

LIFE HISTORY STRATEGIES IN EPHEMEROPTERA AND PLECOPTERA

John E. Brittain

Zoological Museum, University of Oslo, 0562 Oslo 5, Norway

ABSTRACT

The major part of the life of Ephemeroptera (mayflies) and Plecoptera (stoneflies) is spent in the aquatic environment, while their short terrestrial life is primarily concerned with reproduction. Such a complex cycle passing through two different phases, each having its own selection pressures, places evolutionary constraints on life cycle strategies.

Stoneflies are mostly cool water species. They have also evolved brachyptery and mating occurs on the ground or other surface beside the aquatic habitat. In contrast, mayflies are common in tropical waters, show no brachyptery and invariably mate in flight, often at considerable distances from the aquatic habitat.

Water temperature is a major factor governing egg development and although showing the same general relationship between water temperature and the length of egg development mayflies have a greater thermal demand and are more temperature dependent than stoneflies. Nymphal growth rates are also compared and related to their life history strategies.

Univoltine life cycles are most common in both orders, but in mayflies multivoltine cycles are also common, especially in tropical and temperate regions, whereas semivoltine life cycles are generally restricted to certain taxa. In stoneflies, however, semivoltine cycles are common, while multivoltine cycles are rare.

These differences between the two orders explain the greater intrusion of stoneflies into arctic and alpine areas and that of mayflies into the tropics.

INTRODUCTION

The Ephemeroptera and Plecoptera are two small orders of aquatic insects each numbering about 2,000 species. They are widely distributed throughout the world and occur in all continents apart from Antarctica, although poorly represented on oceanic islands. Their conservative dispersal makes them useful objects for biogeographic analysis (e.g. Illies 1965, Rauser 1971, Edmunds 1972).

In contrast to representatives of orders such as the Coleoptera and Hemiptera, they are primary

invaders of the aquatic environment and both orders possessed aquatic nymphs at least 250 million years ago. They have subsequently become highly adapted to the aquatic mode of life, and their immature stages are, with only a few exceptions, exclusively aquatic and restricted to freshwaters. However, both orders have complex life cycles (Wilbur 1980) involving both aquatic and terrestrial phases. Such life cycles create evolutionary dichotomy with selection pressure operating in two, more or less independent, environments. Such dichotomy will theoretically lead to the reduction of either the terrestrial or

aquatic phase. Coordinated evolution between the two phases may occur, but this will retard evolutionary change in general (Istock 1967).

A reduction in one of the phases has clearly happened in both orders, notably in the Ephemeroptera, but also to a considerable degree in the Plecoptera. The adult stage in both orders is of limited duration and has almost the sole function of reproduction, although dispersal is also important.

The life histories of aquatic insects in general and the factors influencing their life histories have been reviewed by Butler (1984) and Sweeney (1984). In the present paper I compare and contrast the life history strategies found in the mayflies and stoneflies. Such a comparison enables one to see present-day distributions in the light of the constraints set by evolutionary history and present selective processes. My main emphasis is on the life history parameters of nymphal growth and egg development and their relationship to temperature. Temperature is also perhaps the major environmental factor controlling zoobenthic populations (Ward & Stanford 1982). The egg stage is especially important as it is more independent of the external environment than either adult or nymphal stages and will thus tend to retain the more primitive characteristics present in their ancestors. However, for a complete understanding of strategies it is necessary to encompass other aspects of life history, such as reproduction, dispersal and nutrition, as well as the overall framework of voltinism.

DISTRIBUTION

Within the limits set by dispersal, distribution patterns are the result of life history strategies. A knowledge of distribution patterns is therefore important in elucidating particular strategies. Stoneflies are primarily cool water species, rarely being reported from waters above 25°C (Hynes 1976, Baumann 1979). Their adaptation to cooler, more oxygen rich environments, renders them more common in lotic habitats than in lakes and ponds than their counterparts. While there are also sev-

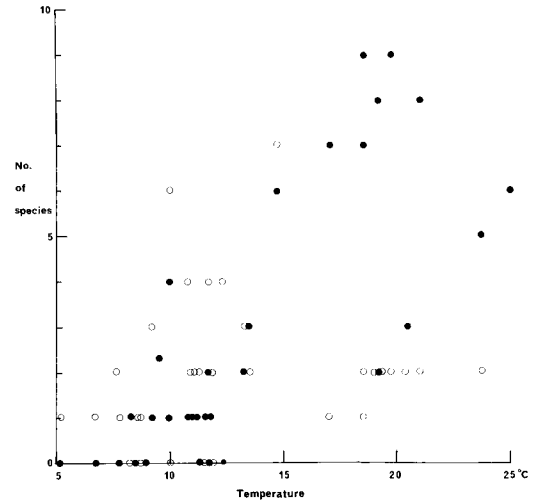


Fig. 1. Relationship between the number of mayfly (filled circles) and stonefly species (open circles) recorded in lakes in southern Norway and the maximum water temperature recorded in each water body (data from Brittain 1974).

eral cool water species among the mayflies, they are as a whole much more common than stoneflies in lakes and ponds. They also extend more widely into the tropics, where stoneflies are usually restricted to alpine or heavily forested areas (Hynes 1976).

There are many studies of the distribution of mayflies and stoneflies along altitudinal and temperature gradients (e.g. Kamler 1965, Ward 1986). These show a greater species richness among Plecoptera in the cooler headwaters and among the Ephemeroptera in the warmer central and lowland reaches. On a larger scale a similar pattern can be seen in the distribution of mayflies and stoneflies in the lakes of southern Norway (Brittain 1974, Fig. 1).

However, distributional patterns are not always simple. For example, the number of mayfly and stonefly species and the proportion of endemics in different geographical regions of Europe is influenced not only by present environmental conditions, but by the Pleistocene glaciation and the presence of subsequent migration routes (Rauser 1971, Illies 1978, Fig. 2). The poorer dispersal ability of stoneflies is reflected in their higher number of endemics, although the survival of isolated stonefly populations during the glacial periods is

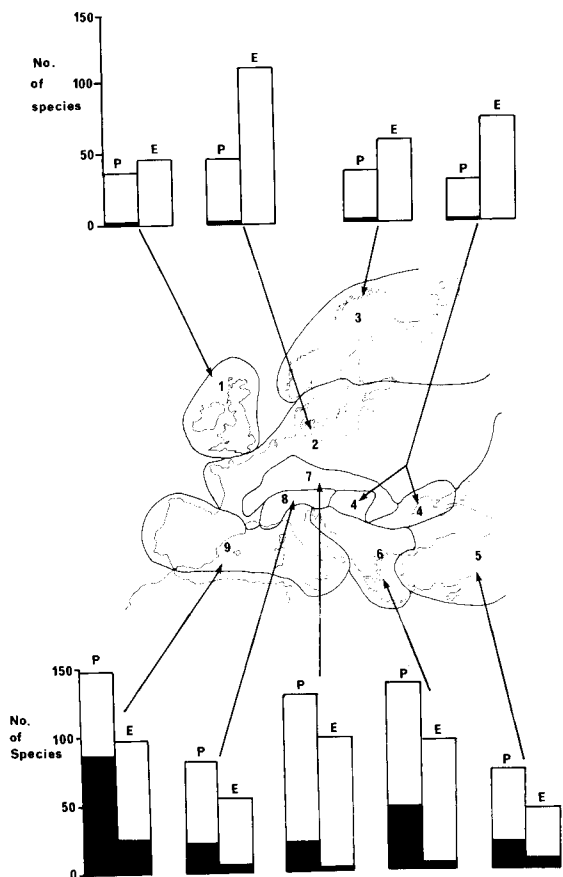


Fig. 2. Number of ephemeropteran (E) and plecopteran (P) species recorded from different geographical regions of Europe. 1 - British Isles, 2 - European lowlands, 3 - Fennoscandia, 4 - Danube lands, 5 - Asia minor, 6 - Balkans, 7 - Prealps/Carpathians, 8 - Alps, 9 - W. Mediterranean. The proportion of endemics is shaded. Data source Illies (1978).

also of significance. The presence of several glacial refuges in central and southern Europe enabled many stonefly species to survive, whereas further north even stoneflies were unable to survive. Mountains running east-west prevented colonization from the south. This has resulted in the greater number of stonefly species in central and southern Europe than in the north and west. In contrast, the number of mayfly species is similar throughout Europe, with a maximum in the central European plains.

THE ADULT STAGE

Adults of both orders are short-lived, but while most adult stoneflies live for several days and even weeks, most adult mayflies live for less than 24 hours (Hynes 1976, Brittain 1980). This is coupled with the fact that no mayflies eat as adults, while most adult stoneflies eat plant material. The lack of nutrition in the adult mayfly clearly limits life length.

Adults in both orders display little diversity in form, greater selective pressure being exerted on the aquatic nymphal stages which in contrast display considerable diversity in both form and mode of life. Nevertheless, many stoneflies have evolved brachyptery, varying from a small reduction in wing length to the absence of wings. Several hypotheses have been put forward to explain brachyptery in Plecoptera (see Hynes 1976). One likely explanation is the advantage conferred by utilizing the energy otherwise necessary for wing production in other somatic growth or in reproductive products. Many stoneflies remain in the vicinity of the stream or lake, mate on or near the ground under stones or in vegetation and therefore do not need the capability of flight. This applies especially to alpine and arctic areas where low air temperatures restrict flight activity. Sexual dimorphism occurs in several species whereby the males are short-winged while females have wings of normal length. This saves the males energy which can be utilized elsewhere, while normal-winged females once mated are able to function as the dispersal agency.

In contrast to stoneflies, mayflies invariably mate in flight, and many complicated behavioural swarming patterns have been evolved (Savolainen 1978). Such patterns serve as isolating mechanisms between closely related species and perform the same function as species specific drumming patterns developed in many stoneflies (e.g. Rupprecht 1978, Stewart & Zeigler 1984). However, the necessity of flight for successful reproduction in non-parthenogenetic species places restrictions on distribution. Climatic conditions, especially air temperatures, are therefore important in ensuring successful reproduction in

mayflies. These differences in mating behaviour between the two orders may explain, at least in part, the greater extension of stoneflies into arctic and alpine regions, where mating on the ground in the shelter of stones or vegetation clearly has distinct advantages. However, by being less predisposed to flight, adult stoneflies are less effective as dispersal agents than their mayfly counterparts. This gives greater importance to the plecopteran nymphal stage as the dispersive life cycle stage. Thus, there is a trade off here between dispersal ability and the potential to reproduce successfully under unfavourable weather conditions.

FECUNDITY

The adults of both orders usually lay high numbers of eggs. In mayflies the eggs and sperm are physiologically mature in the subimago and mating and oviposition usually take place within a few days or even hours of emergence. Among the Plecoptera, many Systellognatha emerge with fully formed eggs and oviposit within 2-3 days. In other species, however, the females mature and even develop their eggs for several days or weeks before oviposition. Fecundity is therefore more difficult to assess in stoneflies. However, although there is overlap in fecundity values found in mayflies and stoneflies (Zwick 1980, Brittain 1982), mayflies generally have higher values. Fecundity values recorded for *Palingenia*, *Hexagenia* and *Epeorus* are in fact greater than most other insect groups except the social Hymenoptera (Brittain 1982). However, most mayflies have fecundities in the range 500-3,000, with the limits being from <100 in *Dolania* to over 12,000 in *Palingenia*. Most stoneflies lie in the range 100-2,000, although up to 3,000 eggs have been recorded in *Paragnetina*.

Fecundity data from a Norwegian subalpine lake for mayflies (Brittain 1980) and stoneflies (see Zwick 1980) demonstrate that although mayfly fecundities are generally higher than in stoneflies in temperate and tropical localities, there may be little or no difference in arctic and alpine habitats (Table 1). Here stoneflies are near-

Table 1. Fecundity values for mayfly and stonefly species found in the subalpine lake, Ovre Heimdalsvatn. Mayfly data is from Brittain (1980) and stonefly data from Zwick (1980) and Brittain - unpubl

EPHEMEROPTERA	
<i>Siphonurus lacustris</i>	624-2792
<i>Leptophlebia marginata</i>	600-2020
<i>L. vespertina</i>	640-1832
<i>Baetis macani</i>	129-258
PLECOPTERA	
<i>Nemoura avicularis</i>	400-900
<i>N. cinerea</i>	1443
<i>Amphinemura standfussi</i>	775
<i>Capnia atra</i>	100-800
<i>Diura bicaudata</i>	365-600

or their environmental optimum whereas mayflies are at the limit of their distribution. Sweeney & Vannote (1978) have in fact suggested that fecundity in aquatic insects will decrease in suboptimal areas and that a species distribution is limited at least in part by reduced fecundity as conditions become suboptimal. It has been subsequently demonstrated that nymphal size in Plecoptera may differ between the extremities and the central areas of a species' distribution (Brittain *et al.* 1984).

In both orders fecundity is related to adult body size (Benech 1972a, Khoo 1964). Most mayfly and stonefly eggs are of similar size as are the first instar nymphs. However, stonefly eggs, for example in the Systellognatha, are often encased in a thicker chitinous layer which undoubtedly protects the eggs from the vagaries of the external environment, perhaps offsetting lower fecundity.

EGG DEVELOPMENT

During the last decade quantitative data on egg development in northern temperate mayflies and stoneflies has been published, enabling a comparison of temperature relationships within and between the two orders. This has the potential to provide new insight into their evolutionary history, biogeography and life history strategies.

In the Plecoptera, hatching success is almost invariably high within the optimal range, which

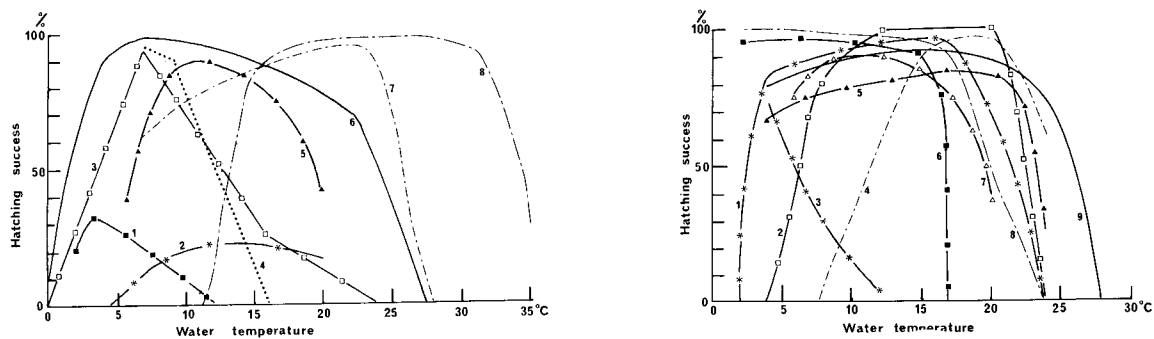


Fig. 3. Egg hatching success in species of Ephemeroptera (left) and Plecoptera (right). Ephemeropteran species: 1. *Rhithrogena loyalea* (Humpesch and Elliott 1980), 2. *R. semicolorata* (Humpesch and Elliott 1980), 3. *Baetis vernus* (Bohle 1968), 4. *Ephemerella ignita* (Bohle 1972), 5. *E. ignita* (Elliott 1978), 6. *Baetis rhodani* (Elliott 1972), 7. *Tricorythodes minutus* (Newell and Minshall 1978), 8. *Hexagenia rigida* (Friesen *et al.* 1979). Plecopteran species: 1. *Taeniopteryx nebulosa* (Brittain 1977), 2. *Siphonoperla burmeisteri* (Lillehammer 1987a), 3. *Isoperla obscura* (Saltveit and Lillehammer 1984), 4. *Dinocras cephalotes* (Lillehammer 1987a), 5. *Nemoura cinerea* (Brittain and Lillehammer – 1987), 6. *Mesocapnia oenone* (Brittain and Mutch 1984), 7. *Nemurella pictetii* (Elliott 1984), 8. *Leuctra digitata* (Lillehammer 1985), 9. *Capnia atra* (Brittain *et al.* 1984).

usually spans the temperature range 10–15°C (Fig. 3). Most species also display high hatching success between 5° and 10°C. The Ephemeroptera so far studied show more variation (Fig. 3, Humpesch 1984). Maximum values for hatching success, although high in some species, are generally lower than in stoneflies. In the Heptageniidae studied hatching success was under 50% (Humpesch 1984). Lower hatching success in mayflies will in part be compensated for by their generally higher fecundity. There are considerable differences in the optimal temperature range of mayfly species and there is no clear temperature interval within which the eggs of most species show high hatching success. In both orders there are species which hatch at low temperature, although some plecopterans show over 90% hatching success even at 2°C, whereas all ephemeropterans tail off at the least by 5°C. At the other end of the temperature scale the opposite situation arises. Whereas most plecopterans show rapidly decreasing hatching success over 20°C, several ephemeropterans have over 50% hatching success at temperatures exceeding 25°C.

The duration of embryonic development or egg incubation period is, in most mayflies and stoneflies so far studied, related to water temperature. In many species the relationship between egg incubation period (Y days) is inversely related to

temperature ($T^{\circ}\text{C}$) and well expressed by the power law equation: $Y = aT^{-b}$ where a and b are constants (see Humpesch 1984). Most studies have been carried out in the laboratory at constant temperatures. The effect of fluctuating temperatures, a feature of field environments, on development is uncertain, and may differ from species to species (see Sweeney 1978 and Humpesch 1982).

It can be fruitful to compare the nature of the relationship in the two orders. Although in most cases the relationship is well expressed by the power-law equation, both the slope and intercept values differ between species. The relationships in four stoneflies and four mayflies are illustrated in Fig. 4. While there is some overlap as shown by *Tricorythodes minutus* and *Dinocras cephalotes*, mayfly relationships appear to have steeper slopes and higher intercept values than stoneflies.

If we plot values of the two constants, “a” which describes the intercept and “b” which describes the slope of the regression line, for all published species, we find that the values of both orders lie along a single new line. Mayfly values are located along the upper section of the relationship, while stonefly values are grouped around the basal area (Fig. 5). Regression analysis of the data for the two orders (Table 2) shows that the individual lines for the two orders are not significantly different ($P < 0.05$). Thus a single regression

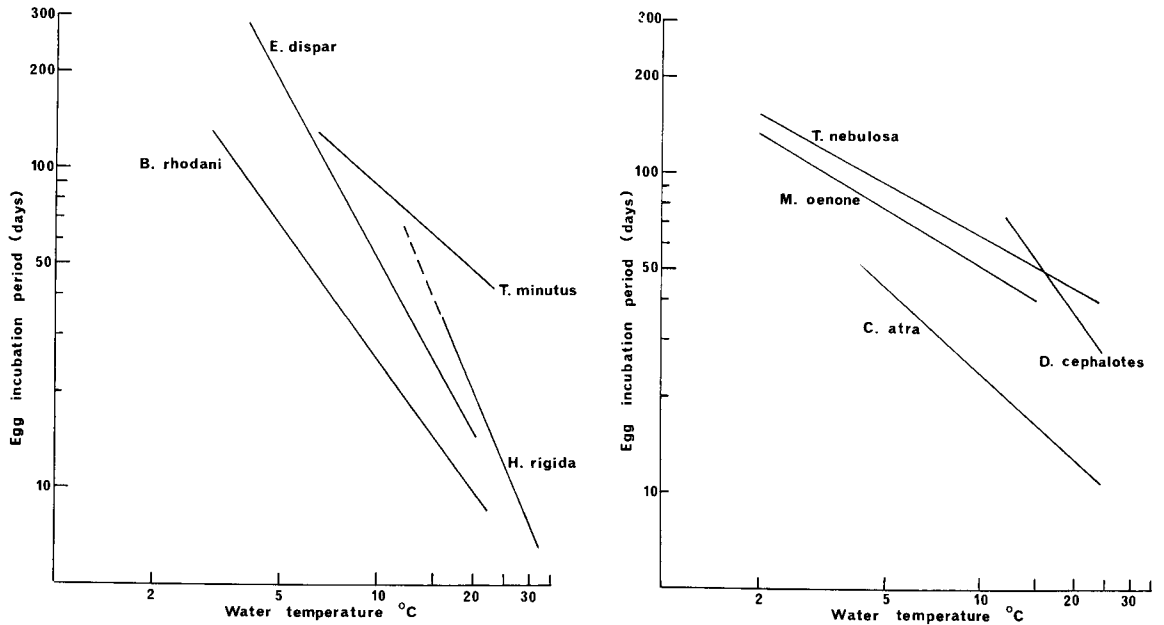


Fig. 4. The relationship between the length of the egg incubation period (50% hatching) and water temperature for species of Ephemeroptera (left) and Plecoptera (right). Data is from the following sources: *Baetis rhodani* (Elliott 1972), *Ecdyonurus dispar* (Humpesch 1980), *Tricorythodes minutus* (Newell and Minshall 1978), *Hexagenia rigida* (Friesen *et al.* 1979), *Taeniopteryx nebulosa* (Brittain 1977), *Mesocapnia oenone* (Brittain and Mutch 1984), *Capnia atra* (Brittain *et al.* 1984), *Dinocras cephalotes* (Lillehammer 1987a).

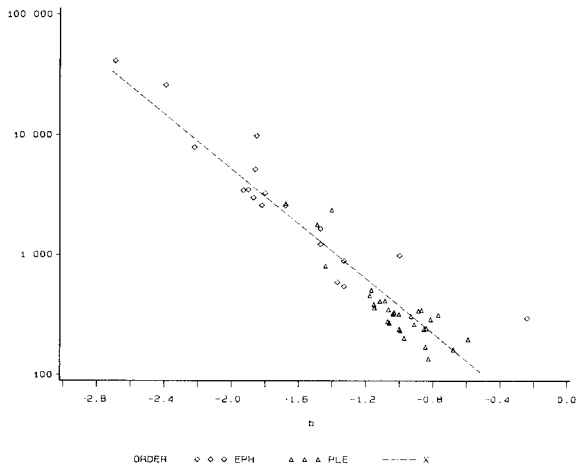


Fig. 5. Relationship between the two constants "a" (intercept) and "b" (regression coefficient) describing the regression equation between the length of the egg incubation period and water temperature in species of Ephemeroptera (diamonds) and Plecoptera (triangles). The composite regression line for the two orders is drawn. Data from the following sources: Benech 1972b, Brittain 1977, 1978, Brittain *et al.* 1984, Brittain and Lillehammer - 1987, Brittain and Mutch 1984, Broch 1986, Elliott 1972, 1978, 1984, 1986, Friesen *et al.* 1979, Haland 1981, Humpesch 1980, Humpesch and Elliott 1980, Lillehammer 1985, 1986, 1987a, b, Mutch and Pritchard 1982, Newell and Minshall 1978, Rekstad 1979, Saltveit pers. comm., Saltveit and Lillehammer 1984, Sweeney 1978, Sweeney and Vannote 1984 (first hatch), Zwick 1981.

Table 2. Regression analysis for the relationship between the two constants 'a' and 'b' in the regression equation for the relationship between water temperature and the length of the egg incubation period in species of Ephemeroptera and Plecoptera. All three regressions are highly significant ($P < 0.0001$). See Fig. 5 for sources of data

Regression	n	Log intercept 'c'	Regression coefficient 'd'	r ²
Ephemeroptera	18	1.84 ± 0.40	- 0.95 ± 0.22	0.83
Plecoptera	31	1.38 ± 0.25	- 1.14 ± 0.23	0.78
Composite regression	49	1.43 ± 0.16	- 1.14 ± 0.12	0.89

quation can be used to express the relationship, which is clearly fundamental to both orders.

What does this relationship mean in evolutionary and ecological terms? The value of the intercept "a" expresses thermal demand, the quantity of heat necessary for egg development. This is often expressed in degree days. A low value of "a" indicates a low thermal requirement for egg development in that particular species and vice versa.

The value of the regression coefficient, "b", indicates the degree of temperature dependency. For example, a steep relationship between the length of the egg incubation period and water temperature, as shown in the mayfly, *Hexagenia rigida* (Friesen *et al.* 1979), shows a high degree of dependence on temperature; that is the amount of heat required for development increases rapidly as temperature decreases. A low value of "b" indicates that the amount of heat required for egg development increases only slightly as the temperature falls. Species showing complete temperature independence would have a "b" value of zero. Several stoneflies and the mayfly *Rhithrogena loyolaea* (Humpesch & Elliott 1980) approach this level with values under 0.8.

Figure 6 illustrates in conceptual terms the actual data plotted in Fig. 5 and shows clearly the

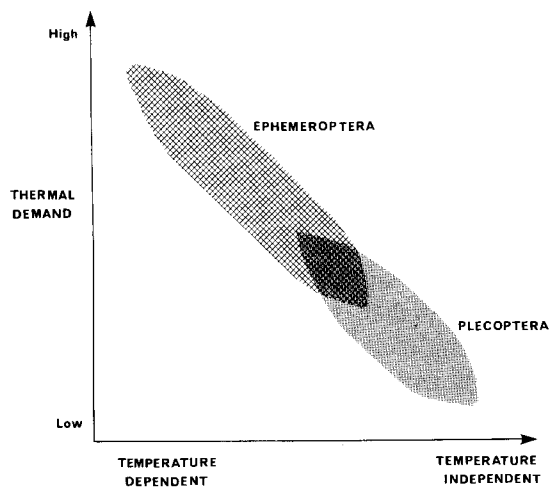


Fig. 6. The overall thermal relationships observed in egg development in Ephemeroptera and Plecoptera based on actual data from the literature (For actual values see Fig. 5).

fundamental difference between the two orders. Ephemeroptera as an order have both higher thermal requirements and are more temperature dependent than Plecoptera. This agrees well with the cold stenotherm nature of stoneflies and their greater extension into arctic and alpine areas. In such habitats most mayflies would have extremely long egg incubation periods if indeed hatching was successful at such low temperatures. Adaption to cold environments in the Plecoptera will, however, place them at a competitive disadvantage in terms of generation time in warmer environments. This will limit their distribution in tropical freshwaters. Among the Plecoptera, the perlids show the greatest extension into the tropics and the perlid for which we have information on egg development, *Dinocras cephalotes*, has the second highest heat requirement of the stoneflies studied (Fig. 4, Lillehammer 1987a).

This fundamental difference between the two orders is thus of major significance in determining potential life history strategies available to members of each order, and probably reflects the early evolutionary history of the two orders. The Odonata, another order of exopterygote aquatic insects, have temperature relationships at an even higher level than Ephemeroptera (Rivard *et al.* 1975, Warninger and Humpesch 1984) and this is reflected in their greater affinity for warm waters compared to both mayflies and stoneflies.

Egg diapause has been demonstrated in both orders, but is not as common as direct development. Where diapause forms part of egg development, temperature relationships will necessarily be more complicated and other factors such as photoperiod may possibly be important (see Hynes 1976, Brittain 1982).

Ovoviviparity is uncommon in mayflies and restricted to the Baetidae while in stoneflies it occurs mostly in the Capniidae, although recorded in other families. Similarly, parthenogenesis occurs in both orders but is of limited extent (Hynes 1976, Zwick 1980, Brittain 1982).

THE NYMPHAL STAGE

Both orders have similar numbers of nymphal instars, generally between 10 and 50 and with most in the range 10–25 (Hynes 1976, Brittain 1982, Butler 1984). The number is not usually constant for a particular species, but varies with sex and development conditions, such as temperature and nutrition. Nymphal diapause has been reported in several stonefly species, but so far no true diapausing stage has been reported in the Ephemeroptera. This gives these stoneflies a greater ability to survive adverse conditions, such as high summer temperatures and drought and to adjust life cycle timing to take advantage of optimal conditions. Egg diapause in mayflies therefore assumes greater significance in life history strategies as both groups have short lived adults.

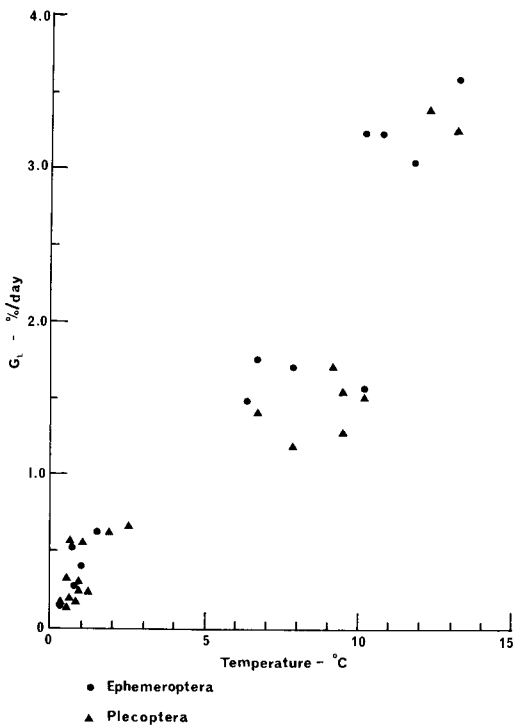


Fig. 7. Specific growth rates, G (% increase in body length/day) for species of Ephemeroptera (Circles) and Plecoptera (Triangles) in the subalpine lake, Ovre Heimdalsvatn, Norway, in relation to mean water temperature. Data for Plecoptera taken from Brittain 1983. Ephemeropteran growth rates have been calculated using the procedure given in Brittain 1983.

Temperature is a major factor governing growth in mayfly and stonefly nymphs, growth rates usually increasing with rising temperature. Growth rates in the two orders are similar at the same water temperature. This is illustrated by field data from Ovre Heimdalsvatn, a Norwegian subalpine lake (Fig. 7). The growth rates increase with increasing temperature, but they fall into three groups, dependent on life cycle type. The highest growth rates occur in the aestival or summer species, *Siphonurus aestivalis*, *S. lacustris*, *Baetis macani* (Ephemeroptera) and *Amphineura standfussi* (Plecoptera), which spend the period of ice cover in the egg stage or as very small nymphs and grow rapidly during the short summer.

The two other groups encompass the hiemal or winter species, *Ameletus inopinatus*, *Leptophlebia marginata*, *L. vespertina* (Ephemeroptera), *Nemoura cinerea*, *N. avicularis*, *Capnia atra* and *Diurra bicaudata* (Plecoptera), which are present as nymphs throughout the long period of ice cover as well as a period during spring and autumn. Their growth during the ice free period reaches values between 1.2 and 1.8% per day, considerably below the level of 3–3.6% per day attained by the summer species. This difference may be due to nutrition. For example, the mayfly *B. macani* utilizes the high production of fresh benthic algae during July and August (Brittain 1975). Also being winter species with adaptation to low temperatures may limit their ability to take full advantage of the higher summer temperatures for growth. Nevertheless, the ability to grow, albeit at low rates from 0.1–0.7% per day during winter enables them to complete their life cycle in this extreme habitat.

Most winter species display some growth during winter, but certain species are able to grow at somewhat higher rates even at temperatures approaching 0°C. The stonefly *Capnia atra* has this ability and its growth has been shown to be independent of temperature in the laboratory (Brittain *et al.* 1986). This is in addition to its relative independence of temperature in the egg stage (Brittain *et al.* 1984). Elliott (1984) has also shown that under optimal conditions in the laboratory the growth of another stonefly, *Nemurella*

pictetii, is little influenced by water temperature.

Omnivory and carnivory are not restricted to stoneflies, but their incidence is much higher than among mayflies. This enables them to obtain food from a variety of sources and at a time of the year when primary production is at a minimum. Also some stoneflies switch from a herbivorous diet in the early instars to a carnivorous one in later instars (see Hynes 1976). In addition many herbivorous stoneflies utilize allochthonous leaf litter. Mayflies utilize algae to a greater degree and are therefore more dependent on aquatic primary production during the summer months. This again contributes to the greater extension of stoneflies into arctic and alpine areas, whereas mayflies are able to make more efficient use of the high aquatic primary production in warmer waters.

Stonefly nymphs show a greater degree of chitinization than the mayflies, which also often have large lamellar gills. Such structural differences probably enable the mayflies to colonise habitats that have lower oxygen concentrations or which have high temperatures which require higher respiratory rates.

LIFE CYCLES

Plecoptera and Ephemeroptera display a wide range of life cycle types. However, although the univoltine or annual life cycle is most common in both orders, mayflies as an order, show a greater propensity for shorter life cycles and stoneflies for longer cycles. Multivoltine life cycles are common in mayflies, especially in warm temperate and tropical waters (Clifford 1982). Even in northern temperate localities mayflies such as the baetid, *Centroptilum luteolum*, can have more than one generation per year (Brittain 1974).

Clifford (1982) gives a figure of 30% for the proportion of published mayfly life cycles which can be classified as multivoltine. In contrast multivoltine life cycles are almost unknown in the Plecoptera (Hynes 1976). At the other end of the scale, however, stoneflies show a much greater ability to lengthen their life cycles at low temperatures to obtain a larger adult body size, thereby

increasing individual fecundity. Only about 4% of published mayfly life cycles are semivoltine (Clifford 1982), while semivoltine life cycles are common in stoneflies especially among Northern Hemisphere Systelognatha. Among arctic and alpine euholognathan stoneflies several species switch from univoltine to semivoltine cycles (see Brittain 1978). There are of course some semivoltine mayflies, but these are not typical of such habitats. Semivoltine mayflies are mostly found in the Ephemeridae, whose longer cycles are associated with large adult body size.

CONCLUSIONS

The emphasis in Plecoptera towards longer life cycles and in Ephemeroptera towards shorter cycles is, at least in part, a function of their inherent temperature and nutritional relationships. Plecoptera are relatively temperature independent organisms and are able to adapt easily to low temperatures and alternative food sources. However, this renders them at a competitive disadvantage in warmer habitats (Table 3). Here, Ephemeroptera come into their own and are able to take advantage of their greater response to higher temperatures and their ability to utilize an abundance of fresh aquatic primary biomass to maintain a high biomass and a short generation time (Table 3). In terms of r- and K-selection (Pianka 1970), Ephemeroptera are thus more r-strategists than Plecoptera.

Adult mating behaviour and differences in dispersal ability between the two orders will serve to reinforce the trend towards the extension of mayflies into the tropics and stoneflies into arctic and alpine areas. Pritchard & Mutch (1985) have suggested that temperature/development relationships in aquatic insects are basically conservative and are as much a reflection of the environment in which the species' ancestors lived than of the environment in which the species now lives. These two orders possibly originated in the Southern Hemisphere. Data on temperature relationships, as well as life cycles and nutrition of species from the Southern Hemisphere are therefore needed to

Table 3. A comparison of the life history strategies typical of Ephemeroptera and Plecoptera

	Ephemeroptera	Plecoptera
Egg development:		
thermal demand	high	low
temp. relationship	temp. dependent	temp. independent
Hatching success	low-moderate	high
Nymphal diapause	no	yes
Carnivorous nymphs	uncommon	common
Adult feeding	no	in most taxa
Adult life-span	hours/days	days/weeks
Mating behaviour	aerial flight	drumming/on ground
Dispersive potential	moderate	low
Fecundity	high	moderate
Emergence	summer	spring
Voltinism	uni-/multi-	uni-/semi-
Warm waters/tropics	many species	few species
Arctic-alpine	few species	several species

complement the relative wealth of information from northern temperate areas. This will ensure further progress in elucidating the evolutionary strategies in the Ephemeroptera and Plecoptera and in explaining more fully past and present distributions.

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