

**TWENTY GENERATIONS OF *PYRRHOSOMA NYMPHULA* (SULZER)  
AND *ENALLAGMA CYATHIGERUM* (CHARPENTIER) (ZYGOPTERA:  
*COENAGRIONIDAE*)\***

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Quantitative studies have been carried out on the larvae of *P. nymphula* and *E. cyathigerum* in a small artificial moorland pond. A double-cylinder toothed sampler appeared to give good quantitative results but it was not a rapid method of collecting and it removed part of the environment. A net caught a higher proportion of larger than of smaller larvae. Artificial vegetation harboured more specimens per unit area than real vegetation. A patch of *Potamogeton natans* is the main egg-laying site of *Pyrrhosoma*. Colonization of mats of artificial *Littorella* indicate passive dispersal soon after hatching. There is little wandering later in life. Development can be completed in one year, but generally requires two. It takes three years when larvae are numerous. Numbers, particularly at the end of a generation, did not vary much from 1955 to 1965, although predation by trout was heavy in the second half of the period and absent during the first. In 1966 and thereafter larvae have been scarcer, probably because there has been much less rooted vegetation.

INTRODUCTION

Hodson's Tarn is an artificial moorland fishpond, a little less than half a hectare in extent and about three metres deep at the deepest point. A regular study of the rooted plants and of the fauna in them started in 1954, and two experiments have been carried out. The first involved the removal of the fish (all *Salmo trutta* except for a few *Anguilla anguilla*) followed by heavy restocking after five years in order to ascertain what effect predation had on the rest of the

\* Dedicated to Franz BERGER on the occasion of his seventieth birthday.

fauna (refs. in MACAN, McCORMACK & MAUDSLEY, 1966/7). The second was concerned with the use of artificial vegetation both as a means of sampling, and of investigating certain problems (MACAN & KITCHING, 1972).

An account of observations on Odonata during the six years from 1955 to 1960 has been published (MACAN, 1964) and accordingly the intention here, after a brief recapitulation, is to examine what may be derived from a twenty-year study that was not revealed in the six-year study and to discuss the results with the new technique.

### PYRRHOSOMA NYMPHULA

#### Recapitulation

The year 1957 was one of exceptional abundance of this species and it was also one in which collections were being made at some ten stations every month. Two new larvae were found at the beginning of July, 27 at the end of that month, but, between 29 August and 5 September, 612 were taken. Other collections (e.g. Table IV) confirm that new larvae begin to appear in large numbers late in August.

GARDNER & MacNEILL (1950) reared in one year a specimen from an egg that hatched on 24 June, and specimens hatching as early as this in Hodson's Tarn may develop in the same way. They have proved impossible to detect, as rapid growth during the summer of hatching would quickly render a specimen indistinguishable from stragglers of the previous year-class. If this quick development does occur it is infrequent, and the usual life histories are shown in Figure 1. Development taking two whole summers was observed in *Carex* up to 1957,

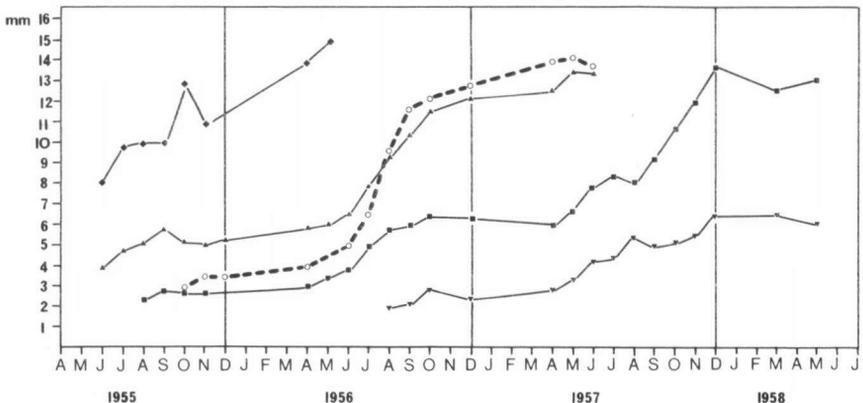


Fig. 1. Hodson's Tarn. *Pyrrhosoma*. Rate of growth: continuous line – in *Carex*, broken line – in *Littorella*.

but the exceptional numbers of that year seem to have led to severe mortality and the next few year-classes achieved full size in one whole summer. This was typical of specimens in *Littorella* until 1957, whose large year-class split into two, some taking one, others two, whole summers to complete development. This phenomenon was not uncommon.

From the fact that these two types of development could be seen proceeding side by side in *Carex* and *Littorella*, it was deduced that there was little lateral dispersal, at least after the first winter. Emergence in 1956 and 1957 extended from early May to the beginning of July, though the main period lasted three to four weeks with a peak at the end of May (MACAN, 1964, fig. 3). In other years peaks were earlier or later (MACAN & MAUDSLEY, 1966). It was noted that, in the years 1958 to 1964, when a recording thermometer was in operation, the earliest date on which temperatures of 6°, 7°, 8° and 9°C were reached varied by five weeks or more. In contrast the dates on which temperatures of 10°, 11° and 12°C were first reached all fell within a period of 22 days. This marked rise always took place in April. When it was early the emergence of *Pyrrhosoma* was early and when it was late emergence was late.

Oviposition in *Potamogeton natans* was observed on a number of occasions. Pairs were often seen resting in *Carex* but never observed to oviposit in that plant, though a careful watch for this was kept. In 1963 a pair was seen to oviposit on a plant of *Littorella* which had failed to take root and had reached the water surface at the end of a stolon from the parent plant. Larvae were abundant at times everywhere in the shallow water but always scarce away from the edge of the tarn.

#### The vegetation

When the tarn was first surveyed, in 1954 and 1955, most of the bottom in shallow water was carpeted by *Littorella uniflora*, except near the inflow where there was a zone of *Carex rostrata*. In the deeper water there was a patch of *Potamogeton natans* near the inflow and a thick forest of *Myriophyllum alterniflorum* covering most of the rest of the tarn. *Nitella flexilis* and *Juncus fluitans* grew in patches in a few places.

In 1957 deterioration of *Myriophyllum* was first noted. By 1961, however, the process had come to an end and in a year or two the plant was growing as vigorously as ever. In 1966 deterioration set in again and after 1968 only a few individual plants, most in shallow water, could be seen. There has been no recovery. *Potamogeton alpinus*, first observed in 1959, spread as *Myriophyllum* receded, but extensive areas of the bottom of the tarn have remained bare. 1966 was also the year in which *Littorella* began to die out, after vigorous growth and considerable increase in area covered during the previous ten years. By autumn it was confined in places to a narrow zone exposed by the fall in water level during dry spells. Since 1968, however, it has been expanding again. The stands of

*Carex* and *P. natans* have been more stable though the shape of the beds and the number of plants per unit area have fluctuated.

#### Methods of collecting

Three methods were used:

- (1) Pond-net with 10 meshes/cm. The net was swept through the vegetation three times along a course 2 m in length. The net is a versatile instrument that yields a large number of animals which can be picked out, counted and sorted in a comparatively short time. The main disadvantage is that a mesh coarse enough to avoid clogging by algae and fine detritus does not retain small animals. Moreover, it does not dislodge all the animals which cling tight to the substratum.
- (2) Saw cylinder sampler (SCS). This quantitative sampler (MACAN 1964) consists of two tubes with sharp teeth at the end. As the sampler is lowered into the vegetation, the inner tube is rotated within the outer and each leaf or stem is severed as the teeth reach it. The instrument has to be driven into the substratum to obtain a seal to retain the sample and the top is also closed. This appears to be a satisfactory device for quantitative sampling, particularly of animals such as odonate larvae that cannot move rapidly, but it has three disadvantages: the area covered is small (75 cm<sup>2</sup>); the separation of the catch from the mud takes time; the environment is damaged.
- (3) Artificial vegetation was made from polypropylene rope, which floats and therefore stands vertical when attached to a lattice that has been weighted and submerged. Strands of appropriate thickness and length to copy *Littorella* and *Carex* were used. The squares of artificial *Littorella* measured 12.5 x 12.5 cm (MACAN & KITCHING, 1972). The advantages of this method are three. Firstly the mat can be lifted off the bottom and then enclosed in a net of sufficiently fine mesh to retain the smallest larvae. Secondly the animals can be removed by simple swilling and there is little debris from which they have to be separated. Thirdly the environment is not altered and the mat can be returned to its previous position.

Sets of five mats were laid at nine stations (Fig. 2), 5 in shallow water (less than 50 cm), 1 suspended in midwater, and 3 in deep water (1.5 - 3 m). Of the last, two were off the dam and one was near the *Potamogeton natans*.

#### Comparison of methods

Net and SCS have been in use since the earliest years but the artificial vegetation has been introduced only recently, in years when the numbers of odonate larvae have been smaller than formerly.

The earlier comparison of net with SCS (MACAN, 1964, p. 333) showed that, when the numbers collected on each occasion on which the two methods

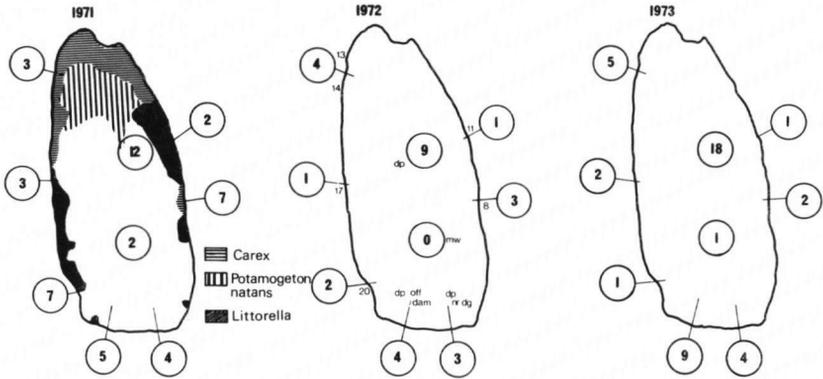


Fig. 2. Hodson's Tarn. *Pyrrhosoma*. Numbers at the beginning of the generation at 9 stations. Abbreviations: *dp* – deep water, *dg* – drainage grid (deep), *mw* – mid water.

were used at more or less the same time and place were added together, the sampler caught twice as many small ones (1-3 mm long) as the net, whereas the net caught twice as many larger ones (over 8 mm). This result is confirmed when the comparison is based on the longer period, 93 twin collections between 1957 and 1971. The ratio for small ones was again 2 : 1 in favour of the SCS, that for the large ones was greater than before, 2.5 : 1 in favour of the net. The figure for the intermediate size group is also higher, 2.1 : 1 in favour of the net compared with the earlier ratio of 1.5 : 1. It is evident that the net cannot be used for quantitative sampling. The net probably catches fewer small specimens because they are nearer the bases of the plants and therefore less likely to be dislodged than larger specimens.

Catches obtained by means of all three methods are shown in Table I. A square of artificial *Littorella* covers twice the area of an SC sample and therefore the figures for that method must be halved. Even when this has been done, there is a preponderance of specimens in the artificial vegetation. When the *Littorella* was sampled for copying, each plant was large and growing close to its neighbours, but later the plants were smaller and further apart. The artificial *Littorella*, therefore, offers thicker cover, which may be why it harbours more specimens. Thus this too is not a reliable quantitative method.

In order to study the occurrence of a species throughout a generation, an investigation for which the artificial vegetation is particularly well suited, it is desirable to sample at as many points as possible, which means reducing the work at any one to a minimum. In fact from autumn 1972 onwards one mat from each group of five was lifted once a fortnight or less often, which means that the shortest interval allowed for recolonization was 10 weeks. In order to give some idea of the degree of accuracy to be expected from one sample,

Table I

Hodsons Tarn *Pyrrhosoma*: numbers caught by three different methods. [The numbers are those taken in 5 mats of artificial vegetation (781 cm<sup>2</sup>), 5 collections with the SCS (375 cm<sup>2</sup>) and a standard sweep with the net].

Season		New generation				Old generation			
		artificial		SCS	net	artificial		SCS	net
		Littorella <i>ev</i>	<i>alt</i>			Littorella <i>ev</i>	<i>alt</i>		
summer	1969	-	-	-	-	12	11	1	16
spring	1970	20	2	1	0	28	7	0	0
autumn	1970	106	59	2	10	26	25	2	2
spring	1971	56	63	6	1	22	12	0	0
summer	1971	-	-	-	-	19	16	3	2
autumn	1971	29	-	1	0	11	-	4	1
<i>Total</i>		<i>211</i>	<i>124</i>	<i>10</i>	<i>11</i>	<i>118</i>	<i>71</i>	<i>10</i>	<i>21</i>

*ev* - 2 threads to every hole, i.e. 288 strands per square measuring 12.5 x 12.5 cm; - *alt* - 2 threads to every alternate hole, i.e. 144 strands. The mats were permanently off post 8. In autumn 1971 the net and SCS samples were taken off post 11 and in autumn 1970 off post 7. At other times all the samples were taken near the same point. The new generation of a spring collection has become the old generation by the summer collection.

numbers, caught in each of five mats when all at one station were lifted at the same time are presented in Table IIa.

For comparison some figures for the SCS have been selected (Table IIb). Both year-classes were large ones and the station off post 11 has also been chosen because of the unusually large number of collections made.

#### New data from the longer survey

There is nothing to add about life history. When latterly numbers fell, development was accomplished during one complete summer in all parts of the tarn.

Collections at both edges of a *Littorella* sward, started in 1957 (MACAN, 1964, tab. V), were continued until 1964, after which the sward was so narrow that the distinction between deep and shallow was not worth making. Whenever larvae were numerous there was, as in 1957, a preponderance in the shallow water during the first winter and an increase in the number near the deep edge of the sward in the following summer.

The main information from long observation concerns the variation in numbers from season to season. Numbers at the end of each year class are shown in Table III. Between 1955 and 1965 numbers do not vary much; the exceptional year-class of 1957 did produce, two years later, the highest total recorded, but it

Table IIa  
Hodsons Tarn *Pyrrhosoma*: artificial *Littorella*. (Number of specimens caught when five mats were lifted at the same time)

		<i>Mats with 288 strands</i>																
		1969 19 & 26 June					10 & 15 Sept.					1970 1, 14, 16 April						
in shallow	<i>og</i>	1	3	5	2	1	4	6	4	8	6	4	8	4	5	3		
water off post 8	<i>ng</i>						0	2	1	3	5	5	3	9	2	3		
		1970 26 June 2 July					4 & 6 Aug.					7 & 8 Oct.						
	<i>og</i>	5	5	0	2	0	4	4	0	5	6	2	10	7	5	2	6	5
	<i>ng</i>						0	1	1	7	5	21	13	20	19	31	28	27
		1971 7 April					21 June					5-31 August						
	<i>og</i>	2	3	3	3	11	2	3	0	5	6	3	5	5	1	0	5	2
	<i>ng</i>	6	8	10	17	15							0	0	0	0	4	0
		1970 15 July					9 & 13 Oct.					1971 7-14 April						
in deepest part	<i>og</i>	0	0	0	0	0	0	1	1	1	3	0	0	0	1	0		
of tarn	<i>ng</i>	0	1	1	1	0	11	13	5	15	6	0	3	1	1	1		
		<i>Mats with 144 strands</i>																
		1970 25 August					15 April											
in deep	<i>og</i>	4	8	10	8	10	1	7	2	1	1							
water of post 11	<i>ng</i>	7	19	14	22	13	15	3	0	2	9							
		1969 30 June 7 July					3 & 15 Sept.					1970 1 & 14 April						
in shallow	<i>og</i>	3	3	3	2	1	1	6	4	0	0	2	1	4	0	0		
water off post 8	<i>ng</i>						0	0	1	3	1	0	1	1	0	0		
		1970 25 June 2 July					4 August					7 & 8 Oct.						
	<i>og</i>	2	0	3	2	4	5	2	1	3	4	6	5	8	3	3		
	<i>ng</i>						3	1	6	1	4	13	14	18	11	3		
		1970 7, 8, 16 Oct.					1971 7 April											
	<i>og</i>	1	2	-	4	3	2	4	3	1	2							
	<i>ng</i>	8	4	2	12	9	12	14	20	7	10							

*ng* - new generation which becomes the old generation (*og*) in midsummer .

Table IIb  
Hodsons Tarn: number of *Pyrrosoma* taken in each collection of the SCS

<i>The 1957 year-class in Littorella off post 11</i>																					
1957	autumn	11	8	5	7	5	17	9	24	7	18	7	14								
1958	autumn	5	14	9	5	5	4	9	7	6	16	4	8	5	10	8	6	9	8	12	4
1959	spring	11	5	3	9	9															
	summer	4	3	0	0	3															
	autumn	3	6	5	2																
1960	spring	2	0	0	0																

<i>The 1963 year-class in Carex between posts 14 and 15</i>													
1963	autumn	2	1	12	5	25							
1964	spring	4	6	3	4	4							
	autumn	2	0	2	1	7							
1965	spring	1	0	1	7	2							
	summer	1	0	0	1	0							
	autumn	5	1	2	1	1							
1966	spring	0	0	0	0	0							

Table IIIa  
Hodsons Tarn: collection with net in spring. (Number of specimens large enough to emerge in the same season. Total at 10 stations)

species	1955	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
<i>P. nymphula</i>	46	66	53	66	93	68	46	46	62	52	50	19	5	2	26	10	7
<i>E. cyathigerum</i>	—	35	60	65	72	70	70	88	48	48	76	30	3	1	3	7	7

is only just twice as great as the lowest. The result of predation, after fish had been introduced in 1960, was a low total during the first two years, but the same level had been reached in the days of slight predation. (In 1955 the last fish had not been removed). In 1966 there was a sudden drop and totals have been low ever since then; the populations in the artificial *Littorella* in 1971, 1972 and 1973 indicate that there has been no recovery up to the time of writing. 1966 was the year when *Littorella* deteriorated suddenly and *Myriophyllum* was in a decline that culminated in its disappearance from most of the centre of the tarn. The smaller totals are attributed to the reduction in the amount of cover.

Many of the small crustaceans on which larvae feed swim in the open water but can cling to vegetation. The disappearance of *Myriophyllum*, their refuge when heavy rain and wind threatened to wash them out of the tarn, must

Table IIIb

Hodsons Tarn *Pyrrosoma*: collections with SCS in spring. (Number of larvae large enough to emerge in the same season)

Year	off B or C	off 14	off 19	off 11
1958	-	-	-	-
1959	-	-	2	4
1960	-	0	5	2
1961	-	2	2	1
1962	-	0	2	2
1963	-	2	3	1
1964	-	3	3	4
1965	-	3	5	4
1966	-	0	0	5
1967	1	0	0	0
1968	0	0	0	2
1969	0	0	1	1
1970	0	0	0	-
1971	1	0	1	-

have reduced their numbers. The larvae were affected not only by this reduction in food supply but also by the greater exposure to predation, as the *Littorella* provided less cover. That the longer life history, due it is thought to food shortage, has not been observed during these recent years of scarcity, indicates that increased predation was an important factor maintaining a smaller population.

#### Deductions from a comparison of methods

The artificial *Littorella* was not a reliable method of ascertaining actual numbers (Tab. I). It would have been admirable for the study of life history had it been brought into use sooner. Its main contribution has been to knowledge of dispersal, the possibility of establishing standard pieces of substratum in places where it does not naturally occur, for example *Littorella* in midwater or in deep regions, providing evidence not obtainable from sampling the natural vegetation. It was unfortunate that the population of *Pyrrosoma* was low during the years when this method of sampling was used.

Observation of the adults indicates that most eggs are laid in the *Potamogeton natans*. In 1971 and 1972 the largest catches of the new generations were made off post 11 in deep water close to the patch of this plant (Fig. 2). This was true also in 1970, in which year, however, there were mats at only three other stations. At the same time larvae were taken at all the stations, including the one suspended in midwater and the two off the dam in the deepest

water. Their numbers did not vary greatly from one place to another (Tab. IV). The obvious explanation of this is that the larvae were floating in the water soon after hatching and that they were carried to all parts of the tarn by currents. The midwater mats could have been reached along the rope to which they were attached but it would have been a very long walk for larvae 1 mm long, and, had this route been used, it is highly unlikely that as many specimens would have reached these mats or have appeared so soon.

The pattern revealed in Table IV was seen also in the other year-classes. The mats in midwater were deserted fairly soon, those on the bottom in deep water early during the second winter. A conspicuous feature of the figures is the drop in numbers in spring and early summer and the recovery later in the summer. Similar fluctuation was evident in the net samples and those obtained with the SC samples. Obviously there is some kind of dispersal at this time from the vegetation where the samples are regularly taken. Until more is known about it, calculations of production must be suspect.

The colonization of artificial vegetation in deep water raises doubts about statements that numbers were always small in the *Myriophyllum* in the early days. This is a difficult plant from which to secure a sample and a net would have missed larvae congregated near the base of the plants. That they do concentrate near the bottom was indicated by an experiment with artificial *Carex* (MACAN & KITCHING, 1972, tab. 2); strands of the normal mats were 45 cm long but a few mats with strands only 8 cm long were made and on these larvae were more numerous than on the others.

The comparison of SCS and net when the two coincided in time and place also throws some light on distribution during the course of a generation. It is instructive to look first at the catches of the small specimens in autumn, that is at the beginning of the generation. The years considered are from 1957 to 1965, after which the catches were too uniformly small to be worth comparing. There were ten collections in the *Carex* and those with the SCS yielded 437 specimens. The 2 poorest catches comprised between 11 and 20 specimens, in two more the catch ranged between 21 and 30 specimens and in the remaining six it was over 40. In marked contrast in seven of the net catches fewer than 10 larvae were collected and the highest catch, 52 in 1960, accounted for more than half the total of 98. It is unclear why the net should occasionally catch as many small larvae as the SCS but generally considerably fewer, but these figures reinforce the earlier conclusion that the net is not a reliable quantitative instrument.

It is more useful to compare these figures for *Carex* with those for *Littorella*. The SCS caught many fewer larvae, 75 in all, and only once did the total exceed 10; in the exceptional year 1957 it was 55. The net totals were smaller but otherwise similar. A glance at the rest of the collections confirms this picture of large numbers of small larvae in the *Carex* and few elsewhere. Large catches in the *Littorella* and other vegetation were frequent in 1957 and rare in other

Table IV  
 Hodsons Tarn *Pyrrhosoma*: 1971 years class.  
 [Numbers taken in one square (12.5 x 12.5 cm) of artificial *Littorella*]

	1971				1972				1973				May 10/16	31							
	Aug 19 25 31	Sept 8 14-22	Oct 5/7 18 26/27	Nov 3	Jan 19	Feb 24 28 Mar 2 5	Mar 10-12 25	Apr 18	May 21 19 27	Aug 16/22	Aug 31 Sept 7	Sept 14/19			Sept 26 Oct 5	Oct 12/19 26 Nov 3	Nov 16 29	Dec 14	Jan 16 30	Feb 20	Mar 8
11 dp	2 15 10	2 4	10 16 11	-	-	2 7 2 0 0	0 0 0 0 0	0 0 0 0 0	7 10 7 4	4	1	1	1	2 8	0 -	1	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0
sh	1 2 1 4	0 0 1 5	0 1 5	11	0	- 7 5 3 1	3 2 1 2	0 0 0 0	2 1 2 0	0 0 0	4 3 4	3	4	1 4 1	4 4 1	10 6 5	4 3 7	5 4 3	7 2 0	2 0 0	0 0 0
8	0 4 0 0	2 8 6 13	4 0 0	1	11	2 1 1 0	4 1 3 4	5 3 4	5 3 4	5 3 4	5 3 4	5 3 4	5 3 4	2 2 2	4 2 0	0 1 3 3	1 2 5 8	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
mw	0 2 1 -	1 5 0 0	-	-	0 0	1 0 0	- 0 0 0	0 0 0 0	0 0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
dg	0 10 1 4	5 7 0 4	0 -	0	0 0	1 0 0 0	0 0 0 0	1 1 1 1	1 1 1 1	1 1 1 1	1 1 1 1	1 1 1 1	1 1 1 1	2 4 2 2	2 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
dp.o.d.	- - - -	- - - -	- - - -	5 2	-	1 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1 1 1 1	1 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
20	1 0 4 3	1 - 1 9	10 -	3 2	1 0 0 0	1 0 0 0	2 2 2	2 2 2	2 2 2	2 2 2	2 2 2	2 2 2	2 2 2	0 6 4	1 0 0 0	0 0 0 0	1 1 1 1	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
17	- 0 - -	- 2 - 4	1 5	1 6	0 2 0 0	2 0 0 0	3 2 2	2 2 2	2 2 2	2 2 2	2 2 2	2 2 2	2 2 2	0 6 4	1 0 0 0	0 0 0 0	1 1 1 1	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
13-14	- - 1 0	2 1 4 2	2 1	3 4	1 1 0 0	2 0 2 0	1 0 0 0	1 0 0 0	1 0 0 0	1 0 0 0	1 0 0 0	1 0 0 0	1 0 0 0	2 2 2	0 0 0 0	1 0 1 0	1 5 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
Total	4 33 18 13	17 31 32 45	37	15 32	15 5 2 3	16 16 16 12	12 11 15	15 16 23	15 7 2 16 11	16 11 8 14	16 11 8 14	16 11 8 14	16 11 8 14	16 23 15 7	2 16 11	2 16 11	16 11 8 14	16 11 8 14	16 11 8 14	16 11 8 14	16 11 8 14

Abbreviations: dp - deep water, sh - shallow water, mw - mid water, dp.o.d. - deep off dam, - dg - deep, beside drainage grid.

years. These findings support the idea put forward earlier that many larvae drift away from the point of hatching soon after that event and that the *Carex* being closest to the *Potamogeton natans*, the point of origin, receives the largest complement.

The total catch of larvae between 4 and 8 mm long, was greater than that of the smallest ones and about twice as many were taken with the SCS outside the *Carex* as in it. There were 51 collections in *Littorella* and 42 in *Carex*. Clearly there has been extensive redistribution of larvae. This, however, appears to be largely confined to the first winter and early spring. In the early years development was requiring two whole summers in the *Carex* and one in the *Littorella*. Had the two populations mixed, the histograms showing number in each size group would have been unintelligible. That they remained clear indicates that the populations were remaining separate.

### ENALLAGMA CYATHIGERUM

The life history was similar but less easy to discern because the range of size in each generation was soon greater than ever it was in *Pyrrhosoma*. Emergence was a little later. Oviposition behaviour was different, the female submerging often after alighting on the small inflorescence of *Myriophyllum* in the middle of the tarn. As a result larvae were widespread, though never numerous in the *Carex*.

The drop in numbers of ultimate-instar larvae before emergence coincided with that of *Pyrrhosoma* (Table IIIa) and was greater, which was to be expected since the disappearance of *Myriophyllum* must have reduced its hunting grounds by a proportion distinctly greater than those of *Pyrrhosoma* suffered.

Table V shows the numbers of the 1972 generation at nine stations of artificial vegetation on successive dates. Numbers were highest at two stations in the deep water off the dam. Adults were always numerous along the dam, which provided protection from the wind on one side or the other. There were no cross winds because the valley was steep and well wooded. The neighbourhood of the dam was also good for oviposition as it was one of the few places where *Myriophyllum* persisted and flowered. *Apium* and some emergent plants also provided routes down into the water.

Up to the end of the year numbers were high at the midwater station. It is not likely that a female would insert eggs into a piece of rope, but the possibility cannot be ruled out. Probably the larvae came from the area off the dam where numbers were high soon after hatching. This should be tested by installing midwater mats after egg-laying is over but before hatching has started.

Numbers at the stations off the dam remained near the maximum till mid January and were still at about half that level six months later. Only once was the highest total not at one or other of these two stations. There is nothing in

Table V  
Hodsons Tarn *Enallagma*: 1972 year class.  
[Numbers taken in one square (12.5 x 12.5 cm) of artificial *Littorella*]

Station	1972			1973			1973			1973			1973			1973			
	Aug 16 22 31	Sept 7 14 19 26	Oct 5 12 19 26	Nov 3 16 29	Dec 14	Jan 16 20	Feb 20	Mar 8 22	Apr 5 18	May 10 31	June 13 14 26	July 11 24	Aug 8 16	Sept 29 5					
off 11 dp	0 0 1	- 4 - 7	- 5 - 0	- 7 -	18 4 12	15 6 - 1 1	0 2 3 - 2 3 2	- 4 2 -											
sh	0 - - 1 - 8 -	2 - 3 4	- 10 5	5 11 8	2 1 - 1 8	1 0 0 - 0 0 1	- 3 3 -												
8	- 0 - 0 - 1 -	1 - 10 -	14 19 9	2 6 21	9 0 - 0 2	1 1 0 - 0 0 0	- 0 - 1												
mw	1 - - 9 - 7 -	18 - 10 -	- 15 20	30 7 4	0 0 - 1 1	1 0 - 1 1 1 0	- 1 - 2												
d.g.	0 - - 28 - 67 -	40 - 48 21	- 49 24	50 56 16	30 13 - 19 21	25 9 - 20 8 9 3	- 5 - 5												
dp.o.d.	- 5 - 24 - 33	- 23 - 60	- 56 38	12 4 9 22	13 7 - 30 4 9 15	- 5 5 3 1 - 2 -													
20	0 - 0 - 2 - 2	- 4 - -	0 2 2	0 1 0 0	4 0 - 1 0 0 0	0 - 1 1 2 3 - 7 -													
17	- 0 - 4 2 - 1	- 0 - -	9 9 2	0 4 3 1	0 - 0 1 1 0 0	0 - 0 1 0 0 - 1 - 4 -													
13-14	0 - 0 - 0 - 3	- 6 - -	16 0 1	5 1 5 1	1 - 0 0 4 2 0 - 0 0 0														
<b>Total</b>	<b>1</b>	<b>48</b>	<b>115</b>	<b>107</b>	<b>109</b>	<b>124</b>	<b>167 101</b>	<b>105</b>	<b>94 78</b>	<b>80</b>	<b>38</b>	<b>29</b>	<b>65</b>	<b>37 23</b>	<b>39</b>	<b>17</b>	<b>20 11</b>	<b>17</b>	<b>27</b>

For abbreviations used cf. Table IV.

these figures to suggest emigration from crowded to less crowded areas and, as in *Pyrrosoma*, there seems to be little lateral movement after the earliest days.

The 1971 year-class reached a total of 160 at seven stations early in November. The larvae were more evenly distributed than in the following year. Numbers were lower up to mid April when they reached a figure almost identical with that attained by the 1972 generation. Then there was a rapid fall and totals ranged between 0 and 5 from 18th May to 3rd November. Thereafter they were higher, ranging up to 17 on 16th November. During summer *Potamogeton alpinus* grows and provides alternative cover, which may be a reason for the drop in numbers in the artificial vegetation.

#### REFERENCES

- GARDNER, A.E. & N. MACNEILL, 1950. The life history of *Pyrrosoma nymphula* (Sulzer) (Odonata). *Ent. Gaz.* 1: 163-182.
- LAWTON, J.H. 1970. A population study on larvae of the damselfly *Pyrrosoma nymphula* (Sulzer) (Odonata: Zygoptera). *Hydrobiologia* 36: 33-52.
- MACAN, T.T., 1964. The Odonata of a moorland fishpond. *Int. Rev. Hydrobiol.* 49: 325-360.
- MACAN, T.T., McCORMACK & R. MAUDSLEY, 1966/7. An experiment with trout in a moorland fishpond. *Salm. Trout Mag.* 1966: 206-211; 1967: 59-69.
- MACAN, T.T. & A. KITCHING, 1972. Some experiments with artificial substrata. *Verh. int. Ver. Limnol.* 18: 213-220.
- MACAN, T.T. & R. MAUDSLEY, 1966. The temperature of a moorland fishpond. *Hydrobiologia* 27: 1-22.