

Temporal Patterns of Emergence in Aquatic Insects

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Abstract

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In aquatic insects, emergence (ecdysis to the adult or subimaginal stage) varies widely in temporal pattern. The comparative study of this pattern is feasible and informative in orders such as Plecoptera, Ephemeroptera, Odonata, Diptera and Trichoptera in which all members of a population pass through the water-surface when emerging. Methods by which emergence rate can be measured are discussed. Four basic temporal patterns of emergence exist. Emergence may be (1) continuous with irregular fluctuations in rate; (2) rhythmic, with a lunar period; (3) sporadic, occurring at irregular intervals of a few days; or (4) seasonal. Examples of each of these patterns are given, and reference is made to the proximate and ultimate environmental factors which may be maintaining the patterns observed. Diurnal rhythms of emergence are excluded from consideration. When emergence is restricted seasonally in temperate latitudes, the degree of its synchronization within the emergence period varies widely but is usually constant and typical for a given species. This has provided the basis for an ecological classification of British Odonata, the validity of which is examined in the light of recent research.

Introduction

The theme of this paper is the temporal restriction of emergence in aquatic insects. Emergence is defined here as the moult which discloses the adult or (in Ephemeroptera) the subimago. By temporal restriction I mean the condition

whereby members of a population tend to emerge within a short space of time owing to the prior operation of some synchronizing process, a condition evident when the temporal spread of emergence is significantly less than that of the late larval stages. The special importance which attaches to emergence in the present discussion is that it provides a well-defined event of short duration by which we can recognize and specify temporal dispersion at the beginning of the reproductive stage.

Though the principles mentioned here apply widely, examples used to illustrate them will, for convenience, be drawn only from those insects with completely aquatic immature stages but aerial, non-swimming adults. Such insects include members of the Plecoptera, Ephemeroptera, Odonata, Diptera and Trichoptera. They are exceptionally well suited for studies of this kind because, when emerging, all individuals in a population pass through the water-surface and thus become unusually accessible to the observer. In the following account prominence will be given to the Odonata, partly because I am relatively familiar with these insects, and partly because certain aspects of emergence are readily quantified in this group.

The temporal patterns discussed here are those in which each 24-hour period represents a unit of observation. The pattern such units form within the emergence period is termed the emergence curve.

Diurnal rhythms of emergence, which are widespread among aquatic insects (Morgan and Waddell 1961; Remmert 1962), need not be considered in this paper. A knowledge of their pattern and operation can however be of relevance in allowing day-groups to be distinguished for sampling purposes, and in providing a background against which other types of rhythmic emergence may be interpreted.

Methods

The accuracy with which emergence rate can be determined depends on an insect's size and emergence habits, and on the site where it is being studied. Field methods fall into one of three categories, considered here in order of their reliability: (1) comprehensive; (2) representative; and (3) indirect.

(1) *Comprehensive methods.* These involve counts of the whole emerging population and are usually feasible only for large insects in small ponds which have accessible margins. Under favourable circumstances, collections of exuviae of Odonata can provide comprehensive counts (Byers 1941; Corbet 1957a; Pajunen 1962).

(2) *Representative methods.* When the emerging population has to be sampled, as with traps, it is necessary that samples remain representative throughout the emergence period. Few species emerge evenly over the whole water-surface, and the ways in which they aggregate must be understood when traps are being designed and deployed. These sources of potential error are compounded when water-level and vegetation change markedly during the emergence period. Such considerations make floating, or mobile traps the best for most purposes (Mundie 1956) although even these may admit bias to the extent that, as relatively protected sites, they are patronized disproportionately during windy weather. Traps which permanently enclose an area of bottom are usually less satisfactory in that they tend to isolate the insects beneath them, but they may be especially useful in small rock pools (Lindeberg 1958). Another factor to be considered is that the emergence curve of a single species may vary considerably from one part of a habitat to another (Hirvenoja 1960). Where certain benthic insects are concerned, these differences are related to the depth at which samples are taken (Fig. 1). To this extent, therefore, they can be allowed for by the investigator.

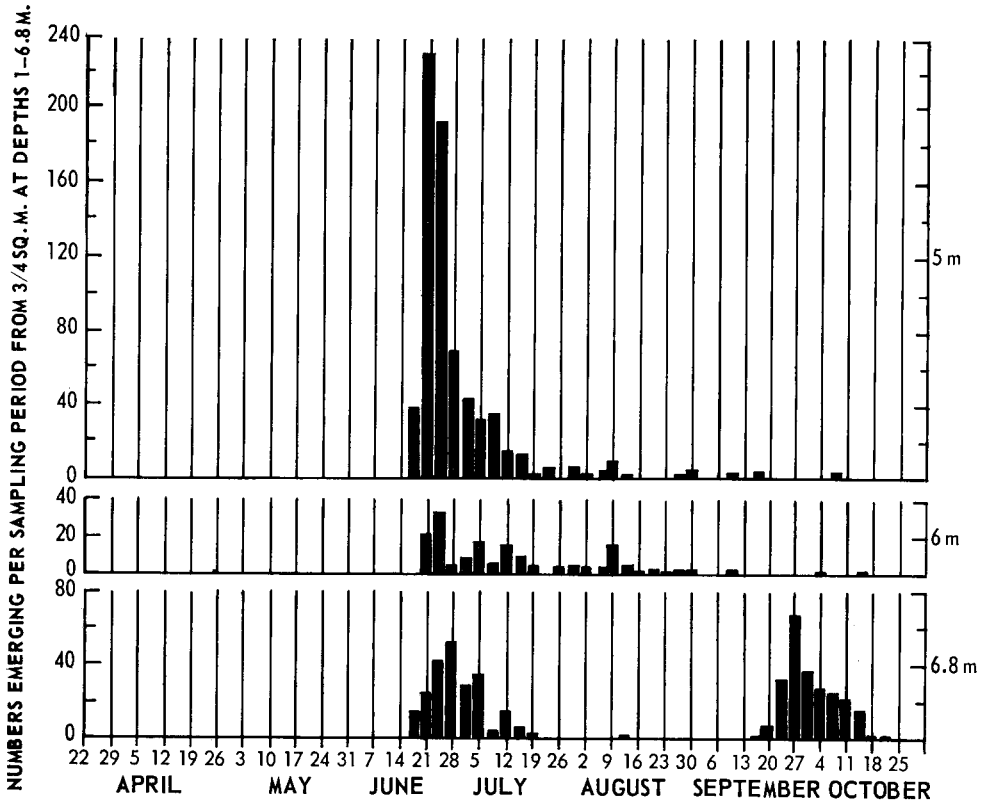


Fig. 1. Emergence of the chironomid, *Tanytarsus holochlorus* Edw., at different depths in a reservoir in southern England, 1951. Adults were collected in submerged traps. (Modified after Mundie 1957.)

(3) *Indirect methods.* If emergence occurs in sites inappropriate for traps, emergence rate has to be deduced from occurrence records of adults. Such methods are subject to least error when the approximate age of the adults can be recognized — either from the knowledge that they are short-lived, as in many Ephemeroptera, or from inspection of age-dependent criteria such as teneral condition, rotation of male hypopygium, presence of a meconium, gonad development, etc. However, results obtained by indirect methods can be subject to wide margins of error. Most age-changes are temperature-dependent (e.g. Provost, Lum and Branch 1961); and the action of water currents and wind often makes it impossible to specify the area from which any one sample was derived.

Thus, when emergence patterns are being compared, due allowance must be made for the ways in which emergence rate was measured.

Patterns of Emergence

The main part of this paper will be devoted to a consideration of the various patterns of emergence which occur in aquatic insects. Four basic temporal patterns of emergence can be recognized: continuous; rhythmic; sporadic; and seasonal. Examples of each pattern will be given and reference made to some of the environmental factors which may be determining it. These factors will be considered under two heads: proximate factors, which regulate emergence rate by evoking specific short-term responses; and ultimate factors, which exert long-term control through natural selection.

1. Continuous emergence

The simplest condition is that in which emergence is continuous and undergoes only slight and irregular fluctuations in rate. It occurs in numerous insects of permanent lakes and rivers near the equator, where physical factors of the environment fluctuate very little during the year. Records of emergence rate exist for a variety of aquatic insects in Lake Victoria, at Jinja, Uganda, a site about 30 miles north of the equator. Though obtained indirectly, from a light-trap on the lake-shore, these records are sufficiently consistent and extensive to show that many insects there emerge continuously. Nightly catches of subimagines of the mayfly, *Euthraulus curtus*, illustrate this clearly (Fig. 2), but comparable examples exist among species of Ephemeroptera (Tjønneland 1960), Plecoptera (Tjønneland 1961), and Trichoptera (Fig. 3). Representative collections of exuviae, made weekly for a year, show that the libellulid dragonfly, *Zygonyx natalensis* (Martin), emerged continuously during that period from the Ripon Falls, a permanent waterfall at Jinja. Such fluctuations in emergence rate as exist in these species (e.g. Fig. 3) probably reflect short-term effects of minor irregularities in the physical and biotic environment, such as occasional storms, unusually heavy predation by shoals of fish, etc. The overall picture, however, is one of stability. It is probably justifiable to regard the other patterns of emergence as derivatives of this basic type.

2. Rhythmic emergence

Emergence is rhythmic if it shows cyclical fluctuations in rate; and the period of these fluctuations characterizes the rhythm. The most widespread emergence rhythms have a diel periodicity (Remmert 1962). This is typically regulated and

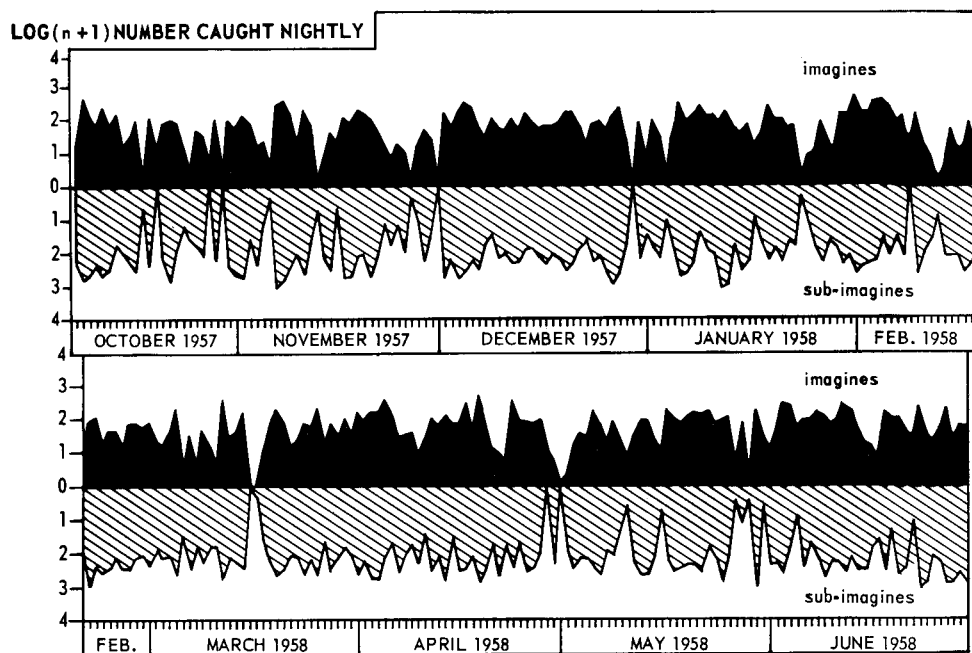


Fig. 2. Continuous emergence. Nightly catches of male imagines and subimagines of the leptohebiid mayfly, *Euthraulus curtus* Kimmins, in a light-trap by Lake Victoria at Jinja, Uganda. Subimagines were less than 24 hours old when caught. (After Tjønneland 1960.)

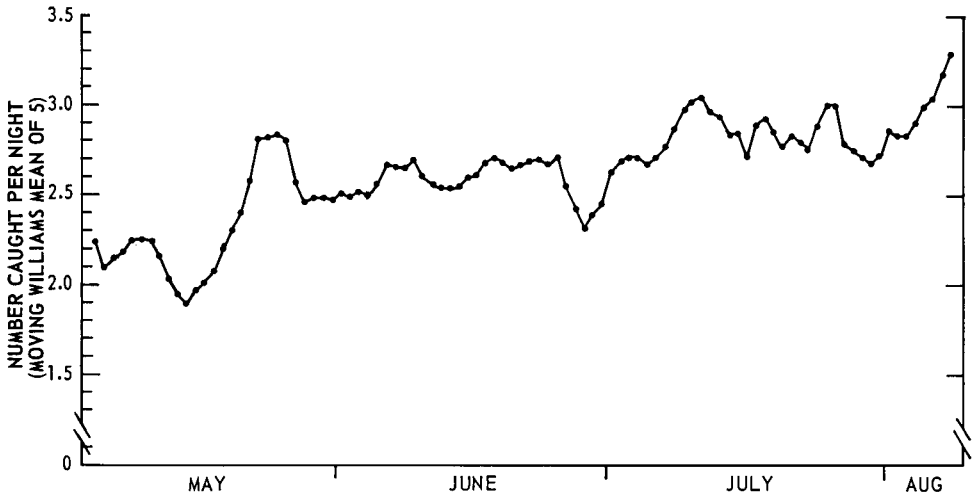


Fig. 3. Continuous emergence. Nightly catches of male and female adults of the hydro-psyche caddisfly, *Cheumatopsyche copiosa* Kimmins, in a light-trap by Lake Victoria at Jinja, Uganda, 1956.

maintained by an 'internal clock' (the endogenous or circadian rhythm) which is 'set' by responses to external time-cues (exogenous factors). The interaction of endogenous and exogenous components in such a rhythm gives it considerable stability and independence from atypical fluctuations in the environment. The only emergence rhythms to be considered here are those with a lunar periodicity, and these also appear to be controlled by endogenous and exogenous factors.

With the exception of the dermestid beetle, *Anthrenus verbasci* (L.) (Blake 1959), no insects are known which exhibit a rhythm with a period exceeding a lunar month. Thus the term 'seasonal' or 'annual rhythm' is generally a misnomer. When emergence recurs seasonally its position is usually dictated by the prevailing environment and therefore varies slightly from year to year.

The best-documented example of lunar periodicity in an aquatic insect is that of the marine chironomid, *Clunio marinus* Haliday, which inhabits the shores of the North Sea. In this species emergence is restricted to two periods in each synodic month, occurring within a few days of new and full moon, respectively (Caspers 1951). A lunar periodicity of emergence has been discerned in other marine or brackish-water insects — another species of *Clunio* in the Pacific Ocean (Oka and Hashimoto 1959), and a biting ceratopogonid, *Culicoides pelilio-uensis* Tokunaga, which inhabits mangrove swamps of the Palau Islands (Tokunaga and Esaki 1936). All these insects live in the tidal zone where direct or indirect lunar effects might be expected. In *Clunio marinus*, for example, emergence coincides with the times of low tide when the algal mats (in which the larvae dwell) are exposed and when, accordingly, emergence is less hazardous (Caspers 1951). It is therefore particularly interesting that lunar rhythms of emergence should occur in several insects inhabiting inland freshwaters, where no such indirect effects of the moon can be discerned.

Lunar emergence rhythms have so far been recognized in several aquatic insects in Lake Victoria (Corbet 1958a). These species differ with respect to the position of the peak (or peaks) of emergence in the synodic month, and also with respect to its synchronization (Fig. 4). A chironomid, *Conochironomus acutistilus* Freeman, has two peaks of emergence, in the first and last quarters

respectively (moon-ages 6 and 21 days), with minima at new and full moon (Tjønneland 1962). The leptocerid caddisfly, *Athripsodes ugandanus* Kimmins, seems to have a similar pattern. A related species, *A. stigma* Kimmins, shows a lunar rhythm on some occasions but not on others, perhaps being in an incipient stage of developing this character.

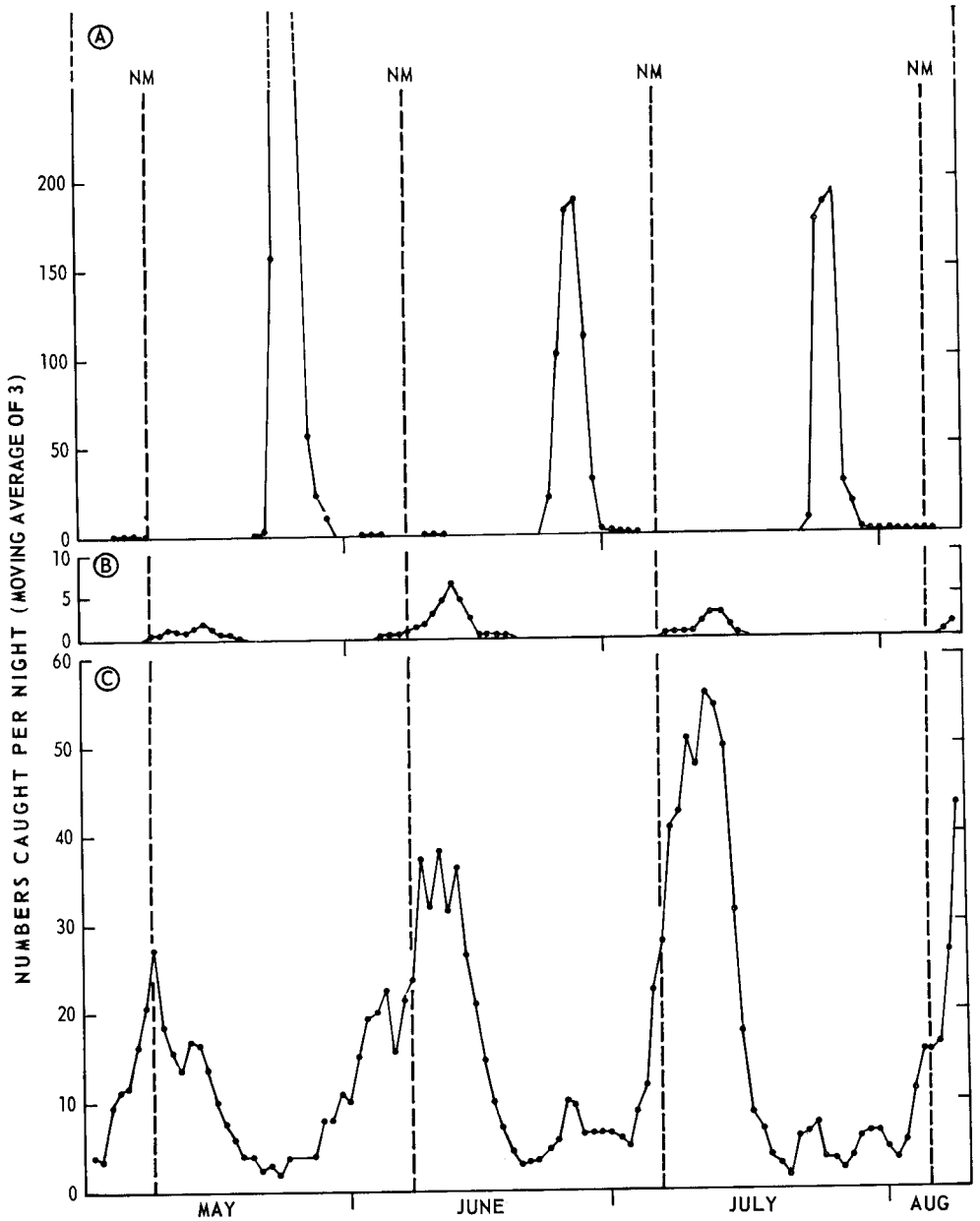


Fig. 4. Rhythmic emergence. Nightly catches of adults in a light-trap by Lake Victoria at Jinja, Uganda, 1956. A: the polymitarcid mayfly, *Povilla adusta* Navás; B: the chironomid, *Clinotanytus claripennis* Kieff.; C: the chironomid, *Tanytarsus balteatus* Freeman. Individuals of *P. adusta* were less than 24 hours old when caught. The times of new moon (NM) are shown by broken lines.

Several authors have suggested that the lunar emergence rhythms of aquatic insects could result simply from the fact that the duration of a generation is an exact multiple of a lunar month. Obviously this suggestion only applies to tropical forms, since in *Clunio marinus*, for example, development may be completed in only two months in summer but takes much longer in larvae obliged to overwinter (Caspers 1951). In Lake Victoria, where water temperature fluctuates very little during the year, the chaoborid, *Chaoborus anomalus* Edw., completes a generation in two lunar months (Macdonald 1956), and the mayfly *Povilla adusta* in five (Corbet 1957c). It is important to stress, however, that in these examples, and probably in all comparable ones, the temporal variation accumulated during the larval stage is too wide to allow a recognizable periodicity to persist for more than a few generations. Similarly, the periodic emergence of *Chaoborus flavicans* (Meigen) and *C. punctipennis* (Say) in southern Ontario, Canada (Judd 1960) cannot be an expression only of the emergence of age-groups, since at this latitude growth must begin anew each spring, and a summer generation is completed in about two months (see Miller 1941; Macdonald 1956), yet emergence peaks are only one month apart. There can be little doubt that most, if not all, emergence rhythms can be explained only on the assumption that some synchronizing factor operates during development.

The proximate factors controlling lunar emergence rhythms in freshwater insects are almost unknown, and present a promising field for research. Observations made by Hartland Rowe (1958) on the mayfly *Povilla adusta*, suggest that in this insect emergence may be under control of an endogenous rhythm positioned in early larval life by a refined response to photoperiod. Experimental work by Hauenschild (1960) on the platynereid worm, *Platynereis dumerilii*, has established the feasibility of this explanation, but the confirmatory work on *Povilla* still has to be performed. Whatever the time-cue controlling the rhythm may be, it is likely that most lunar insects in non-tidal waters use variants of the same system, because there are so few other discernible environmental changes to which they could respond. The lunar cycle of rainfall, discovered recently by Adderley and Bowen (1962) and Bradley, Woodbury and Brier (1962), is essentially a statistical phenomenon, apparent only in aggregate records collected over many years. It is not sufficiently regular or well-marked to serve as a proximate stimulus.

The ultimate factors which impose a lunar rhythm are not obvious. They might be of two kinds: those concerned with the direct effect of physical factors on the emerging insects, or those related to the phenomenon of synchronization *per se*. It is possible that, over a long period, the periodicity of rainfall mentioned above might exercise selection in favour of a lunar emergence rhythm. The only other physical factor known to change extensively according to moon phase near the equator is nocturnal illumination. Hora (1927) suggested that the post-sunset illumination characteristic of nights near full moon might facilitate the swarming and oviposition of certain mayflies, and it is possible that the short-lived adults of *Povilla adusta*, which swarm shortly after sunset (Hartland-Rowe 1958), may benefit from their lunar rhythm in such a way. For insects such as *Clinotanypus claripennis* and *Chaoborus edulis* (Edw.) which emerge near new moon and swarm in the daytime, any direct influence of the moon phase must be different. It might, for example, be connected with the need for females to enjoy the protection of darkness while ovipositing. On the other hand, direct effects of physical factors are unlikely to be responsible for the lunar rhythm of the chironomid, *Chironomus brevibucca* (Kieff.), since this emerges at full moon in Lake Bangweulu, Northern Rhodesia (Fryer 1959) but at new moon in

Lake Victoria. Here the selective importance of synchronization itself may be a determining factor.

Synchronization might prove of selective value in several ways. Irrespective of its adaptive value, rhythmic emergence might tend to become established in a population from time to time simply because individuals carrying a gene which tied emergence to a certain moon phase would mate with each other more often than with others not so endowed. Some such mechanism may be maintaining the two peaks of emergence in *Conochironomus acutistilus*. It has often been suggested that the adaptive (as distinct from merely selective) value of synchronization resides in the greater opportunities for mating which it provides. If this were so, one would expect synchronization to be developed best in insects of which the adults are short-lived and spatially dispersed. So far it has proved difficult to investigate this hypothesis because spatial dispersion cannot be adequately determined. Other ways in which synchronization might be of adaptive value concern the regulation of predation and density. These two aspects are considered later in the section devoted to seasonal emergence.

3. Sporadic emergence

A few aquatic insects appear to emerge in short bursts separated by irregular intervals of a few days during which little or no emergence occurs. As far as I know, incisive evidence for sporadic emergence is still lacking, because observations made so far have been obtained using indirect methods. There are indications, however, that it may exist in certain mayflies, chironomids and caddisflies, some of which constitute a classified nuisance to man.

The best-known examples are North American mayflies of the ephemerid genus *Hexagenia*, adults of which appear at intervals in distressingly large numbers along the margins of large lakes and rivers. Sporadic appearance at a fixed observation site on a lake-shore could be the result, not of irregular emergence, but of sporadic flight activity or of the uneven aggregation of adults by wind, Hunt (1953) having remarked that even slight air movements can effect a redistribution of adult *Hexagenia limbata* (Serville) around a lake. Support for this interpretation is found in work by Neave (1932) who observed that on Lake Winnipeg the largest numbers of this species did not appear simultaneously at all places. On the Upper Mississippi River, however, Fremling (1960) noted that emergence (inferred from flight activity) occurred in waves, at intervals of about 6-11 days along a stretch of some 600 miles. Fremling (1960), like Needham (1920) who investigated this problem elsewhere, could find no correlation between emergence-times and temperature (of air and water), water-level or phase of the moon, although Hunt (1953) states that in lakes in southern Michigan emergence was always heaviest when the air and water temperatures exceeded 70°F. (ca. 21°C.). There can be little doubt that air temperature contributes to the synchronized appearance of adults during the long flying season, because duration of the subimaginal stage is temperature-dependent (Lyman 1944). But evidently its mode of operation is complex or indirect. This important question still requires critical investigation.

In the Victoria Nile near Jinja, Uganda the mayflies *Tricorythus tinctus* and *Centroptilum notabile* Kimmins appear to show sporadic emergence of a similar type (Fig. 5; Tjønneland 1960). Both species inhabit rivers, and it has been suggested that rate of water-flow, one of the very few short-term variables in such an environment, may be the factor to which they are responding. Unfortunately this hypothesis is difficult to examine in the field because the delay between stimulus and emergence is not known. If these tropical species are indeed

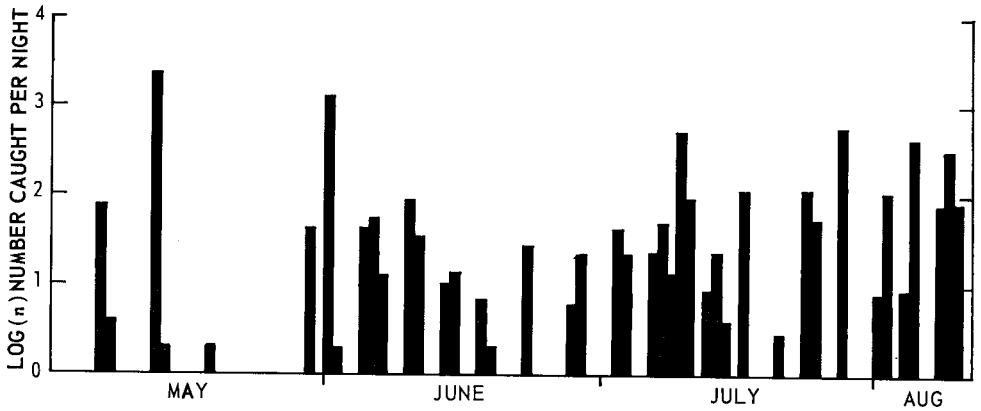


Fig. 5. Sporadic emergence. Nightly catches of male and female imagines and sub-imagines of the tricorythid mayfly, *Tricorythus tinctus* Kimmins, in a light-trap by Lake Victoria at Jinja, Uganda, 1956.

exhibiting sporadic emergence, its biological significance is almost certainly related to some advantage of synchronization *per se*.

To confirm the existence of sporadic emergence, representative or comprehensive methods of observation are needed, so that the masking effects of adult activity can be eliminated. A salutary warning in this regard is provided by the demonstration that the sporadic appearance of certain chironomids expresses corresponding changes in the strength, time and direction of the winds that transport them after emergence (Lewis, Henry and Grindley 1954; Nielsen 1962).

4. Seasonal emergence

In considering seasonal emergence our first concern is with the two physical factors which impose the greatest seasonal restriction on insects. These are rainfall, in tropical regions, and temperature, in higher latitudes.

Rainfall. Few of the insects treated here are sufficiently robust to inhabit temporary bodies of water in the tropics. Those that do so must possess either a resistant stage in which to survive the dry season or a migratory one able to follow the moving rain belt. Certain dragonflies possess each of these adaptations (Corbet 1962). Some species of *Lestes* and *Gynacantha* spend the dry season as adults, resting in forest from which they venture for only a few minutes each day at sunrise and sunset. Shortly before the rains break the females lay drought-resistant eggs in sites later to be flooded. The migratory dragonflies are mainly Libellulidae. In a single temporary pool adults may be ovipositing during several weeks of the rainy season. The eggs are usually laid on the water-surface and hatch promptly. Hence the temporal variation accumulated before emergence is considerable (Fig. 6). It is likely that species with each type of life-history show a widely dispersed emergence, and that this is of no biological disadvantage to them. The specializations they need are evidently directed mainly towards the temporal restriction of the larval stage, which is dependent on ephemeral bodies of water. The long-lived adults appear to have independent means of spatial and temporal aggregation. *Pantala flavescens*, for example, migrates immediately after emergence and appears to be transported and re-aggregated by rain-bearing winds.

Temperature. Restriction of emergence to the warmer months of the year is a phenomenon typical of insects in temperate regions, and is the aspect of emergence which concerns us most in North America and in the present discussion.

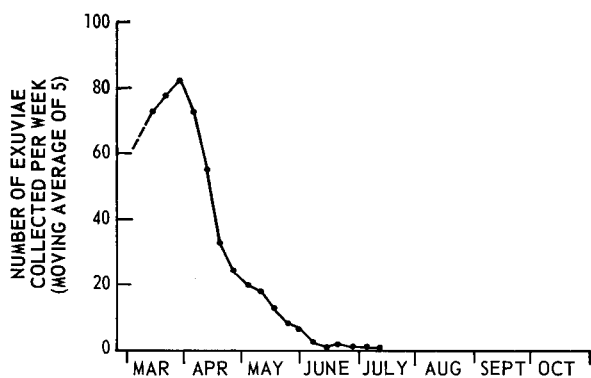


Fig. 6. Seasonal emergence. Weekly exuvial collections of the libellid dragonfly, *Pantala flavescens* Fbr., from a pool at Jinja, Uganda, 1955.

It is instructive to consider restriction of emergence as being related progressively to latitude, or to its climatological equivalent. In the lowest temperate latitudes, emergence of some aquatic insects is interrupted for only a few colder weeks each year, but is otherwise virtually continuous. Towards higher latitudes the emergence period becomes progressively shorter until in extreme cases it may last only one or two days (e.g. Johnson 1963). Although this general picture is probably valid for most groups of aquatic insects, there are apparent exceptions where individual species are concerned. These, however, are no more than reflections of the fact that species have upper as well as lower temperature thresholds for emergence and that they can exist in localities where both operate. In his now classic study, Ide (1935) showed conclusively that the emergence period of the northern mayfly, *Iron pleuralis* Bks., became progressively shorter towards the lower reaches of the water-course he studied and that this was correlated with the higher temperatures there. This example does not contradict the principle outlined above, since emergence of *Iron pleuralis* is seasonally-restricted in all parts of its range, and therefore different from the continuous emergence shown by tropical species. This shortening of the emergence period, and the synchronization of emergence within it, are expressions of the increasingly complex and efficient methods of seasonal regulation employed by insects of temperate latitudes. I shall now consider the possibility that one can learn something about the responses involved in this seasonal regulation from inspection of the shape of the emergence curve, and also the feasibility of attempting an ecological classification of an insect group on this basis.

Many emergence curves of aquatic insects in north-temperate regions have been published (e.g. Hirvenoja 1960a, b; Ide 1935, 1940; Judd 1953, 1960, 1961, 1962; Macan 1958, 1960; Mundie 1957; Robert 1958). Most have been obtained by representative methods and probably give a pattern very close to that of the whole population sampled. A striking feature of these and other similar data is the degree to which the duration of emergence varies. In a single habitat one species may emerge for several months and another for several days. An equally noteworthy feature is the extent to which the synchronization of emergence can differ within the emergence period (Fig. 7).

Proximate factors responsible for such patterns of emergence must be looked for among those acting in a short-term way, since the variability of first dates of emergence and the existence of multivoltinism eliminate the possibility of an annual rhythm (*sensu stricto*) being involved in most cases. Seasonally varying

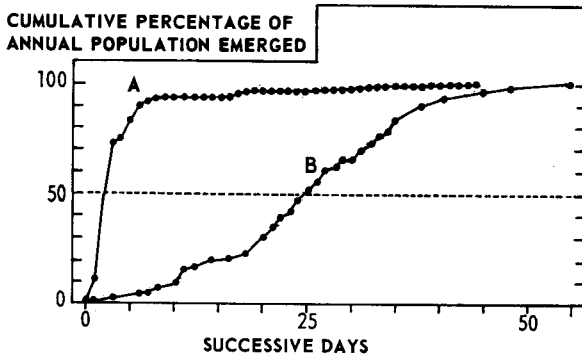


Fig. 7. Seasonal emergence of two aeshnid dragonflies, as expressed by comprehensive daily exuvial collections from ponds in southern England. *A*: *Anax imperator* Leach, emerging between 25 May and 7 July 1953. *B*: *Aesbna cyanea* (Müller), emerging between 29 June and 22 August 1957. In the spring species (*A*) 50% of the annual population had emerged by the third day, whereas in the summer species (*B*) this value was not reached until the 25th day of emergence. (Modified after Corbet and Corbet 1958.)

factors most likely to be responsible are temperature and photoperiod, acting independently or in concert. Emergence curves, considered in relation to the seasonal distribution of immature stages, can provide useful means of inferring the mode of action of such factors. As I wish to discuss the implications of this statement in some detail, I shall restrict my remarks to a single group — the Odonata. It is likely, however, that the principles discussed apply to other groups of aquatic insects also.

Anax imperator and *Aesbna cyanea*, the dragonflies with such different emergence curves (Fig. 7), differ also in their life-histories. In *A. imperator* (at a site in southern England, 50°N.) at least 90% of individuals emerging in a given year had spent their last winter in the final larval instar, which they had entered the previous autumn. These emerged synchronously at the beginning of the emergence period. The remainder, comprising less than 10%, which had spent this winter in the penultimate instar and entered the final instar before June, had spent only about 45 days (instead of 9 months) in the final instar. This second group showed poor synchronization and emerged later, being responsible for the protracted 'tail' of the emergence curve.

The temporal pattern of emergence in *A. imperator* has been shown to be the consequence of two phenomena: (1) the majority of a year-group overwintering in the final larval instar and thus responding synchronously to the rising temperatures which induce metamorphosis in spring; and (2) larvae which enter the final instar after May postponing metamorphosis until the following year (Corbet 1957a). In *Aesbna cyanea*, on the other hand, there appears to be no such rigorous control of the destiny of overwintering larvae: it appears that they can overwinter in several instars and still emerge the following year (Corbet 1959; Schaller 1960). Extending these ideas to other species of north-temperate Odonata, we find that a series exists in which synchronization of emergence is correlated with the number of larval instars which can precede emergence in one year. At one extreme are certain Gomphidae in which emergence lasts for only one or two days and in which the last winter must be spent in the final instar. At the other are trivoltine Coenagrionidae such as *Ischnura elegans* (v.d. Lind.) in southern France (Aguesse 1955). Recognition of this relationship led to an ecological classification of British Odonata according to which two major types

were recognized: 'spring' and 'summer' species (Corbet 1954). This represented a preliminary attempt to classify a natural group on the basis of seasonal regulation.

According to this classification, spring species were defined as those which possessed a diapause in the final instar; summer species as those which did not. Summer species, essentially a heterogeneous group, were divided further according to the normal duration of larval development (Corbet 1958). The two groups recognized were (a) univoltine species, and (b) species requiring more than one year to complete a generation. It had been observed that some summer species, although lacking a final instar diapause, were able to reduce temporal variation before emergence. One way in which this could theoretically have been achieved in the examples studied was for the last few stages before emergence to have had a series of rising temperature thresholds for development (Corbet 1957b). Such a system is similar in principle to that suggested by Lloyd (1941) to account for discontinuous emergence in the chironomid *Spaniotoma minima* Meig. It can only operate when temperatures are rising and is less efficient when growth is rapid. Hence univoltine dragonflies, which grow quickly, were considered unable to utilize such a system effectively at British latitudes. On theoretical grounds, emergence was thought to be most closely synchronized in spring species and least so in univoltine summer species. Also, when emergence was closely synchronized, it was expected that adult life would be relatively short and *vice versa*. An attractive feature of such a classification is that, if validly based, it should reveal the successive stages involved in the colonization of higher latitudes from the tropics, and the ways in which life-histories become modified in the process.

To date, the validity of the spring and summer species classification has been investigated only in Britain and there only in a few species. A much broader treatment is needed, involving more species and, particularly, those of different latitudes. In these respects North America is an appropriate study-ground for such a problem, and in the last few years these questions have been taken up in this continent. Recently, Jenner and his associates have been analyzing the factors controlling seasonal regulation of certain Odonata in North Carolina, at about 36°N. A finding of great significance is that in some species the development rate in each of several later instars is a direct function of the current photoperiod (Jenner 1958, 1960). This pattern of response has been found also by Montgomery and Macklin (1962) in Indiana at 41°N., and may prove to be a general feature of Odonata, and perhaps other slow-growing insects. If so, it will necessitate a revision and reassessment of earlier work in which insufficient allowance was made for its possible operation (e.g. Corbet 1956). It is already clear that in Odonata diapause, or its equivalent, can be controlled by a continuously-variable response to photoperiod quite unlike the all-or-nothing threshold which determines it in many other insects. It is also evident that the instar is not necessarily a sound division for purposes of diapause analysis and that if, as seems likely, spring species represent a valid ecological group, they can no longer be defined as possessing a diapause only in the final instar, since development may be subject to environmentally-induced delay in earlier instars as well. Probably spring species will best be defined as those in which all, or a majority, of a population spends the winter before emergence in the final larval instar, irrespective of how this may be achieved. It may be also, that spring species (in this modified sense) differ from others not so much by emergence always being more closely synchronized, as by the synchronization being achieved in a much simpler way. Other species may approach this degree of synchronization, but perhaps only by utilizing more complex responses. Thus it may transpire that spring species constitute a mean-

ingful entity, but that summer species comprise a heterogeneous assemblage of categories yet to be recognized.

The ultimate factors which impose synchronized emergence are doubtless manifold and differ from species to species. In considering some of these, we should remember that synchrony may have drawbacks as well as advantages, and that its selective value, if any, may sometimes hang on a fine balance. Some of the more evident consequences of restricted emergence are mentioned below, under two heads. Those in the second refer to the synchronization which may arise from rhythmic, as well as from seasonal emergence.

(1) *The seasonal position of the emergence period* will determine the physical and biotic environment that adults encounter. In the former, temperature and the duration of day, night and twilight will affect the type and pattern of adult activities. In the latter, the coincident plants will be those available for emergence supports, shelter, or sites for swarming, oviposition, and the demarcation of territories. The coincident animals will determine the amount of predation or parasitism which occurs, and the intensity of interspecific competition for available shared resources; for species in which sexual recognition is poor, the coincident animals may influence the frequency of abortive sexual interaction or interspecific crossing.

(2) *The synchronization of emergence within the emergence period* has consequences which increase both survival and mortality.

Depending on the environment, synchronization of emergence may increase or reduce predation. Mass emergence of gomphid dragonflies along a river bank may attract large numbers of non-territorial birds to feed on them (Martin 1895; Lyon 1915); but where a pair of birds successfully defends a territory which includes an emergence site, mass emergence reduces mortality when more individuals emerge than can be eaten in a single day (Corbet 1957a).

Synchronized emergence increases the frequency of intraspecific encounters. One manifestation of this is the density-dependent mortality arising from competition for emergence sites, a factor which in *Anax imperator* may cause the death of up to 16% of a day-group (Corbet 1957a). Another is the overcrowding which occurs among newly-hatched larvae at the oviposition-site. It is, however, encounters between adults that are usually regarded as being of greatest significance. Coincidence of the sexes, especially in rare or short-lived species, is necessary if the reproductive potential is to be realized. On the other hand, by leading to dispersal or interference with mating and oviposition, intraspecific encounters can provide a homeostatic device which limits population size. Wynne-Edwards (1962) has suggested that aggregation before reproduction is a device which presents an arena for intraspecific competition resulting in the consequent dispersal of the less successful individuals. In the case of Odonata, this consequence is evident in territorial behaviour of mature males, an activity closely similar in most respects to the swarming of other insects. What may prove to be a special case of this phenomenon, and one in which synchronized emergence plays the major part, is the facultative migration of the Holarctic libellulid dragonfly, *Libellula quadrimaculata* L. Migrations are believed to begin with the mass departure of newly-emerged adults from a breeding site, and such migrations occur after mass emergences, when synchronization has been accentuated by unusual meteorological conditions in early spring (Fraenkel 1932). Thus it appears that, for a given density, it is the temporal pattern of emergence which determines whether or not migration will ensue.

In this brief treatment of a very extensive theme, I have tried to show that the study of temporal patterns of emergence in aquatic insects can yield information about several facets of their biology. The changes in structure and behaviour which precede the last moult have long received detailed study and are considered of great significance in the life-history. My purpose here has been to draw attention to the no less important changes which occur in the temporal dispersion of a population at this time. Their successful implementation can determine such factors as the environment the adults will encounter and the one they will manufacture for themselves, the distances they will travel, their mortality, and the size of the next generation.

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