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 nympal 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-

Dr. W. Junk b.v. Publishers - The Hague, The Netherlands
Habitat descriptions

and Community Reactions (below 1972) have been made

...
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 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 January, with Lyn Corun and Llyn Dinlas being the coldest, while the temperature rose to above 20°C in the late summer and autumn.

Regional weather factors such as periods of anticyclonic weather or periods of low pressure, would appear to be more important than local differences such as the peaks and troughs in the Llyn Dinlas records, which are 35 km distant and surrounded by mountains. Llyn Dinlas is only 5 km above sea level. Nevertheless, there are some differences between the two lakes. In March the temperatures in Llyn Dinlas were lower than in July and August. In January, Llyn Dinlas was warmer than Llyn Corun, although the differences were small.

The overall pattern is the same, but while the maximum temperatures in Llyn Dinlas and Llyn Corun are similar, the minimum temperatures are lower. In Llyn Dinlas, there is a greater diurnal temperature variation caused by the warmer weather, while in Llyn Corun, the diurnal variation is smaller. The minimum temperatures of Llyn Corun remain above 20°C throughout the night.

The monthly maximum and minimum temperatures show the same differences as the daily maximum and minimum temperatures. The monthly maximum temperatures were higher than the daily maximum temperatures, while the monthly minimum temperatures were lower than the daily minimum temperatures.

Table 1: Dates on which temperature exceeded 20°C in Llyn Dinlas and Llyn Corun.

<table>
<thead>
<tr>
<th>Month</th>
<th>Llyn Dinlas</th>
<th>Llyn Corun</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>July</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>August</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>September</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>October</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>November</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>December</td>
<td>10th</td>
<td>10th</td>
</tr>
</tbody>
</table>

Table 2: Dates on which temperature fell below 0°C in Llyn Dinlas and Llyn Corun.

<table>
<thead>
<tr>
<th>Month</th>
<th>Llyn Dinlas</th>
<th>Llyn Corun</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>February</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>March</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>April</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>May</td>
<td>10th</td>
<td>10th</td>
</tr>
<tr>
<td>June</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>July</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>August</td>
<td>10th</td>
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<td>October</td>
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<td>November</td>
<td>10th</td>
<td>10th</td>
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<tr>
<td>December</td>
<td>10th</td>
<td>10th</td>
</tr>
</tbody>
</table>
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 convective 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).

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 tendency 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.
Introduction

Laboratory studies

Depending on the prevailing weather conditions, minimum and maximum values could be reached at different times during the day. Minimum temperatures were lower during winter months, while maximum temperatures were higher during summer months. After the sun rose around 6 am, temperatures usually began to rise rapidly soon after. The air temperature in Lijn Coton and Lijn Dhans is shown in the graph:

- **Graph**: Temperatures usually begin to rise rapidly soon after the sun rose around 6 am. Temperatures reach their peak around 10 am. Temperatures drop sharply after 4 pm, and temperatures drop sharply after 4 pm. Temperatures drop sharply after 4 pm.

**Legend for Graph**
- **C.M.**: Cattle milk
- **D.M.**: Dairy milk
- **C.1.**: Cattel 1
- **C.2.**: Cattel 2
- **C.3.**: Cattel 3

**Graph**: Temperatures during July and August 1999

- **Graph**: Temperatures during July and August 1999

**Data for Graph**
- **July**: Temperatures in Lijn Coton and Lijn Dhans during July
- **August**: Temperatures in Lijn Coton and Lijn Dhans during August

**Note**: Temperatures in Lijn Coton and Lijn Dhans during July and August 1999.
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 exclusively 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 appropriate 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.

<table>
<thead>
<tr>
<th>Date</th>
<th>20°C</th>
<th>Llyn Dinas temperatures</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 May</td>
<td>0.49 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>14 May</td>
<td>0.49 ± 0.04 (10)</td>
<td></td>
</tr>
<tr>
<td>21 Aug</td>
<td>2.96 ± 0.47 (10)</td>
<td></td>
</tr>
<tr>
<td>27 Oct</td>
<td>3.65 ± 0.48 (30)</td>
<td></td>
</tr>
<tr>
<td>21 Dec</td>
<td>4.46 ± 0.64 (23)</td>
<td></td>
</tr>
<tr>
<td>25 Feb</td>
<td>5.05 ± 0.60 (10)</td>
<td></td>
</tr>
<tr>
<td>10 Apr</td>
<td>5.70 ± 0.45 (3)</td>
<td></td>
</tr>
<tr>
<td>4 June</td>
<td>5.00 (3)</td>
<td></td>
</tr>
<tr>
<td>21 July</td>
<td>All died</td>
<td></td>
</tr>
</tbody>
</table>

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 (a———a) 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
Before emergence is possible, the effect of temperature was not immediate. It must be noted that emergence would appear to be unimportant prior to emergence. Phloem transport, at least during the first month, is an important factor associated with the regulation of an experimental factor. However, clear data indicate that emergence is possible by keeping mean temperatures at 6°C.

Two simple experiments were set up to test the effect of temperature on the emergence of L. vestimenta. The second experiment, with L. vestimenta, was collected from L. vestimenta in the second to delay the onset of emergence. For the first one, an attempt was made to advance emergence and the temperature was kept at 6°C. The results showed there were no nymphs collected from L. vestimenta. The first experiment showed that there were no nymphs collected from L. vestimenta. The second experiment showed that there were no nymphs collected from L. vestimenta.

It is probable that L. vestimenta contains a leaf or leaflike structure that is more important in the field than it is observed in the field and before any emergence and been observed.
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—sensu 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.

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.
not. Monthly, before June (Lindeman 1942, Hudson 1949). The
sea-water temperature was only slightly less than that of
the open ocean, except in May, when the water was a few
degrees warmer than the open ocean. This is because
the water is not as well mixed in the lagoon as in the
open ocean.

Discussion

The water temperature in the lagoon was consistently
higher than in the open ocean, and this may be due to
the following factors:

1. The water is not as well mixed in the lagoon as in the
open ocean.

2. The water temperature in the lagoon is influenced by
the temperature of the surrounding land.

3. The water temperature in the lagoon is influenced by
the temperature of the surrounding land.

4. The water temperature in the lagoon is influenced by
the temperature of the surrounding land.

5. The water temperature in the lagoon is influenced by
the temperature of the surrounding land.

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the temperature of the surrounding land.

9. The water temperature in the lagoon is influenced by
the temperature of the surrounding land.

10. The water temperature in the lagoon is influenced by
the temperature of the surrounding land.
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 Plecoptera and Ephemeroptera 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.

**Acknowledgements**

I am most grateful to Professor T. B. Reynolds for advice during the study and for helpful comments on the manuscript. Dr Alan Buse kindly made available the meteorological data for Cwm Dyli. Laboratory facilities were provided by the late Professor F. W. R. Brambell and by Professor J. M. Dodd. The work was carried out during the tenure of an N.E.R.C. Research Studentship.

**Summary**

1. Temperature data are presented for two lakes in North Wales, Llyn Coron and Llyn Dinas. Both lakes are low-lying, 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
References


