1978; Keffermuller and Da Terra 1978; Cowie et al. 1978; Newell and Minshall 1978a; Soldan 1978a,b,c,d,'79; Braasch 1977, 1978a,b; McCafferty and Provonsha 1978; McCafferty and Edmunds Jr. 1979; Morihara and McCafferty 1979).

Studies on mayfly population started with observation on burrowing behaviour, habitat specialization and Swarming of certain species of Palingenia in remarkable details by Swammerdam (1675). Subsequent works on different aspects of Biology including Swarming have been reviewed by Needham et al (1935), While some other studies on adaptation to running-water and influence by physical and chemical factors have been reviewed subsequently (Hynes 1970). Studies on seasonal distribution and relative abundance showed overlapping broods for certain species (Harker 1953) and a lunar rhythm was observed in the emergence patterns of Povilla adusta Navas, a burrowing mayfly from equatorial Africa (Hartland-Rowe 1955). Many workers attempted to correlate the density of Ephemeropteran larvae to the abiotic and biotic factors. Thus the relation of abundance to detrital content (Egglishaw 1964; Egglishaw and Morgan 1965), pH and altitude (Agnew 1962) were demonstrated. Baetis rhodani showed considerable resistance to organic pollution (Brinkhurst 1965). The seasonal distribution of thirtyfour species of adult mayflies from North Arkansas was described (Hubbard 1966), while life cycle data were presented on a ephemerid species from United Kingdom (Gledhill 1959). The relationship of various Ephemeropteran genera was established with reference to habitat differentiation (Egglishaw and Mackay 1967). Relationship between larval production and rate of flow, floods and damming in Ephemeroptera were established in West Pakistan (Ali 1968a,b,c,'69), while in another study the community dynamics of benthic fauna in relation to various environmental factors were discussed (Minshall 1968). It was shown that among ephemeropterans certain species showed preferences for particular aquatic weeds and soft-wood trees (Petr 1968,'69). Landa (1968) established 4 major types of life cycle patterns with many sub-types for the principal Central European species. Nutrient levels, physico-chemical parameters, substrate, silting and organic pollution were found to be related to the differential abundance, diversity and distribution of many species, genera and families of ephemeropteran larvae in different parts of the world (Minshall and Kuehne 1969; Cummins and Lauff 1969; Chutter 1969; Langford and Bray 1969). Nature of substrate, nature and quantity of allochthonous input and current speed were found to be important factors controlling ephemerid standing crop, diversity and biomass (Petr 1970; Macan 1974). Necessity of a holistic approach to ephemerid research with more of nymphal studies and phylogeny were emphasized (Edmunds Jr. 1973a). Patterns of life cycles and the biotic and abiotic factors influencing them, growth, reproductive potential and other aspects of biology were dealt with in a number of studies from France (Benech 1972), Austria (Humpesch 1979), Ireland (Fahy 1973), England (Bass 1976, Brittain 1976a,b), Poland (Sowa 1975), Scandinavian countries (Bengtsson 1973; Kjellberg 1973; Brittain 1973, '74b,'75, Jensen 1978), Czechoslovakia (Sukop 1973), U.S.A. (Pescador and Peters 1974; Hall et al 1975; Bertholomae and Meier 1977; Flowers and Hilsenhoff 1978), Canada (Clifford et al 1973; Clifford 1976; Corkum 1978; Clifford et al. 1979), Japan (Okazawa 1974; Miyata 1976), New Zealand (Winterbourn 1974), West Africa and Ghana (Corbet et al 1974; Hynes 1975) and Madagascar (Ramanakasina 1973). All these studies point out the fact that although the life cycle patterns were extremely variable even for the same genus or species under differing conditions of altitude, latitude, topography, vegetation, substrate, temperature and photoperiod, they nevertheless fit into a range of basic patterns as outlined in the Landa classification. On the other hand, a comprehensive study on a Malayan river by Bishop (1973) showed that most of the forms living therein had a asynchronous growth and continuous life cycles. Data available on mayfly subimagos and imagos indicate that emergence occurs mostly after sunset and exhibits diel and seasonal variations although governed to a large extent by latitude, temperature, light intensity, rainfall, spates and other weather conditions (Boerger and Clifford 1975; Illies and Mastellar 1977; Peters and Peters 1977; Kraft et al 1978; Illies 1978; Savolainen 1978; Sandrock 1978). It was also observed in a couple of studies that emerging adults mostly fly upstream (Madsen et al 1973; Thomas 1975). A number of investigations from various countries indicated that substrate particle size, detrital content and other organic components, lake inflow, firmness of substate including the presence of submerged trees were found instrumental in controlling the diversity, abundance and distribution of ephemerid larvae (Mackay and Kalff 1969; Petr 1973; '74; Barber and Kevern 1973; Ward 1975; Fahy 1975; Sowa 1975; Moore 1978). Studies on the effects and aspects of recovery of mayfly larvae in regard to temperature, oxygen, pH and Calcium concentration revealed that these parameters acted as limiting factors on certain species and not on some others with certain degree of local differences (Lehmkuhl 1976; Sutcliffe and Carrick 1973; Csoknya and Hallasy 1974; Ziemann 1975; Brittain 1976a, b; Herricks and Cairns Jr. 1977; Newell and Minshall 1978b). It is well known that sediments influence the distribution of ephemerids/macrobenthos (Brusven and Prather 1974). Nevertheless, reduction of ephemerid fauna from stream channelization and spates were always followed by quick recovery in number and biomass through increased drift and recolonization (Luedtke et al 1976; Hart and Brusven 1976). On the other hand, ephemerid populations were reported to be severely effected by insecticides, urban pollutants, mine acid drainage, crude oil and agricultural pollutants (Herricks and Cairns Jr. 1974; Echaubard and Neveu 1975; Macan 1976; Napier Jr. and Hummon 1976; Ferrarese and Sambugar 1976/77; Ferguson and Fox 1978). As an outcome of such studies on the effects and tolerance levels of different toxic substances, ephemerids are found to be useful as indicators and indices of water quality and saprobity (Olive and Smith 1975; Hubbard and Peters 1978b). Seasonal, vertical, horizontal and altitudinal distributions of Ephemeroptera and their microdistribution within a habitat, along with their importance in longitudinal zonation of streams were recorded in a number of publications (Harrison and Rankin 1975, '76; Ulfstrand 1975; Hynes et al 1976; Wise 1976; Minshall and Minshall 1977). In recent years some data have been presented on these insects regarding their colonization and life in temporary streams (Williams and Hynes 1976a,b), while estimates of production, bioenergetics and community analyses are some of the current areas of interest on the functional aspects of ephemeropteran research (Illies 1975; Tsuda et al 1975; Hopkins 1976; Bagge and Salmala 1978; Iversen et al 1978; Rosenberg and Wiens 1978; Marcuzzi and Faccipieri 1978; Cianciaria 1979; Short and Ward 1980; Vannote et al 1980).

Early studies on the trophic relations of ephemerids showed that they were a group of important fish food organisms in many temperate waters and that they themselves were generally herbivores (Needham et al 1935). Diatoms were the major food items in the guts of Blastuus cupidus larvae which were also devoured by the fishes (Traver 1925). Algae together with amorphous detritus and leaf fargments were found to be the major food items of many mayfly larvae (Jones 1949, '50), whereas a number of algal genera were recorded in the gut of others (Jones 1951). The larvae of Baetis rhodani Pictet and Cloeon dipterum L. were found to feed predominantly on detritus, the amount of algae in the gut being less, and many diatoms passed undigested through the gut. The functioning of mouth parts were also studied in these two species (Brown 1960, '61). Many mayfly larvae fed primarily on diatoms in spring and early summer but detritus in other seasons while in this study a diurnal rhythm in algal feeding was also observed in Paraleptophlabia spp. which fed more on algae at night (Chapman and Demory 1963). On the other hand, Centroptiloides bifurcata (E.P.) nymphs were found to be carnivorous, feeding on other ephemerids, simuliids and chironomids (Agnew 1962). The role of mayfly larvae as primary consumers in streams where autumn shed leaves are used as food was discussed by Kaushik and Hynes (1968). Mayfly larvae belonging to different species, genera and families were found to be mostly herbivore-detritvores (Minshall 1967) and the nature of food items sometimes showed seasonal and individual variations in the amount and variety of food substances (Gilpin and Brusven 1970; Pescador and Peters 1974; Koslucker and Minshall 1973; Winterbourn 1974; Hall et al. 1975). Nymphs of Siphloplecton basale were found to shift from an exclusive diet of detritus in late winter to that of live diatom cells in spring months (Clifford 1976), while Baetis rhodani changed from a diatom diet in January to detritus in March-May (Dumont and Verneaux, 1976). Bacteria was not found to be a major source of

~~of~~ nutrition for Ephemeroptera (Baker and Bradnam 1976). Thus with the exception of certain carnivorous species, most ephemeropteran larvae were detritivores or herbivore-detritivores, some showing seasonal or occasional changes in proportion of algae to detritus in gut (Shapas and Hilsenhoff 1976). Recently the feeding biology of benthic herbivores was reviewed in detail with the methods of assessing gut contents along with aspects of relative importance, selectivity and differential digestion (Moore 1977a). Baetis spp were found to feed more on detritus and sand, whereas some Leptophlebiidae more on algae, the most important factor effecting algal consumption being food availability although other factors like water velocity, temperature, daylength and density of algal flora were also considered important (Moore 1977b, c; Moore 1979). Assimilation rates and efficiencies of Tricorythodes minutus were worked out for different food items like mixed diatoms, blue green algae and Nitzschia (Mc Cullough et al 1979). Trophic structure of invertebrates in a woodland stream, U.S.A. showed that mayflies belong to three categories of feeding habits - herbivore, carnivore and detritivores - with certain degree of overlap (Coffman et al 1971) and the relation of invertebrate community to the dead leaves, in another study, falling into streams (Kaushik and Hynes 1971) was discussed. A review of trophic relations of aquatic insects pointed out the fact that they fall into few general categories-herbidetriti- and carnivororus-on the basis of food items and shredders, collectors, scrapers and predators based on feeding mechanisms. This study also postulated that ephemerids are trophic generalists, ingesting anything available withinx certain particle sizes and texture limits in a given general food compartment (Cummins 1973). Conversion of detritus to food in stream ecosystems in fine particle feeders or collectors were discussed in detail (Cummins et al 1973). Calorific values of many common mayflies like Cloeon dipterum, Caenis robusta, *Baetis rhodani* and others were worked out based on a number of studies (Sherstyuk and Zimbalevskaya 1973; Caspers 1975a,b). Data were presented on the detrital processing by a small woodland stream and the role of macroinvertebrates (Peterson and Cummins 1974) and the amount of utilizable energy in detritus and its variations in different localities (Calow 1975b). It was also seen that cellulase activity was slight to absent in certain Ephemeroptera and no relationship could be established between cellulase activity and abundance of cellulose in diet (Monk 1976) while in another study *Ephemera vulgata* and *Cloeon* sp. showed high activity levels of a trypsin-like enzyme (Dabrowski and Glogowski 1977). More evidences are available in recent years to show that ephemeropteran nymphs belonging to various families, genera and species constitute an important source of food for a number of fishes like various salmonids, Cyprinids and others (Hopkins 1970; Clady and Hutchinson 1976; Mathur 1977), plecopterans (Siegfried and Knight 1976) mammals (Whitaker *et al* 1975), trichopterans (Crosby 1975) and triclads (Reynoldson and Bellamy 1975).

Although it was known for a long time that ephemerid larvae show the phenomenon of drift (Needham 1928), probably the first important study was that of Müller (1954) who postulated that competition among individuals for food and space causes drift and therefore the significance of drift was associated with population regulation. Subsequent studies from U.S.A., U.K., U.S.S.R. and Japan revealed that ephermerid larvae showed a definite diel rhythm in drift which is controlled by light intensity and that actively swimming forms like *Baetis* larvae were represented more in the drift samples. It was also proposed in some of these studies that drift rate is a function of production rate (Waters 1961, '62; Kljutschareva 1963; Minckley 1964; Ohgushi and Saito 1963; Elliott 1965). It was shown that generally egg laying females moved upsteam and nymphs downstream prior to emergence (Hynes 1970). Thus it was concluded that drift is not the result of a non-directional, random activity, but a definite directional downward displacement through all the water strata, mostly controlled by exogenous stimuli, light intensity being one of them (Waters 1965, '66; Bailey 1966; Holt and Waters 1967). A curvilinear relationship was found to exist between quantity of drift and the standing crop density, suggesting that drift is density-related (Dimond 1967), although discharge rates were found to be more associated with increased drift (Elliott 1967). The latter author also showed that density of drifting larvae is more at night, reflecting their negative phototactic behaviour due to which they aggregate more on top of stones and aquatic plants to forage, during which period they are dislodged, thereby causing greater drift density. Reduction in stream flow (Minshall and Winger 1968) and freshets of rain resulting in increased stream flow (Anderson and Lehmkuhl 1968) were observed to considerably increase drift intensity. Temperature was the major factor controlling the drift of a day active invertebrate, whereas illumination, population density and temperature had significant influences on rates of night drifting mayfly larvae (Waters 1968; Pearson and Franklin 1968). Drift was found to exhibit a light controlled, labile, exogenously mediated activity rhythm in a stream ecosystem which was effected even by illumination from moonlight and the loss of a minor portion of the fauna in drift probably reflects the activity by insects which exposes them to other factors like current, and competition of space and food (Bishop 1969; Bishop and Hynes 1969). Recolonization by macroinvertebrates including some ephemeropterans in a Welsh stream most probably occurred from hyporheal areas deep down in the gravel, and not from drifting or egglaying by flying adults (Hynes 1968). Moonlight was found not to depress drift rates (Chaston 1969; Dennert *et al* 1969). Reviews on drift of stream insects as a regular phenomenon in running water with diel and seasonal periodicities (Waters 1972; Müller 1974) and yet another synopsis on the drift and diel cycles of North American invertebrate taxa (Adamus and Gaufin 1976) were worth mentioning in the context of drift studies. Increase in water temperature and thermal shocks were found to alter the drift rates only in certain species while in others generally did not influence drift patterns and rates to a significant extent (Wojtalik and Waters 1970; Durett and Pearson 1975; Sherberger *et al* 1977). The effect of damming was apparent in the composition of drift fauna and also in the non-faunal elements (Armitage 1977). The feeding relationships of trouts to the drift of invertebrates and the extent of utilization were stressed (Elliott 1973; Griffith 1974). A number of studies from different countries indicated that among Ephemeroptera *Baetis* spp. were almost always found to be an important component in the drift; in general ephemerids were mostly night active, showing even two or more noctural peaks and at times related to benthos density, although moonlight is known to generally suppress drift activity (Dorgelo and Lair 1973; Kroger 1974; Neveu and Echaubard 1975; Hynes 1975; Dorgelo 1975-76; Zimmer 1976; Cowell and Carew 1976). Drift samples were found to be appreciably constant over a limited period and there was a general reduction in drift rates during winter, which subsequently increased in spring and summer with increasing temperature (Clifford 1972a,b; Pearson and Kramer 1972; Cloud Jr. and Stewart 1974; Chutter 1975; Zelinka 1976). Drift rates and patterns were also considerably influenced by food levels and availability, high flow which was found to initiate and subsequently reduce it, temperature changes, light intensity, life-cycle, microdistribution and the behavioural characteristics of individual species (Lehmkuhl and Anderson 1972; Hinckley and Kennedy 1972; Hildebrand 1974; Keller 1975). Increased activity was not found to be correlated with emergence (Steine 1972) whereas in a different context a shift in activity over the seasons was related to food searching and emergence (Solem 1973). Upstream movements, either through flights of imagines or by larval migrations were found to be essential to compensate the induced downstream drift (Russev 1972), and in another study the distances travelled by drifting invertebrates were estimated by Elliott 1971). Recently, spraying of some insecticides was reported to increase drift rates significantly (Courtemanch and Gibbs 1980).