DIURNAL VARIATION IN THE EMERGENCE OF SOME AQUATIC INSECTS

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I. Introduction

(1) *Previous Observations*

Various workers have shown that a definite diurnal rhythm exists in the emergence of aquatic insects. Phillipp (1938) has studied the phenomenon under laboratory conditions, Miller (1941), Scott and Opdyke (1941) and Morgan (1958) under lake conditions, Sprules (1947) under stream conditions, and Caspers (1951) and Palmén (1955) in brackish water. The findings of these observers differ considerably and much has still to be learnt about the time of emergence of individual species. In this paper the diurnal periodicity of the emergence of many of the commoner species occurring in a small Scottish loch is recorded. The original study was carried out to determine the availability of emerging insects as trout food at different times of day and the diurnal periodicity of the total emerging fauna was determined during twice monthly periods in 1954 and 1955 (Morgan and Waddell, 1960). The information given in this paper has been extracted from these records, and in a few cases supplementary observations were made on particular species to obtain more information about the fauna which emerges in the spring.

(2) *Site*

The observations were made at Loch Dunmore, near Pitlochry, Perthshire. This is a small loch, 4·5 acres in area, situated in a mixed wood of coniferous and deciduous trees at a height of 350 feet above sea level. Much of the mud bottom is at an even

depth of 6 feet (1·8 m.), which is also the greatest depth recorded, and the loch supports a rich growth of macrophytes. The *pH* ranges from 6·9–7·7 and the alkalinity from 20–30 mg. $CaCO_3$/l. A detailed description of the loch has been given by Morgan and Waddell (1960).

Insect emergence from different habitats was observed by the operation of traps at different sites, the characters of which can be summarised as follows :

Site 1.—Depth of water 10 inches (25 cm.). Bottom of mud covered with a dense growth of *Apium inundatum* (L.) Rehb.

Site 2.—Depth of water 4 inches to 1 foot (10–30 cm.). Bottom of mud covered with leaves and twigs from the surrounding trees with a scattered growth of *Menyanthes trifoliata* L., *Apium inundatum*, *Sparganium minimum* Fries, *Littorella uniflora* Aschers, *Elodea canadensis* Michx., *Myriophyllum spicatum* L. and *Nymphaea alba* L.

Site 3.—Depth of water 6 feet (1·8 m.). Bottom of mud covered with a scattered growth of *Chara delicatula* Agardh.

Site 4.—Depth of water 6 feet. Bottom of mud covered with *Myriophyllum spicatum*.

Site 5.—Depth of water 6 feet. Bottom of mud covered with *Potamogeton natans* L.

Site 6.—Depth of water 6 feet. Bottom of mud covered with a dense growth of *Elodea canadensis*.

II. Methods

The emerging insects were caught in floating emergence traps which had a clear " Perspex " top and sides covered with " Tygan " plastic screen cloth (24 meshes to the inch). Detailed accounts of the traps and the methods of dealing with the catch have been given by Morgan and Waddell (1960). Traps of area 4 square feet, 5 square feet and 7·5 square feet were used.

The daily variation in the time of emergence was investigated by emptying the traps every two hours over a period of 54 hours but only the results obtained during the last 48 hours were used. This was done to reduce the possibility of any small insects, in particular *Tanytarsus* spp., being left in the trap after the removal of the previous day's catch at the beginning of the period of observation. During darkness the traps were tilted with their tops towards a Tilley lamp and the insects, which were attracted towards the light, removed by use of an entomological aspirator. This followed the normal procedure of removing the traps to the boat-house for emptying.

Diurnal studies were carried out at the beginning and end of the month from May to September in 1955, at the end of March and beginning of April 1957 and at the end of April and beginning of May 1958.

Unless stated otherwise, the times given in this paper are British Summer Time (one hour ahead of Greenwich Mean Time).

Continuous records of air temperature and the water temperature at a depth of one foot at site 2 were taken on a Negretti and Zambra " Mersteel " Recorder.

III. Diurnal Emergence Periods

Since the emergence pattern of each species was similar at all sites at the same time of year, the data collected at different sites have been grouped together for each species. When the data on the same species collected at different times of year were similar these were also summed. The catches in each two-hour period are shown in Tables I, II and III. In these tables the time of year at which the diurnal studies were carried out is shown for each species. This does not always cover the whole of the seasonal emergence period of a species and in some cases results were only available for one generation.

The nomenclature used for the Chironomidae is based on that followed by Goetghebuer (1936–50), except that *Chironomus* Meig. is used instead of *Tendipes* Meig. and

(following Freeman, 1957) the sub-genus *Dicrotendipes* Kieff. is used instead of the sub-genus *Limnochironomus* Kieff.

(1) *Ephemeroptera*

Leptophlebia vespertina (L.) (Table I).—Subimagines were caught mainly between 10.00 and 16.00 hours, the majority of insects emerging between 10.00 and 14.00 hours. This species emerged at the shallow water sites only, being more common at site 2, where there was less vegetation.

Leptophlebia marginata (L.).—A few observations indicated that this species also emerged in the middle of the day (Table I). At other lochs where this species was more abundant subimagines were frequently seen emerging from the shallows between 11.00 and 14.00 hours. Although this species can emerge at the water surface, the last instar nymph often crawled a few centimetres out of the water up some support before the sub-imagines emerged.

Caenis horaria (L.) (Table II).—This species was caught at all sites but most commonly from the deeper water, particularly site 3. Most of the subimagines were caught in the evening, chiefly between 20.00 and 22.00 hours. These records agree with the findings of Kimmins (1954), who observed that the duns of *C. horaria* emerged between 19.00 and 21.30 hours G.M.T. in mid June. Subimaginal ecdysis, mating, egg-laying and death took place within about two hours of emergence from the last instar nymph, the spent imagines littering the water surface.

Cloëon simile Etn.—This species was caught during each period of diurnal study from the beginning of May to the end of September, the majority of subimagines emerging between 10.00 and 16.00 hours (Table I). No difference was discernible in the time of maximum emergence in different months. *C. simile* was common at the shallow and weedy site 1.

Cloëon dipterum (L.) (Table I).—The small numbers caught indicated that the time of emergence was similar to that of *C. simile*. It was also caught most frequently at site 1.

(2) *Odonata*

Enallagma cyathigerum (Charp.).—Since the Zygoptera emerge by climbing up the bank or up supports from shallow water, this species was only caught at sites 1 and 2. Emerging nymphs left the water between 08.00 and 14.00 hours (Table I). Corbet (1952) observed that the nymph of *Pyrrhosoma nymphula* (Sulzer) began to leave the water about 08.30 hours (B.S.T.) and that the daily maximum lay between 09.00 and 10.00 hours. *P. nymphula* nymphs were seen leaving the water between 09.00 and 10.00 hours at Loch Dunmore.

(3) *Trichoptera*

Limnephilus marmoratus Curtis (Table II).—This species was caught most frequently in traps set over *Potamogeton natans* and *Myriophyllum spicatum* growing in deeper water and was more frequent from the weedy site 1 than from sites 2 and 3.

Athripsodes aterrima (Steph.) (*Leptocerus aterrimus*) (Table I).—The last instar larvae migrate inshore or up weed stems to pupate (Morgan, 1956) so that most of the emergence took place from shallow water.

Mystacides azurea (L.).—In contrast to *Athripsodes aterrima* this leptocerid was caught between 16.00 and 02.00 hours, the maximum emergence occurring between 20.00 and 24.00 hours (Table II).

Cyrnus flavidus McLach. (Table II).—The majority were caught between 20.00 and 02.00 hours, the emergence rate being slightly higher before midnight. During this period imagines were seen swimming rapidly over the water surface, gyrating in

the manner of *Gyrinus* beetles. *C. flavidus* emerged at all sites but was most common in traps over vegetation.

Oxyethira costalis (Curt.).—The time of the diurnal maximum in the emergence of *O. costalis* varied with the time of year (Table II). During June and July, when the first generation was emerging, the maximum emergence occurred between 22.00 and 24.00 hours but during August, when the second generation was emerging, the maximum occurred between 20.00 and 22.00 hours. The change in the time of the period of peak emergence coincides with the change in the time of sunset. This species was most common at the deeper water sites.

A small number of imagines of other species of Trichoptera caught during the two-hourly observations indicated that most of these emerged in the late evening.

(4) *Diptera : Culicidae*

Chaoborus flavicans (Meig.) (Table III).—This species emerged at all sites but most commonly at sites 5, 4 and 1, in that order. The emergence occurred during darkness, chiefly between 24.00 and 04.00 hours. No other species showed a maximum emergence during this period and it is unfortunate that *C. flavicans* was not caught in greater numbers.

A small number of the culicids *Dixa filicornis* Edw. and *D. aestivalis* Meig. were also caught. The former was unusual since it was only caught in the early morning and the latter was caught during the same period as *C. flavicans*.

(5) *Diptera : Chironomidae : Tanypodinae*

Ablabesmyia monilis L. (Table II).—Emergence occurred principally during darkness and the period of maximum emergence was more extended than in most species of chironomid, which had a maximum in the late evening. *A. monilis* occurred at all sites but emerged most commonly from *Myriophyllum spicatum* at site 4.

Ablabesmyia phatta Egg. (Table II).—The emergence of this species, which occurred after dusk, was less extensive than that of the closely related *A. monilis*.

Ablabesmyia barbitarsis (Zett.) (Table I).—This species was studied in late April and early May, 1958. Earlier observations had indicated that it emerged during daylight, and the traps were emptied every two hours only, between 08.00 and 18.00 hours G.M.T. Seven insects were caught between 18.00 and 08.00 hours and eighteen between 08.00 and 18.00 hours. Emergence was therefore greatest during daylight and it is possible that the seven insects which were caught between 18.00 and 08.00 hours also emerged during daylight. At the end of April sunrise was at 04.40 hours G.M.T. and sunset at 19.49 hours G.M.T. *A. barbitarsis* occurred most commonly at sites 1 and 5.

Ablabesmyia cingulata Walk. (Table III).—This insect emerged at all times of day, there being little variation in the numbers caught in each two hour period. The maximum between 04.00 and 06.00 hours was caused by a total of 15 taken in this period in June which statistical analysis showed to be significantly higher than the catches at any other time of day. In the collections taken in May, July and August there was no significant variation from one time of day to another. *A. cingulata* emerged chiefly from shallow water, being more common from the less weedy site 2 than site 1.

Procladius simplicistilus Freeman (Table I).—This species occurred most frequently at sites 3 and 6.

Procladius choreus (Meig.).—The question whether *P. choreus* and *Procladius crassinervis* (Zett.) should be regarded as distinct species has been discussed by Mundie (1957). The two forms proved difficult to separate in the collections from Loch Dunmore, as many individuals which were intermediate in character were caught. In June and July, when they were caught during diurnal observations, there was a

preponderance of *P. choreus* and forms approximating to it. Thus the name *P. choreus* is used here.

The June and July catches have been recorded separately (Table III). In June there was a distinct tendency towards an evening emergence but in July there was little variation throughout the day and night. In July the imagines were almost entirely the true *P. choreus* form, whereas there was a greater preponderance of intermediate forms in June. The only catches of the true *P. crassinervis* were three imagines on 23rd and 24th May which emerged at 08.00–10.00, 16.00–18.00 and 20.00–22.00 hours respectively. From the Dunmore records it can be concluded that the true *P. choreus* form emerges at a steady rate throughout the day and night in July but it would be unwise to comment further on the June results in view of the present uncertainty of the taxonomy of this species complex.

Mundie (1959) found that at 5 and 13·5 m. at Lac la Ronge, in Saskatchewan, the pupae of *P. choreus* rose to the surface between 9.00 p.m. and 3.00 a.m. but that there was a delay in the emergence of the adults. Pupae caught at the water surface at 10.00 p.m. and brought ashore did not produce adults for 18–24 hours after capture. A simple calculation gives the emergence period of the adults as between 15.00 and 03.00 hours. The longer emergence period found at Loch Dunmore may be due to a similar but more extended delay in the production of adults once the pupae reached the water surface. It would be useful to have information about the behaviour of the pupae of *Ablabesmyia cingulata*, which also had a long emergence period.

Procladius sagittalis (Kieff.) was also recorded at Dunmore, with forms intermediate in character between this species and *P. choreus*. The forms caught in August were predominantly *P. sagittalis* and the emergence was scattered throughout the day and night.

Psilotanypus lugens Kieff. (Table I).—This species was caught during May, the greatest number occurring at the beginning of the month. It was most common at site 2 and least common at site 1.

(6) *Diptera : Chironomidae : Orthocladiinae*

The most common Orthocladiinae were *Psectrocladius* spp., of which *P. psilopterus* Kieff., *P. limbatellus* (Holmgr.) and *P. sordidellus* (Zett.) were the most abundant.

Psectrocladius psilopterus.—The captures of this species are the first records for the British Isles. Table III shows the daily periodicity of emergence of the second generation of *P. psilopterus*, based on the catches taken over *Myriophyllum spicatum* in deeper water. The maximum emergence occurred between 20.00 and 22.00 hours, with a secondary peak between 04.00 and 06.00 hours. This was the only species to show bimodal emergence activity. Scott and Opdyke (1941) found that the Diptera as a whole emerged in the greatest numbers between 18.00 and 24.00 hours with a smaller increase between 04.00 and 06.00 hours, though they do not state whether the same species were common to both periods. In view of this behaviour it is unfortunate that *P. psilopterus* was not caught during diurnal studies at other times and that no information is available about the diurnal emergence of the first generation, which emerges in large numbers in late May and early June at site 5.

Psectrocladius sordidellus and *Psectrocladius limbatellus*.—Although these species were caught in large numbers during studies on seasonal emergence, insufficient were caught during two-hourly collections to allow the determination of the diurnal pattern of emergence. Further, the females of the two species could not be separated satisfactorily and only data obtained about males could be used. The information available showed that these species were caught at all times of day, but there was some indication of a late evening maximum in the emergence of *P. sordidellus*.

Psectrocladius obvius (Walk.) (Table I).—Only a small number were caught and these indicated maximum emergence at midday.

(7) *Diptera : Chironomidae : Chironominae*

Pseudochironomus prasinatus (Staeg.) (Table III).—The intensity of emergence was greatest between 12.00 and 24.00 hours, 29 insects emerging over this period out of a total of 32. This species was most common at site 3.

Chironomus anthracinus Zett. (Table I).—The diurnal emergence of this species was investigated on 29th March and 2nd April, 1957, and the times given are G.M.T. This species was only caught during the period 08.00–18.00 hours and emergence was maximal about midday. It is interesting that far the greatest numbers of this species were caught over decaying *Myriophyllum spicatum* in 6 feet (1·8 m.) depth of water. Other workers (Brundin, 1949 ; Thienemann, 1954 ; and Jónasson 1955) have found this species in the profundal of lakes. Thienemann (*loc. cit.*: 34) associates it with habitats where the oxygen concentration falls to very low levels from time to time.

Chironomus (*Einfeldia*) *longipes* Staeg. (Table II).—This species, which was caught mainly from shallow water, emerged just before and after midnight.

Chironomus (*Dicrotendipes*) *pulsus* Walk. var. (Table I).—At the beginning of May emergence extended from 06.00 to 24.00 hours with the highest rate in the middle of the day. It is interesting to compare these results with those for *Chironomus* (*Dicrotendipes*) *pulsus* var. *objectans* Walk. caught at the beginning of June (Table II). There is a distinct tendency for emergence of the latter variety to be at a maximum during the period 22.00–24.00 hours. Both the dark variety of Walker and the variety *objectans* emerged chiefly from site 3, though a few emerged from the other deep water sites. The emergence of *C. pulsus* var. *objectans* occurred one month after that of *C. pulsus* Walk. var. and it is unlikely that this time interval would be long enough for the variety *objectans* to be a second generation hatched from eggs laid by females of the Walker variety in early May. This and the difference in time of emergence during the day suggest that the variety and the typical species may be living independently within the same habitat and that they are sibling species, each having only one generation within a year.

Microtendipes chloris Meig.—A small number of *Microtendipes chloris* var. *lugubris* (Kieff.) caught in March and April and of *M. chloris* caught in late June and early July indicated that a similar difference in diurnal emergence time may exist between this species and its variety. The insects emerging in March and April were caught at midday and those in June and July during darkness. In this species, however, the eggs from the generation of *M. chloris* var. *lugubris* could give rise to the *M. chloris* generation later in the year, as there is a three months' interval. The observations on the last two species indicate the value of ecological data to the taxonomist in determining whether a form is a variety or a true species.

Chironomus (*Cryptochironomus*) *krusemani* Goetgh. (Table II).—*C. krusemani* was common at sites 3, 4 and 6. The only previous record of this species is furnished by the type material from Belgium (Goetghebuer, 1935). There were two generations within a year and the diurnal periodicity for each generation is shown. The first generation shows a distinct maximum between 22.00 and 24.00 hours, the majority of imagines emerging between 22.00 and 02.00 hours. At the beginning of August the peak emergence for the second generation occurred between 20.00 and 22.00 hours, an advance of two hours over that for the first generation. This change in the time of the period of maximum emergence rate corresponds to the change in the times of sunset ; on 15th June sunset occurs at 22.04 hours and on 10th August at 21.06 hours. As the time interval between successive observations was two hours, it was not possible to record a relationship with the time of sunset more precisely. A similar time difference of about two hours was observed between the maximum period of emergence of the first and second generations of *Chironomus halophilus* Kieff., *Microtendipes pedellus* (Deg.), *Polypedilum nubeculosus* Meig., *Lenzia flavipes* Deg., *Tanytarsus heusdensis* Goetgh. and *Monotanytarsus inopertus* (Walk.) by Palmén (1955).

In the generation of *Cryptochironomus krusemani* emerging in June there was a considerable emergence over the midday period with a secondary peak between 10.00 and 12.00 hours. The midday emergence was absent in the second generation and none of the other species studied had an emergence pattern similar to that of the first generation.

Chironomus (*Cryptochironomus*) *edwardsi* (Krusem.) (Table II).—This species, which emerged chiefly at the shallow water site 2, also had two generations within the year. The diurnal periodicity of these two generations closely resembles that of *Cryptochironomus krusemani*.

Polypedilum arundineti Goetgh. (Table II).—Most of the imagines emerged between 22.00 and 02.00 hours, and particularly between 22.00 and 24.00 hours, which again coincides with the time of change from light to darkness. The majority were caught at site 1.

Polypedilum nubeculosus Meig. (Table II).—This species was caught at site 3 at the beginning of June and had a similar diurnal pattern to that of *P. arundineti*. In the Baltic in June, Palmén (1955) found that nearly all the imagines of this species emerged between 21.00 and 03.00 hours.

Lauterborniella orophilus Edw. (Table I).—This species was very common at site 3. Emergence was highest during daylight, rising steadily to a maximum in the afternoon, between 14.00 and 16.00 hours, falling to a low level during darkness and to a minimum just before dawn.

Tanytarsus samboni Edw. (Table II).—This species was caught in large numbers at site 3 and records were obtained at the beginning and end of May when the first generation was emerging. By far the greatest emergence took place between 20.00 and 22.00 hours although some occurred at all times of day. The period of maximum emergence again extended over the time of sunset, which occurs at 21.20 hours on 15th May. None of the second generation of *T. samboni* was caught during two-hourly collection periods.

Tanytarsus (?) *glabrescens* Edw.—The most common species of *Tanytarsus* at Loch Dunmore was one very closely resembling *T. glabrescens*, but differing slightly in the form of appendage 2*a* of the hypopygium. As the only British specimen of *T. glabrescens* available for comparison is the type specimen in the British Museum, it would be unwise to separate the Loch Dunmore specimens as a new species or variety until further specimens of *T. glabrescens* have been collected from a range of localities. *T.* (?) *glabrescens* was common at all the deeper water sites, being particularly abundant at site 3 where the bottom was mud with a sparse growth of *Chara delicatula*. Records of the diurnal periodicity of emergence of the two generations of this species are given in Table II from which it will be seen that the time of the period of maximum emergence of the second generation again moves forward with the change in the time of sunset.

Tanytarsus (*Xenotanytarsus*) *miriforceps* Kieff. (Table I).—This species, which had previously only been recorded from Germany, emerged commonly in April particularly at sites 3, 4 and 6. Emergence took place between 08.00 and 18.00 hours with a distinct maximum between 12.00 and 14.00 hours.

Several other species of *Chironomus* were taken in small numbers during two-hourly collections and most of these were caught in the period coinciding with sunset.

(8) *General Remarks*

The following generalisations can be made about the diurnal emergence of the various groups of insects considered.

The Ephemeroptera emerged in the middle of the day, with the exception of *Caenis horaria*, which emerged during the evening, as did the stream-dwelling forms observed by Sprules (1947).

Diurnal observations were only available for one species of Odonata and this emerged between 08.00 and 14.00 hours as did *Pyrrhosoma nymphula* (Corbet, 1952).

The Trichoptera generally emerged between dusk and midnight, as did both the stream-dwelling caddis observed by Sprules (1947) and the lake-dwelling caddis (Scott and Opdyke, 1941). The exception at Loch Dunmore was *Athripsodes aterrima* which emerged in the middle of the day. Most of the caddis are crepuscular in their habits but *A. aterrima* flies during daylight (Morgan, 1956). On the other hand *Mystacides azurea*, which also swarms during daylight, appears to emerge at dusk. It would be interesting to have records of the time of emergence of the other day-flying caddis such as *Tinodes waeneri* (L.) and *Apatania wallengreni* McLach. The relation of the time of maximal emergence of different generations of *Oxyethira costalis* to the time of sunset was similar to that recorded by Palmén (1955) for several chironomid species.

There was considerable difference in the time of emergence of various species of chironomids, which can be divided roughly into three groups :

(1) species which emerged in the period immediately following sunset, e.g. *Chironomus* (*Cryptochironomus*) *krusemani*, *Chironomus* (*Cryptochironomus*) *edwardsi*, *Polypedilum arundineti*, *Tanytarsus samboni* and *Tanytarsus* (?) *glabrescens* ;

(2) species which emerged during the period of high light intensity and maximum water temperature in the late morning and early afternoon, e.g. *Ablabesmyia barbitarsis*, *Procladius simplicistilus*, *Psilotanypus lugens*, *Chironomus anthracinus*, *Chironomus* (*Dicrotendipes*) *pulsus*, *Lauterborniella orophilus* and *Tanytarsus miriforceps* ; the period of high emergence usually extended over a longer time than for those species emerging at sunset ; Phillipp (1938) reported similar results with *Chironomus thummi* under laboratory conditions ;

(3) species which emerged more or less constantly during day and night, e.g. *Ablabesmyia cingulata* and possibly *Procladius choreus*.

Ablabesmyia monilis and *Psectrocladius psilopterus* did not fit into any of these groups, the first emerging throughout the whole period of darkness and the second showing two emergence peaks, the main one at sunset and a secondary one between 04.00 and 06.00 hours.

Emergence of Chironomidae was reported by Miller (1941), in Ontario, to be maximal at 04.00–07.00 hours, at which time it was minimal for most of the species from Loch Dunmore. The results of Sprules (1947), also in Ontario, and Palmén (1955), in the Baltic, were similar to those for the Loch Dunmore species belonging to group 1. Sprules found the maximum emergence of Chironomidae occurred between 22.00 and 23.00 hours and stated that " The emergence began to build up to this maximum between 8.00 and 9.00 p.m., which corresponds with the onset of sundown and indicates that the final impetus for emergence is related to a decrease in light intensity ". Palmén (*loc. cit.*) observed a very definite diel peak for nine species of chironomids during the hours following sunset, the bulk of emergence being about midnight. The onset coincided with the day to night change in illumination and the timing mechanism was independent of temperature within the range met under field conditions. In contrast to the times of emergence of *Tanytarsus* spp. at Loch Dunmore, Lewis (1957) observed, on the Nile, that the mass emergence of *T. lewisi* Freeman usually occurred in the early morning, chiefly before sunrise. Lindeberg (1958) shows figures of diurnal periodicity for three species of chironomid, two of which showed no definite maximum restricted to a short period of the day, but in all cases very few midges emerged between 02.00 and 06.00 hours.

IV. Factors Affecting Emergence

Measurement of the daily variation of the temperature in shallow water from May to August, 1955, for the days on which two-hourly collections were made, showed no relation between the time of maximum emergence of the Chironomid species and the time of maximum or minimum water temperature. Maximum and minimum temperatures occurred at the same time in May and June but maximum emergence occurred between 20.00 and 22.00 hours in the first month and between 22.00 and 24.00 hours in the second, and the same was true for August and July.

The period of maximum emergence does, however, show a relation to change in the time of sunset. For the species with two generations, one in June and the other in August, the time of maximum emergence shifted between generations, in step with the change in the time of sunset. It seems reasonable to assume that emergence is regulated in the species that emerge in the late evening by the change in light intensity at dusk. The time of sunset changes less from day to day than any other physical factor which is likely to affect emergence and the change in light intensity at that time is both large and rapid.

Palmén (1958) has shown that the diel rhythm persists for at least six days when the larvae and pupae of *Allochironomus crassiforceps* Kieff. are kept in complete darkness, indicating that in this species the rhythm is already imprinted upon the last instar larvae.

The period between 02.00 and 08.00 hours was generally the time of minimum emergence for all groups of insects. Air and water temperatures are at a minimum within this period and it may be that conditions are then unfavourable for emerging insects; also dawn occurs within this period, and it is possible that the change from darkness to light may inhibit insect emergence. Generally very few insects were seen flying at this time of day. By contrast Miller (1941) found the maximum emergence of Chironomidae, during a couple of days in July, to occur between 04.00 and 07.00 hours, with very little outside this period, and Scott and Opdyke (1941) reported a secondary increase, between 2nd and 10th August, in the emergence of Diptera, between 04.00 and 06.00 hours, the minimum occurring at midday. Sprules (1947), between 3rd and 7th July, caught least insects between 15.00 and 18.00 hours. It is clear from the study recorded in this paper that there is considerable variation in diurnal emergence from species to species and that differences occur from one time of year to another. Thus in diurnal studies it is necessary to treat the species separately and, wherever possible, to carry out observations at least once a month during the whole emergence season.

Those insects which emerge over midday and the early afternoon do so when the water temperature is still rising to its maximum. Maximum emergence was reached at 10.00–12.00 hours in *Procladius simplicistilus* and *Chironomus* (*Dicrotendipes*) *pulsus* var., at 12.00–14.00 hours in *Leptophlebia vespertina*, *Cloëon simile*, *Psilotanypus lugens*, *Chironomus anthracinus* and *Tanytarsus* (*Xenotanytarsus*) *miriforceps*, and at 14.00–16.00 hours in *Lauterborniella orophilus*. In each case this was before the time of maximum water temperature, which was at 15.00 hours in April, 16.00 hours in May and June and 18.00 hours in July and August. Where the diurnal emergence was observed in May, June, July and August, as for *Cloëon simile*, no difference in the time of maximum emergence was discernible in different months. The time of maximum light intensity occurs at the same time (13.00 hours B.S.T.) throughout the summer and it may well be that the time of emergence of the daytime emerging insects is also determined by light intensity. It may also be that insects which emerge at other times of day, such as *Caenis horaria*, are reacting to a particular light intensity. Palmén (1955) found that the time interval between successive emergence maxima of six species of chironomid remained constant at 24 hours at different water temperatures. This was also true of the Loch Dunmore species with more than one generation. The June and August generations of *Chironomus* (*Cryptochironomus*) *krusemani*, *Chironomus*

(*Cryptochironomus*) *edwardsi* and *Tanytarsus* (?) *glabrescens* maintained a twenty-four hour rhythm although the mean of the daily maximum and minimum temperatures were 16·8 and 15° C. in June, whereas the corresponding figures in August were 19·2 and 17° C. The same was found to be true of the two generations of the caddis *Oxyethira costalis*.

Most of the chironomid species which have their maximum emergence period over the middle of the day had completed their emergence before the end of May (Table I), but none of the species which emerge shortly after sunset were caught in large numbers before the middle of this month (Table II). Also *Microtendipes chloris* var. *lugubris*, during March and April, and *Chironomus pulsus* var., during May, emerged in the middle of the day whereas *Microtendipes chloris* and *Chironomus pulsus* var. *objectans* emerged after dusk during June. Before May the number of nights when the air temperature falls to 0° C. or below is high (Table IV). This would be a disadvantage to

TABLE IV.—*The proportion of nights when the minimum air temperature was 0° C. or less over the period 1953–1957*

Month	Percentage
March	0–61*
April	30–43
May	0–13

* No air frost was recorded during March 1957.

insects emerging after dusk, whereas those emerging in the middle of the day emerge when the air is warmer and are able to take shelter before dusk. From early May onwards, physical conditions are normally favourable for emerging insects in the late evening. Temperatures are higher and the rate of loss of water from newly emerged insects will be higher at midday than at the lower temperature and higher humidity in the late evening. In addition, although there is often a regular evening rise of fish over this period (van Someren, 1940), visibility is then poor and the mass emergence of an insect species after sunset must be of considerable survival value to that species. In this connection, laboratory experiments by Brett and Ali (1958) have indicated that the eye of salmonids may take some time to become completely adapted to darkness. On the other hand, it is possible that predation by other insects on the newly emerged imagines may be high, as it was observed at Loch Dunmore that the Empididae were very active between dusk and midnight in late July and most of August. However, those species which emerge over the whole twenty-four-hour period with no precise maxima are often very successful species as judged by their abundance, e.g. *Ablabesmyia cingulata* and *Procladius choreus* at Loch Dunmore. It is noticeable that these are Tanypodinae and it may be that the survival rate of the species wirh carnivorous larvae is greater than that of those with herbivorous larvae, and that the former may thus be able to withstand a higher mortality during the pupal and early adult stages.

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VI. Summary

1. Observations were carried out on the diurnal emergence of insects at a small woodland loch near Pitlochry, Perthshire. Data were obtained on the emergence periods of five species of Ephemeroptera, one species of Odonata, five species of Trichoptera, one species of Culicidae and twenty two species of Chironomidae.

2. All Ephemeroptera emerged in the middle of the day except *Caenis horaria*, which did so in the evening; the single member of the Odonata, *Enallagma cyathigerum*, emerged between 08.00 and 14.00 hours; the Trichoptera emerged chiefly after dusk, except that *Athripsodes aterrima* did so between 08.00 and 18.00 hours; the single member of the Culicidae, *Chaoborus flavicans*, emerged between midnight and dawn. The Chironomidae could be divided into two main groups, those species with maximum emergence over midday and those with maximum emergence in the period immediately after sunset, with a smaller third group whose emergence varied little with time of day. A few species of chironomid showed increased emergence at other times.

3. The timing of late evening emergences was related to the rapid change of light intensity at sunset. The change in time of the maximum emergence of the two generations of some chironomids and Trichoptera was related to the time of sunset. It is suggested that those species with emergence maxima at other times of day may also have been responding to a particular light intensity.

4. In general, emergence was at a minimum over the period 02.00–08.00 hours. This is the period when water and air temperatures are lowest and it is possible that the change from darkness to light at dawn may inhibit emergence in many species.

5. It is suggested that the midday spring emergence of some Chironomidae is of considerable survival value at this time of year when the number of nights when air temperature falls below 0° C. is high. During the summer, when late evening temperatures are much higher, a maximum emergence after dusk is probably of greater survival value than one at midday.

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TABLE I.—*The insects with a maximum emergence at midday*

Species	Number caught in each two-hour period												Time of year
	0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24	
EPHEMEROPTERA													
Leptophlebia marginata	0	0	0	0	0	5	4	0	0	0	0	0	April
L. vespertina	0	0	0	1	0	40	51	7	0	0	0	0	End May-beginning July
Cloëon dipterum	0	0	0	0	0	6	2	5	2	0	2	1	End July and August
C. simile	0	0	0	3	7	25	49	22	11	6	2	0	Beginning May-end September
ODONATA													
Enallagma cyathigerum	0	0	0	0	2	4	2	0	0	0	0	0	End June and beginning July
TRICHOPTERA													
Athripsodes aterrima	0	1	0	0	10	13	8	5	9	2	1	0	June and July
DIPTERA : CHIRONOMIDAE													
TANYPODINAE													
*Ablabesmyia barbitarsis**	.	.	.	.	4	2	4	5	3	.	.	.	25th and 26th April, 1st and 2nd May
Procladius simplicistilus	0	0	0	0	3	12	10	7	4	0	0	0	25th and 26th April, 1st and 2nd May
Psilotanypus lugens	0	0	0	0	1	7	25	14	12	0	2	0	May
ORTHOCLADIINAE													
Psectrocladius obvius	0	0	0	0	2	0	3	2	1	0	0	1	End June-end July
CHIRONOMINAE													
Chironomus anthracinus	0	0	0	0	9	50	67	32	5	0	0	0	29th March and 2nd April
C. (Dicrotendipes) pulsus	0	0	0	1	1	17	12	11	4	6	4	1	5–7th May
Lauterborniella orophilus	4	0	2	4	10	25	28	49	30	18	7	5	End May-end June
Tanytarsus (Xenotanytarsus) miriforceps	0	0	0	0	4	7	21	8	3	0	0	0	25th and 26th April, 1st and 2nd May

* The trap was only emptied every two hours from 08.00–18.00 hours (*see text*).

TABLE II.—*Species with a maximum emergence rate in the late evening*

Species	Number caught in each two-hour period												Time of year
	0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24	
EPHEMEROPTERA													
Caenis horaria	1	0	1	1	0	0	0	1	0	38	177	45	Beginning June–beginning August
TRICHOPTERA													
Limnephilus marmoratus	3	1	0	0	0	0	0	0	0	0	0	10	End May–end July
Mystacides azurea	1	0	0	0	0	0	0	0	2	1	7	4	End July and end August
Cyrnus flavidus	5	1	1	0	0	1	0	0	0	0	8	8	End June–end August
Oxyethira costalis													
(1st generation)	12	2	1	3	0	0	1	1	3	3	8	18	End June and July
(2nd generation)	2	1	0	0	0	0	0	1	1	0	22	7	August
DIPTERA : CHIRONOMIDAE													
TANYPODINAE													
Ablabesmyia monilis	13	7	2	2	2	0	0	0	0	1	11	18	End May–beginning August
A. phatta	1	0	0	0	1	0	0	0	0	0	0	6	July
CHIRONOMINAE													
Chironomus (*Einfeldia*) *longipes*	9	0	0	0	0	0	0	0	0	0	0	9	23rd–25th June
C. (*Dicrotendipes*) *pulsus* var. *objectans*	2	0	0	0	0	1	0	0	0	2	5	13	June
C. (*Cryptochironomus*) *krusemani*													
(1st generation)	17	8	1	0	3	12	2	6	6	0	3	35	June
(2nd generation)	1	1	1	0	0	0	0	1	0	1	19	2	9–11th August
C. (*Cryptochironomus*) *edwardsi* (1st generation)	2	0	0	0	0	0	0	0	0	0	2	6	23rd–25th June
(2nd generation)	2	2	1	0	0	0	1	0	1	2	38	3	August
Polypedilum arundineti	8	0	0	2	0	0	0	0	2	2	2	20	June
P. nubeculosus	0	0	0	0	0	1	1	2	2	1	3	11	7–9th June
Tanytarsus samboni (1st generation)	19	3	1	6	1	1	2	6	5	13	142	35	May
T. (?) *glabrescens*													
(1st generation)	25	11	15	7	9	47	38	38	31	39	91	213	7–9th June
(2nd generation)	2	0	0	0	0	0	1	3	0	7	92	4	9–11th August

TABLE III.—*Insects emerging at other times of day*

Species	Number caught in each two-hour period												Time of year
	0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24	
DIPTERA : CULICIDAE													
Chaoborus flavicans .	7	4	1	0	0	0	0	0	0	0	0	1	End July–end August
DIPTERA : CHIRONOMIDAE													
TANYPODINAE													
Ablabesmyia cingulata .	9	11	24	12	14	10	16	9	17	19	18	19	Beginning May–end August
Procladius choreus .	1	0	0	1	0	0	2	0	1	7	5	8	June
	5	3	2	3	0	6	7	6	10	7	4	8	July
ORTHOCLADIINAE													
Psectrocladius psilopterus (2nd generation)	1	2	22	4	5	4	2	0	7	2	65	4	9–11th August
CHIRONOMINAE													
Pseudochironomus prasinatus	0	2	1	0	0	1	3	4	10	3	9	4	June