SOME ASPECTS OF THE BIOLOGY OF *EPHEMERA DANICA* MÜLL (EPHEMERIDAE: EPHEMEROPTERA) IN IRISH WATERS

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ABSTRACT

From the anglers point of view the mayfly *Ephemera danica* is one of the most important insects found in Irish waters. During the past decade it has shown marked fluctuations in abundance and it some waters it has practically disappeared. Laboratory reared nymphs emerged to adults after two years while a batch of nymphs, reared from the egg, took only eleven months to develop to adults in a small limestone lake. It is concluded that the life cycle of *Ephemera danica* is flexible, achieving development in a shorter time in places where food is abundant and habitat conditions are ideal. The principal factors affecting the abundance of *Ephemera danica* in Irish lakes are discussed.

INTRODUCTION

The mayfly *Ephemera danica* is the only burrowing species of Ephemeroptera found in Irish waters. It shows a preference for habitats characterised by high alkalinity (100-240 mg/l Ca CO_3) and high pH values (7.9-8.5). The central plain of Ireland is saucer shaped, lying on a geological base of Carboniferous limestone (Fig. 1). The majority of rivers and lakes occupying this area contain populations of *Ephemera danica*. These waters also hold good stocks of large, fast-growing, brown trout (*Salmo trutta* L.) which can reach 2 kg in weight in five years of growth. With an abundance of other invertebrate food to feed on, it is only during hatches of *Ephemera danica* that these large trout can be readily taken while fly fishing. The mayfly season (mid-May to mid-June) is considered

one of the most important annual angling events by both resident and visiting trout anglers.

During the past decade, the hatches of *Ephemera danica* have shown marked fluctuations in abundance and in some instances they have almost disappeared. Since the mayfly is of such importance to the larger Irish trout fisheries, the Inland Fisheries Trust, a semi-state body charged with the development and management of these waters, decided to initiate research into the basic biology of *Ephemera danica* in Irish waters. These studies form the basis of the present paper.

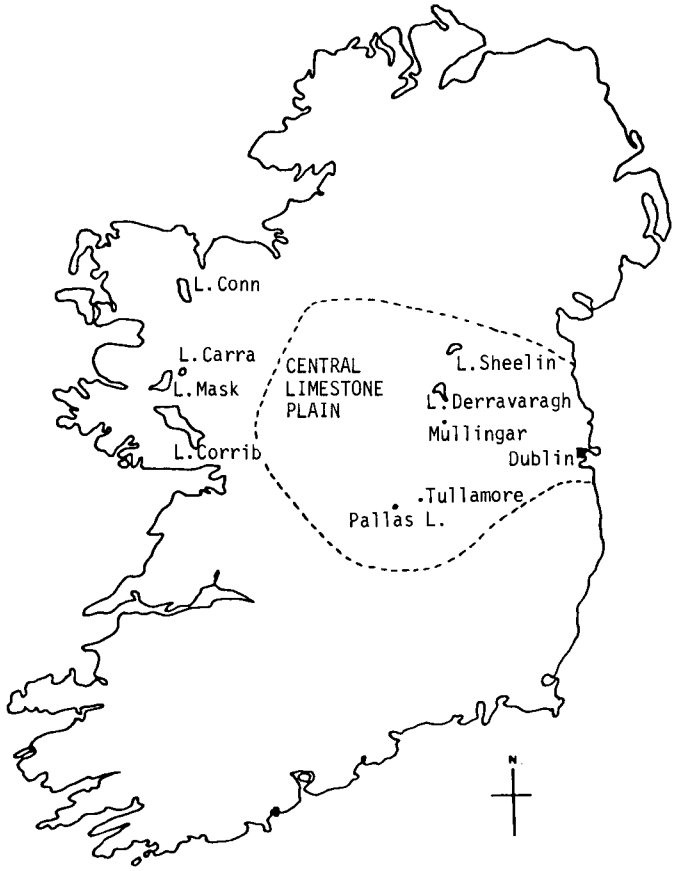

Figure 1. General map of Ireland showing central limestone plain and waters mentioned in text.

ANALYSIS OF QUALITATIVE COLLECTIONS

In the period March 1974 to June 1976 the field staff of the Inland Fisheries Trust collected in excess of 5,000 specimens of *Ephemera danica* from waters throughout Ireland. The majority of mayflies collected were in the nymphal stages; however, some 500 adult mayflies were also included. Length frequency analysis of these insects showed some interesting trends.

In the case of the adult *Ephemera danica* there was a sexually dimorphic growth pattern present. The males averaged from 14 to 18 mm in length and were 4 to 6 mm smaller than their female counterparts. The specimens from the western lakes were smaller than those collected from midland waters. River adults were significantly larger than those taken in still water.

The length frequency analysis of the nymphs showed that in many of the waters examined, for each month sampled, two distinct size groups were present (Fig. 2). The size discrepancy was too large to be explained in terms of the sexually dimorphic growth pattern mentioned earlier. It was proposed that two distinct age groups of *Ephemera danica* nymphs were present. A set of field experiments were designed to test this hypothesis.

FIELD STUDIES

A one square metre section of Lough Sheelin, a large, 1862 hectare, limestone lake, was cordoned off using a metal frame and tygon sheeting. Metal plates were attached to the legs of the frame and these were sunk into the lake bottom. When in place these metal plates protruded approximately 20 centimetres above the substratum. A tight-fitting wooden cover, containing a trap door, completed the structure. The cover served a dual purpose in that it ensured the capture of all emerging adults and also prevented adults from laying eggs in the experimental area.

The trap was in place from May 1975 until November 1976 when a series of severe winter storms irreparably damaged the frame and covering. Samples taken from areas lying adjacent to the trap showed that two size groups of nymphs were present.

In May/June 1975 108 adults emerged from the enclosed area. The wooden cover was removed in July 1975 and it was not replaced until early May 1976. Twenty five adults emerged from the trap during the 1976 emergence period. This experiment showed that at least a percentage of the mayfly population spent in excess of one year as nymphs.

To verify the length of the *Ephemera danica* life cycle the

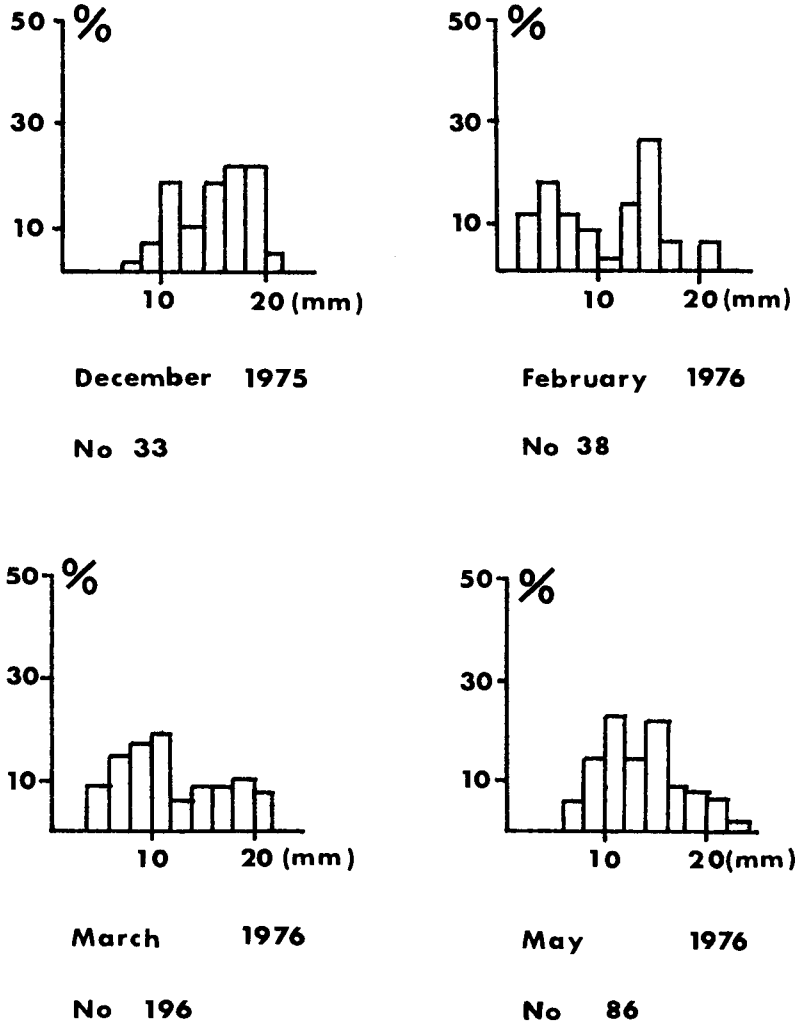

Figure 2. Cumulative length frequency histograms of mayfly nymphs collected from the western lakes (Loughs Mask, Carra and Conn) in Decmeber 1975 and February, March and May 1976.

insects were reared from the egg to the adult stage under experimental conditions. A technique based on that used by Lunn (Hills 1934) was developed for collecting fertilized ova.

COLLECTION AND SUBSEQUENT DEVELOPMENT OF FERTILIZED OVA

Having completed metamorphosis from the subimago (Green Drake) to the imago (Gnat), the male spinners of *Ephemera danica* gather in large clouds and swarm. As they do so, they display a most characteristic rise and fall motion. The females join the swarm as they are ready to mate.

Each female that enters the swarm is immediately persued by a group of males. One of these approaches the female from underneath and grasps her with his long forelegs in the region of her thorax. The male then tilts his abdomen upwards and partly forwards over its back and clasps the eight or ninth segment of the female abdomen with his abdominal forceps or claspers (Whelan 1975). If only one male is attached to the female copulation is effected while the pair continue flying. However, it is more usual for three to four male spinners to grasp onto the female or to the original copulating male. The attendant males force the female to the ground where copulation is completed. It is at this stage that fertilized females may be gathered.

When a suitable number have been collected they are transported to the laboratory, placed on containers of water and their abdomens gently stimulated until they are seen to emit a steady, cone-shaped, stream of eggs.

Estimates for the fecundity of *Ephemera* have ranged between 2,300 and 6,500 eggs per female (Clifford and Boerger 1974, Halford 1889, Hills 1934, Peart 1916, Percival and Whitehead 1926). Detailed examination of adult females collected during the course of the project has shown that fecundity values in Irish specimens of *Ephemera danica* range between 1,700 and 3,000 eggs per female or between 94 and 136 egg/mm body length. These estimates are based on total egg counts from eleven selected individuals.

The ova of *Ephemera danica* are adhesive and it has been found that plastic containers offer a very suitable substratum for them. After several hours, a transparent egg mat is formed. The ova are now firmly attached to the containers and it is necessary to dissect sections of the mat if specimens are required for microscopic examination.

After eight days of incubation the first outlines of an S-shaped larva appear in the ova. By the fourteenth day, a wedge-shaped larva is present. These larvae show signs of segmentation, and can be made

to move by light or heat stimuli. The eggs hatch after eighteen days at 15°C. Newly hatched nymphs are characterised by five pigment spots on the head and a mottled brown, wedge-shaped oesophagus.

ADULTS REARED FROM THE EGG

Aquaria which contained suitable burrowing substrata and also a variety of aquatic plants were prepared and set up in the grounds of the laboratory. They were, therefore, subject to normal climatic variation.

First instar *Ephemera danica* nymphs were placed into the aquaria on the 10th June 1976. A table outlining their subsequent growth is shown (Table 1).

Table 1. Mean size of laboratory reared mayfly nymphs.

Date	Mean Size of Mayfly Nymphs	Number of Nymphs Measured
29.06.76	1.5 mm	40
09.08.76	3.0 mm	40
15.09.76	4.5 mm	25
01.11.76	5.7 mm	14
07.06.77	12.2 mm	12

No attempt was made to artificially feed these nymphs, however, as previously stated, the aquaria in which they were held contained natural plant detritus. It was noticed when sub-sampling the nymphs present, that many were concentrated around the roots of the *Potamogeton* sp. present in the aquaria.

From the five thousand first instar nymphs stocked five hatched as adult insects in June 1978. There were three males (mean length 14.9 mm) and two females (mean length 18.5 mm) present. The nymphs of these adults had spent a full two years as larvae.

MASS REARING OF *EPHEMERA DANICA*

Following the success attained in artificially rearing

and propagating mayfly eggs during 1976, experiments were carried out in late May and early June of 1977 to ascertain the feasibility of mass rearing *Ephemera danica* to the first nymphal instar stage. Between May 23 and 30 some 230 fertilized female adult mayflies were collected. These were transported to the Inland Fisheries Trust fish farm at Mullingar and spawned into plastic containers. Approximately ten females were placed on each container and moved about the water's surface to ensure even dispersion of the eggs. The containers were placed in troughs in the trout hatchery. A constant flow of water insured sufficient oxygenation and it was hoped to leave the boxes undisturbed for at least ten to twelve days.

Thirty of the female mayflies collected were spawned in the laboratory and the eggs from these were held in an aerated plastic aquarium.

Fourteen days after fertilization, June 10, the eggs held at the laboratory hatched. The eggs at the fish farm hatched between June 12 and June 20, eighteen to twenty days after fertilization. The hatchery water was an average 3.5°C cooler than the laboratory water during the incubation period.

The half a million first instar *Ephemera danica* nymphs resulting from this experiment were subsequently stocked into Pallas Lake, a small 10 hectare limestone lake. Although *Ephemera danica* had never been recorded from Pallas Lake a biological survey showed that the resident fauna was similar in composition and abundance to many of the larger midland limestone lakes, which had established populations of *Ephemera danica*.

Between May 19 and May 21, 1978 small hatches of adult *Ephemera danica* were recorded from Pallas Lake. These mayflies, which were stocked as first instar nymphs in June 1977, had hatched after a nymphal life of only eleven months.

DISCUSSION

Results from research carried out prior to 1978 indicated that the life cycle of *Ephemera danica* was completed in two years. The occurrence of small nymphs during the adult hatching period and the results obtained from rearing experiments in 1975/78 seemed to rule out the possibility of *Ephemera danica* completing its growth cycle in one year. The hatch of *Ephemera danica* recorded from Pallas Lake in June 1978 showed that under favourable environmental conditions adults can emerge after spending only eleven months as nymphs.

It is often assumed that the life cycle of an insect is a species characteristic whereas in fact many life cycles are extremely flexible, achieving development in a shorter time in places where

food is abundant and environmental conditions are ideal. One species of dragonfly may complete its development in one, two or three years (Macan, personal communication).

Many of the water keepers on the English chalk streams during the nineteenth and early twentieth centuries were ardent entomologists and it is to them credit must be given for the initial research into the life cycle of *Ephemera danica* (Halford 1889, Hills 1934, Peart 1916, Percival and Whitehead 1926). They maintained that the life cycle was completed in two years. However, their only proof of this was the occurrence of juvenile nymphs during the adult hatching period. Previous research has shown that river mayfly adults are consistently larger than their lake counterparts. This size differential may be due to a faster nymphal growth rate in the river environment.

It has been recently demonstrated that the progeny of river mayflies, given virgin growing conditions, can hatch after one year. Damerham Fisheries are small, artifically constructed, "put and take" ponds lying adjacent to the River Allen, which is itself a tributary of the English Hampshire Avon. The lakes were excavated in midwinter and by the following June gnats, from the adjacent stream, were seen ovipositing on the newly constructed ponds. One year later there was a substantial hatch of *Ephemera danica*, providing an unexpected bonus to the fishery owners. A mayfly hatch, although not as large as the original emergence, has become a regular feature on these lakes (Walker 1978).

Peart (1916) also records that ponds constructed near a stream containing *Ephemera danica* produced a hatch of adult mayfly after they had been only one year in existence. He discounts the possibility that the larval stages of *Ephemera danica* had gained access to the ponds.

The life cycle of the large North American species of mayfly, *Hexagenia limbata* has also caused much discussion and controversy. Both one and two year life cycles have been documented for this insect. Some authors claimed that it had a one year cycle in the Southern States of America and a two year cycle in the Northern States and Canada. (Craven and Brown 1969, Neave 1932 and Swanson 1967). A recent intensive study has shown that both one and two year cycles may occur in any given population of these insects. Temperature is the principal factor regulating their growth. The majority of the mayflies take two years to complete their development while the nymphs hatching from eggs laid in the early part of the adult emergence period completed their development in one year (Rutter and Wissing 1975). One factor which emerges from much of the research to date on the various species of mayflies is the correlation between the rate of nymphal growth and water temperature (Brittain 1972; Rutter and Wissing 1975).

Analysis has shown that two separate regimes of temperatures are present in the Irish midland and western lakes. The western lakes display a higher mean winter temperature. They become warmer at a slower rate than the midland lakes in spring but they ultimately reach a higher mean summer temperature. The drop in temperature in the autumn is more pronounced in the midland lakes.

The temperature regime present in the western lakes facilitates the early hatching of eggs laid in the summer or early autumn. Initial growth continues for a longer period and adults may emerge after twelve to eighteen months. This leads to a situation where a staggered mayfly emergence is present, with peaks in May and August. From the results obtained in the case of the American mayfly, *Hexagenia limbata* it is reasonable to assume that the time of egg laying and first instar nymph hatching regulates the length of the life cycle and so the time of adult emergence. In the midland lakes the temperature regime limits adult emergence to a confined period from mid-May to mid-June.

Natural fluctuations in the intensity of *Ephemera danica* hatches have been recorded from many waters in Britain and Ireland during the nineteenth and twentieth centuries. The mayfly disappeared on sections of the river Test between 1893 and 1917. Poor weather conditions during the period 1893-1906 were considered responsible for this drop in numbers (Hill 1934). Minor fluctuations in abundance have also occurred in the past ten years.

Past annual reports of the Inland Fisheries Trust record occasions when adverse weather conditions effected mayfly populations. Unusually cold weather in the May/June period of 1962 prevented the imagines from laying their eggs. Mayfly populations were diminished in 1963 and 1964, but normal mayfly hatches were recorded from 1965 to 1972. The fluctuations in abundance of both mayflies and Trichoptera experienced at this time promoted the authors of the 1962 and 1963 Inland Fisheries Trust reports to write an explanatory note on cycles in insects population abundance (I.F.T. 1962 and 1963). Weather conditions were assumed to regulate either directly or indirectly the intensity of insect hatches during any given year.

The next major natural catastrophe occurred in 1972 when gale force winds drowned millions of emerging adult mayflies and prevented those that survived from making their egg-laying flight to the lake margins (Table 2).

On Lough Sheelin the mayfly has failed to appear in any significant numbers since that time. Other waters, such as Lough Derravaragh, were also badly hit by the storm but in recent years moderate hatches of mayflies have occurred.

Table 2. Wind velocities in the Irish midlands May 1972.

Date	Mean Wind Speed (m/sec)	Highest Gust (m/sec)	Beaufort Number	Description
22.5.72	5.2	16	7	Near Gale
23.5.72	6.4	20	8	Gale
24.5.72	7.6	24	9	Strong Gale
25.5.72	8.1	28	10	Storm
26.5.72	10.7	25	10	Storm
27.5.72	8.6	20	8	Gale
28.5.72	6.8	19	8	Gale
29.5.72	8.7	23	9	Strong Gale
20.5.72	8.7	20	8	Gale

The reason for the disappearance of *Ephemera danica* from Lough Sheelin may be attributed to three main causes, the storm of 1972, cultural eutrophication, and increased predation from both brown trout and perch populations.

Increased cultural eutrophication became evident in Lough Sheelin during the spring of 1971 when blue green algal blooms and high chlorophyll *a* levels were recorded. The situation improved somewhat during 1972 but in January 1973 intensive algal blooms reappeared.

Britt (1955a) observed that the populations of *Hexagenia* in Lake Erie were decimated during the early fifties as a result of intense cultural eutrophication. The low numbers of mayfly nymphs resulting from the 1972 egg laying season on Lough Sheelin were subjected to changing environmental conditions which favoured the more pollution resistant organisms such as Chironomidae and Oligochaeta.

Another factor which must be taken into account when discussing the fate of *Ephemera danica* in Lough Sheelin is the increase in the population density of both perch (*Perca fluviatilis* L.) and brown trout (*Salmo trutta* L.) that occurred in the early seventies. This followed many years of predator control which resulted in a dramatic reduction of the pike (*Esox lucius* L.) stocks in 1970-71. Stocking of large numbers of artificially reared fish farm trout began in 1970, reaching a peak in 1973 when 35,000 summerlings, 80,000 fingerlings, 128,800 spring yearlings and 61,000 autumn yearlings were placed in the lake. The numbers of perch present in Lough Sheelin increased dramatically from 1974 to 1976. The

weight of perch captured during predator control operations was 1,112 kg in 1974, 8,330 kg in 1975 and 8,338 kg in 1976. The perch feeds on a mixed diet of invertebrates and fish, whereas the pike, after its first year, is mainly a fish feeder. The increased population density of both perch and brown trout must have resulted in a greater cropping of the invertebrate populations present in the lake. For a species such as *Ephemera danica* whose survival was already under pressure from changing environmental conditions, the unprecedented rise in predation levels must have further decreased the possibility of its reappearance in significant numbers.

The results of the project to date indicate that *Ephemera danica* populations are exceptionally sensitive to environmental change. Natural fluctuations in abundance occur and where these coincide with habitat or species dominance changes, they can result in the disappearance of the species.

In Lough Sheelin at the present time (1979) levels of nutrient input are still excessively high. The lake is subject to continuing cultural eutrophication and so the chances of the mayfly re-establishing itself as an angling species are presently poor. However, the technique developed for the artificial rearing of *Ephemera danica* may enable its eventual re-introduction into areas where suitable habitats are available.

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RESUME

Du point de vue des pêcheurs à la ligne, l'éphéméroptére, *Ephemera danica*, est un des insectes les plus importants que l'on trouve en Irlande. Pendant les dix dernieres années, l'abondance de l'insecte a beaucoup varié et dans certaines eaux il a presque disparu. Des nymphes élevées au laboratoire ont atteint le stade adulte en deux ans. Il n'a fallu qu'onze mois pour le développement complet d'un certain nombre de nymphs élevées depous 'oeuf et

placées dans un petit lac a pH éleve. On en conclut que le cycle de vie d'*Ephemera danica* est flexible et que l'insecte atteint son développement en un temps plus court quand la nourriture est abondante et les conditions d'habitat idéales. Le travail se termine avec une discussion des prineipaux facteurs qui influencent l'abondance d'*Ephemere danica* dans les eaux irlandaises.

ZUSSAMENFASSUNG

Vom Standpunkt des Anglers aus gesehen ist die Eintagsfliege *Ephemera danica* eines der wichtigsten Insekten, die sich in irischen Gewässern befinden. Während des letzten Jahrzehnts zeigte sie markante Abundanzfluktuierungen, und in einigen Gewässern ist sie praktisch ganz ausgestorben. Nymphen, die in einem Labor aufgezogen wurden, traten nach zwei Jahren als ausgewachsene Tiere zutage, während ein Schub von Nymphen die aus Eiern aufgezogen worden waren, nur elf Monate brauchte um sich in einem kleinen Kalksteinsee zu ausgewachsenen Tieren zu entwickeln. Daraus läßt sich schließen, daß der Lebenszyklus von *Ephemera danica* flexibel ist. Ihre Entwicklung vollzieht sich schneller in Plätzen, die reichlich Nahrung enthalten und ideale Lebensbedingungen bieten. In der vorliegenden Arbeit werden die wichtigsten Faktoren erörtert, die die Abundanz von *Ephemera danica* in irischen Seen beeinflussen.

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