BIOLOGY OF MAYFLIES

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PERSPECTIVES AND OVERVIEW

The insect order Ephemeroptera, or mayflies as they are usually called, have attracted man's attention for centuries. As early as 1675, Swammerdam wrote *Ephemeri vita* (212), which contains an amazingly detailed study of the biology and anatomy of the mayfly *Palingenia.* Mayflies date from Carboniferous and Permian times and represent the oldest of the existing winged insects. They are unique among the insects in having two winged adult stages, the subimago and imago. Adult mayflies do not feed; they rely on reserves built up during their nymphal life. They live from 1–2 hours to a few days and even up to 14 days in some ovoviviparous species. Thus mayflies spend most of their life in the aquatic environment, either as eggs or as nymphs, and the major part of this review concerns itself with their aquatic life. The nymphal life span in mayflies varies from 3–4 weeks to about 2½ years. The length of egg development varies from ovoviviparity, in which the eggs hatch immediately after oviposition, to a period of up to 10–11 months in some arctic/alpine species.

Because of their winged adult stage and a propensity for drift as nymphs, mayflies are often among the first macroinvertebrates to colonize virgin habitats (89, 128, 241). However, over longer distances their dispersal capacity is limited, owing to the fragile nature and short life of the adults. Mayfly faunas on oceanic islands and isolated mountain areas are poor in species and usually restricted to the Baetidae and/or Caenidae (62). Their conservative dispersal makes them useful subjects for biogeographical analysis (62).

The mayflies are a small insect order containing somewhat over 2000 valid species, which are grouped into approximately 200 genera and 19 families (102, 152). Despite their poor fossil record, the conservative dispersal, together with the wide range of morphological, anatomical and

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behavioral data on their eggs, nymphs, and adults, has permitted consider-able phylogenetic analysis during the last decade (130, 152, 188).

Mayflies are found in almost all types of freshwater habitats throughout the world, with the exception of Antarctica, the high Arctic, and many small oceanic islands. Some species also occur in brackish waters. A South American baetid is apparently semiterrestrial [Peters in (188)].

In the Arctic and in mountain areas above the tree line, there are few mayfly species (22, 46, 127). Their greatest diversity is in lotic habitats in temperate regions, where they are an important link in the food chain, from primary production to secondary consumers such as fish. More recently their potential as indicators of pollution has attracted increasing attention.

The literature on mayflies is extensive, especially in North America and Europe. An insight into the breadth of modern studies on the mayflies is provided by the proceedings of the three international mayfly conferences (78, 175, 180). The last attempt to review the data on mayfly biology on a worldwide basis was by Illies in 1968 (113). Therefore, in the present review I have concentrated on the data published during the last decade.

ADULTS

The adult mayfly has two main functions, mating and oviposition. This produces a general uniformity in adult structure. The prominent turbinate eyes of males, especially well-developed in the Baetidae and some Leptoph-lebiidae, provide both high acuity and good sensitivity (100). This enables them to detect and capture single females in a swarm at low light intensities.

The forelegs of most mayflies also show sexual differences; those of the male are unusually long for grasping and holding the female during mating. In the Polymitarcyidae the middle and hind legs of the male and all the legs of the female are reduced, and in *Dolania* (Behningiidae) all the legs of both sexes are reduced. Another interesting aspect of the biology of *Dolania* and several members of the Polymitarcyidae and Palingeniidae is that the females remain in the subimaginal stage (181). The reason for two adult stages has provoked much discussion. It has been suggested that this primi-tive trait is maintained because there has not been the selective pressure on the short-lived stages to produce just a single molt (195). Another explana-tion is that two molts are necessary to complete the elongation of the caudal filaments and forelegs of the adults because such a drastic increase in their length from those of the nymphs is not possible in a single molt (146).

Most mayflies have two pairs of wings, but in the Caenidae, Tricory-thidae, Baetidae, and some Leptophlebiidae the hind wings are reduced or even absent (66).

Fecundity

Spermatogenesis and oogenesis are completed in the final nymphal instar, and the eggs and sperm are physiologically mature in the subimago (19, 200). Several workers have obtained viable offspring by artificial fertilization. Although most species have fecundities in the range 500–3000 (43), values range from less than 100 in *Dolania* to 12,000 in *Palingenia* (123, 181). There is a general trend for the females of the larger species to produce more eggs, and the fecundity values recorded for *Palingenia, Hexagenia,* and *Epeorus* are greater than in most other insect groups except the social Hymenoptera (43). Most workers have found a positive correlation between fecundity and female size within a particular population. In species with a long emergence period or with a bivoltine life cycle giving two summer emergence periods, early emerging females are larger and therefore more fecund than those emerging later (9, 214, 216). In some species of *Baetis* with long emergence periods, female size and fecundity increase again in the autumn concomitant with falling temperatures (9, 115). Two explanations have been offered: either a temperature effect on the number of ovarioles (214) or a combination of high water temperatures and low water flow produce premature emergence (115).

Mating and Swarming

The swarming and mating behavior of mayflies has been the subject of a number of reviews (19, 31, 90, 194). Swarming is a male activity, apart from the Caenidae and Tricorythidae where both males and females may participate. The females fly into these swarms and mating occurs almost immediately and usually in flight. Swarming may take place over the water itself, over the shore area, or even remote from the water. For instance, the swarms of *Baetis, Paraleptophlebia,* and *Rhithrogena* have been observed up to several kilometers from the nymphal habitat (65, 66). Most swarms are orientated according to terrain markers such as areas of vegetation, the shoreline, and trees (194). The time of swarming varies considerably, although dusk is the most common time of day in temperate areas. Light intensity and temperature are major factors in determining the timing of swarming.

Oviposition

The majority of mayflies, including most Ephemeridae, Heptageniidae, and Leptophlebiidae, oviposit by descending to the water and releasing a few eggs at a time by dipping their abdomen into the water. Species of *Ephemerella, Siphlonurus,* and *Centroptilum,* however, release all their eggs in a single batch that separates immediately on contact with water. In *Ha-*

broleptoides and some Heptageniidae (71, 184) the female, resting on a stone above the water, dips her abdomen into the water to lay the eggs. This is taken a stage further in several species of *Baetis* (9, 66, 69) in which the female actually goes underwater and lays its eggs on suitable stones. Such behavior may permit assessment of water quality before oviposition (207).

Parthenogenesis

Parthenogenesis has been reported in about 50 mayfly species, although it is not obligatory in most cases. In nonobligatory parthenogenesis, eggs develop more slowly than fertilized eggs and fewer of them hatch (59, 107, 178). Because of the low level of hatching success, this type of parthenogenesis is unlikely to be of importance in population dynamics.

Parthenogenesis is apparently obligatory in all or certain populations of five species: *Ameletus ludens, Baetis hageni, B. macdunnoughi,* and *Cloeon triangulifer* from North America and in *Caenis cuniana* from Brazil (11, 71). *Caenis cuniana* was reared through several parthenogenetic generations in the laboratory, and only females were obtained (86). In the species in which parthenogenesis appears to be obligatory, hatching success is usually high and similar to the fertilized eggs of nonparthenogenetic species. Gibbs (88) studied the emergence of *C. triangulifer* and found the emergence period to be unusually long (June–November). She suggested that this was due to the removal of the necessity for synchronous emergence of the sexes; it has been suggested that parthenogenesis may also lead to decay of the diel flight activity pattern (221).

EGGS

Mayfly eggs vary from ovoid to nearly rectangular. Their length generally ranges between 150 and 200 μm, although the eggs of some larger species (e.g. *Hexagenia*) are 250–300 μm wide, and even up to 1 mm long in the Behningiidae (59, 122, 124, 125). As most mayfly eggs are laid freely on the water surface, they have a variety of attachment structures that enable them to adhere to submerged objects or to the substratum.

Differences in egg morphology have enabled the construction of identification keys, purely on the basis of eggs. This has provided a useful complement, not only to studies of phylogeny (125) but also to taxonomy, as identification of female adults according to external characters is often difficult. In addition, the eggs are already developed in the mature nymphs, providing the possibility of associating nymphal and adult stages when rearing is not possible. Recent comparative morphological studies of mayfly spermatozoa (200) indicate similar possibilities for males.

Development

Until the last decade there had been no detailed work on egg development. Even today, we have very limited information, almost exclusively from temperate areas in Europe and North America (71). Most eggs hatch within the range 3–21°C. Among the European exceptions are *Baetis rhodani* whose hatching success is high even at 25°C; *Rhithrogena loyolea,* with eggs that hatch in the narrow range 2–10°C; and *R. semicolorata* which has a lower hatching limit of 5°C (71). In *Hexagenia rigida,* a North American species, the eggs hatch successfully between 12 and 32°C and even at 36°C if incubation is started at lower temperatures (85). Eggs of *Tortopus incertus* do not complete development at 14°C, whereas at 19°C hatching occurs (224). In *Tricorythodes minutus* eggs hatch between 7.5 and 23°C, but mortality is least at 23°C (171).

Hatching success is variable, ranging from over 90% in *Baetis rhodani* and *Hexagenia rigida* to less than 50% in the Heptageniidae studied. This type of difference clearly has repercussions for population dynamics. Excluding the few ovoviviparous species, the total length of the egg development period varies from a week in *Hexagenia rigida* to almost a year in *Parameletus columbiae* (61, 85). Temperature is the major factor determining the length of the period of egg development in mayflies. There is no indication that photoperiod influences egg development time. In most species the temperature relationship can be well described by the power law or as a hyperbola (71).

Egg diapause has only been studied in detail in *Ephemerella ignita* and *Baetis vernus* (15, 16), although there is much indirect evidence from field data and from limited laboratory studies. However, one should be cautious in putting forward egg diapause as an explanation for the absence of small nymphs in field collections. For example, on the basis of field data (129), it was suggested that *Ecdyonurus dispar* and *E. insignis* spend the winter in egg diapause; but Humpesch (106, 108) has shown that the eggs hatch directly without diapause. The small nymphs may be deep down in the substratum or are perhaps too small to be detected by normal sampling methods. Nevertheless, Clifford (42) makes the conservative estimate from published field data that 15 species of mayfly display summer egg diapause. This aspect of mayfly biology clearly warrants further study. Assessment from field data whether winter egg diapause occurs is more difficult owing to the irregularity and even absence of winter samples. However, many species undoubtedly spend the winter months either in the egg stage or as very small nymphs, particularly in arctic/alpine areas (23, 61).

The actual period over which hatching takes place may often be short.

For example, at temperatures above 5°C most eggs of *Baetis rhodani* hatch in less than ten days (10, 69). The occurrence of small nymphs of this species in field collections over several months is often due to slow growth in part of the population rather than to a long hatching period. This is not always the case, however, as shown in British *Ephemerella ignita* (70). In the Nearctic *Leptophlebia cupida,* extended hatching has been demonstrated in the laboratory (44).

Ovoviviparity is rare in the mayflies and is restricted to the Baetidae. In Europe, *Cloeon dipterum* is the only species known to be ovoviviparous (58). The female imago of *C. dipterum* oviposits 10–14 days after mating, and as soon as the eggs come into contact with water they hatch. In America a number of species in the genus *Callibaetis* are ovoviviparous (66). Here again the female imagos are especially long-lived, which, coupled with the comparatively short life of the males, leads to abnormal sex ratios in field collections.

NYMPHS

In contrast to the adults, mayfly nymphs show considerable diversity in habit and appearance. Differences do not always follow taxonomic lines, and convergent and parallel evolution appears to be common.

Growth and Development

Mayflies have a large number of postembryonic molts. Estimates of the number of nymphal instars vary between 10 and 50; most are in the range 15–25 (77). However, because of size overlap between instars, which necessitates the rearing of individual nymphs from hatching to emergence, the exact number of instars has only been determined in a few species (24, 44, 57). Many workers have therefore distinguished developmental stages on the basis of morphological characters (77). Although these may encompass several instars, they have proved useful in analyzing complex life cycle patterns (153, 210), in elaborating the effect of environmental factors on growth and survival (36), and in comparing field and laboratory data (36, 178). The number of instars does not appear to be constant for a particular species but probably varies within certain limits. Instar number can vary even when nymphs are reared under the same conditions (24, 44, 57). Environmental conditions, such as food quality and temperature, also affect instar number. Because of its simplicity, by far the most common measure of development and growth in mayflies has been body length, although head width and other body dimensions have also been used. However, growth of the various body parts is not always isometric (40). A number of authors have also used body weight, and the length-weight relationship is usually

well expressed by a power function where the value of b is close to 3 (108, 198).

As one might expect from the variability and flexibility of mayfly life cycles, nymphal growth rates are influenced by several environmental factors. However, in most species that have been studied in detail, temperature, in terms of mean values, the scale of diurnal fluctuations, or total day degrees, is the major growth regulator (24, 44, 52, 75, 105, 108, 155, 176, 210, 214, 215, 233). Other factors, such as food and current velocity, may exert a modifying influence on growth rates (36, 105, 108, 126). In a few species growth rates appear to be independent of water temperatures, particularly in those that continue growing at the same rate during the winter months (150, 157, 236). No true diapausing nymphal stage has been reported in the Ephemeroptera. However, growth rates are often very low during the winter because of low temperatures. Judging from field data nymphal growth in some species may be inhibited by high summer temperatures, although extended hatching could create a similar picture.

Respiration

The gills of mayflies are very diverse in form, ranging from a single plate in *Ameletus* to fibrillar tufts in *Hexagenia* (188). Respiratory tufts are sometimes developed on other parts of the body besides the abdomen, such as those at the base of the coxa in *Isonychia* and *Dactylobaetis* (66, 188). In several families the second abdominal gill has developed into an operculate gill cover for the remaining gills and in certain Heptageniidae the gills are markedly expanded so that they together form an adhesion disc. In many of the Siphlonuridae the gills are used as swimming paddles, which has been put forward as their original function (188). In respiration the gills may either function as respiratory organs or as ventilatory organs for the other respiratory exchange surfaces.

Mayflies have solved the problem of respiratory regulation in two ways. Some species, mostly from lentic habitats, are respiratory regulators (74, 167). These species may be unable to regulate oxygen consumption on nonoptimal substrata or in the absence of substratum (73), a fact which is particularly important when interpreting the results of laboratory respiration studies. Other species, primarily associated with running waters, are unable to physiologically regulate oxygen consumption over concentration gradients. The mayflies that have immovable gills are usually restricted to environments with high current velocities, and their oxygen consumption can often be directly related to current speed (109). This gives them the opportunity of regulating their oxygen consumption by positioning themselves with respect to the current (240). Factors affecting respiration rates include temperature, light intensity, and growth stage (37, 54, 97, 226, 229).

High rates of oxygen consumption are often reported in association with emergence and gonad maturation (37, 54, 229). At that time water temperatures are also usually high, which means that low oxygen concentrations can be critical (170, 184).

Many burrowing Ephemeridae and pond-dwelling Baetidae are able to survive moderately low oxygen concentrations, especially for short periods (74, 87, 170). However, so far only one species, *Cloeon dipterum,* has been shown to survive long-term anoxia and respire anaerobically (168, 169). This adaptation is part of the overwintering strategy of *C. dipterum* in small ponds that experience low oxygen concentrations during winter ice cover. In addition to an ability to survive anoxia at low temperatures, the nymphs display special behavioral adaptations under anoxic conditions, which enable them to move into microhabitats more likely to contain oxygen. Although unable to move into microhabitats more likely to contain oxygen. Although unable to survive long-term anoxia, the mayfly *Leptophlebia vespertina* also displays similar behavioral adaptions under conditions of low oxygen (30).

Population Movements

All mayfly populations undertake movements at some time during their life; they may be random or directional, daily or seasonal. Due to frequent nonrandom oviposition, a redistribution of small nymphs takes place in many mayfly populations (213, 241). During the final stages of nymphal life there is also a movement to and a concentration in the shallower areas of lakes and rivers. In running waters, springtime mass movements of mayfly nymphs along the banks of the main river and into slower flowing tributary streams or into areas flooded by spring snow-melt have been reported (98, 173). In running water, mayfly nymphs may move down into the substratum in response to spates (185) or as part of a daily rhythm (35). Generally, however, mayflies do not extend far down into the substratum (110, 161).

Mayflies, especially *Baetis,* are a major component of invertebrate drift in running waters. Their drift shows a strong diurnal periodicity, with a peak during the hours of darkness (2, 45, 67). At high latitudes the drift activity of certain Ephemeroptera becomes desynchronized in continuous daylight (162). Drift rates are not constant for a particular species, and the larger size classes are usually more in evidence. Behavioral drift may serve, as in mass movements along the substratum, to relocate the population in areas suitable for that particular stage (93, 136, 227). In addition to photoperiod and stage of development, several other factors have been shown to influence mayfly drift including changes in current velocity and discharge (34, 39, 176), increased sediment loading (38, 189), temperature

changes (119), oxygen conditions (240), nymphal morphology (38), nymphal density (91), and food availability (17, 119). Within the mayflies there is a gradation in the tendency to leave the substratum and enter the water column, and this appears to be related more to behavioral patterns than to density (51). Recently the presence of predatory stoneflies has been shown to increase drift rates (53, 177).

The potential reduction of upstream populations of both eggs and nymphs by drift has initiated a search for compensatory mechanisms. Drift may well be simply a method of reducing competition which is related to benthic population densities (91). However, there is clear evidence of other explanations in some cases. Upstream movement of nymphs has been demonstrated in several mayfly species (68, 109) and may at least partially compensate for drift. Another compensatory mechanism is the upstream flight of imagos before oviposition. Upstream flight has been demonstrated in a wide range of habitats, from small streams to large rivers, both in treeless mountain areas and in lowland forests (144, 163, 191, 217). However, although common, the phenomenon of upstream flight is not by any means universal (67, 91, 176, 181).

EMERGENCE

Emergence, the transition from the aquatic nymph to the terrestrial subimago, is a critical period for mayflies. Their movement up to the water surface, often during daylight, makes them especially vulnerable to aquatic and aerial predators. Shedding of the nymphal skin usually occurs at the water surface on some object such as a stone or macrophyte stem or in mid-water. The latter is more typical of the burrowing species which inhabit deeper waters and of a number of river species. Genera such as *Siphlonurus, Isonychia,* and *Baetisca* crawl completely out of the water before they molt (66, 178). The mechanism of molting has been well described (113).

Diel Patterns
In temperate regions the crepuscular emergence of mayflies is well known. However, dusk is not the only time of day that mayflies emerge, although most species exhibit clear diel patterns of emergence which are, with few exceptions (20, 84), characteristic for a given species, genus, or even a whole family. For example, the emergence of the short-lived Caenidae invariably takes place either at dawn or dusk and appears to be controlled by light intensity (164). Several baetid and leptophlebiid genera emerge around midday (e.g. 13, 84, 99, 104, 164, 218). In temperate areas the higher daytime air temperatures are less restrictive for flight activity, although the adults are probably more susceptible to predation (65). In the arctic summer, with perpetual daylight, *Baetis pumilis, B. macani,* and *Heptagenia*

sulphurea still maintain a synchronized daily rhythm of emergence with a distinct afternoon peak (218). This suggests either an endogenous circadian rhythm (162), also postulated for *Dolania* (181), or a response to the limited diurnal fluctuations in temperature and light intensity. In *Baetis alpinus,* which normally emerges in the afternoon under constant temperature, the rhythm of emergence was disturbed in permanent light and suppressed in permanent darkness (104). Nymphs of *Dolania* appear to require both light and temperature cues for successful emergence (181).

In the tropics and warm temperate regions, nighttime air temperatures are less restrictive, and in order to escape from daytime predators it seems that most longer-lived forms emerge during the first two hours of darkness (65, 72). The shorter-lived genera, such as *Caenis,* are subject to fewer restraints on their emergence and there are few constant differences between tropical and temperate species (65).

The daily emergence of males and females is usually synchronous, especially in the short-lived forms, although there may be an excess of males at the start of the day's emergence (13, 84). In the Behningiidae, females oviposit as subimagos and therefore the males, which molt to imago, emerge well before the females (181).

Seasonal Patterns

As well as diel patterns, mayflies have distinct and finite emergence periods, especially in temperate and arctic areas. In cold temperate and arctic areas, mayfly emergence is more or less restricted to the summer months, owing to the physical barrier of ice cover and the low air temperatures during the rest of the year (13, 26, 228). Probably only a few species, such as *Baetis macani,* are able to emerge at water temperatures below 7°C (13, 23). As one approaches the tropics, and also in more oceanic climates, there are fewer restrictions and emergence may occur throughout much of the year, although most emergence still occurs during the warmer months (42, 216). In the tropics emergence is often nonseasonal (220, 221), although some species have clear emergence patterns. The lunar rhythm of emergence of the African species, *Povilla adusta,* is well known from a number of lakes (50, 96). In other African lakes, however, emergence of *P. adusta* is less synchronized (50, 182). The burrowing mayflies of the Ephemeridae, Polymitarcyidae, and Oligoneuriidae are well known for their sporadic mass emergence (20, 66). The mass emergence of *Hexagenia* from the Mississippi River, USA, has been well documented (82), although the mechanism producing such synchronicity is unknown (219).

Latitudinal and altitudinal differences result in differences in the timing of emergence. For example in both American and European *Leptophlebia,* emergence occurs progressively later as one moves northwards (21, 22, 44, 120). In a similar way, the onset of emergence is delayed with increasing

altitude. In habitats with several mayfly species, peak emergence of the major species may be separated in time, especially in congeneric species (e.g. 13, 26–28, 109, 216). Such serial emergence appears to be a constant feature from year to year; changing temperature conditions only affect the absolute dates of the emergence peaks rather than the serial pattern itself (26, 27).

The length and pattern of emergence varies in seasonal species, and it has been suggested that emergence falls into two main categories: synchronized and dispersed (95). It is thought (142) that such differences represent two approaches for reducing adult mortality: synchronous emergence attempting to saturate a potential predator, and dispersed emergence seeking to lower the possibility of predator-prey encounters. However, emergence pattern can vary with abundance, locality, and from year to year within the same species (27, 112, 131, 216). The degree of developmental heterogeneity in the preemergence nymphal population also has a major influence on emergence patterns (27, 28, 95, 116), and emergence should be viewed as an intergral part of the species' overall life cycle strategy (28). In species with well defined emergence periods, males and females usually emerge synchronously, although there is often a tendency for the cumulative emergence curve of males to lie somewhat ahead of the females' (27, 44, 95, 216).

Water temperature thresholds, often in conjunction with rising temperatures, are important for both seasonal and daily emergence of many mayflies (20, 25, 82, 104, 114, 131, 141, 181, 218). It has been shown in the laboratory that emergence can be hastened or delayed by changing the experimental water temperatures (25, 214). Also, field data often show earlier ephemeropteran emergence in warmer years (27, 114). However, it has been argued that other factors such as stable flow conditions and food are of equal importance in inducing emergence in the laboratory (131). Nevertheless, the later emergence of the same species at higher altitude lends support to the effect of temperature, either through threshold temperatures or through nymphal growth and development (233).

Photoperiod has also been suggested as a potential factor regulating seasonal emergence in mayflies (131, 157), but little concrete data are available and successful emergence has been shown in nymphs reared in complete darkness (24). Other abiotic factors, such as wind, humidity, precipitation, turbidity and irradiance, may also affect daily emergence totals (20, 27, 131, 181, 218, 220).

LIFE CYCLES

Types

There is an extensive literature on mayfly life cycles, mostly from temperate areas in Europe and North America (42). Care should be taken when interpreting mayfly life cycles, especially when based solely on field observa-

tions. Hynes (109) has rightly emphasized that a combination of field and laboratory work yields much more information than either does alone. Particular care is necessary in interpreting the length of egg development from field data, as shown by the recent studies of Humpesch (106) The use of inadequate sampling methods for the smaller instars can also be a source of error (208).

Several authors have classified ephemeropteran life cycles; most use a combination of voltinism, duration of egg development, and nymphal growth rates as criteria (42, 129, 140, 204). Multivoltine species usually have two or three generations in temperate regions, often a slow growing winter generation and one or two rapidly growing summer generations. Limited data from the tropics, where many species are nonseasonal, indicates that some species go through about four and possibly up to six generations during the course of a year (12, 50). However, analysis of field data is difficult, and there is certainly need for complementary laboratory studies. In temperate areas the univoltine life cycle is the most widespread. Several authors have distinguished two main types of univoltive cycles: in the first, overwintering occurs during the nymphal stage after a relatively short egg development period, and in the second, hatching occurs in the spring after a long period of egg development. Semivoltinism appears to be relatively uncommon in mayflies. The maximum generation time so far recorded is 3 yr, and even in such populations there are usually both 2 and 3 yr cohorts.

Mayfly life cycles show a distinct trend from the tropics to the arctic (42). In the tropics, nonseasonal multivoltine cycles predominate; seasonality becomes more distinct in mountainous and continental areas. In oceanic climates, such as in New Zealand, synchronization may be poorly developed (242). As one approaches the Arctic, univoltine cycles dominate even more (22, 42, 227).

Flexibility

Some mayflies, for example the widespread Palearctic *Leptophlebia* species, have a univoltine winter cycle over a wide range of latitudes and climates (21, 22, 120, 129, 204). A similar constancy is found in the Nearctic *Leptophlebia cupida* (44).

However, a number of successful species display a considerable degree of life cycle flexibility throughout their distributional range. This is perhaps best exemplified by many of the Baetidae. The European species, *Baetis rhodani,* is a typical univoltine winter species in northern and mountain areas, while in much of Europe it has both a winter generation and a summer generation (140). In more southerly locations there are two summer generations as well as the winter generation. The real flexibility of

Baetis rhodani's life cycle has been shown by Humpesch (105), who showed variation from year to year depending on temperature conditions. For example, in an Austrian stream he was able to distinguish 10 cohorts over a 30 month period, and the duration of these cohorts varied from 2.5 to 8 months.

Several Ephemeridae are also known to exhibit a degree of life cycle flexibility, and there has been much confusion concerning life cycle length in certain species. For example, the European species, *Ephemera danica*, may have a one, two, or three year cycle, and two of these cycles are often present in the same habitat (e.g. 210, 216, 237). A similar situation exists for the North American *Hexagenia*.

Temporal separation of life cycles is one of the most common mechanisms permitting coexistence among closely related mayflies. For example, the European *Leptophlebia* spp. have essentially similar life cycles. However, when they occur together their cycles are out of step, *L. marginata* always being larger and emerging earlier than *L. vespertina* (21, 22, 26). Preliminary data (28) suggest that *L. marginata* has a lower temperature threshold for growth. Such differences have also been observed in North American *Paraleptophlebia* species (48, 52). Differences in life cycle, although often the most obvious, are usually not the only differences between coexisting species. For example, in a Norwegian mountain lake differences in nutrition, fecundity, predation pressure, and size at maturity were found among the mayfly species (28).

RELATIONSHIPS

Nutrition

The majority of mayfly nymphs are herbivores, feeding on detritus and periphyton. This explains the relative uniformity of mouthpart construction within the order (206). The modifications that are present are a result of different food gathering mechanisms rather than differences in diet (201, 206). The herbivorous mayflies fall into two main categories: collectors and scrapers (55, 64). Among the collectors, several genera are filter-feeders, with setae on the mouthparts or forelegs acting as filters (230). Within the Oligoneuridae, Leptophlebiidae, Siphlonuridae, and the Heptageniidae, there are several genera that are probably filter-feeders (230). By using their gills to produce a current of water through their burrows, several of the Ephemeridae and Polymitarcyidae may, at least for part of their food supply, be regarded as filter-feeders. The higher caloric and organic matter content of *Hexagenia* gut contents compared to the sediments they inhabit lends support to this hypothesis (248). To supplement their diet, *Povilla* nymphs, especially the larger ones, leave their burrows at night and graze

on periphyton (12, 182, 183). Most mayflies, however, are fine-particle detritivores (55). These include many Siphlonurinae, Baetidae, Leptophlebiidae, Metretopodidae, Emphemerellidae, Caenidae, and Baetiscidae, as well as some Heptageniidae (64). The other major feeding group within the mayflies, the scrapers, utilize the periphyton present on mineral and organic surfaces (55). These include representatives of several mayfly families, notably the Baetidae, Heptageniidae, Leptophlebiidae, and Caeniidae (66). Shredders are probably also represented among mayflies.

True omnivory is of limited occurrence in the mayflies and is restricted to some species in genera such as *Isonychia, Siphlonurus, Stenonema,* and *Ephemera* (55, 66). The predatory habit is also relatively uncommon in the mayflies. In North America, *Dolania, Analetris,* and the heptageniids, *Pseudiron, Spinadis,* and *Anepeorus,* feed largely on chironomid larvae (66, 134, 223). The baetid genera *Centroptiloides* and *Raptobaetopus* have carnivorous nymphs (1, 80, 165). Within the Prosopistomatidae there are also carnivorous species, although within the single genus *Prosopistoma* there are both detritivores and carnivores (80). Several species, such as *Siphlonurus occidentalis* and *Stenonema fuscum,* may change from a predominantly detrital diet in the early instars to one containing a significant proportion or even a dominance of animal material in the mature nymphs (3). First instar nymphs consume small algae and finely divided detritus (24, 44, 59, 154). However, it has been suggested that the first instar nymphs of *Povilla adusta* do not feed, but rely on the vitelline cells in the midgut (182). Even within the detritivore/herbivore category, diet may change with season, habitat, and stage of development. Seasonal differences are often a reflection of food availability (33, 44, 120, 154, 159), thus emphasizing the opportunistic nature of mayfly nutrition. This is further demonstrated by laboratory studies in which nymphs have been reared on single species algal cultures, or even on artificial fish foods and cereals (36, 44, 155, 222). However, within the range of food available, there is often evidence of selection (33, 36, 248). Food selection may clearly be advantageous, as growth may be influenced by different foods (3, 36, 155).

The time for food to pass through the gut is often short, and in *Baetis, Cloeon,* and *Tricorythodes* it has been shown to be only about 30 min (33, 155). However, in *Hexagenia* it varies between 4 and 12 hr, depending on temperature (247). Apart from their temperature dependence, these differences probably reflect differences in food quality, digestibility, and specialization (174). This is supported by the fact that *Hexagenia* nymphs feed continuously during the day and night and that at most temperatures they ingest over 100% of their dry body weight per day (247). In contrast, values for several species of the surface-dwelling collector *Stenonema* are much lower and vary between 2% and 22% of dry body weight per day (55, 222).

The carnivorous *Dolania,* feeding more intermittently but on a higher energy diet, has consumption indices similar to those of *Stenonema* (97).

In all these studies there arises the question of what fraction of the food ingested is actually digested and absorbed. Two detritivores, *Habroleptoides modesta* and *Habrophlebia lauta,* have been observed to eat their own feces directly from the anus (184)—probably a mechanism for increasing the efficiency of digestion. Brown (32) has shown that several algal species are efficiently digested by *Cloeon dipterum,* although narrow filamentous forms and small cells remain viable after excretion. He suggested that such algae pass between the mouthparts without being damaged and that in the absence of a cellulase they were unable to be digested. Subsequent studies have shown little or no cellulase activity in mayflies (158). Nevertheless, organic compounds leaked or secreted by the algae may be of nutritional importance (55). In contrast to cellulase activity the proteolytic activity of trypsin- and pepsin-like enzymes is very high in the Ephemeroptera (56). Bacteria and fungi are another potential food source for mayfly nymphs. However, no evidence for the digestion of bacteria was found in *Baetis* or *Ephemerella* (5), and a hypomycete mycelium alone was insufficient to support the growth of *Stenonema* (55).

Predation

Mayflies are susceptible to predation throughout their life cycle. We know least about egg predation, although both true predators and grazing and collecting herbivores undoubtedly take their toll (139). Mayfly nymphs are eaten by a wide range of aquatic invertebrate predators, including stoneflies, caddisflies, alderflies, dragonflies, water beetles, leeches, triclads, and crayfish. Mayflies are also important fish food organisms (see 109). In many cases the degree of predation is closely related to the mayflies' size and abundance and therefore varies with habitat and with season (29, 147).

Birds and winged insects, such as Odonata, also prey on mayflies (e.g. 151, 154). Birds may take both the aquatic nymphs and the aerial adults. Several other animal groups, including spiders, amphibians, marsupials, and insectivorous mammals such as bats, shrews, and mice, have been reported to take mayflies. Many parasites also utilize these food chain links (4).

Despite the numerous records of predation on mayflies, its effect on their population dynamics is poorly known. In an English pond, Macan (138) found little change in *Leptophlebia* populations after a change in trout densities, although the mayflies were one of the trout's main food items. However, on the stony shores of nearby productive lakes the lack of aquatic insects, including mayflies, was attributed to predation by groups such as

triclads and molluscs (139). In a Norwegian mountain lake, trout consumed 30–40% of the total annual mayfly production (26, 28, 29).

Symbiosis, Phoresy, and Parasitism

There is a wide range of organisms that live on or in mayflies. They include the normal spectrum of protozoan, nematode, and trematode parasites as well as phoretic and commensal relationships with other organisms (4, 47, 179). Unfortunately, much of the literature is restricted to occurrence records. The more detailed studies have been on phoretic Diptera (60, 202, 209, 211, 239). Svensson's investigation of the relationship between the chironomid *Epoicocladius flavens* and the mayfly *Ephemera danica* in southern Sweden is particularly noteworthy (209, 211). Chironomids in the genus *Symbiocladius* are ectoparasites and may cause sterility (202), but *Epoicocladius* does not appear to be detrimental to its host. In fact the cleaning effect, especially of the gills, may facilitate oxygen uptake in the mayfly. The semivoltinism of *E. danica* (210) compared to the univoltinism or bivoltinism of *Epoicocladius* considerably lessens the problem of life cycle synchronization for the chironomid. In contrast, the apparently bivoltine ectoparasite *Symbiocladius equitans* from North America has hosts with much shorter generation times, and in one area the winter generation of *S. equitans* infests *Rhithrogena* nymphs while the summer generation lives on *Heptagenia* (239).

Blackflies are also phoretic on mayflies, although far more is known about the parasite than the host because of their medical importance. Although blackflies and mayflies occur together throughout the world, phoretic relationships are restricted to upland areas in Africa and Central Asia.

Mayflies can also be commensal, and a baetid, *Symbiocloeon heardi,* from Thailand lives between the gills of a freshwater mussel (166). The mayfly has a number of morphological adaptations to life inside the mollusc, such as a strongly hooked apex to the tarsal claws in order to hold on to the mussel's gills. The mayfly profits from the food filtered by the mussel, and the relationship may be obligatory for the mayfly.

DISTRIBUTION AND ABUNDANCE

The distribution and abundance of mayflies has received considerable attention. Within the basic zoogeographical limitations, abiotic factors, notably temperature, substratum, water quality, and in running water current speed, appear to be the most important. Other factors such as ice, floods, drought, food, and competition may also influence abundance and distribution. These factors have been treated in detail by Hynes (109), with many examples drawn from mayflies. In addition to subsequent papers dealing

specifically with mayfly zonation (14, 22, 127, 187, 196, 203, 231, 243, 245), numerous studies have been made on macroinvertebrate zonation in the temperate regions of the world. Generally, the number of mayfly species increases with decreasing altitude. As shown by several authors (22, 112, 118) increasing temperature, by creating more emergence slots and enabling additional species to grow and complete their life cycles, is important. Differences in the trophic nature of the community can change the nature of the mayfly community. For example, a change from a predominantly autotrophic alpine to a heterotrophic subalpine stream community would result in a shift from grazers to collectors.

Many lotic mayflies are either dorsoventrally flattened or streamlined as an adaptation to life in swift current (109). Although this is generally true, such a body form does not necessarily indicate a preference for current habitats (143). The importance of respiration in microhabitat selection should not be forgotten, both with respect to substratum and in terms of respiratory regulation (73, 126, 240). The physical substratum also traps different amounts of detritus and silt and this is a major factor influencing microdistribution (e.g. 6, 26, 196, 197). The richest mayfly community is often found in association with aquatic vegetation (6, 41, 132, 145, 246), which, as well as providing shelter, functions as a detrital trap and as a substratum for periphyton. Removal of aquatic macrophytes may therefore lead to an impoverished mayfly community (49). For burrowing mayflies, the presence of the correct substratum is obviously a major determinant of both macro- and microdistribution (183, 193, 213). In lentic habitats and in slow-flowing waters, oxygen concentrations may become critical in certain areas (20, 183, 213). In lakes the highest mayfly diversity occurs in the shallow littoral areas. At deeper levels the mayfly fauna, although often reaching high densities, is usually poor in species. Mayflies are generally absent from the profundal of lakes.

Many mayflies can tolerate a wide range of salinities, and a few species within the Baetidae, Caenidae, and Leptophlebiidae occur in brackish water habitats (81, 137). The chloride cells in the integument of mayfly nymphs participate in osmoregulation, and their density appears to be related to the osmotic strength of the medium (238).

Clifford (41) has reviewed numerical abundance values in the Holarctic Ephemeroptera. *Baetis* and *Ephemerella* were the most reported genera and *Baetis, Ephemerella,* and *Caenis* accounted for a major part of the higher values. The genus *Baetis* provides the most data and has the highest average annual abundance value. Its species richness and life cycle plasticity undoubtedly contribute to its success.

Mayflies constitute a major part of the macroinvertebrate biomass and production in freshwater habitats. Seasonal variation in density and

biomass and annual production are strongly influenced by life cycle parameters, indicating the importance of correct life cycle information in production studies (42, 234, 235). Most mayfly production values are in the range 0.1–10.0 g dry wt/m^2/yr (108, 234). The errors that may arise due to drift and to exuvia loss in estimating mayfly production have been demonstrated (93, 155). Emergence biomass has also been used as a measure of production in mayfly communities (e.g. 26, 114).

HUMAN INFLUENCE

Man is having an increasing effect on the distribution and abundance of mayflies and, by virtue of their widespread occurrence and importance in aquatic food webs and particularly in fish production, mayflies have been widely used as indicators of water quality (149). Mayflies play a central role in the saprobic system that is especially well-developed in Eastern Europe (18, 192, 205). Mayflies often occur in habitats of a particular trophic status (139, 148), and increased eutrophication caused by man's activities can lead to the reduction or even extinction of certain species (160, 244). Even under slight pollution the mayfly community may be changed, initially often resulting in higher densities and production (225, 246). However, it is not long before the mayfly fauna becomes impoverished or even totally exterminated. *Baetis* species are often among the most tolerant of mayflies to pollution.

In North America the use of mayflies as indicators of water quality has not escaped attention (82, 103, 135). Until recently, however, this work has been hampered by problems of species identification. The mass emergence of burrowing mayflies from Lake Erie and the Mississippi River has provided a useful barometer of water quality. Organic and nutrient enrichment of Lake Erie in the 1940s and 1950s led to an increase in the intensity and frequency of mass emergence of *Hexagenia* until in 1953 prolonged periods of oxygen depletion in the hypolimnion caused the population to crash to virtual extinction (244). In the Mississippi River, mass emergence still occurs, but it is largely restricted to less polluted, upper reaches (82). Notably in North America, numerous laboratory bioassays have been made using mayflies, particularly *Hexagenia*. The lethal concentrations of a number of pollutants, such as heavy metals and detergents as well as naturally occurring compounds such as hydrogen sulphide, have been determined (see 149). DDT and other pesticides also affect non-target organisms such as mayflies (111, 199). For example, Canadian studies in connection with blackfly control have demonstrated catastrophic drift and reduced biomass in mayfly populations over large distances in rivers treated with methoxychlor (79).

Contamination by petroleum products is a new threat to aquatic ecosystems in certain areas (7). Although most mayflies are adversely affected, a few species may show small increases owing to the extensive algal growth that often occurs on oiled substrata (190). Acidification of freshwaters is also a threat, especially in some areas of Europe and North America. Many mayflies are affected adversely by low pH and emergence is a particularly critical period (8). In the northeastern USA, *Eurylophella funeralis* was the only mayfly to survive in near normal numbers after experimental acidification of a stream. However, its growth rate decreased and recruitment to the next generation was severely reduced (76). In Scandinavia the mayfly fauna of affected areas is poor in mayfly species, and in lotic habitats *Baetis* are notable by their absence and are often replaced by *Leptophlebia* and *Siphlonurus* (94; Brittain unpublished data). Although it was suggested that the absence of *Baetis* from acid streams was due to the lack of periphyton (207), more recent evidence implicates direct chemical action on the mayflies themselves (92, 156).

The impoundment and diversion of watercourses for water supply and power is commonplace and can have profound effects on the mayfly community, especially when there is a hypolimnion drain (121, 232). An increase in winter temperatures and a fall in summer temperatures may remove obligatory life cycle thresholds and produce changes in energy budgeting, leading to extinction (133, 214, 232). Heated effluent usually has detrimental effects on diversity and production (172), although in some cases the observed effects may be small (131). The seasonality of the climate (continental or oceanic) of the actual area may also determine the degree of disturbance. In reservoirs themselves, lentic conditions and increased water level fluctuations usually produce a depauperate mayfly fauna, especially for species typical of stony substrata (117), although there may be an increase in the abundance of burrowing and silt-dwelling species. The flooding of new areas can create new habitats for mayflies, and in many of the large African reservoirs the mayfly *Povilla adusta* has developed large populations, which burrow into the submerged trees and play an important role in tree breakdown (183).

POSTSCRIPT

All biological studies must have a firm basis in taxonomy, and species identification has been, and still is in large areas of the world, a major obstacle to progress in mayfly biology. This is especially true of the nymphs.

Our ideas of mayfly biology are largely based on data from the temperate areas of Europe and North America. In order to obtain a more balanced

picture we need more information from the tropics, the Arctic, and from much of the southern hemisphere.

In the same way as taxonomy presents an obstacle to further progress in biology, so the lack of accurate life history information hinders progress in explaining community processes and in monitoring and assessing man's impact on aquatic ecosystems (235). While field data on mayfly life cycles is extensive, there is often considerable doubt as to whether the species in question is in the egg stage or is present as early instar nymphs. In such cases laboratory studies can provide the answer, and much can be gained from a combined laboratory and field approach. The culture techniques being developed for the eggs and nymphs of mayflies (83, 85, 106, 237) are an important aid to progress in this field, in addition to their value in bioassay work. We also need to know the ecological requirements of each life cycle stage in order to assess the effect of manmade perturbations (133, 135).

By virtue of their high and easily measured fecundity, mayflies are interesting objects for population dynamics. Data on *Hexagenia* indicate that population regulation occurs in the nymphal stage (101). However, although total life cycle mortality has been estimated in several species (9, 28, 43), we know little about the causes of mortality and how mortality varies with population density.

We already know of several cases where the mayfly fauna has either been drastically changed or exterminated (63). This is especially true of large rivers because of their restricted number and their vulnerability to pollution (63, 135). For example, the genus *Palingenia* studied by Swammerdam in the 17th century, which I mentioned at the beginning of this review, is now extinct in the Netherlands and western Europe (186). Nevertheless, research activity during the last decade or so has set us on the right course towards solving both the academic problems that concern us as biologists and the more applied problems of resource management in freshwater systems. To fulfill both these goals we must continue to increase our knowledge of mayfly biology.

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