with best wishes, John Brittain

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THE TEMPERATURE OF TWO WELSH LAKES AND ITS EFFECT ON THE DISTRIBUTION OF TWO FRESHWATER INSECTS

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Abstract

Temperature data are presented from the littoral zones of two lakes in North Wales, Llyn Coron and Llyn Dinas. Recording, mainly on a continuous basis, was over a two year period. Despite their different situations, the lakes had similar temperature regimes. Regional weather factors were of greater importance than local variations. However, some differences were present, especially during the summer months. Laboratory experiments were conducted to determine the temperature relationships of *Nemoura avicularis* Morton (Plecoptera) and *Leptophlebia vespertina* (L.) (Ephemeroptera), common species in Llyn Dinas but absent from Llyn Coron. Aspects considered included nymphal temperature tolerance and the effect of temperature on egg development and emergence. From the background of the results, it was concluded that the differences in temperature regime between the two lakes were insufficient to explain the absence of the two species from Llyn Coron.

Introduction

The distribution of many animals would appear to be limited by temperature. Although the relationship is sometimes indirect, temperature is obviously a factor of great ecological importance. Temperature may influence the distribution of a freshwater organism in one of two main ways; either temperatures may be lethal to a certain stage in the life cycle, or the growth rate of the animal may be affected, such that its life cycle is not synchronised with other environmental parameters. Obviously, these two are linked in many situations.

Temperature was one of the factors considered in a study of the distribution of lake dwelling Plecoptera and Ephemeroptera in North Wales (Brittain 1971). Special attention was paid to *Nemoura avicularis* Morton (Plecoptera) and *Leptophlebia vespertina* (L.) (Ephemeroptera). Two lakes, Llyn Dinas and Llyn Coron, were selected for intensive study since both species were common in the former lake but absent from the latter. Temperature as a possible factor producing this distribution was investigated by a combination of field recording and laboratory experiments.

Although a number of studies have now been carried out in Britain on the temperature conditions existing in small lentic water bodies (Macan & Maudsley 1966, Moss 1969, Martin 1972) and in running waters (Macan 1958, Smith 1968, Crisp & LeCren 1970, Langford 1970), few investigations have been published concerning the temperatures prevailing in larger water bodies. The only data are those given for Scottish lochs by Gorham (1958) and for Windermere by Jenkin (1942) and Macan (1970). The last mentioned reference refers to daily spot readings taken by the shore of Windermere and the other two concern recordings made from above the deeper parts of the lakes in question. In the present study recordings were made, largely on a continuous basis, in the littoral zone; the region where Plecoptera, Ephemeroptera and many other aquatic insects have their greatest density. Condi-

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tions in deeper waters are likely to differ from those in the littoral zone. For example, it might be expected that littoral temperatures, especially when there is little wind, would follow air temperatures more closely and have higher maximum temperatures during the summer and lower minimum temperatures during the winter.

Several studies have been made, particularly with stream dwelling species, on the relationship between temperature and the distribution of mayflies and stoneflies (e.g. Ide 1935, Sprules 1947, Macan 1960, Kamler 1965, Clifford 1969, Knight & Gaufin 1966, Langford 1971). The effect of temperature upon the various stages and upon the life cycle as a whole has also received attention (Pleskot 1951, 1958 & 1961, Harker 1952, Macan 1957, 1958, Illies 1959 and Nebeker 1971). Temperature as a factor controlling emergence, has been suggested by Macan & Maudsley (1966) and Morgan & Waddell (1961). Morgan (1964) suggested that temperature may regulate the initiation of emergence and daylength its cessation. Macan (1966) analysed the emergence period of two *Leptophlebia* species in relation to the temperatures prevailing in Hodson's Tarn. He concluded that the time of emergence was related to the date when the water temperature reached 11°C, rather than to the number of accumulated degree hours.

However, most of the studies have been predominantly field investigations and there have not been many controlled laboratory experiments to test hypotheses based on field data. The work of Whitney (1939) on the thermal resistance of various mayfly species was until recently one of the few laboratory studies in this field. Some American workers have conducted laboratory experiments with special reference to thermal discharges from power stations and other forms of artificial heating (Nebeker & Lemke 1968, Heiman & Knight 1972). Recently, comprehensive combined field and laboratory studies on the effects of temperature on the development of the eggs of the mayflies, *Baetis rhodani* (Elliott 1972, Benech 1972) and *Ephmerella ignita* (Bohle 1972) have been made.

Habitat descriptions

1. Llyn Dinas

Llyn Dinas is situated at an altitude of 53.5 m in the Gwynant valley (map reference SH 615495). It lies in the heart of Snowdonia, an area of mountain and moorland terrain in North Wales which reaches elevations of over 1000 m. The river Glaslyn rises on steep slopes at around 1000 m and then flows rapidly down into the Gwynant valley at about 75 m, where the flow becomes less rapid. The river then passes through Llyn Gwynant before it enters Llyn Dinas. Rainfall is high in the area (Fig. 1), reaching over 4000 mm./yr. around the mountain summits. Therefore, especially during spates, considerable quantities of suspended material are carried down the river Glaslyn and into Llyn Gwynant and Llyn Dinas causing them to silt up rapidly. Llyn Dinas has a maximum depth of 8.5 m. (Ferrar 1961) and its area is 31.10 ha. The lake's main axis, like that of the valley, runs SW-NE. The shores of the lake are mainly rocky, grading into mud and silt substrata at a depth of about 1 m. An average calcium level of 2 mg./l. and an electrical conductivity at 25°C. of 38 μmhos. reflect the oligotrophic nature of this habitat.

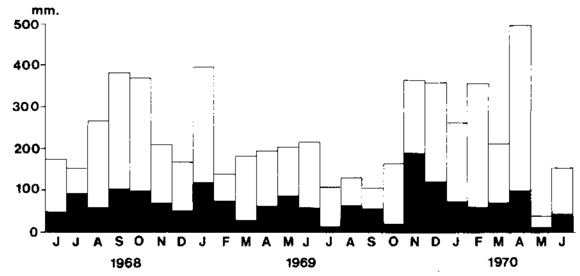

Fig. 1. Monthly rainfall at Valley (shaded) and Cwm Dyli (unshaded), June 1968-June 1970.

2. Llyn Coron

Llyn Coron, formed by the inland progession of coastal sand dunes damming the river Ffraw, is situated in south-west Anglesey at an altitude of 10 m. above sea-level. The climate is maritime and strong winds are common owing to the island's exposed position. Rainfall is less than that in Snowdonia and is in the order of 800 mm./yr. (Fig. 1). All the streams that enter Llyn Coron are small and slow-flowing. In the more exposed areas the shoreline is stony, but where sheltered, reed beds have developed on the mud and sand substratum. Llyn Coron has an area of 26.09 ha and a mean depth of 4.6 m. (Greenly 1919). The lake is moderately productive, having an average calcium concentration of 33 mg./l. and an electrical conductivity at 25°C. of 320 μmhos. By virtue of its proximity to the sea its chloride content is high (about 34 mg./l.).

A more detailed description of both Llyn Dinas and Llyn Coron, together with further information on their biotic and abiotic aspects, is given in Brittain (1971). The nearest meteorological stations to Llyn Dinas and Llyn Coron were Cwm Dyli and Valley respectively. The former is situated in the Gwynant valley 5.5 km. from Llyn Dinas and daily maximum and minimum air temperatures and rainfall data were available. From Valley, 8 km. N.W. of Llyn Coron, a considerable number of parameters were available, many recorded on a continuous or hourly basis.

Comparison of temperature regimes in the two lakes

Introduction

To investigate the possible effects of temperature on the distribution of *Leptophlebia vespertina* and *Nemoura avicularis,* it was necessary to determine the temperature regimes existing in Llyn Dinas and Llyn Coron. The temperature of these two lakes was measured, mostly on a continuous basis, over a two year period from June 1968 to June 1970. Recordings were made continuously as, particularly during the summer months, it may be of importance whether a certain maximum temperature is maintained for several hours or even days, or is attained only for a short period. Weekly or even daily maximum-minimum reading would not distinguish these two situations. Spot readings are of even less value unless the diurnal temperature pattern is constant and well-known. (Macan & Maudsley 1966). Recordings were made on the substratum in the littoral zone of the lake at a depth of about 0.4 metres. Either surface or mid-depth temperatures, those often given in limnological investigations, would not necessarily be the temperatures experienced by the eggs and nymphs of mayflies and stoneflies.

Methods

Three types of instrument were used in measuring the temperatures in Llyn Dinas and Llyn Coron, the first being two Cambridge thermographs. These instruments recorded continuously, but the mechanical clock only ran for 7-10 days and so the clock had to be rewound and the chart replaced about once a week. The recorder itself was housed in a wooden box to protect it from the weather. However, during periods of heavy rain at Llyn Dinas the lake level often rose very rapidly, flooding the recorder owing to the lead being only 2 metres in length. After about 18 months' continuous use in the field the mild steel capillary system became too eroded to be of use. (A capillary system in stainless steel is now available.) Thermographs were in operation at Llyn Coron from 11 June 1968 until 29 January 1970, and at Llyn Dinas from 11 June 1968 until 2 October 1968.

Mid-way through the study a Grant miniature temperature recorder was used. The thermistor probe was covered in stainless steel and recorded for 30 secs every 30 mins. Although more expensive than the thermographs, it had several advantages. Being smaller it was more easily concealed and protected from the weather. The 20 metre lead prevented flooding of the recorder, while the chart and mercury battery had to be replaced only once every three months. This instrument recorded temperatures at Llyn Dinas from 16 May to 20 August 1969 and from 14 October 1969 until 11 November 1969; and at Llyn Coron, during 1970 from 29 January until 12 June.

During the periods when two continuous recorders were unavailable a maximum-minimum thermometer was used in Llyn Dinas. It was read and re-set weekly, and was in use from 7 October 1968 until 16 May 1969, from 20 August to 14 October 1969, and finally from 11 November 1969 until 16 June 1970.

All the three instruments were checked regularly against an accurate mercury thermometer. The recordings were made on the N.W. shore of Llyn Dinas adjacent to the road and on the N.W. shore of Llyn Coron 100 m. from the outflow.

Results and Discussion

The temperature recordings obtained from Llyn Dinas and Llyn Coron are summarized in Fig. 2. During the two years of recording from June 1968 until June 1970 each lake passed through two complete temperature cycles. Both lakes were warmest during June, July and August. Then temperatures fell gradually until the

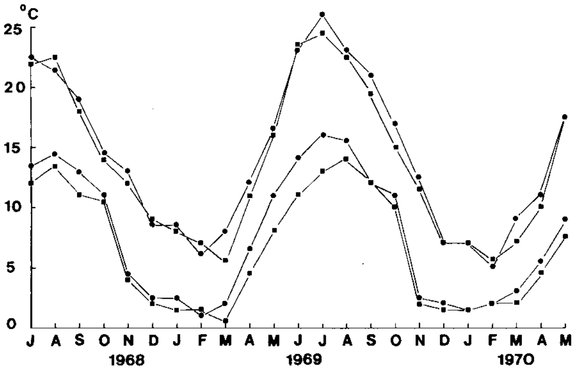

Fig. 2. Monthly maximum and minimum water temperatures in Llyn Coron (●———●) and Llyn Dinas (■———■), July 1968-May 1970.

beginning of November when there was a more rapid fall to about 5°C. The temperature remained low until March, although in both years there was a mild period during late January. The coldest temperatures were recorded in early January and in February. Ice formed on both Llyn Dinas and Llyn Coron during the coldest weather, but it was never very thick and rarely remained on the lakes for more than a few days. In March the temperature began to rise again until by May temperatures of 15°C. and above were attained.

The temperature cycle is very similar in the two lakes. Regional weather factors, such as periods of anticyclonic weather or periods of low pressure, would appear to be more important than local differences as the peaks and troughs in the Llyn Coron records are mirrored in those of Llyn Dinas, which is 35 km. distant and surrounded by mountain peaks. However, although surrounded by mountains, Llyn Dinas is only 55 metres above sea level. Nevertheless, there are some differences between the two sets of records if they are examined in detail. In Table 1 the dates are given on which Llyn Dinas and Llyn Coron reached 10°C., 15°C. and 20°C. during the spring and early summer and in the autumn when the temperature fell to 15°C. and 10°C. Comparison of the dates shows that Llyn Coron was invariably the first to reach a certain temperature during the spring. The time differential was usually only a few days, although after the cold spring of 1970, Llyn Coron reached 10°C. on 17 April, while the same temperature was not attained in Llyn Dinas until the end of the month. In the autumn, the two lakes cool down at similar rates. The monthly maximum and minimum temperatures show these same differences and similarities (Fig. 2).

Taken as a whole the temperature regimes in the two lakes are very similar, but especially during the summer months certain differences are apparent. The daily maximum and minimum temperatures for the months of June, July and August 1969 are given in Figs. 3 and 4.

Table 1. Dates on which temperature rises or falls to standard temperatures in Llyn Dinas and Llyn Coron.

Temperature falls to:	10°C.		5°C.	
	Dinas	Coron	Dinas	Coron
Autumn 1968	30 Oct-8 Nov	2 Nov	8-15 Nov	18 Nov
Autumn 1969	31 Oct	5 Nov	18-25 Nov	17 Nov

Temperature rises to:	10°C.		15°C.		20°C.	
	Dinas	Coron	Dinas	Coron	Dinas	Coron
Spring 1969	10-18 Apr	7 Apr	20 May	10 May	11 Jun	8 Jun
Spring 1970	28 Apr-6 May	17 Apr	12-19 May	7 May	28 May-4 Jun	3 Jun

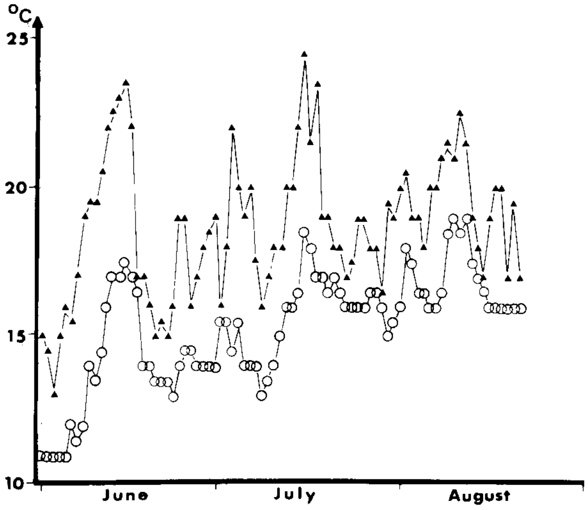

Fig. 3. Daily maximum (▲——▲) and minimum (o——o) water temperatures in Llyn Dinas for June, July and August 1969.

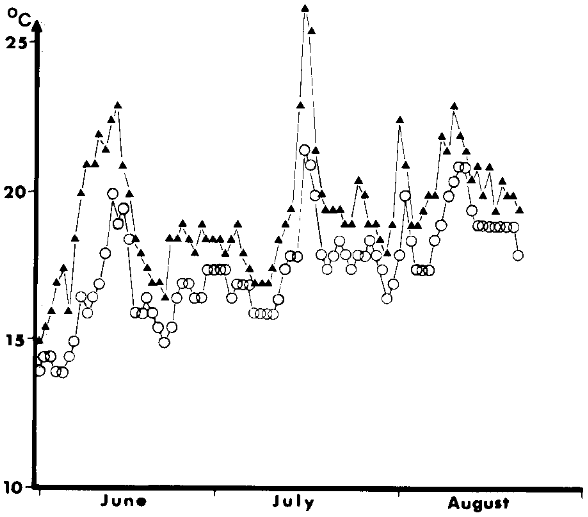

Fig. 4. Daily maximum (▲——▲) and minimum (o——o) water temperatures in Llyn Coron for June, July and August 1969.

The overall pattern is the same, but while the maximum temperatures are similar, the minimum temperatures differ. In Llyn Dinas there is a greater diurnal temperature variation caused by there being lower minimum values during the night and early morning. Thus, during periods of warm anticyclonic weather, when temperatures exceed 20°C. during the day, the temperature falls to below 20°C. in Llyn Dinas during the night while Llyn Coron may remain above 20°C. throughout the night.

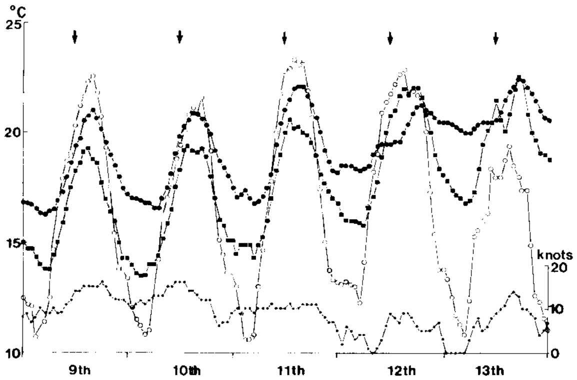

Fig. 5. Water temperatures in Llyn Coron (●——●) and Llyn Dinas (■——■), and air temperatures (o——o) and wind velocity (•——•) at Valley, 9-13 June 1969. A vertical arrow indicates 1200 hours G.M.T.

This type of situation is clearly seen in Fig. 5, which gives hourly temperatures in Llyn Dinas and Llyn Coron during a period of fine weather.

Absolute differences in the number of degree hours above 0° C. between the two lakes are greater during the summer. The values are given in Fig. 6. The overall difference is 8% which means a difference in the region of 7,000 degree hours per year. This corresponds to an average permanent temperature difference of 0.83° C., or alternatively to a 3-4 week time period.

The importance of air temperature in determining lake temperature is clearly seen when Figs. 3 and 4 are compared with Fig. 7. The first point is that the same major peaks and troughs are reflected in air and lake temperatures from both areas. However, absolute air temperatures are lower in Cwm Dyli. Most minimum temperatures at Cwm Dyli are under 10° C. The position of Cwm Dyli in the steep sided Gwynant valley no doubt leads to frequent temperature inversion. Maximum temperatures also differ, again being higher at Valley than at Cwm Dyli. This may be explained by the blocking of the sun by the mountains for part of the day and by the formation of convectional cloud around Snowdon and the neighbouring peaks during fine weather. Comparison of the daily maximum and minimum temperatures in the two lakes shows that minimum air temperatures have a more pronounced effect upon lake temperature than the maximum air temperatures. In Fig. 5 the short-term relationship between a number of parameters recorded at Valley and the temperatures prevailing in Llyn Coron and Llyn Dinas is plotted. During the first three days air and lake temperatures were well synchronised at Valley and Llyn Coron respectively. However, on 12 and 13 June the situation changed. What was before a more or less constant breeze, producing mixing of the surface waters and the littoral areas, diminished, especially during the critical cooling down period after midnight. Therefore, minimum temperatures in Llyn Coron were higher on 12 and 13 June. On 13th, when temperatures did not fall below 20° C. during the night, day lake temperatures equalled or even exceeded air temperatures. Over a longer period the residual heat in even a small lake can also be noticeable. For example, in Cwm Dyli temperatures began falling by the end of August 1969 (Fig. 7), but in Llyn Dinas there is no such clear indication (Fig. 3).

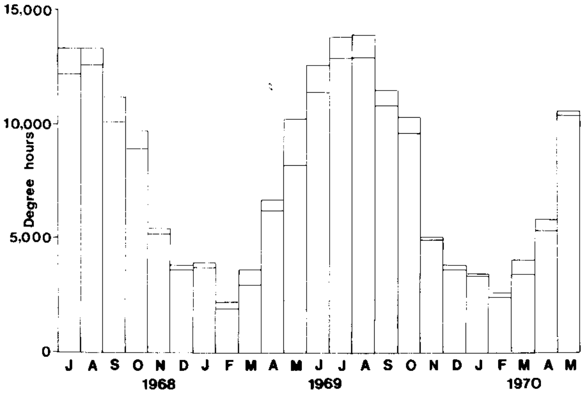

Fig. 6. Monthly totals of degree hours above 0° C. for Llyn Coron and Llyn Dinas, July 1968-May 1970. With the exception of February 1969 and 1970, the higher totals are from Llyn Coron.

The rate of water renewal is undoubtedly more rapid in Llyn Dinas than in Llyn Coron, owing to the presence of larger and faster-flowing inflows resulting from steeper terrain and a higher level of precipitation in the catchment area (Fig. 1). The inflowing water will also be cooler in Llyn Dinas because of its origin at higher altitudes and its rapid progression down into the Gwynant valley. There is unlikely to be a major warming of the waters by their passage through Llyn Gwynant as this lake can be seen, as can Llyn Dinas, as an extension or widening of the river Glaslyn. Llyn Coron is more circular in shape and thus there will be less tendancy for the formation of a through current.

Wind may have a stronger influence on Llyn Coron, which is situated in open terrain exposed to the prevailing south-westerlies and is only 3 km. from the coast. The Gwynant valley runs SW-NE, but Llyn Dinas is situated further inland. However, an accurate assessment of the comparative effect of wind on the two lakes is impossible

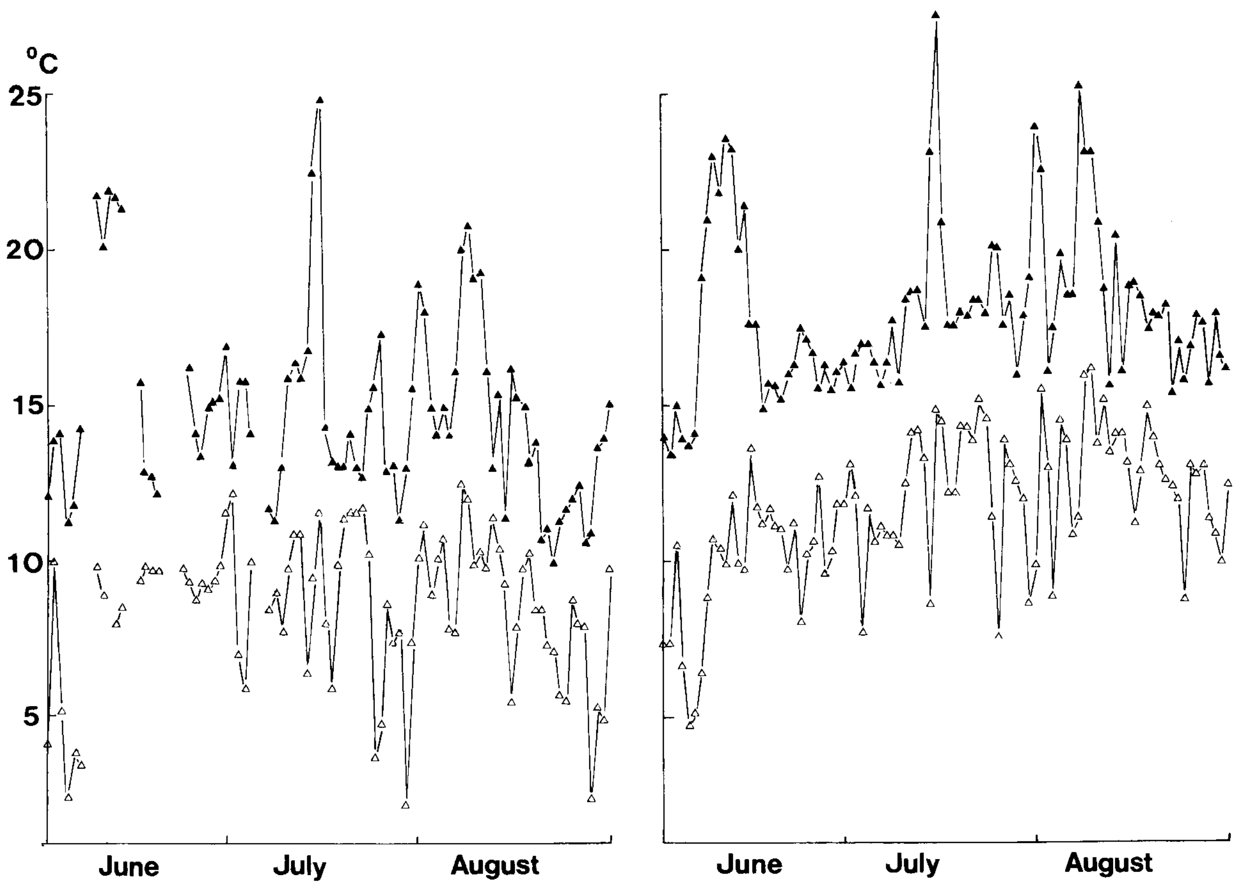

Fig. 7. Daily maximum (▲———▲) and minimum (△———△) air temperatures at Cwm Dyli (left) and Valley (right) for June, July and August 1969.

without more detailed meteorological data than are available.

During the summer of 1969 only Llyn Coron exceeded 25°C. and for a period of 8½ hours (the maximum recorded in Dinas during 1969 was 24.5°C.). A temperature of 20°C. was exceeded several times in both lakes. During the summer of 1969 there were 319 hours above 20°C. in Llyn Coron, while in Llyn Dinas there were 144 hours. The longest continuous periods above 20°C. were, in Llyn Coron, 96 hours and in Llyn Dinas 28 hours.

Returning to Fig. 5, some generalisations can be made about the diurnal pattern of temperature variation. During warm, sunny weather, diurnal fluctuations are pronounced. On such occasions maximum temperatures were reached in both lakes around 1500 hours G.M.T., while minimum temperatures were recorded in the early morning between 0100 hours and 0500 hours G.M.T. Temperatures usually began to rise rapidly soon after the sun rose, about 0400 hours during June. During periods of unsettled weather and in the winter months diurnal fluctuations were less distinctive and maximum and minimum values could be reached at different times depending on the prevailing weather conditions.

Laboratory studies

Introduction

Concurrent with the determination of the temperature regimes of Llyn Coron and Llyn Dinas a series of preliminary laboratory experiments were carried out to give guidance in the interpretation of the field results. Unless otherwise stated, laboratory cultures of the mayfly, *Leptophlebia vespertina,* and the stonefly, *Nemoura avicularis,* were kept in the conditions outlined in earlier publications (Brittain 1972, 1973), which also contain information on the biology and life cycle of these two species. Both are univoltine, peak emergence of *N. avicu-*

laris taking place in April and that of *L. vespertina* in early June. Their eggs hatch in about 3 weeks at temperatures prevailing in the field at the time of incubation. Thus the majority of the year is spent in the nymphal stage. For *N. avicularis,* the three warmest months, June, July and August are spent almost exclusivly as early instar nymphs. In the case of *L. vespertina* both eggs and nymphs are present during the three warmest months.

Total Life Cycle

Eggs of *Nemoura avicularis* kept at a constant temperature of 20°C. hatched in 12-16 days, while those kept at lower temperatures took longer to hatch. For example, the incubation period was 26 days at 15°C. and 20 days at the temperatures prevailing in Llyn Dinas at that time (between 12 and 21°C.) (Brittain 1973). However, the advantage gained in rapid hatching was soon lost. After the first few instars the nymphal growth rate at 20°C., as compared with a population kept at field temperatures, decreased considerably (Table 2). Ultimately none of the nymphs reared at 20°C. emerged. Those which survived the mortality of the first few weeks remained in the nymphal stage as late as July when the last few nymphs died. Nymphs kept at normal field temperatures emerged mainly in March and none remained in the nymphal stage beyond early April. Thus *N. avicularis* was unable to complete its life cycle at a constant temperature of 20°C. No similar experiment was conducted with *L. vespertina* owing to the shortage of eggs. However, some nymphs were reared at Llyn Coron temperatures and their growth was normal and emergence occurred at the appropiate time.

Table 2. Mean size (in mm) ± standard deviation of laboratory populations of *Nemoura avicularis* at 20°C. and at field temperatures (Llyn Dinas). Number of nymphs are given in parentheses.

Date	20°C	Dinas temperatures
1 May	0.49 ± 0.04	
14 May	-	0.49 ± 0.04 (10)
21 Aug	-	2.96 ± 0.47 (10)
27 Oct	3.65 ± 0.48 (30)	6.07 ± 0.64 (10)
21 Dec	4.46 ± 0.64 (23)	7.30 ± 0.63 (10)
25 Feb	5.05 ± 0.60 (10)	8.80 ± 0.63 (10)
10 Apr	5.70 ± 0.45 (3)	All emerged
4 June	6.00 (3)	
21 July	All died	

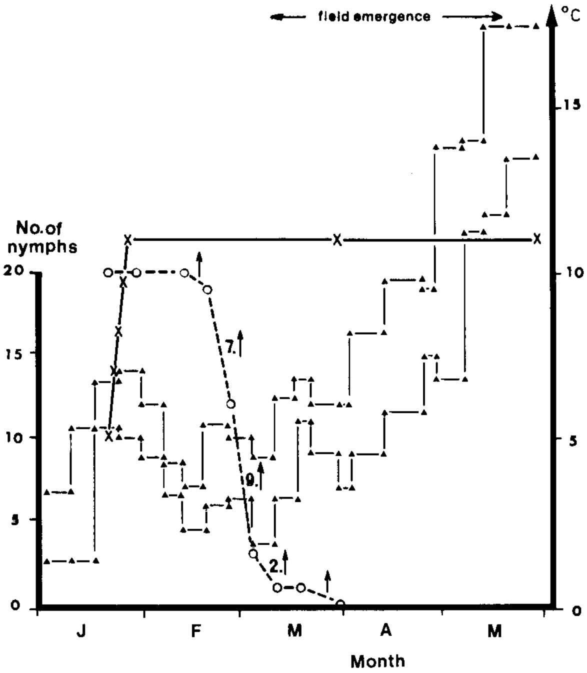

Fig. 8. Advancement of emergence in *N. avicularis.* The number of nymphs remaining (o———o), the experimental temperature (x———x) and maximum and minimum field temperatures from Llyn Dinas (▲———▲) are given. Emergence is indicated by a vertical arrow and when more than one nymph emerged the number is given.

Emergence

Prior to emergence the nymphs of both *Nemoura avicularis* and *Leptophlebia vespertina* move into shallower water (Macan & Maudsley 1968, Brittain 1971). The cause of such movements is not definitively known, but temperature, photoperiod and maturation may all be involved. Once in shallow waters temperature would appear to be the dominating factor determining when emergence takes place. A laboratory experiment was set up to evaluate the effect of temperature on the emergence of *N. avicularis.* During January, when field temperatures were around 5°C., twenty nymphs, by now more or less fully grown, were collected from Llyn Dinas and placed in controlled conditions in the laboratory. They were kept in total darkness and the temperature was raised from 5°C. by 1°C. per day until 11°C. was reached. Once at 11°C. the temperature was held constant, and any emergence noted. The results are shown in Fig. 8. By placing the nymphs in a higher temperature the peak of emergence was advanced by over a month. Nineteen out of the 20 experimental animals had emerged before any emergence had been observed in the field and before any of a laboratory population at field temperatures had emerged (Brittain 1973). Thus it is probable that low temperatures in the field during February and early March delay emergence until April.

Two simple experiments were set up to test the effect of temperature on the emergence of *L. vespertina.* In the first one an attempt was made to advance emergence and in the second to delay the onset of emergence. For the first experiment 20 nymphs were collected from Llyn Dinas during January and placed in the same conditions as were the nymphs of *N. avicularis* in the experiment above. By placing the nymphs in a higher temperature (11°C.) the peak of emergence was advanced by over six weeks and 14 out of the 16 nymphs that emerged did so before any emergence was observed in the field (Fig. 9). In addition, all 16 emerged before any of a laboratory population kept at field temperatures had emerged (Brittain 1972). The second experiment with *L. vespertina* was very preliminary as only small numbers of nymphs were available. Nymphs were collected from Llyn Dinas in April, about a month before emergence was due to begin. They were kept at a constant temperature of 6°C. throughout the summer and there was no emergence until the temperature was raised from 6°C. to 12°C. in late September. As soon as the temperature was raised all the nymphs emerged during the following month. Thus emergence was delayed by about four months by keeping nymphs at 6°C.

From these experiments it is clear that temperature is an important factor concerned with the regulation of emergence. Photoperiod, at least during the four months prior to emergence, would appear to be unimportant. As the effect of temperature was not immediate, it must be necessary for certain maturation processes to occur before emergence is possible.

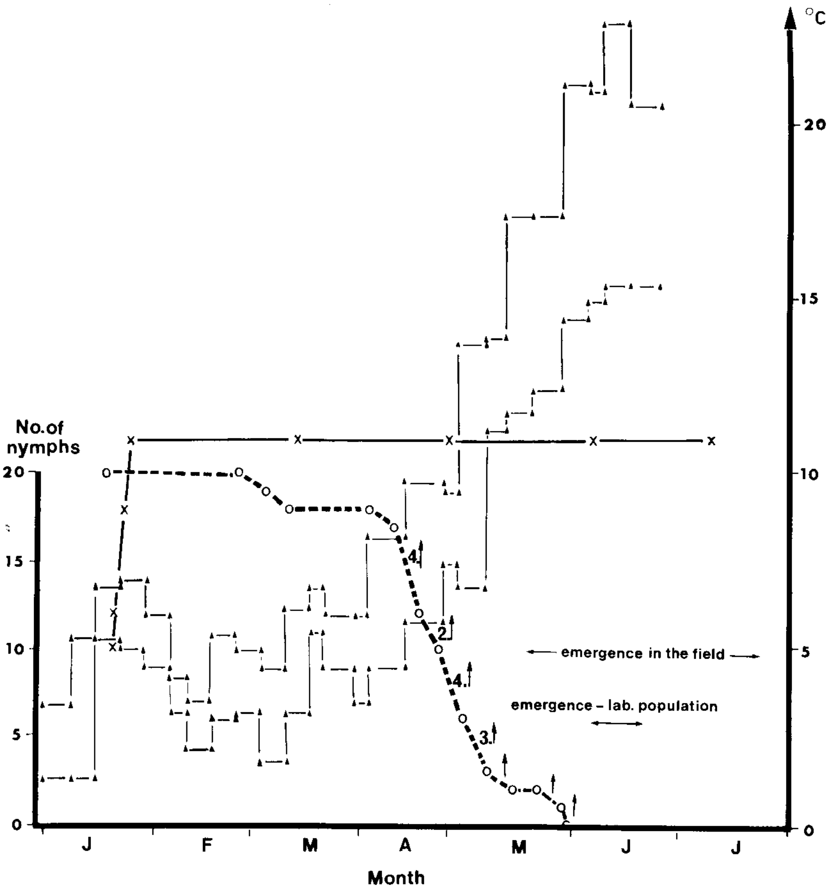

Fig. 9. Advancement of emergence in *L. vespertina.* Symbols as in Fig. 8.

Temperature tolerance of the nymphs

During October, 30 nymphs of *Nemoura avicularis* were collected from Llyn Dinas. Ten were kept at temperatures approximating those of Llyn Dinas and thus served as the control group. The remaining 20 were divided into two equal groups; one in which the temperature was raised at a rate of 1°C. per day until 20°C. was reached, and another where the temperature was elevated at the same rate until 25°C. The two latter groups were then kept at 20°C. and 25°C. respectively throughout the rest of the experiment. There was no mortality until 18 days after the experimental temperatures had been attained, when some of those at 25°C. began to die (Fig. 10). The first mortality in the 20°C. group occurred after 41 days. The maximum survival times at 25°C. and 20°C. were 43 days and 155 days respectively, while the times taken for 50% to die (the L.D. 50-sensuo Fry 1947) were respectively 31 and 73 days.

Thirty nymphs of *Leptophlebia vespertina* were collected from Llyn Dinas at the same time as those of *N. avicularis* and then subjected to the same three regimes; field temperatures, 20°C. and 25°C. The results are given in Fig. 11. The survival of *L. vespertina* was better than that of *N. avicularis*. The L.D. 50s at 20°C. and 25°C. were 159 and 37 days respectively. Because of their longer survival at constantly high temperatures, this experiment continued until the normal emergence period in May and early June. Seven out of the ten nymphs in the control group emerged successfully as did one of the nymphs in the 20°C. group.

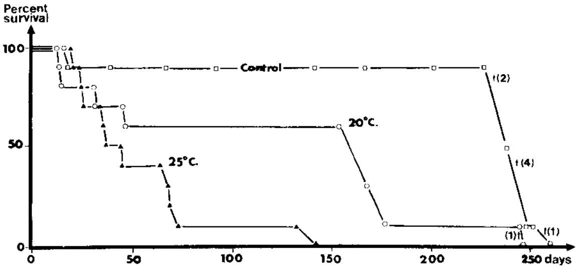

Fig. 11. Temperature tolerance of *L. vespertina* nymphs at 20°C. and 25°C. Emergence, with the number in parentheses, is indicated by a vertical arrow.

Another aspect of temperature tolerance, besides that of being kept at a constantly high temperature, is that of being subject to an ever increasing temperature. As this aspect is not so relevant to the field situation only one experiment, with *L. vespertina,* was carried out. During May 10 nymphs were subjected to an increase of 1°C. per day, beginning at the temperature prevailing in Llyn Dinas. Mature nymphs were excluded from this experiment as emergence, due to the rise in temperature, would obscure the result. (However, experiments with mature nymphs showed similar results, although most emerged before temperatures became lethal.) There was no mortality until 27°C. was reached, after which there was a rapid increase in mortality. The L.D. 50 was 32°C. and the last nymphs died at 33°C.

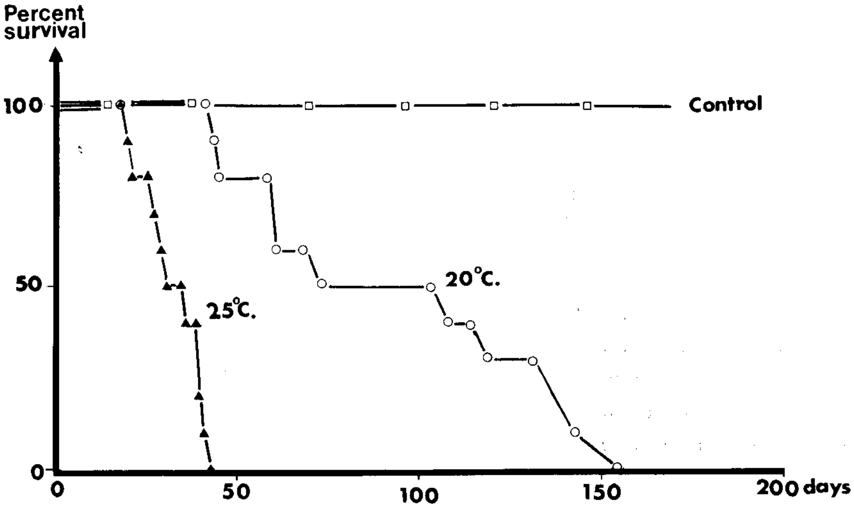

Fig. 10. Temperature tolerance of *N. avicularis* nymphs at 20°C. and 25°C.

Discussion

In both Hodson's Tarn (Macan & Maudsley 1966) and two Leicestershire ponds (Martin 1972) the temperature regimes were grouped into four periods corresponding to the conventional seasons. These were: 1. Period of increasing temperature, March to May; 2. Plateau of high temperature, June to August; 3. Period of falling temperature, September to November; 4. Period of low temperatures, December to February. The temperature regimes of Llyn Coron and Llyn Dinas can also be similarly grouped. However, March, especially for Llyn Dinas, was one dominted by low temperatures andit was only at the end of March that temperatures began to rise significantly; also, the first half of June was a period of rising temperature. Thus in the warming-up phase the temperature regimes of the two lakes were 2-4 weeks behind that of the smaller water bodies. This fits in well with Gorham's (1958) conclusion that the larger and deeper the water body, the later the attainment of maximum summer temperatures. During the autumn there is less variation, no doubt on account of the higher frequency of strong winds at that time of the year and the exposed situations of the two lakes. Once the lake has reached summer temperatures the temperature regime of the lake littoral is likely to resemble that of a smaller water body in periods of still weather, but in windy periods there will be some mixing with the cooler, deeper water layers in lakes.

Air temperature was a major factor, if not the major factor, determining water temperature in previous investigations of smaller water bodies (Macan & Maudsley 1966, Moss 1969, Martin 1972) and this was also the case for the littoral zone of the two lakes, Llyn Dinas and Llyn Coron.

Although there were nearly twice as many hours above 20°C. in Llyn Coron than in Llyn Dinas, this must be related to the survival times of the animals at such a temperature. It is always difficult to compare and evaluate the results obtained from field recording with those obtained in the laboratory, but such comparisons may suggest the ecological role of an environmental parameter. In the summer of 1969 there were, in total, 319 hours (13.3 days) above 20°C. in Llyn Coron and the longest continuous period was 96 hours during August. From laboratory studies it was shown that even at a constant temperature of 25°C. no mortality occurred in the nymphs of *N. avicularis*, the most sensitive of the two species, until 18 days at 25°C. In the long term, therefore, high water temperature was unlikely to adversely affect these two insect species.

A temperature of 25°C. was rarely exceeded in the littoral zone of Llyn Coron (only for an 8 hour period during the summer of 1969 when 26.3°C. was reached), whereas in laboratory experiments where nymphs were subjected to a rise in temperature of 1°C. per day no mortality occurred until 27°C. was reached and the L.D. was 32°C. This comparison, of course, assumes that there is no effect on the nymphs before death occurs and that the response to high temperature is the same throughout the egg stage and the nymphal life. On the first point it has been demonstrated that at a constant temperature of 20°C. *N. avicularis* cannot complete its life cycle as growth and maturation is hindered. However, there is considerable difference between a constant temperature of 20°C. throughout the life cycle and, as exists in Llyn Coron, about 13 days annually at or above 20°C. Concerning the second point, it is generally held, though backed up by little experimental evidence, that the eggs and young nymphs are more resistant to higher temperature than the older nymphs as they are often present during the summer months-perhaps a circular argument? In fact, Heiman & Knight (1972) tentatively suggest that newly-hatched nymphs of an American stonefly species are more susceptible to high temperatures than either the eggs or the later nymphal stages. They also found that temperature tolerance, apart from the period immediately after hatching, was maximal in the summer and the autumn, minimal during the spring and intermediate during the winter. However, such relationships are likely to differ from species to species.

If the temperatures in a lake such as Llyn Coron are not high enough to slow down or inhibit growth, they may increase the growth rate. Emergence might then take place earlier and synchronisation of the life cycle with other environmental variables may be upset. This possibility is doubtful as many species of Ephemeroptera and Plecoptera show considerable plasticity in their life cycles. For example, certain Baetidae are able to produce a variable number of generations per year depending on the prevailing temperature (Pleskot 1958, Brown 1961, Macan 1961). In Scandinavia, where a more continental climate than in Britain generally prevails the life cycle of many Ephemeroptera and Plecoptera is altered to some extent. In the subalpine areas of southern Norway and in northern Sweden, where the lakes are ice covered until May or early June, nymphs of *Nemoura avicularis* do not emerge before June (Ulfstrand 1969, Brittain 1974, Lillehammer 1975), compared with British populations which emerge in March. A similar situation is also found with the mayfly *Leptophlebia vespertina* (Kjellberg 1972, Brittain 1974), whereby the emergence period is much later in Scandinavia than in Britain. However, although the actual time differs the water temperatures prevailing at the time of emergence are remarkably similar, thus again making the point that once the nymph has passed a certain stage in maturation then it is principally water temperature that determines when emergence takes place.

The difference over a period of 12 months in degree hours between the two lakes corresponds to 3-4 weeks. Thus, assuming a direct linear relationship between the number of degree hours and both egg incubation time and nymphal growth and maturation, emergence would occur 3-4 weeks earlier in Llyn Coron than in Llyn Dinas. However, the relationship is unlikely to be linear and higher temperatures can actually slow down or even inhibit growth (cf. growth of *N. avicularis* at 20°C.). In addition, as suggested above, there is probably a threshold temperature for emergence no matter how many degree hours have been received. In practice, however, a habitat with a lower number of accumulated degree hours will usually also reach a certain temperature at a later date. In the case of the two lakes in the present study, there was 1-2 weeks' difference between the dates on which 10°C. was reached, but the accumulated degree hours represented a difference of approximately double this period. Therefore, in this case a threshold temperature for emergence would be of advantage, necessitating less change in the timing of the other life cycle stages. Langford (1970, 1971) studied the temperature of the river Severn upstream and downstream of a heated discharge from a power station and its effect on the Plecopteran and Ephemeropteran fauna. In terms of degree hours above 0°C., the annual difference between the river above and below the discharge varied between 11 and 29%. From faunal studies Langford concluded that the heated effluent had no significant effects on the distribution and ecology of the 8 species he investigated, suggesting that the ability of each species to tolerate wide temperature range in different life cycle stages is sufficient to enable the species to withstand and survive unnatural temperature conditions, provided that these temperatures are not sustained, or lethal to any stages.

If the same species can adjust their life cycles to suit conditions both in continental Scandinavia and in Llyn Dinas, it is likely that adaptation is possible to a slightly different temperature regime in a nearby lake. The possibility that the species may be near the limit of their temperature tolerance in Llyn Dinas is not supported by the laboratory studies or by their abundance in Llyn Dinas. Thus in the light of other investigations and the preliminary laboratory experiments carried out in the present study, the differences in the thermal conditions of Llyn Dinas and Llyn Coron are insufficient to account for the absence of *L. vespertina* and *N. avicularis* from Llyn Coron.

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Summary

1. Temperature data are presented for two lakes in North Wales, Llyn Coron and Llyn Dinas. Both lakes are lowlying, but the former is moderately productive and situated among lowlands on the island of Anglesey, while the latter is oligotrophic and lies in the Snowdonia mountain area.

2. *Leptophlebia vespertina* (L.) (Ephemeroptera) and *Nemoura avicularis* Morton (Plecoptera) were common in Llyn Dinas, but absent from Llyn Coron. The hypothesis that temperature was responsible for such a distribution was investigated by a combination of field recording and laboratory experiments.

3. The temperatures prevailing in the littoral zones of the two lakes were measured, mostly on a continuous basis, from June 1968 to June 1970.

4. On comparison, the two temperature regimes were found to be on the whole very similar. Regional weather factors appeared to be more important than local variation.

5. Nevertheless, especially during the summer months, there were certain differences in detail. For example, in warm anticyclonic summer weather when water temperatures exceeded 20°C. during the day the temperature fell to below 20°C. in Llyn Dinas during the night, while

Llyn Coron often remained above 20° C. throughout the night. Air temperature was important in producing these differences and at certain times wind strength also played a role.

6. The average difference in degree hours above 0° C. between the two lakes was 8%, which is equivalent to approximately 7,000 degree hours per year, or 3-4 weeks on a yearly basis.

7. In the summer of 1969 there were 319 hours (13.3 days) above 20° C. in Llyn Coron, while in Llyn Dinas there were 144 hours. The longest continuous periods above 20° C. were, in Llyn Coron 96 hours and in Llyn Dinas 28 hours.

8. During warm, sunny weather, diurnal fluctuations were pronounced, with maximum temperatures around 1500 hours G.M.T. and minimum temperatures between 0100 and 0500 hours G.M.T.

9. In the laboratory *N. avicularis* was unable to complete its life cycle at a constant temperature of 20° C., although egg hatching and early growth were normal.

10. Emergence of both *N. avicularis* and *L. vespertina* was advanced by keeping nymphs at higher temperatures than those prevailing in Llyn Dinas.

11. For *N. avicularis*, the L.D. 50s at 20° C. and 25° C. were respectively 73 and 31 days. For *L. vespertina*, the equivalent periods were 159 and 37 days. Thus, high water temperature was unlikely to adversely affect these two insect species.

12. Both species are capable of adapting their life cycle to a range of temperature regimes in central and northern Europe and so it is likely that adaptation is possible to a slightly different temperature regime in a nearby lake. The possibility that the species may be near the limit of their temperature tolerance in Llyn Dinas is not supported by the laboratory studies or by their abundance in Llyn Dinas. Therefore, differences in the thermal conditions of Llyn Dinas and Llyn Coron are considered insufficient to account for the absence of *L. vespertina* and *N. avicularis* from Llyn Coron.

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