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The fauna in the vegetation of a moorland fishpond

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With 9 figures and 8 tables in the text

Contents

1. Introduction

Whether the purpose of a study is the academic one of discovering more about the structure and composition of a community or whether it is the practical one of finding out what there is for fish to eat, the following fundamental information is required:

1. What species are present;
2. What the life histories of at least the common species are;
3. How numbers of each species vary:
   a) from place to place within the piece of water;
   b) at different stages of the aquatic life;
   c) from year to year.

In order to find out about life history it is necessary to count and measure specimens. If, later, and this is a stage that the present investigation has not reached, specimens in each length-group are weighed, data are to hand for a calculation of biomass and production.

The overall purpose of the present investigation was to study the population of a fishpond in which there were no fish with a view to finding out what the effects of predation were when fish were introduced. A study of Hodson's Tarn started in 1955, and in October 1960 500 small *Salmo trutta* were introduced into it. The present paper describes the fauna of the tarn up to 1960, that is during the period when there were no fish in it, though one or two observations made later are included. Actually the tarn was never completely free of fish, as it proved impossible to prevent *Anguilla* migrating into it, but it is believed that there were never more than a few of these.

Attention was confined to the animals of the vegetation, and among them microscopic groups such as the Protozoa have been ignored. Chironomidae have not been identified. The resulting gaps are regrettable, but it seemed essential to limit the investigation to what could be achieved by the personnel available. The entomostraca have been studied by Mr. W. J. P. SMYLY (1957) and an account of the water mites will be published by Mr T. GLEDHILL.

The Odonata are the subject of an earlier paper, in which the fishpond and the methods of collecting used are described (MACAN 1964). A list of the species taken and comparison with other ponds and with lakes are given by MACAN (1963).

2. Description of the tarn

The tarn is 4427 m² in extent and 3 m deep at the deepest point. It is a typical artificial moorland fishpond, poor in electrolytes, though not extremely acid. For faunistic purposes four types of vegetation can be recognized:

1. emergent: beds of *Carex rostrata* fringe the margin near the inflow end, and there is one patch nearer the dam. There are also patches of *Eleocharis palustris* and *Glyceria fluitans* at the edge in shallow water. The

Glyceria has been dying out while the investigation has been in progress and *Carex* stands have become less dense (600);

2. floating-leaved: there is a big bed of *Potamogeton natans* between the *Carex* beds at the inflow end. It has been extending during the period of observation and has invaded areas where previously only *Carex* grew, as this plant has grown less dense (600);

3. sward: most of the shallow water down to a depth of about 1 m is covered by *Littorella uniflora,* growing with great vigour. The leaves are up to 15 cm long, in places there are upwards of 1000 plants/m^2, the number per unit area has been increasing in those parts of the tarn in which plants were fairly scattered at the start of the investigation, and the patches have been increasing in area (500);

4. Milfoil: *Myriophyllum alterniflorum* grows in most of the deeper parts of the tarn, generally thickly. Towards the end of the period under review the forestlike cover provided by this plant became thinner, so much so that collecting in it was discontinued. At the time of writing (1963) it is as flourishing as it was at the beginning (2400).

The figures in parentheses at the end of each of the four preceding sentences indicate the area covered in m^2. They are approximations to the nearest hundred of the figures quoted by MACAN (1964). The use of a more exact figure would give a misleading impression of accuracy by minimizing the difficulty of determining a precise boundary to the area covered by any one kind of plant and ignoring that this may have increased during the course of the investigation.

Posts were driven in at intervals around the tarn and numbers on them were useful for indicating the positions of collecting stations.

In the exceptionally cold winter of 1962/63 ice came and went again in both November and December, and was continuous from late December to early March, but in mild winters it covers the tarn for a much shorter period. A thermograph was installed in 1957 and there are records for all subsequent years. It is convenient to consider here the years 1958 to 1962 inclusive, since temperature could not have been affected by the introduction of fish. The date on which the water begins to warm up is variable; for example, 6° C was reached in late January in 1960 but not until the end of March in 1958. There was a similar wide gap between the earliest and latest dates on which the next three temperatures were reached: 7° C 7 weeks, 8° C 5 weeks, 9° C 6 weeks. In contrast, in each of the five years, 10° C was reached some time in mid-April and there were only two weeks between the earliest and the latest date. 13° C was invariably reached between mid-April and early May, but after that the gap widened again; for example, in 1959 13° C was not reached until 6 May but thereafter for the next nine days the average rise was 1° C per day. In 1958 13° C was reached at the beginning of May, but 14° C not until over a month later.

In every year except 1961 the temperature rose above 20° C. In 1959 there were 340 hours above 20° C though 23° C was not reached. In 1960 there were 226 hours above 20° C but for 4 hours the temperature was between 25° and 26° C.

From 16° C downwards there is less difference between the earliest and latest date when each temperature is reached than during the warming-up period.

The level of these artificial tarns in the Lake District generally fluctuates very little, but that of Hodson's Tarn fell to about 25 cm below normal level during dry spells, because there was a leak in the dam.

3. Methods

3.1. The aquatic stages

Most of the collecting was done with a pond-net which, at each station, was pushed along a line 2 m long. The advantages of the net are that it collects a large number of animals without bringing in much debris from which they have to be sorted, and without harming the vegetation. The disadvantages are that it is not quantitative, that its mesh had to be coarse enough (10 meshes/1 cm) to allow the smallest animals to pass through because a finer one was clogged by epiphytic algae, and that it is subject to certain errors, which are discussed by Macan (1963, p. 282).

Quantitative samples were obtained by a sampler (SCS) which, designed for the purpose, has been described elsewhere (Macan 1964). It appeared to fulfil its intended function well, but it had the disadvantage that it was sealed by being driven into the mud in which the plant was growing. Sorting the animals from the leaves, roots and mud so obtained took time, and the complete removal of the plant carpet from the area sampled also set a limit to the number of samples that could be taken. Consequently the total number of specimens caught by this sampler was small.

Collections with the net were made at about 11 stations at the beginning but, as experience accumulated, some of these were abandoned and others added, the final number being 13. In 1955 the tarn was visited once a fortnight and collections made from about half the stations. It soon became apparent that collections from every station once a month were preferable, and this was the regime in 1956 and 1957. These having yielded all the information thought to be necessary to work out life histories, three collections a year were deemed sufficient for 1958, 1959, and 1960: in spring (late April or early May); in summer (mid June to early July); and autumn (mid September to early October).

Collections with the SCS did not start until the autumn of 1957 and none were made in spring or summer until 1959.

3.2. Emerging adults

Frames of wood enclosing $^1/_8$ or $^1/_2$ m², and provided with little curtains to prevent waves washing anything in or out of them, were moored at various points in the tarn. Wide variation in the catch at different places made it clear that the frames were valueless as indicators of absolute numbers, but visits to them almost every day during the critical period in 1956 and 1957, and the removal of every cast skin, gave valuable information about the emergence period of several species. The method, however, was time-consuming, and, from 1959 onwards, emerging adults were caught in a floating cage that was visited once a week.

4. The Fauna

4.1. The species considered individually

It is convenient, for the presentation of the results, to distinguish the following categories:

4.11. Abundant species:

4.111. genera in which there is more than one species;

4.112. genera in which there is one species.

4.12. Species which, though never abundant, are taken regularly.

4.13. Species taken occasionally in small numbers.

This appears to provide reasonably clear-cut distinctions, but some scarce species have been treated with the abundant ones in the first group is another species in the same genus is abundant.

4.11. Abundant species

4.111. Genera in which there is more than one species

"Gause's hypothesis" of British ecologists, or "Monard's principle" of continental workers has been renamed "The competitive exclusion principle" by Hardin (1960) in a critical essay. If it is valid, which one school of thought doubts (see Macan 1963, pp. 100—107, for a discussion of freshwater aspects of the idea), when two species in the same genus are found in a place such as Hodson's Tarn, they should differ in their ways of life.

The following genera are represented by more than one species: *Leptophlebia, Cloeon, Corixa, Deronectes, Haliplus,* and *Phryganea.* Modern authors (for example Southwood and Leston 1959) have split *Corixa* into several genera, but, as I have no reason to suppose that the splitting and lumping which have alternated in the past have come to an end, I have retained the genus *Corixa* in an older wider sense. *Enallagma cyathigerum* and *Pyrrhosoma nymphula* (Odonata), discussed elsewhere (Macan 1964), are always placed in different genera, as far as I know, yet they have identical feeding habits and life histories not sufficiently dissimilar to take them out of competition with each other. They differ in oviposition habits, which lead to *Enallagma* occurring predominantly in deeper parts of the tarn, whereas *Pyrrhosoma* is confined to the shallower.

Leptophlebia

Since this was one of the most numerous organisms in the tarn, and since the certain distinction of *L. marginata* and *L. vespertina* is time-consuming, the two were not separated in many of the collections.

Life history. Hatching had started by the end of July in 1957 (table 1), but to judge from the number of very small nymphs, it did not reach a peak before September. How far the further increase in November is due to more specimens, and how far to the attainment of a size at which the nymphs could not pass through the net, is not known. There was some growth throughout the winter and an increase in the rate in the spring. In Windermere (MOON 1938) hatching is later and nymphs correspondingly smaller on any given date.

Adults emerge from about mid April to late June, with a peak in the second half of May (fig. 1). In 1956 particular care with the identity of

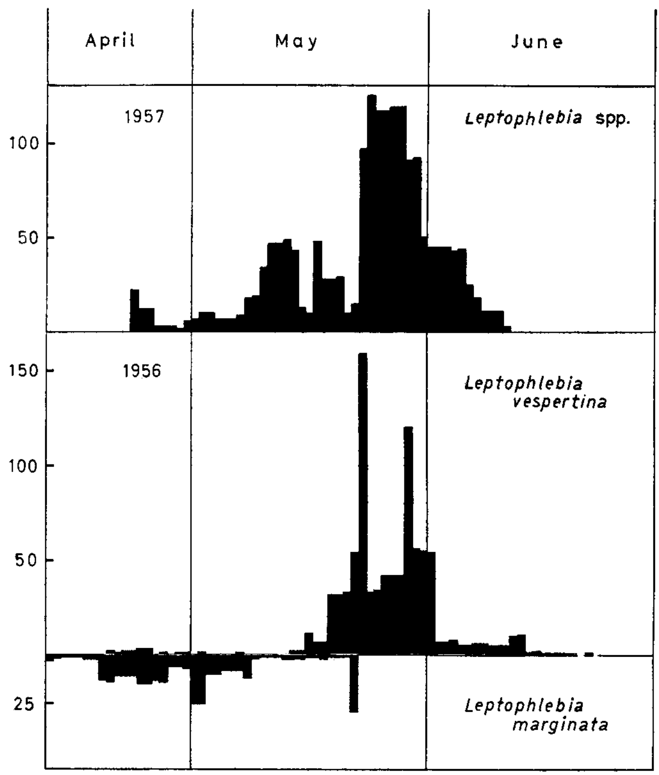

Fig. 1. *Leptophlebia*. Number of cast skins in frames on successive days.

the specimens made it clear that the main emergence of *L. marginata* is nearly a month earlier than the main emergence of *L. vespertina* (fig. 1).

Distribution. There was a marked preponderance of the 1957 year-class in *Littorella* (table 1), but comparison with other years shows that this must have been due to an accident of oviposition or survival, because there was no station in shallow water where nymphs were not taken in

Table 1. *Leptophlebia* spp. in HODSONS TARN. 1957 Year-class

Date	*Litt.* 6—7 sh	*Litt.* 6—7 dp	*Litt.* 9—10	*Litt.* 10—12	*Litt.* 18—20	*Glyc.* 16—17	*Glyc.* 7—9	*Carex* A—C	*Carex* 14—15	*Carex* 4—5	*Pot. natans*	*Myr.* 3—20	*Myr.* 7—20	total
1957														
30 July — 1 Aug.	3		9	0	1	4	0	0	1	1	0	0	0	19
29 Aug. — 5 Sept.	—		57	123	156	31	29	0	5	31	0	9	20	461
1—8 October	909	240	—	—	—	140	709	75	39	154	40	56	69	2431
6—13 November	1,747	544	638	463	275	387	551	84	254	170	89	56	57	5315
9—13 December	541	775	—	516	411	412	422	98	93	—	138	42	26	3474
1958														
3—7 March	547	208	—	230	—	56	154	118	109	203	94	—	53	1772
28 April — 2 May	301	151	173	227	163	539	247	39	132	168	0	1	3	2144

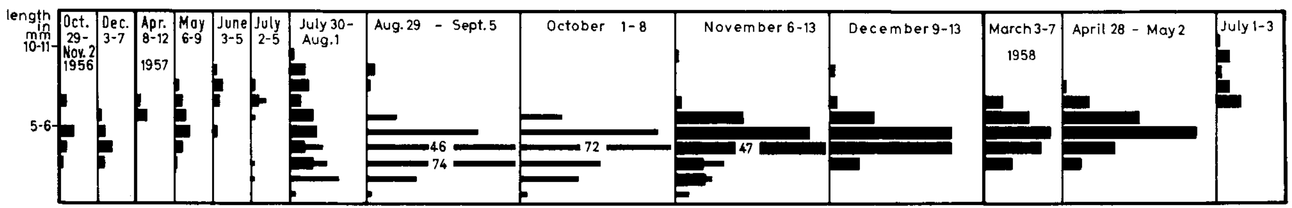

Fig. 2. *Cloeon dipterum* (broad) and *Cloeon* sp. (narrow): numbers in 1-mm-size-groups in successive months. Scale: distance between first two vertical lines = 10 specimens.

large numbers at some time during the five years of the investigation. In deeper water, that is in *Potamogeton natans* and *Myriophyllum*, recently emerged nymphs were always scarce. The figures in table 1 suggest that some of them later migrated into the middle of the tarn and returned before emergence but that most spent their whole lives in shallow water. Oviposition was not observed.

Difference between the two species. No difference in habitat was observed. *L. marginata* emerged before *L. vespertina* and there was some evidence that it hatched earlier and was larger at all times of the growing period.

Cloeon dipterum

Life history. The smaller specimens were not always identified and the smallest could not be. These unnamed specimens fit the figure for *C. dipterum* (fig. 2), not that for *C. simile*, and presumably, therefore, belong to the former species.

In 1960, the only year when adults were caught in the cage in any number, emergence started early in June and lasted two months with a peak in the middle of the period. This suggests one generation a year. On the other hand the capture of small nymphs in July and large ones in September in 1957 (fig. 2) suggests a quick summer generation. Since in 1956 nymphs were few and in subsequent years collections were made less often, there is not enough evidence for a firm conclusion. It is possible, however, that, as Brown (1961) found, *C. dipterum* has one generation per year in a cool summer, but two in a warm one such as 1957 was.

Distribution. Nymphs were found everywhere but particularly in *Carex* and *Potamogeton natans*. The smallest nymphs were notably abundant in *Carex*.

Cloeon simile

The nymphs, like those of *C. dipterum*, change little in size during the winter, but they start to grow earlier in the spring. Few specimens were taken in frames or cages but males were caught dancing near the tarn. This occurred in late May, and in 1956, when specimens were abundant, the last dancer was captured on 17 June. Emergence is several weeks earlier than that of *C. dipterum*. It is evident from fig. 3 that there is a summer generation that emerges in the autumn. In 1962 a swarm was noted on 26 September.

Distribution. This species was also recorded at all stations but its greatest numbers were in the vegetation in the deep water (fig. 9).

Difference between the two species. There is a difference of habitat and furthermore *C. simile* starts to grow in the spring sooner than *C. dipterum*.

Corixa

Only *C. castanea* and *C. scotti* occurred in sufficient numbers to warrant analysis, but three more species in the genus occurred regularly (table 4) in small numbers and there were six casuals in the family (table 5).

Life history. Nymphs, in which stage the two species were not distinguished, were found from June to October with a peak in June, July and August. Numbers of adult *C. castanea* began to rise in late July, but those of *C. scotti* generally changed little. A sudden increase in the numbers of this latter species between early October and early November 1957 was too late to be due to local breeding, and, together with another in May 1960, was probably due to immigration.

Distribution. No specimen of *C. castanea* was ever taken in the *Myriophyllum* and few in *Potamogeton natans*. It was numerous everywhere in the shallow water round the edge of the tarn (tables 2, 3). *C. scotti* occurred here also but tended to be most abundant in deeper water; the two largest average catches were, for example, in *Littorella* 6—7 deep and *Potamogeton natans* (fig. 9). This relationship between the two species is not quite the same as that described by MACAN (1938 p. 16), who writes: "*S. scotti* occurs where vegetation is sparse or absent, *S. castanea* where vegetation is dense."

Deronectes

As the only other species in the sub-family were no more than occasional visitors (table 5), it is likely that all records of "*Hydroporus* larvae" refer to *Deronectes*. They were taken as early as mid May and as late as the beginning of November, but the peak of abundance was in July and August. The highest total was 31 at 12 stations in August 1956. Nearly half were taken in *Myriophyllum* on that occasion but in other collections distribution was more uniform except that specimens were rarely taken in *Carex*. However the small number of larvae relative to adults taken suggests that most occurred somewhere where the net did not catch them. As the two could not be distinguished in the larval stage, the life histories could not be made out.

The highest catch of adult *D. assimilis* was 119 at 11 stations in December 1956, and the lowest 6 at 11 stations in April 1957 and 1959. Generally about 20 specimens were taken and no consistent pattern of rise and fall with the seasons could be observed. The beetles were most abundant in *Littorella* (fig. 9).

D. duodecimpustulatus was scarcer than the preceding, and, though there were only two occasions (April 1959 and May 1960) when no specimens were caught, the highest total was 9. Its distribution is similar to that of *D. assimilis*, and it is impossible to make out whether the two differ in way of life.

Table 2. *Corixa castanea* in Hodsons Tarn. Numbers caught in the net in autumn.

	Litt. 6—7 sh	*Litt.* 6—7 dp	*Litt.* 9—10	*Litt.* 10—12	*Litt.* 18—20	*Glyc.* 7—9	*Glyc.* 16—17	*Carex* A—C	*Carex* 14—15	*Carex* 4—5	*Pot. natans*	total
1956 Sept. 24—28	16		—	5	12	24	8	10	20	—	3	98
1957 October 1—8	25	5	—	—	—	48	42	31	8	7	1	167
1958 Sept. 10—12	21	11	—	11	3	12	29	11	10	1	0	109
1959 October 2—5	—	12	7	11	3	—	—	7	10	0	1	51
1960 Sept. 20—29	8	0	—	0	0	4	5	3	7	13	0	40
Average	18·0	7·0	7·0	7·0	4·5	22·0	21·0	12·4	11·0	5·2	1·0	
	excluding 1956											

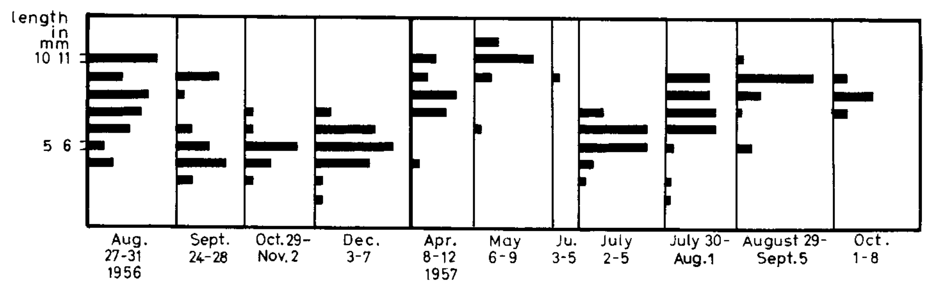

Fig. 3. *Cloeon simile*. Numbers in 1-mm size-groups in successive months. Scale: distance between first two vertical lines = 10 specimens.

Table 3. *Corixa castanea* in Hodsons Tarn. Numbers caught in net in spring and summer.

	Litt. 6—7 sh	*Litt.* 6—7 dp	*Litt.* 9—10	*Litt.* 10—12	*Litt.* 18—20	*Glyc.* 7—9	*Glyc.* 16—17	*Carex* A—C	*Carex* 14—15	*Carex* 4—5	*Pot. natans*	total
1956 April 10—13	7		6	2	2	3	—	8	23	1	2	54
June 19—26	7		6	4	7	5	—	2	2	2	2	37
1957 April 8—12	0		—	0	—	3	0	0	0	0	0	3
May 6—9	—		1	0	0	2	1	2	1	—	0	7
June 3—5	3		—	0	0	1	0	2	3	0	0	9
1958 March 3—7	7	11	—	0	—	1	3	5	13	1	0	41
April 28 — May 2	1	2	4	4	1	2	4	6	6	0	0	30
July 1—3	1	0	—	7	4	4	13	6	0	0	0	35
1959 April 20—21	3	11	—	0	1	—	4	6	7	5	0	37
June 16—18	2	0	—	10	2	1	3	4	3	0	0	25
1960 May 9—11	3	1	2	1	7	0	1	5	1	2	0	24
July 6—8	4	0	1	1	0	1	1	2	0	1	3	14
Average	3·0	3·6	3·3	2·4	2·4	2·1	3·0	4·0	4·9	1·1	0·6	

(Averages for Litt. 6—7 sh and 6—7 dp: excluding 1956 and 1957)

For 1956 and 1957, each *Litt.* 6—7 value is printed once across the sh and dp columns together.

Haliplus

One of the surprising things about the collections was the very small number of larvae taken: 8 in the six years. It was therefore impossible to make out the life history and we were also unable to separate the two species in the larval stage.

The highest total of adult *H. fulvus* was 57 at 12 stations in June 1959, the lowest 9 at 10 stations in September 1960, but generally between 20 and 40 specimens were taken, and no seasonal trend was evident.

H. fulvus was most abundant in *Glyceria* and *Eleocharis* (fig. 9). It was much less plentiful in the deep than in the shallow station between posts 6 and 7, and only 1 specimen was taken in the *Myriophyllum*. It is evidently a species that inhabits shallow water mainly among emergent vegetation.

Five specimens of *H. confinis* were the most ever taken in one series of collections and frequently none were recorded. It was nonetheless a regular member of the fauna turning up every year. Whether its way of life differs from that of *H. fulvus* cannot be determined.

Phryganea striata and *P. varia*

Both species occurred in the emergence trap, *P. striata* late in May, *P. varia* in June and early August. The larvae were not distinguished. The development of the 1957 year class, shown in fig. 4, is typical. Most eggs

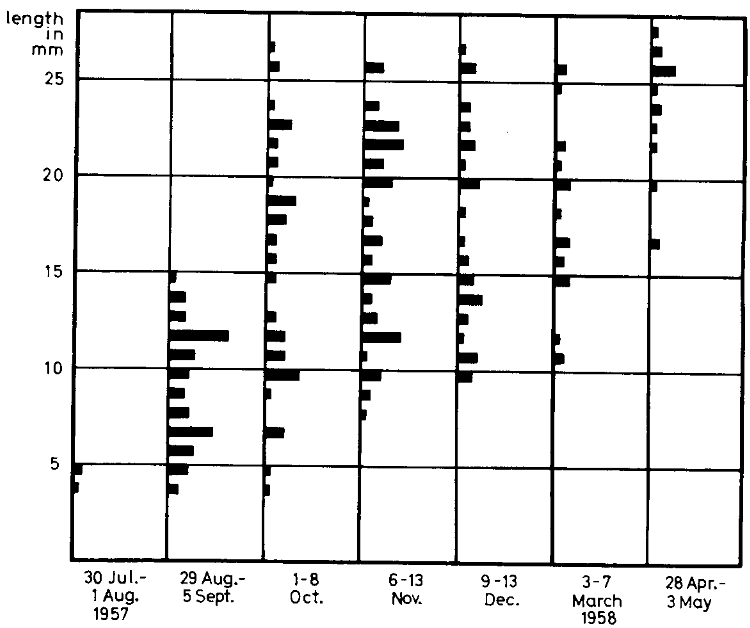

Fig. 4. *Phryganea* spp. Numbers in 1-mm size-groups.
Scale: distance between vertical lines = 20 specimens.

hatch in August and there is growth up to October, after which comes a pause until March. Growth must then be rapid before pupation.

Phryganea larvae were found everywhere, but were most abundant in *Glyceria* and *Eleocharis*, and in *Carex* (fig. 9).

Chironomid and ceratopogonid larvae

Species, of which 45 were recorded from Three Dubs Tarn, were not identified.

Larvae of chironomids were most abundant in *Littorella* and least in the emergent vegetation, with *Potamogeton natans* and *Myriophyllum* coming together in between. Larvae of ceratopogonids were most numerous in *Potamogeton* and rather scarce in the *Myriophyllum*.

Numbers of both tended to reach a maximum sometime during the summer and to fall in the winter. The largest catch of chironomid larvae was in June 1959 (table 6), and of ceratopogonid larvae in June 1956 when 44 were taken at 12 stations, but, as many larvae were small enough to pass through the net, nothing is known about the relation between numbers present and numbers caught. Pupae of chironomids were recorded in all months from April to November inclusive.

4.112 Genera in which there is one species

Limnephilus marmoratus

Eggs start to hatch towards the end of July and the larvae continue to grow at least till December (fig. 5). Adults occurred in the emergence trap throughout June and July.

The larvae were most numerous in emergent vegetation.

Triaenodes bicolor

Adults first appear in the emergence trap in June and most are caught in July. The new generation of larvae is abundant in August but there is little growth till the following spring. In late April some specimens start to grow fast but others are slower and there is soon a big range in size (fig. 6). The decrease in numbers in winter is seen each year and presumably indicates that the larvae have retired to some place where they are less likely to be taken with the net. This species is abundant everywhere but least in *Littorella* (fig. 9).

Holocentropus dubius

Emergence took place in June and the first young larvae were collected in July. Growth of most specimens was rapid and many were almost full grown by the end of the year (fig. 7).

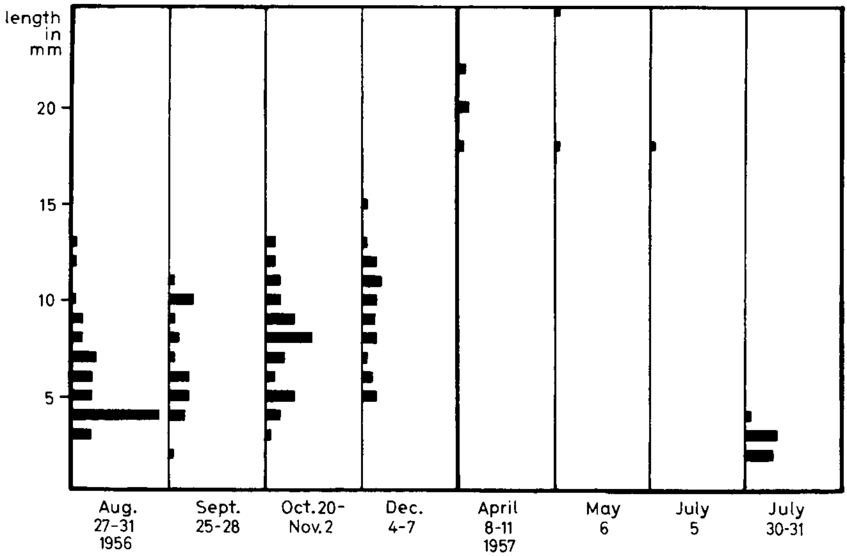

Fig. 5. *Limnephilus marmoratus.* Numbers in 1-mm size-groups.
Scale: distance between vertical lines = 20 specimens.

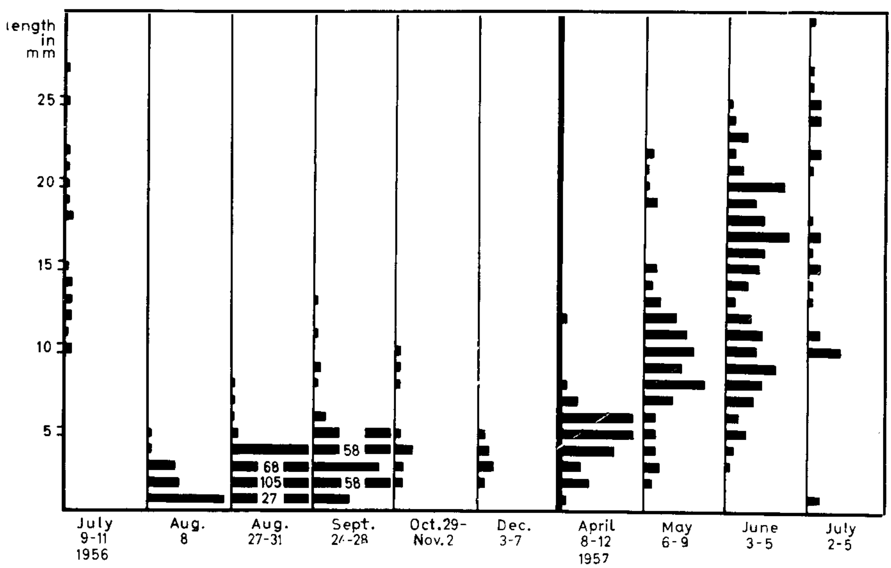

Fig. 6. *Triaenodes bicolor.* Numbers in 1-mm size-groups.
Scale: distance between vertical lines = 20 specimens.

This was one of the few species that were most abundant in the deeper parts of the tarn (fig. 9).

Leptocerus aterrimus

MORGAN (1956) reports that this species laid its eggs all over two Scottish lochans, 15 and 1.8 hectares in extent, but that, from October to April, no larvae were found in water deeper than 2.4 m. Most were between 1.2 and 1.8 m. In June many larvae moved into shallow water and pupated. Adults emerged in June, July and August at the lower of the two lochs and a month later at the higher. Eggs hatched within three weeks and the species overwintered as a small or medium-sized larva. Growth took place before October and after April.

The sequence of events in Hodson's Tarn is evidently similar, and numbers caught rise sharply in June or July. In one or other of these months

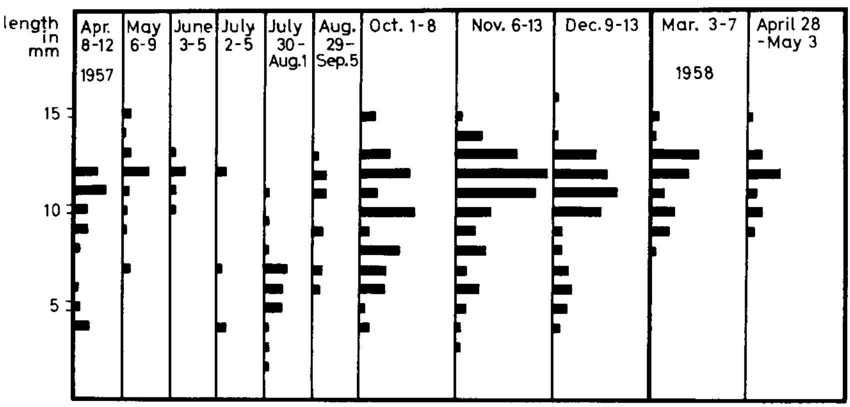

Fig. 7. *Holocentropus dubius*. Numbers in 1-mm size-groups.
Scale: distance between first two vertical lines = 10 specimens.

42 specimens were taken at 7 stations in 1955 and the totals were similar in 1956 (36) and 1958 (49) when, however, collections were made at more stations. In 1959 and 1960 only 3 and 1 specimens respectively were taken during the whole season.

Numbers were low in the *Potamogeton natans* and the *Carex* at the inflow end of the tarn, not much higher in *Myriophyllum* and greatest in *Littorella*.

Notonecta obliqua

Eggs hatch in May and adults appear in July.

Nymphs lurk at the surface waiting for their prey, and the territory of a specimen seems to be larger in each instar. Whether a nymph enlarges its territory by eating its neighbours was not ascertained.

Between 30 July and 1 August 1957, 19 adults were captured, the largest total in any year, but this, the product of an unusually great number of nymphs, was only half as great a month later. Whether the adults killed one another, or whether some flew away, was not discovered.

Nymphs occurred all over the tarn.

Limnaea pereger

Egg-masses appear late in April and snails of the new generation were first recorded early in June. After the eggs have been laid, the adults die. Growth is slow and some specimens are far from full size in October.

Generally numbers are highest in midsummer and then fall fairly rapidly to a level which does not change much to the end of the generation. In 1957, when the summer total was low, the decline was less and the final numbers (29 at 13 stations at the end of April 1958) were similar to those of the preceding and succeeding year-classes.

The largest populations just before egg-laying were nearly always in *Littorella,* but there were only three stations, *Myriophyllum* 3—20, *Littorella* 18—20 and *Carex* 4—5, at which the resulting young were not taken in abundance at least once during the investigation. There was always a good summer population in *Potamogeton natans* and *Carex* A—C, but survival over the winter was always poor in the former and often poor in the latter.

Erpobdella octoculata

Distribution. *Erpobdella* occurred everywhere, but most abundantly in *Potamogeton natans,* where 25 % of the total was taken. Numbers were similar in *Myriophyllum* and *Littorella,* and somewhat higher in emergent vegetation than in these two plants.

Life history. The numbers caught are not sufficient to warrant any conclusion except that the life history is probably the same as that observed in Berkshire by MANN (1953). The new generation emerges in late summer and most of its members reproduce in the following July. A few of them survive to breed a second time in their third summer. A small proportion of specimens does not attain maturity after one year and breeds in the third and fourth summer.

Nymphula nympheata

According to WESENBERG-LUND (1943) adults appear in July and larvae soon afterwards. After a period of growth the caterpillars go to the bottom to spend the winter. Activity is renewed in the spring and pupation takes place about midsummer.

In Hodson's Tarn the largest catches were in late August or September and numbers had dropped considerably in October. Presumably they had entered the winter resting period, and there was considerable mortality during this to judge from the numbers taken in the following year. Autumn totals were 72, 26, 82 and 73, in 1955, 1956, 1957 and 1958 respectively. In 1959 and 1960 there were few specimens, but this could have been due to the lateness of the date. On the other hand the numbers taken at other times suggest a diminishing population. The greatest number ever taken after the winter was 18 in June 1956.

This was the only species confined to one part of the tarn. It makes its case from the leaves of *Potamogeton natans* and there was probably nothing else in the tarn that would have served this purpose. The specimens found in *Carex* are easily accounted for by the fact that some specimens of *Potamogeton natans* grew among that plant. Altogether 4 specimens were found in other parts of the tarn, whither they could have been blown by the wind or carried by scientific apparatus.

Rana temporaria and *Bufo bufo*

Frogs and toads spawned in the tarn each year but the tadpoles were not distinguished. Tadpoles could be seen swimming all over the tarn or resting on the surface of the vegetation. Even after dispersal from the neighbourhood of the spawn-jelly, they tended to aggregate, and it was obvious to the naked eye that this made quantitative estimation impossible. This was confirmed by a haul of 533 tadpoles in *Littorella* in May 1960, contrasted with a next-highest total in this or any other year, of 28.

No tadpoles were seen after early July.

Triturus helveticus

The highest total was four newts at 10 stations in April 1956. Adults were scarcer after July but some were taken in later months up to December.

Most larvae were taken in *Littorella,* few in *Myriophyllum.*

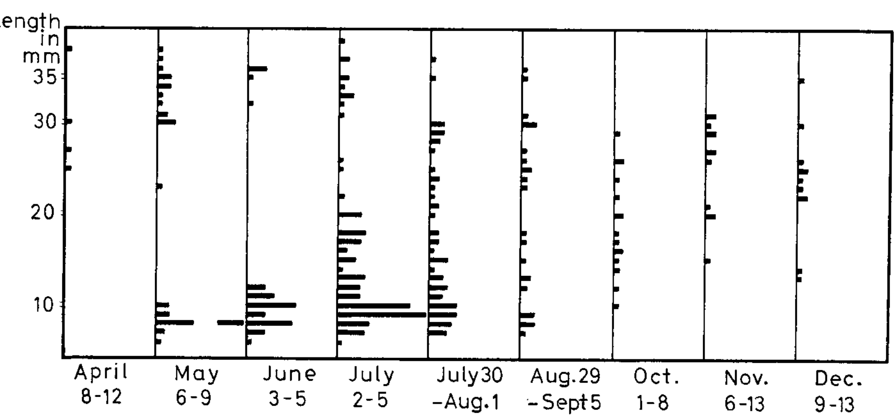

Fig. 8. *Triturus helveticus* Numbers in 1-mm size-groups in 1957. Scale: distance between vertical lines = 20 specimens.

Small larvae appear first in May and are ready to leave the water in August, but larvae which hatch late in the season overwinter and metamorphose in the following summer (fig. 8).

Gammarus pulex

Gammarus is found everywhere but in greatest numbers in *Carex*, possibly because this is nearest the inflow, which is the animal's main breeding place.

4.12 Species which, though never abundant, are taken regularly

The species in this category and the number of each caught each year are shown in table 4. (It will be remembered that collections were more frequent during the first three years than during the last three.) *Dytiscus* larvae were taken each year and their occurrence in every month suggests that *D. marginalis* as well as *D. semisulcatus* was breeding in the tarn. Therefore only two of the seven species were not found every year and it would be rash to infer from this that they were absent, as numbers were always low.

Table 4. Hodsons Tarn.
Numbers per annum of species taken regularly but always in small numbers.
a = adult, l = larva.

	1955	1956	1957	1958	1959	1960
Corixa distincta	9	2	6	5	2	12
Corixa linnei	3	6	1	5	5	9
Corixa dentipes	20	8	7	1	8	3
Dytiscus semisulcatus	1	2	—	—	1	—
Acilius sulcatus	—	—	2	1(1)	2(a)+1(1)	4(1)
Rantus exsoletus	1	5	4	7	6	7
Nemoura cinerea	—	—	1	3	1	—

These species, then, are characteristic members of the tarn fauna notable for regularity of occurrence combined with consistently low numbers.

Larvae thought to be those of *Rantus* were taken every year. *Gyrinus* larvae were taken every year in all parts of the tarn except *Myriophyllum*. They occurred from April to September. Twenty in 1956 was the greatest number taken in one season. The species was not identified.

4.13 Species taken occasionally in small numbers

The list of casuals is shown in table 5. *Theromyzon tessulatum* travels from place to place attached to the back of the throat of ducks; the occurrence of the single *Glossiphonia* was more unexpected. All the other casuals can fly. *Plea* caused surprise, as only two specimens had been taken previously in some twenty years collecting water-bugs in the Lake District.

For the sake of completeness it should be mentioned that occasional hydroptilid, hydrophilid and tabanid larvae were taken. Rhabdocoeles were recorded from time to time but, as they were small enough to pass through the net, they could have been commoner than the figures show. The same

Table 5. HODSONS TARN. Total number of casual species taken.

	1955	1956	1957	1958	1959	1960
Corixa praeusta	—	1	—	2	—	—
punctata	—	—	1	—	—	—
sahlbergi	—	—	—	—	3	—
fossarum	—	—	—	—	—	1
Glaenocorisa propinqua	—	—	—	—	—	1
Cymatia bonsdorffi	—	—	—	—	—	1
Notonecta glauca	—	—	—	1	—	—
Nepa cinerea (nymph)	—	—	—	1	—	—
Plea leachi	—	1	—	—	1	2
Agabus sturmi	—	2	—	—	—	—
Hydroporus palustris	1	—	—	—	—	—
gyllenhalii	—	1	—	—	—	—
Glossiphonia complanata	—	1	—	—	—	—
Theromyzon tessulatum	—	—	—	2	—	1

applies to small oligochaetes, a few of which were identified as *Stylaria lacustris*. In the early years some specimens of *Hydra* were noted, but this is another species for which the net is not a reliable instrument of capture.

4.2. The fauna considered as a whole

When basic facts of the type just discussed have been gathered, progress can be made in two main directions. One is the study of production; the other a study of the community — an examination of how far it is legitimate to refer to the assemblage found as a community, an attempt to define the community or communities, and to discover what factors govern presence or absence and the relative numbers of those species that do occur. Work on one body of water permits only limited conclusions about presence and absence and relative numbers; the pioneer cannot do much more than put facts on record and leave explanations to those who, coming later, can make comparison.

Whichever line a worker decides to follow, he must give careful attention to life-histories; in both production and community studies due consideration must be given to the dimension of time.

Both lines must be based on numerical data, community studies demanding comprehensiveness to which some accuracy may be sacrificed, production studies the greatest accuracy possible but only of the numerous species. Production studies require that the animals should be weighed, and, at this has not yet been done, the emphasis here is on community studies.

4.21 Life histories

Classification is necessary in order that ideas may be presented coherently, but it brings in its train the danger that too much emphasis is placed on features common to species that fall into one category and too little on those in which they differ. Life histories can be divided into three main groups according to whether they take over one, one, or less than one year for completion.

1. Development takes longer than one year. *Pyrrhosoma nymphula, Enallagma cyathigerum, Aeshna juncea* and *Erpobdella octoculata.* The two small dragon flies are on the wing in summer, and their eggs hatch in late summer and autumn. After that the life history is versatile. Some nymphs may grow enough before the onset of winter to be ready to emerge in the following year, but generally the overwintering nymphs are small, growth takes place in the second summer, and emergence in the summer after that. If conditions are unfavourable, however, the whole process may take a year longer. *Aeshna* is different in that the flight period is later and the first winter is spent in the egg.

2. One generation in one year.

a. Summer species. Most animals in the tarn lay eggs early in the summer, complete development before autumn, and overwinter as adults. Larvae of *Triturus* can overwinter if they have not metamorphosed before a certain date, and growth of *Limnaea pereger* goes on late into the winter and possibly all through it.

Lestes sponsa, which overwinters as an egg, is the only insect in this group with an aerial adult.

b. Winter species. All the insects whose adults are not aquatic, except *Lestes sponsa,* overwinter as larvae and disappear from the water or become very scarce for a shorter or longer period during the summer. Of the insects whose adults are aquatic, only *Dytiscus semisulcatus* occurs in the larval stage in winter.

3. More than one generation in a year. In a cold summer *Cloeon dipterum* is probably a typical winter species, but in a warmer one it can complete a quick generation within the summer. *C. simile* regularly has a life history of this type.

Gammarus pulex produces a number of broods during its long breeding season (Hynes 1955).

A life history may be anachronistic, having remained unchanged after the passing of conditions to which it was adapted (NIELSEN 1951), but it is difficult to believe that such rigidity does not lead to the disappearance of the species before long. Generally then it may be supposed that a life history has been modified so that the species is ready to breed at the most favourable time and to offer the greatest resistance when conditions are unfavourable. Climate, of which temperature is probably the most important component in fresh water, may be the overriding factor, but biotic influences may be paramount, and there is adaptation to make the best use of the food supply when most is available or to avoid the time of greatest activity of some predator. Much also depends on whether the adult lives in the water or not. A cold-water stenotherm such as *Salmo trutta* or *Planaria alpina* breeds in winter. An Ephemeropteran or Plecopteran could not do this because the adult could not emerge through the ice, and if, because the water was flowing or there was no ice for some other reason, it could, it might find the air temperature so low that the activity necessary for reproduction was not possible. For this reason insects of all kinds with aerial adults are on the wing in summer and spend twe winter as a larva or as an egg. In contrast, if the adult is aquatic, that seems to be the stage most resistant to winter conditions to judge from the number of species which pass the winter in it.

It is easy to propound such speculations, but less easy to interpret observed facts in their light. For one thing it is difficult to discern what adaptation there has been, owing to the impossibility of knowing exactly the circumstances under which any particular species lived previously; one may see what it is adapted to now but one cannot know what it became adapted from. Some species are northern in origin and accordingly cold-water stenotherms. If their adults are not aquatic, they are winter species with an early emergence and sometimes a long period in the egg, which seems to be the stage most resistant to unfavourably high temperatures (MACAN 1963 p. 142). Possibly the two species of *Leptophlebia* belong to this category, for there is a long period in summer when there are no nymphs, and MOON records later hatching in Windermere, which cools down more slowly in winter. Of the other winter species, *Phryganea* and *Limnephilus* could belong to this category but their small numbers make any conclusion uncertain. *Triaenodes* assuredly does not, for larvae are found as late as July, in which month most emergence takes place, and, moreover, the small numbers found in winter (fig. 6) indicate hibernation of some kind, like that recorded in *Nymphula.* Nor is *Holocentropus,* whose adults emerge in June and whose small larvae appear in July, a cold-water stenotherm. These and perhaps all the other species in the tarn, entered Britain from more southerly latitudes after the Ice Age and have a higher optimum temperature, though what it may be there is no means of knowing. Their problem is that of tiding over a period of unfavourably low rather than one of unfavourably high temperature. *Lestes sponsa,* with its overwintering diapause egg (CORBET 1956) and quick growth after hatching in the spring, has a life history well adapted to the climate of Hodson's Tarn, but there may be disadvantages in the rigidity of it. Range northwards may be limited by a summer temperature insufficiently high to bring the adults out before the air temperature is too low for them (CORBET, LONGFIELD and MOORE 1960, p. 145). *Holocentropus* overwinters as a larva, which is likely to be a more vulnerable stage than the egg of *Lestes,* but it can take advantage of a warm autumn or spring to continue growth beyond the usual time, which *Lestes* cannot do. It is noteworthy in this connexion that versatility characterizes the life histories of *Enallagma, Cloeon dipterum,* and *Triturus.* The first two would benefit from warmer water, for it would enable them to breed more often.

Why some species should be able to breed so much faster than others is a physiological problem far beyond the scope of the present field study.

CORBET (CORBET, LONGFIELD, and MOORE 1960) has suggested that, by reaching a late instar before the winter, a large dragonfly will gain the advantage of being too large for many carnivores to eat it during the long period of inactivity.

Larvae of *Dystiscus semisulcatus* can overwinter because, at winter temperatures, they are active enough to be able to obtain enough food to stay alive, which larvae of *D. marginalis* are not (BLUNCK 1924). The species extends to the Mediterranean region (BALFOUR-BROWNE 1950) and therefore it is unlikely to be a cold-water stenotherm. Perhaps the ability to overwinter as a larva has developed to enable the species to exploit the resources of the environment at a time of year when others cannot.

4.22 The community

4.221 Sources of information

Definition of a community requires first a reliable species list with some indication of abundance, which must be available for different times of year because life histories are so diverse. It is also desirable to know how much these figures vary during a period of several years.

Information of this kind is set out in table 6, in which catches with the net are summarized, and in table 7 in which those made with the SC sampler are set out in full.

I have compared elsewhere (MACAN 1963 p. 282) the number of specimens caught in the net (3 sweeps along a line 2 m long) and in a SCS sampling (the numbers all converted to total in 5 samples) at the same time and almost the same place. The net caught more of everything except *Erpobdella octoculata,* whose numbers in the sampler were 4.5 times those

Table 6. HODSONS TARN. Collections with net.
Numbers at 10 stations. The lines show the numbers at successive times for each generation. The first one (except that against *Leptophlebia*) refers to the year at the head of the column, but any labelled "following spring" refer to the next year.

		1955	1956	1957	1958	1959	1960
Leptophlebia spp.	following spring	1170	669	1649	744	440	—
Phryganea spp.	autumn	93	150	50	215	30	111
	following spring	13	5	21	24	7	—
Limnephilus marmora-	autumn	146	38	10	18	(2)	61
tus	following spring	16	4	1	5	17	—
Triaenodes bicolor	autumn	136	145	221	165	73	32
	following spring	75	52	200	16	50	—
Holocentropus dubius	autumn	157	37	64	18	5	32
	following spring	20	22	34	4	8	—
Cloeon dipterum	autumn	9	9	146	57	265	169
	following spring	24	4	64	94	104	—
Cloeon simile	autumn	0	18	9	3	4	1
	following spring	2	13	6	1	1	—
Corixa nymphs	summer	222	263	200	295	470	253
Corixa castanea	autumn	93	98	167	90	64	40
	following spring	54	3	23	34	20	—
Corixa scotti	autumn	6	3	18	4	16	10
	following spring	9	10	30	7	59	—
Notonecta obliqua	nymphs summer	10	55	175	58	30	15
	adults autumn	6	8	9	12	4	10
	adults following spring	3	2	7	3	3	—
Limnaea pereger	summer	88	106	18	120	95	357
	autumn	38	80	14	73	32	176
	following spring	9	22	22	28	70	—
Triturus helveticus	summer	42	25	91	35	25	34
	autumn	5	25	15	21	3	5
	following spring	3	3	9	8	6	—
Gammarus pulex	spring	23	60	23	10	10	10
	summer	370	80	32	1	12	11
	autumn	93	34	21	5	8	7
Chironomid larvae	spring	124	150	204	178	127	126
	summer	?	208	159	382	429	180
	autumn	104	285	302	291	48	180
Lestes	summer	41	140	100	120	100	60
Enallagma cyathigerum	summer; specim. nearly 1 year old	450	270	240	380	220	340
Pyrrhosoma nymphula	ditto	—	210	130	610	310	170
Erpobdella octoculata	summer	2	3	10	3	6	3
Tadpoles	summer	0	5	2	15	30	1
Haliplus fulvus	summer	53	36	38	26	48	20
Deronectes assimilis	summer	22	16	14	20	19	15
Deronectes duodecim-pustulatus	summer	2	2	6	3	5	8

in the net. The explanation of this offered is that the leech's clinging powers are great enough to prevent a net from dislodging it, so that only a proportion of the population in a given area is caught. At the other extreme comes *Corixa castanea*, of which 27 specimens were taken in the net to every 1 in the SCS. Probably *Corixa* tends to flee over the surface of the vegetation rather than to seek cover in it, and, by the time a sampler has been brought up and lowered, corixids have moved away to another area. The remaining ratios are closer together. *Limnaea pereger* is probably the best test organism because it can introduce no error into either method of collection by clinging to the vegetation or by attempting to flee. Four specimens were taken in the net to one in the SCS. A similar ratio was found for *Deronectes* spp, *Haliplus fulvus* and *Leptophlebia* spp. The ratio was a little lower for the Trichoptera, ranging from 2.4:1 for *Phryganea* to 1.5:1 for *Triaenodes*, and it was 2.4:1 for large specimens of *Pyrrhosoma*. There lower ratios are attributed to clinging powers, whereby a certain proportion of specimens avoid capture by the net. In contrast the ratio for *Enallagma* was 8:1. It is thought that the passage of the net causes this species to try to escape by swimming, which, since it cannot swim fast, renders it more liable to capture at the next sweep. It seems unlikely, in the thick *Littorella* at least, that *Enallagma* can escape from the sampler.

If a ratio of 4:1 is right, the net covers 4×375 cm^2 $=$ 1500 cm^2.

Not only method of sampling but time of sampling can affect results. Ideally the worker who wishes to calculate production should know for each of the abundant species how many there were at the beginning and end of a generation and the shape of the mortality curve in between. Only a sampling program that took account of the life history of each species could achieve this, which means that any investigation not carried out by a large team must choose between exact study of a few species and a less exact one of a number. In the present instance the second course has been followed.

Almost all the animals in tables 6 and 7 have a large number of progeny, and it is likely that there are many deaths in the earliest stages and relatively few later on. The exact date of a sampling carried out soon after hatching must therefore make a big difference to the number of specimens caught, and there are certainly errors from this source in table 6. Later in the generation time of sampling is much less important.

Another error is introduced into the figures in table 6 (which are the numbers at 10 stations) by the fact that not all of the 13 stations were visited each time a series of collections was made. Generally this error is quite small but occasionally it has happened that the program omitted all the stations where a particular species was numerous, which introduces a substantial error. Such figures are enclosed in brackets. The 1955 collections are less satisfactory for comparative purposes than the rest, because samples were taken once a fortnight, not once a month as in subsequent years, at about half the total number of stations. It was not possible to collect at the shallowest stations in the autumn of 1959, because the water level was too low; and in 1960 there was no collecting in *Myriophyllum* because it had become so sparse.

Table 6 includes all the abundant species except *Leptocerus* and *Nymphula. Leptocerus* evidently spends most of its life at depths where the methods of sampling used reached only a proportion of the population, and, as there is no means of knowing the size of the proportion, the figures are without significance. *Nymphula* was almost confined to one species of plant (fig. 9), and an average based on numbers at 10 stations would therefore be misleading as a basis for comparison with the other species, all of which are more widely distributed.

Table 7 includes all the species taken except those that belong to the mud, not the weed, fauna, such as oligochaetes, *Pisidium, Sialis, Caenis horaria, Donacia, Chrysogaster* and an unidentified dipterous larva. This has necessitated omitting the chironomids and ceratopogonids, since it was impossible to separate those species which lived on plants from those which lived in the mud.

The first five in table 6 are winter species which are scarce or absent in midsummer. Accordingly there are only two lines of figures, the upper showing the total at ten stations in autumn, that is at the beginning of the generation, the second showing it in the spring, that is near the end. The first line for *Leptophlebia* has been left out, because, as a glance at table 1 will show, the collections were made too early. The numbers caught in the SCS (table 7) are unreliable for the further reason that, when the range within the individual samples of one series is compared with the confidence limits (cf MACAN 1964, p. 190), distribution is found not to be random. That of older nymphs generally is. The remaining species appear earlier in autumn, and the figures in table 6 give a fairer picture, though subject to the error already mentioned. For example, in 1957 over 800 larvae of *Triaenodes* were collected early in September but the number had dropped to about 200 at the beginning of October. That this high mortality could have been due to large numbers is suggested by the figures in the year before when the total was less and there was no reduction at all in the corresponding period.

Spring and autumn counts only are given for the two species of *Cloeon,* because numbers in summer, when one generation may be finishing and another starting, indicate nothing.

The species of *Corixa, Notonecta, Limnaea,* and *Triturus* are summer growers whose numbers are likely to be high in summer, when the young are present, and to decline through the winter. *Gammarus pulex* should be

Table 7. Hodsons Tarn. Numbers/m² taken with SCS. When the autumn collection comes first, "following spring" and "summer" refer to the year after the one shown at the head of the column. Generally there were 5 collections to one sample and the figures have been multiplied by 26. 6 to give numbers/m². In the first two years there were more collections per sample and consequently a single specimen is represented by a lower figure.

		1957		1958			1959				1960		
		Littorella 10—12	*Carex* A—B	*Littorella* 10—12	*Littorella* off 19	*Carex* A—B	*Littorella* 10—12	*Littorella* off 19	*Carex* 14—15	*Potamogeton natans*	*Littorella* 10—12	*Littorella* off 19	*Carex* A – C
Leptophlebia spp.	autumn	4640	6479	4410	—	9954	7965	7290	8370	1350	2484	1917	5940
	following spring	—	—	459	162	—	27	27	1215	—			
Phryganea spp.	autumn	10	57	56	—	126	27	0	0	27	27	27	0
	following spring	—	—	54	54	—	0	0	27	—			
	summer	—	—	27	27	—	—	—	—	—			
Limnephilus marmoratus	autumn	0	38	14	—	9	0	0	0	0	0	0	27
	following spring	—	—	27	54	—	27	0	0	—			
Triaenodes bicolor	autumn	530	627	98	—	54	0	0	324	0	0	0	108
	following spring	—	—	0	0	—	0	27	0	—			
	summer	—	—	0	81	—	—	—	—	—			
Holocentropus dubius	autumn	10	0	0	—	9	0	0	27	135	27	0	0
	following spring	—	—	0	0	—	0	0	81	—			
Cloeon dipterum	autumn	40	133	49	—	198	0	108	540	567	0	0	54
	following spring	—	—	0	27	—	0	0	135	—			
	summer	—	—	0	27	—	-	—	—	—			
Cloeon simile	autumn	0	0	0	—	0	0	0	0	0	0	0	0
	following spring	—	—	0	0	—	0	0	0	—			
	summer	—	—	0	0	—	-	—	—	—			
Corixa nymphs	summer	—	—	—	—	—	27	27	—	—	—	—	—
	autumn	20	0	14	—	0	0	0	0	0	0	0	0
Corixa castanea	autumn	30	19	0	—	27	0	27	0	0	0	0	54
	following spring	—	—	0	0	—	0	0	0	—			

Notonecta obliqua	autumn	10	0	0	—	0	0	0	0	0	0	0	0
Limnaea pereger	summer	—	—	—	—	—	0	0	—	—	—	—	—
	autumn	0	0	0	—	45	81	0	27	27	162	0	81
	following spring	—	—	108	0	—	0	81	0	—			
Triturus helveticus	autumn	10	0	0	—	0	0	0	0	0	0	0	0
	following spring	—	—	0	0	—	0	27	0	—			
	summer	—	—	81	0	—	—	—	—	—			
Gammarus pulex	spring	—	—	—	—	—	0	0	—	—	0	0	27
	autumn	0	19	14	—	18	0	0	216	81	27	0	0
Lestes sponsa	spring	—	—	—	—	—	54	108	—	—	0	0	81
	summer	—	—	—	—	—	0	0	—	—	—	—	—
Enallagma cyathigerum	autumn	270	0	490	—	54	729	891	27	270	243	837	0
	following spring	—	—	432	243	—	945	675	0	—			
	summer	—	—	540	324	—	—	—	—	—			
Pyrrhosoma nymphula	autumn	1450	1311	1113	—	2790	675	486	2565	405	81	243	810
	following spring	—	—	1161	1620	—	162	270	702	—			
	summer	—	—	297	999	—	—	—	—	—			
Erpobdella octoculata	autumn	30	114	0	—	54	0	27	135	27	0	54	54
	following spring	—	—	0	0	—	27	0	108	—			
	summer	—	—	0	54	—	—	—	—	—			
Haliplus spp.	autumn	20	38	14	—	0	0	0	0	0	27	0	27
	following spring	—	—	27	0	—	0	0	0	—			
Deronectes assimilis	autumn	10	0	7	—	0	27	0	0	0	0	0	0
	following spring	—	—	0	0	—	0	0	0	—			
Deronectes duodecimpustulatus	autumn	20	0	0	—	0	0	27	0	0	0	0	0
	following spring	—	—	0	0	—	27	0	0	—			
Hydracarina	autumn	120	171	84	—	216	27	0	108	297	27	0	135
	following spring	—	—	27	0	—	27	27	0	—			
Libellulids	summer	—	—	—	—	—	27	0	—	—	—	—	—
	autumn	0	0	7	—	0	27	162	27	0	0	54	0
	following spring	—	—	0	0	—	0	0	0	—			

Also taken: 30 *Leptocerus*, *Littorella* off 11, Autumn 1957
7 *Leptocerus*, *Littorella* off 11, Autumn 1958
27 *Gyrinus* l. *Littorella* off 11, Summer 1959
54 *Hydroporus* l *Littorella* off 19, Spring 1960
27 Tadpoles, *Carex* 14—15, Spring 1960
27 *Theromyzon tessulatum*, *Carex* 14—15, Spring 1960
108 Tabanid l. *Carex* A—C, Spring 1960
135 *Aeshna cyanea*, *Carex* A—C, Autumn 1960

similar, though it starts breeding earlier, at the beginning of the year, and goes on longer, not pausing till October (Hynes 1955). Chironomids are inserted at this point because their greatest abundance is reached in summer, but the total is made up of a number of species, most of which probably have different life histories (Macan, 1949, p. 169). *Lestes* is an extreme example of a summer grower and in spring and autumn it is present only in the egg stage. Numbers of the other two species of dragon-fly are also quoted only for summer, because they have been discussed in detail elsewhere. Numbers of *Erpobdella* were not large enough to justify the presentation of extensive data, and summer figures only are quoted also for the three beetles at the end, partly because the life history is not known, and partly because numbers remained remarkably similar throughout the year.

4.222 Discussion of the data presented

The numbers of *Enallagma* and *Pyrrhosoma* (Macan 1964) that emerge from the tarn each year do not vary much and bear no relation to the size of the generation earlier on. This is not true of all species, though there is a tendency for numbers at the end of a generation to range less than at the beginning. *Triaenodes* and *Cloeon dipterum* are two species whose final populations differed greatly in size; in 1957 the generation of both *Leptophlebia* and *Triaenodes* maintained an unusually high level throughout. In general there was no correlation between the size on any generation and the one that followed it. One the biggest catches of *Cloeon dipterum* was made in 1957, in which year the population at the end of the winter was by far the smallest recorded. The size of a population appears to depend less on the number of eggs laid than on conditions during development. It should be pointed out in this connexion that most of the animals under discussion are insects, that Hodson's Tarn is one of a number of similar tarns lying close to each other, and, therefore, that immigrants may make good any deficit in the number of eggs laid by autochthonous specimens.

Some species, notably the three beetles which come last in table 6, were taken each year in numbers that were surprisingly similar. *Triaenodes bicolor* and *Cloeon dipterum* fluctuated more in numbers than other species.

Some tended to remain steady with an occasional notably bad (*Corixa castanea*, spring 1957, see also table 3) or notably good (*Notonecta obliqua*, *Pyrrhosoma*, 1957) year. *Gammarus pulex* was less abundant at the end of six years than at the beginning, whereas *Limnaea pereger* was showing in 1960 the beginnings of an upward trend that has continued.

No generalizations are possible. Attention is drawn to these fluctuations as an essential part of the picture of the community in the tarn.

4.223 Tentative explanations

The first step is observation an record; the stage of explanation has not yet been reached in the present investigation, but some possible correlations are worth mentioning here. Numbers of *Pyrrhosoma* were unusually high in 1957 (the bulge appears in 1958 in the table, which includes only specimens nearly 1 year old) and this was attributed less to the warm sunny conditions which characterized that year than to the low level of the water at the time of oviposition. As a result of this, leaves of *Littorella* were projecting above the surface, and the adults of *Pyrrhosoma* were able to lay eggs over considerable areas of the tarn where in other years they could not because there was nothing on which they might alight. Numbers of *Leptophlebia, Triaenodes* and *Cloeon dipterum* were also high but, as nothing is known about their oviposition habits, it is not possible to decide whether this was due to conditions generally favourable to the adults or to the low water level. The success of *Notonecta,* whose nymphs were far more abundant in 1957 than in any other year, can most plausibly be attributed to an unusually large immigration of adults just before the time for egg-laying. The success of *Triturus,* also abundant in 1957, is more likely to be related to generally favourable conditions. The number of *Corixa castanea* in the autumn of 1957 was the highest recorded but this could have been due to immigration of adults from other ponds.

The decline of *Gammarus* was possibly related to the gradual growth of *Littorella* over the loose stones under which it shelters. 1957 was the year in which many species were more numerous than usual and few scarcer; notable among the latter are *Phryganea* spp., *Limnephilus marmoratus* and *Limnaea pereger.* The large numbers of many species persisted throughout the generation. The result of the big year-class of *Pyrrhosoma* was that in *Littorella* some specimens took a year longer than usual to complete development, an in *Carex* many specimens died, both of which events are tentatively attributed to shortage of food. No comparable effect in any other species was observed.

1958 was a cold wet summer and most species were scarcer than during the year before. It is noteworthy, however, that two species which were numerous, *Phryganea* and *Limnaea pereger,* had been among the few which had been scarce the year before. Fewer predators cannot account for the larger numbers of these two but no other species, and it is not easy to see how weather could have exerted a selective action. It is most plausible to postulate some relation to the events of the year before, but far-fetched to suggest that the generally low populations of 1958 might be due to exhaustion after the exuberance of the previous season.

1959, memorable for being dry and sunny from mid-May to mid-October, might have been expected to be as productive as 1957. That it was not was possibly due to the low water level in late summer and autumn, which greatly reduced the living space of species hatching at that time and perhaps fell low enough to kill many eggs laid when there was more water in the tarn.

The species in table 4 are never numerous but all are regular inhabitants which must not be ignored in any account of the community of the tarn. On the other hand the species in table 5 are no more than casual visitors. A striking feature of this list, which is the product of extensive collecting over six years, is its shortness (contrast, for example, the list of species recorded by Thienemann [1948] in a small garden tank that was dry each winter) and I suggest that this may be a characteristic feature of places with an established stable community. Immigrants are rarely caught because, when they arrive in such a place, they soon leave it. This seemed the most likely explanation of the capture of many species of corixid in places liable to sudden catastrophe and of few in more stable places (Macan 1961). I believe this to be true also of Hodson's Tarn but have no experimental proof that scarcity of invaders is not due to few invasions.

4.224 Fauna of different types of vegetation

Hitherto the animals in the tarn have been written of as if they could all be regarded as belonging to one community. This assumption demands examination. Fig. 9 shows the number of specimens of the commoner species at thirteen stations, the figures being obtained by taking an average of all the specimens caught at each station up to 1959 (after which there was no sampling in *Myriophyllum* because it had become too thin). It is necessary, before drawing conclusions from it, to be certain that an average based on five years' collecting has some meaning. A careful examination of the data has not revealed anything constant about the abundance of *Limnaea pereger*, and large numbers of it at any one station appear to be due to some chance some time between oviposition and the first week or two of active life. An average based on more or fewer years might differ markedly from one based on five. Likewise, exceptional conditions during the period of oviposition led in 1957 to a distribution of *Pyrrhosoma* that was unlike that of earlier years and would have made an average meaningless had the species been included in fig. 9. Examination of the data for other species has not revealed irregularities of this kind, and the average gives a fair representation of distribution each year. An occasional year of exceptional abundance may cause a peak to be higher than it would be without that year, but it does not produce one in a place where there would not otherwise be one. Therefore it is legitimate to draw conclusions from fig. 9.

Nymphula, as already noted, is the only species limited to one kind of plant. The remaining species fall fairly clearly into two classes — they

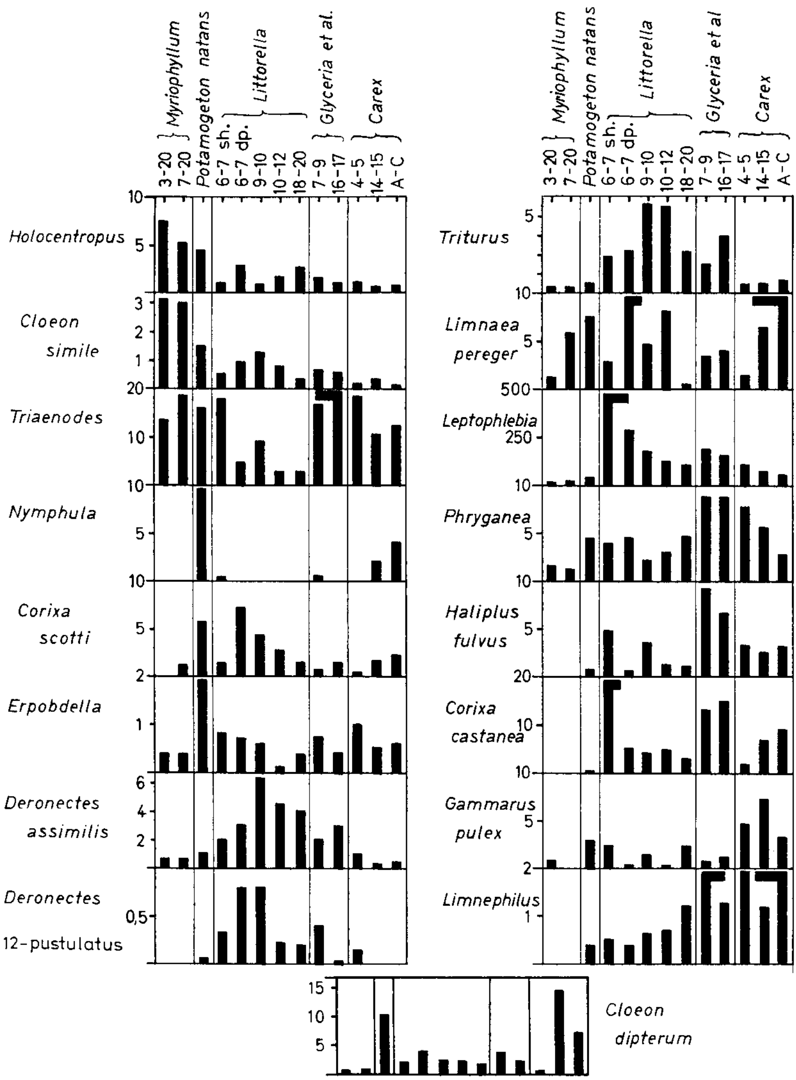

Fig. 9. Average number of specimens up to the end of 1959 at different stations.

might even be called communities — according to whether or not they are abundant in deeper water. The first six in fig. 9 are, and to them may be added of the rarities (table 4) *Corixa distincta* and *C. dentipes. Holocentropus, Cloeon simile* and *Triaenodes* are the only three species in fig. 9 taken in numbers in *Myriophyllum.* Others are *Enallagma,* which oviposits there, and *Lestes* whose nymphs migrate into it from the shallow water where the eggs are laid. *Corixa scotti* and *Erpobdella* were numerous in the *Potamogeton natans.*

Limnaea pereger and perhaps *Phryganea* spp. form a connecting link between these species and the rest, which are confined to or almost confined to shallow water. The species are arranged in fig. 9 in such a way that those predominantly in *Littorella* come first and there is a series with increasing abundance in *Carex* and *Glyceria*. The first three, that is the two species of *Deronectes* and newt larvae, show a fairly marked predominance in *Littorella*, but the species that are commonest in *Carex* tend to occur in fair numbers in *Littorella* also.

Pyrrhosoma was generally most numerous in *Carex* but abounded in *Littorella* one year when its leaves were exposed during the egg-laying season. All the species in table 4, except *Corixa distincta* and *C. dentipes* already mentioned, were found mainly in *Carex*.

The relatively high numbers of *Gammarus* in *Carex* could be due to its being a stream species whose population is constantly augmented from the stream which flows into the tarn near two of the *Carex* stations. The occasional larva of *Baetis rhodani* recorded almost certainly came from the stream. The abundance of *Erpobdella* in *Potamogeton natans* might be attributable to the suitable substratum provided by the flat leaves of that plant. *Enallagma* occurs in shallow and deep water, *Pyrrhosoma* in shallow because that is where the two species lay their eggs and the nymphs do not move from the place where they hatch. *Lestes*, in contrast, spreads all over the tarn from a limited breeding area. It may be deduced, then, that if the tarn were a reservoir with vertical sides enclosing only the vegetation now growing in deep water, there would be few species other than the first six in fig. 9, *Corixa distincta* and *C. punctata, Enallagma cyathigerum*, and *Leptocerus aterrimus*. *Lestes sponsa*, though numerous in *Myriophyllum* in the real tarn, would not occur in it.

The fauna of a tarn that was uniformly shallow so that there was no *Myriophyllum* or *Potamogeton natans* is less easy to predict. *Nymphula* would not be present if there were no *Potamogeton*. The other species abundant in deep water all extend into shallow water, but whether all could maintain themselves if deep water was not there to provide a favourable invasion base cannot be decided. *Cloeon simile* would come into competition with *C. dipterum* and *Corixa scotti* with *C. castanea*.

Similarly no certain conclusions about the fauna of a tarn in which all the vegetation was either emergent or *Littorella* can be made. Possibly both species of *Deronectes* would be absent if there were only *Carex*, and most of the less common species (table 4) would be absent if there were only *Littorella*. The one fairly marked difference that comes out of this general survey is that between the communities of the shallow marginal and the deeper areas.

4.225 Calculation of total numbers

In table 8 an attempt is made to give a picture more accurate than any hitherto of the total number of specimens in different parts of the tarn. It has seemed preferable to take an actual year rather than to base calculations on an average, and the autumn of 1958 has been chosen because 20 individual samples instead of the usual 5 were taken then. Net collections (table 6) indicate that its main divergence from the average was the large number of *Pyrrhosoma*, whose nymphs I have calculated (MACAN 1964, p. 9) were about twenty times more abundant than usual in *Littorella*.

Table 8. HODSONS TARN. Totals in different types of vegetation in September 1958. The figures for *Littorella* and *Carex* are those in table 7 multiplied by 500 and 600 respectively, to give the total in the plant mentioned. The figures for *Potomogeton natans* and *Myriophyllum* have been obtained by comparing the numbers caught in the net at the various stations. They are based primarily on the catches made in September 1958 but some account has been taken of the ratios of the average catch at each station.

	Littorella	*Carex*	*Pot. natans*	*Myr.*	Total
Leptophlebia	2,205,000	4,977,000	800,000	700,000	8,682,000
Phryganea spp.	28,000	63,000	30,000	30,000	151,000
Limnephilus	7,000	4,500	1,000	—	12,500
Triaenodes	49,000	27,000	25,000	80,000	181,000
Holocentropus	3,500	4,500	4,000	16,000	28,000
Limnaea pereger	13,000	22,500	55,000	56,000	146,500
Gammarus	7,000	9,000	2,000	—	18,000
Enallagma	245,000	27,000	48,000	160,000	480,000
Pyrrhosoma	556,500	1,395,000	600,000	50,000	2,601,500
Haliplus fulvus	7,000	4,000	2,000	—	13,000
Deronectes assimilis	3,500	350	700	2,800	7,350

The figures in table 8 for *Littorella* and *Carex* are those in table 7 multiplied by 500 or 600, the approximate areas covered by those two plants respectively. Figures for *Potamogeton natans* and *Myriophyllum* have been obtained from the net samples by assuming that the ratio of specimens caught in them to those caught in *Carex* with net and with SCS is the same. It was difficult to collect in the *Myriophyllum* in a way comparable to that used in other plants, and this certainly introduces an error into the calculation, an error which is magnified by the fact that the area covered by *Myriophyllum* was 4 times as great as that covered by any other kind of plant. However, in any attempt to base total numbers on comparatively small samples the best that can be hoped for is a result of the right order of magnitude.

4.226 Numbers in different species of plants

A further step, one of practical importance to fishermen, is to discover, from all the sources available, whether, over the years, one kind of plant harbours more animals than any other. To this end, all the animals caught with the net at each station during spring in the five years from 1956 to 1960 have been added together. Similar totals for each station having been obtained for summer and autumn, the stations have been arranged in order according to the totals. In the summer the first five places are occupied by the five stations in the *Littorella* and the next two by the two in *Glyceria*. *Carex*, *Potamogeton natans* and *Myriophyllum* follow in that order. The ratios of the numbers of animals in these plants, averages being taken when there was more than one station, are 3:2:1.5:1.5:1. However the ratios are not the same at other times of year. In the spring most animals are taken in one of the *Glyceria* stations, and the other lies in third place. In the autumn stations in *Carex* occupy fourth and fifth places. This suggests that the *Carex* is favoured by ovipositing females but that survival of the resulting progeny is better elsewhere.

Less is produced in deeper water, where some of the most abundant of the inhabitants of the tarn, such as *Leptophlebia*, *Pyrrhosoma* and *Corixa castanea*, are scarce or absent, but none of the shallow-water plants appears better than the others as a harbourage for the organisms that fish eat.

4.227 Comparison with Grib Sø

In Grib Sø, which is ringed with *Phragmites* and floored with *Fontinalis* to a depth of 2 m, there were more animals in November than in October and the totals were some 4500/m^2 in *Fontinalis* and 1000/m^2 in the reedswamp. This is somewhat less than was generally found in the autumn collections in Hodson's Tarn (table 7). In spring and summer the numbers were more nearly similar. *Leptophlebia* was abundant in both places, but otherwise there was no close resemblance, *Asellus*, *Cordulia* and *Holocentropus* being plentiful in Grib Sø and Zygoptera scarce.

Esox lucius and *Perca fluviatilis* inhabit Grib Sø (Berg and Petersen 1956).

4.228 Seasonal pattern of production

Few species were true winter growers, though one that was, *Leptophlebia*, occurred in greater abundance than anything else, and sometimes contributed half the population. Most were summer growers, and evidently the pattern of production is quite different from that of a stream such as the Afon Hirnant where Hynes (1961) found that winter growers contributed far more to the total production than summer growers.

From the practical point of view winter growers are important in that they provide fish with a source of food at a time when other kinds are hard to get; a tarn occupied entirely by summer growers which overwinter as an egg, such as *Lestes*, would not support a population of fish.

5. Acknowledgements

I have listed the names of those who have helped with this survey in the earlier publication, and I am glad to take this second opportunity to thank them. I also record with gratitude assistance with the preparation of this account from Miss Rachel Maudsley and Miss Rachel Cruttwell.

6. Summary

1. Hodson's tarn is a moorland fishpond, poor in electrolytes, just under half a hectare in extent, and 3 m deep at the deepest point.
2. The main plants are *Carex* and *Littorella* in shallow, *Potamogeton natans* and *Myriophyllum* in deep water.
3. An account, dealing mainly with life history and distribution in different parts of the tarn, is given of the larger animals inhabiting vegetation. When there are two species in one genus, differences in their way of life are discussed. There were no *Salmo trutta* in the tarn during the period of observation.
4. Development may be completed in more than one, one, or less than one year. Species completing development in one year may be further classified into winter and summer species. Winter species are mostly insects whose adults are not aquatic and which pass the winter, during which they may or may not grow, in the larval stage. Summer species are mostly insects whose adults are aquatic, and other animals which grow in summer and overwinter as adults. Life history is discussed in relation to adaptation.
5. Table 6 shows the numbers caught in a net, table 7 the numbers caught in a quantitative sampler. Some species vary greatly in numbers at different times of the life history and at the same time from year to year, others vary little. Any definition of the community must take account of these variations.
6. The size of a year-class seems to depend more on conditions in the tarn than on the number of parents. The number completing development of two species of Zygoptera does not vary much from year to year and bears no relation to the initial size of the year-class. In other species large year-classes remain large throughout.
7. Only tentative explanations are offered. Numbers of emerging Odonata are thought to depend on food supply. A large year-class was attributed to a fall in water level, which exposed an unusually large area of the tarn for oviposition. Many species were more abundant than usual in a warm sunny summer. Invasion from elsewhere is thought to have been the reason for several large catches.
8. The number of species of which only a few specimens have been taken on one or two occasions (table 5) is small. It is suggested that invaders entering a pond where the fauna is well established soon leave again.
9. Some of the most numerous animals, such as *Leptophlebia, Pyrrhosoma* and *Corixa castanea* are largely confined to shallow water. *Nymphula* larvae (Lepidoptera) are confined to *Potamogeton natans*. There is a marked difference

between the fauna in the deeper and shallower parts of the tarn, and otherwise a slight difference between the fauna of the different species of plants (fig. 9).

10. An attempt is made to calculate total numbers (table 8).
11. The greatest number of animals is found in *Littorella* in summer, but when catches at other times of year are considered, no species in shallow water is found better as a harbourage for animals than any other.
12. Total numbers per unit area (table 7) are similar to those in the Danish Grib Sø.
13. Summer species contribute more to production than winter species.

7. Zusammenfassung

Hodson's Tarn ist ein Moor-Fischteich mit weniger als 0,5 ha Oberfläche, dabei 3 m Maximaltiefe und ist arm an Elektrolyten. Die häufigsten Pflanzen sind *Carex* und *Littorella* im flachen Wasser und *Potamogeton natans* sowie *Myriophyllum* im tieferen.

Es wird ein Bericht gegeben über die Entwicklung und Verteilung der größeren pflanzenbewohnenden Tiere in verschiedenen Teilen des Gewässers. Sofern zwei Arten von einer Gattung vorkommen, werden in ihrem Verhalten die auftretenden Unterschiede besprochen. Während der Beobachtungszeit kam kein *Salmo trutta* im Teich vor. Die Entwicklung der tierischen Organismen kann in einem Jahre bzw. in mehr oder weniger als einem Jahre erfolgen. Arten, die ihre Entwicklung während eines Jahres durchlaufen, können in Winter- und Sommerarten unterschieden werden. Winterarten sind meistens Insekten, deren Imagines nicht aquatisch sind und die den Winter mit oder ohne Wachstum als Larven verbringen. Zu den Sommerarten gehören größtenteils Insekten, deren Imagines aquatisch sind, aber auch andere Tiere, die im Winter und Sommer als Imagines weiterwachsen. Die Entwicklung dieser Organismen wird unter Berücksichtigung der Adaptation diskutiert. Tab. 6 zeigt die Individuenzahlen, die in einem Netz gefangen wurden, Tab. 7 die mit dem quantitativen Fanggerät festgestellten. Die Mengen einiger Arten ändern sich stark zu verschiedenen Zeiten der Lebensentwicklung und zur selben Zeit von Jahr zu Jahr, andere variieren wenig. Jede Definition der Gemeinschaft oder Gesellschaft muß diese Variationen berücksichtigen.

Die Größe einer Jahresklasse scheint mehr von den Bedingungen des Teiches als von der Zahl der Elternorganismen abhängig zu sein. Die Zahl von zwei Zygoptera-Arten, die ihre Entwicklung abschließen, ändert sich von Jahr zu Jahr nur wenig und steht in keiner Beziehung zum ursprünglichen Umfang der Jahresklasse. Bei anderen Arten bleibt die Größe der Jahresklassen ständig erhalten. Erklärungen für diese Befunde werden nur andeutungsweise gegeben. Die Zahl der schlüpfenden Odonaten ist vermutlich vom Nahrungsangebot abhängig. Die Entwicklung einer großen Jahresklasse wurde auf den Abfall des Wasserspiegels zurückgeführt, wodurch ein außergewöhnlich großes Gebiet am Teich für die Eiablagerung zur Verfügung stand. Viele Arten kamen in einem warmen Sommer in größerer Häufigkeit als gewöhnlich vor. Die Invasion von anderen Wohnstätten mag die Ursache für einige Massenfänge sein. Die Zahl der Arten, von denen nur wenige Exemplare bei ein oder zwei Gelegenheiten (Tab. 5) gefangen wurden, ist gering. Es wird vermutet, daß Einwanderer, die in einem Teich ankommen, dessen Fauna voll aufgefüllt ist, ihn bald wieder verlassen.

Einige der häufigsten Tiere, z. B. *Leptophlebia, Pyrrhosoma* und *Corixa* *castanea*, bleiben größtenteils auf flaches Wasser beschränkt. Larven von *Nymphula* (Lepidoptera) kommen ausschließlich auf *Potamogeton natans* vor. Es besteht ein ausgesprochener Unterschied zwischen der Fauna der tieferen und flacheren Teile des Teiches, und andererseits sind nur geringe Unterschiede zwischen der Fauna verschiedener Pflanzenarten festzustellen (Abb. 9). Es wird der Versuch unternommen, die Gesamtzahlen der Organismen zu berechnen (Tab. 8). Die größte Zahl an tierischen Organismen tritt im Sommer zwischen *Littorella* auf; aber wenn man die Tierfänge von anderen Jahreszeiten vergleicht, so besteht keine Bevorzugung von einzelnen Pflanzenarten durch die Tiere. Die Gesamtzahlen der Organismen je Areal-Einheit (Tab. 7) sind denjenigen des dänischen Grib Sø ähnlich. Sommerarten weisen eine stärkere Entwicklung auf als Winterarten.

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