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The influence of predation on the fauna of a moorland fishpond

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With 1 figure and 9 tables in the text

Contents

MACAN (1964, 1965) has described the fauna of the weeds in a small fishpond while it was free of fish. Now the changes that followed the introduction of fish are discussed. The present paper takes account of all the animals except the Heteroptera, which will be the subject of a separate article.

1. Description of the tarn

Hodson's Tarn is small moorland fishpond, filled with soft water poor in electrolytes. Comparison of the extent of the drainage area with the size of the tarn reveals that the water may be replaced within 24 hours on a wet day. The greatest depth is about 3 metres.

In 1961 the temperature never reached 19° C; in the other years it spent the following number of hours above 20° C:

1959	1960	1963	1958	1964	1962
340	226	152	70	30	22

In 1960 it was above 25° C for four hours; in 1959 it never reached 23° C.

The outline of the tarn and the vegetation were surveyed in 1955, and a second survey was completed in 1964. This showed the area of the tarn to be 4080 m^2, nearly 10 % less than the figure previously quoted. Much of this was due to the exclusion of an area of *Carex* included in 1955, some was due to encroachment by marginal vegetation elsewhere, and some to a small error in the original survey.

Four types of vegetation were recognized by MACAN (1964), and the changes which they have undergone can now be described (see also fig. 1):

1. Emergent — mainly *Carex rostrata*. The band around the inflow end of the tarn has been advancing towards the middle into the *Potamogeton natans*. The sedge has grown thinner near the bank, and in places there is no vegetation at all. On the other side it has not replaced *Potamogeton natans* and the two are now much more intermixed than they were.

Of the two other emergents, *Glyceria fluitans* has almost disappeared, but *Eleocharis* has spread. In most places, however, the stems are far apart in a thick carpet of *Littorella*, and these areas have been included in the category "sward".

The area of emergent vegetation is still approximately 600 m^2, the area gained being balanced by the area no longer regarded as providing an aquatic biotope.

2. Floating-leaved — *Potamogeton natans* has spread in all directions particularly into the shallow water where *Carex* is now much less dense than formerly. It does not grow thickly in this new part of its range nor in that part of the old one which *Carex* has invaded. If the area is taken to be that part of the tarn where only *P. natans* leaves break the surface, it covers now 400 m^2, which is less than formerly because the amount lost to *Carex* has not been made up by the amount gained along the open margin in deeper water. There is more *Juncus fluitans* and *Nitella* growing among the *P. natans* than in earlier years.

3. Sward — *Littorella uniflora* has spread with vigour, covering on both sides of the tarn areas of deeper water where previously there was little vegetation. Between posts 1 and 4 (fig. 1) it now grows thickly over an area where there were bare stones in 1955. It extends beyond the edge of the *Myriophyllum* between posts 16 and 20 and has invaded the emergent vegetation off posts A and 9. The total area of sward is now some 900 m^2, nearly twice as much as in 1955.

4. Milfoil — *Myriophyllum alterniflorum*. It was noted in 1958 that the stand of this plant was thinner than it had been, and in 1960 its disappearance seemed imminent. By 1962 it had completely recovered, and it now grows thickly on the left-hand side of the tarn (posts 13—21) and less thickly on the right-hand side (posts 1—12). Much of the bottom here is covered by *Nitella*, which grows among the *Myriophyllum* everywhere. *Juncus fluitans* was also abundant in the upper half of the tarn in 1964, as it had been in 1955 though not in the years in between.

A patch of *Potamogeton alpinus* was first noted in the middle of the tarn in 1959. It has been spreading ever since and in 1964 covered over 50 m^2 in the area where it was first observed, as well as a few smaller areas elsewhere.

Potamogeton berchtoldii and *Utricularia vulgaris* agg. were two species noticed among the *Myriophyllum* for the first time in 1964.

The area covered by *Myriophyllum* and *Potamogeton alpinus* in 1964 was 2000 m^2, some 300 m^2 less than in 1955. *P. natans* and *Littorella* had taken over the ground lost.

About 200 m^2 were reckoned to be bare in 1964, less than half as much as in 1955. The areas were in the *Carex* and off posts 9—12 between the *Littorella* and the *Myriophyllum*. It is, however, difficult to decide how far apart plants must be before the surveyor starts measuring the extent of bare bottom.

The importance of a fifth category of vegetation was not realized until the effects of predation were becoming manifest. Several species found refuge in the marginal vegetation and occurred nowhere else. The main plant was *Sphagnum*. Where the land was flat, this was long and loose and, together with *Carex rostrata* and *Juncus articulatus*, formed an area which was aquatic to small animals but not to those as large as a fish. Where the land was steep *Sphagnum* grew compactly together with *Scorpidium* (*Hypnum*) *scorpioides*.

2. Methods

Most of the collections were made with a net wielded in a way that gave roughly comparable results. A quantitative sampler (SCS) sampled much more accurately but brought in fewer specimens.

Fish were caught in gill nets.

3. History of observations

The tarn was emptied in 1948 and refilled the following year. In 1954, during the course of some preliminary observations, it became evident that this had not rid the tarn of all fish, as had been supposed. Twelve proved to have survived and the last of them was not caught until early in 1957.

In the autumn of 1960 500 *Salmo trutta*, hatched the same year, were introduced into the tarn followed by a further 500 a year later.

The netting of these fish to discover what they had been eating was started in spring 1961 but the work had to be discontinued that winter and the next. Regular collections every week in summer and nearly every fortnight in winter for twelve months did not start until 1963.

By October 1964 451 fish had been caught and, as only about 10 % of them belonged to the 1961 year-class, it was thought likely that survival of this had been poor and that not many fish remained in the tarn.

Collections of the rest of the fauna were made in late April or early May, late June or early July, and late September or early October, except in 1962 when the summer collection had to be omitted. As the work proceeded, it was found desirable to increase the number of stations from which collections were made and the final number was 14 (fig. 1).

4. Food of fish

During the summer fish fed extensively at the surface, where they found animals that had originated outside the tarn, as well as chironomid

Table 1. Food of *Salmo trutta* in Hodson's Tarn.

The total number of fish caught was 451. The figure in the left hand column is obtained by subtracting from this figure the number of fish caught during the period when the species in question was absent or so small that fish were not eating it.

Almost all the consumption of specimens in the lowest block (the last six species) took place in the first year.

	Total no. of fish caught in period when spp. eaten	Total no. of fish containing spp.	Total no. of specimens eaten	Highest no. in one fish
Allochthonous food	337	202	2,827	183
Eurycercus lamellatus	332	241	10,327	460
Chironomid larvae	424	312	6,972	463
Chironomid pupae and adults	337	262	6,183	420
Leptophlebia spp.	215	168	2,294	180
Hydroptilid larvae	305	155	1,042	80
Limnaea pereger	404	182	803	27
Ceratopogonid larvae	261	123	683	91
Phryganea spp.	286	89	322	30
Enallagma cyathigerum	403	126	287	9
Pyrrhosoma nymphula	354	61	156	19
Holocentropus dubius	327	49	112	24
Erpobdella octoculata	451	37	45	6
Haliplus larvae	—	29	130	42
Pisidium spp.	—	41	96	—
Sialis lutaria	—	65	92	—
Triaenodes larvae	—	26	79	16
Leptocerus larvae	—	44	78	9
Haliplus fulvus	—	26	73	19
Corixa spp.	—	33	45	—
Libellulid ny.	—	21	31	3
Entomostraca (exclud. *Eurycercus*)	—	21	25	—
Hydracarina	—	12	18	—
Nemoura ny.	—	12	15	—
Ostracods	—	11	14	—
Gammarus pulex	—	9	14	3
Triturus helveticus adults	—	10	13	3
Deronectes 12-pustulatus	—	11	12	2
Cloeon spp. nymphs	—	9	9	—
Limnephilus larvae	—	5	6	—
Oligochaeta	—	5	6	—
Aeschna nymphs	—	4	4	—
Hydroporus adults	—	3	3	—
Triturus helveticus larvae	—	1	1	—
Tabanid larva	—	1	1	—
Chaoborus pupa	—	1	1	—
Hydrophilid larva	—	1	1	—

Table 1.

	Total no of fish caught in period when spp. eaten	Total no. of fish containing spp.	Total no. of specimens eaten	Highest no. in one fish
Agabus affinis	—	1	1	—
Donacia sp. adults	—	39	46	—
Gerris sp.	—	8	8	—
Velia caprai	—	5	5	—
Gyrinus sp. adults	—	1	1	—
Leptophlebia adults	—	13	25	—
Trichoptera adults	—	13	15	—
Enallagma adults	—	2	6	—
Plecoptera adults	—	5	5	—
Pyrrhosoma adults	—	1	3	—
Lestes adults	—	1	1	—
Notonecta nymphs	83	1	3	3
Deronectes assimilis	83	13	18	2
Dytiscid larvae	83	21	80	13
Lestes sponsa ny.	83	12	27	8
Corixa nymphs	83	10	35	14
Caenis horaria ny.	30	4	28	10

larvae, pupae and adults. Apart from this they did not prey much on the mud-dwellers (chironomid larvae, *Sialis, Pisidium,* Oligochaeta), and their consumption of plankton species was negligible. The main source of food was the fauna of the weeds, that is the animals with which the survey has mainly been concerned (table 1). In general only the larger specimens of each species were taken. Many *Eurycercus lamellatus* were consumed, but the number of other entomostraca taken was trifling. No species of moderate size escaped predation, but some species were more successful at this than others. It is hoped to revert to this topic in a later publication.

5. The effects of predation

In the previous account the animals were placed in three categories according to their abundance, and it is convenient to retain this system but to present it in the reverse order.

5.1 Casual species

There were 14 species in the earlier account (Macan 1965, table 5) but nine of these, being Heteroptera, are discussed elsewhere. Of the remaining five, three were Coleoptera and two Hirudinea. One leech occurred twice during the fish-free period, all the others once. Not more than two specimens of any species were taken in a single collection. None of these casual species was taken in 1957 and 1959. After the introduction of fish, there were three consecutive years in which none was captured. In 1964, by which time predation had become less intense everywhere, and particularly in the shallowest water owing to the increased size of the fish, *Agabus sturmi* and *Glossiphonia complanata,* both recorded in previous years, and *Agabus bipustulatus,* a newcomer, were collected. In addition to these, another species previously unknown in the tarn, *Agabus affinis,* was found inside a fish. This capture lends support to a suggestion put forward during the course of the work on the Heteroptera that casuals apparently became scarcer because fish caught them before the human collector did.

5.2 Species taken regularly but always in small numbers

Before fish were introduced, there were three species of Heteroptera, three of Coleoptera and one of Plecoptera (Macan 1965, table 4). Of the three Coleoptera, *Rantus exsoletus* was taken every year, the highest total being 7, *Dytiscus semisulcatus* (*punctulatus*) and *Acilius sulcatus* less often. Apart from 1 *Rantus* in 1961, no adults of these species have been seen since fish were introduced. Possibly the larval stage, which is obvious to the human eye and therefore no doubt to the fish's eye as well, is the one mainly affected by predation. Large numbers of larvae were found in trout in 1961 (table 1) and thereafter very few. None have been taken in the standard collections though occasionally specimens have been seen.

The abundance of two other species remained unchanged. *Haliplus confinis,* treated previously in another section so that comparison might be made with *H. fulvus,* is one of them. The other is *Nemoura cinerea* (Plecoptera), the total numbers of which caught in 1961 (8) and 1962 (5) were in fact higher than any reached in the years without fish.

5.3 Abundant species

In table 2 the species are arranged so that those greatly affected by predation come first and those slightly affected last, and it is logical to regard them as forming a continuous series. In the text, however, it is convenient to separate them at arbitrarily chosen points into those greatly, moderately or scarcely reduced in numbers.

5.31 Species greatly reduced in numbers

Larvae of *Rana* and *Bufo.* As tadpoles tend to aggregate, a better impression of the effect of predation can be gained from observation than from the net collections. When there were no fish, tadpoles could be seen swimming all over the tarn until the end of June, when tiny adults were common round the edge. After the fish had been introduced, tadpoles could only be found at a few places at the extreme edge, where the vegetation prevented the approach of fish.

Table 2. Collections with net. Numbers at 10 stations. The lines show the numbers at successive times for each generation, and, therefore, "following spring" refers to the year after the one shown at the head of the column. Data for 1956—1960 are taken from table 6 in Macan (1965). (sp. = spring; f. sp. = following spring; su = summer; au = autumn)

		1955-1960 lowest	1955-1960 highest	1961	1962	1963	1964
Deronectes assimilis	sp.	6	22	13	0	0	0
	su.	14	22	5	—	0	0
	au.	8	25	5	1	0	0
Cloeon dipterum	au.	9	265	8	0	0	3
	f. sp.	4	104	2	0	0	—
Gammarus pulex	sp.	10	60	4	1	0	0
	su.	1	370	3	—	0	1
	au.	5	93	8	2	0	3
Dytiscid larvae	su.	20	102	20	—	2	14
Phryganea spp.	au.	30	215	6	17	26	35
	f. sp.	5	24	0	1	4	—
Limnephilus marmoratus	au.	10	146	10	23	39	219
	f. sp.	1	17	1	0	1	—
Triaenodes bicolor	au.	32	221	4	16	13	10
	f. sp.	16	200	8	5	6	—
Holocentropus dubius	au.	5	157	5	1	9	40
	f. sp.	4	34	1	0	12	—
Haliplus fulvus	sp.	18	36	24	44	4	18
	su.	20	53	15	—	16	16
	au.	9	39	17	8	22	35
Pyrrhosoma nymphula	su.	130	610	157	—	55	407
Enallagma cyathigerum	su.	220	450	333	—	53	139
Deronectes 12-pustulatus	sp.	0	3	2	5	2	0
	su.	2	8	5	—	1	1
	au.	1	5	3	1	3	1
Erpobdella octoculata	sp.	1	8	6	11	3	6
	su.	2	10	6	—	3	0
	au.	8	14	14	11	7	7
Triturus helveticus	su.	25	91	51	—	25	20
	au.	3	25	6	4	9	1
	f. sp.	3	9	3	2	3	—
Cloeon simile	au.	0	18	1	4	5	133
	f. sp.	1	13	1	10	28	—
Limnaea pereger	su.	18	357	202	—	134	55
	au.	14	176	137	287	193	5
	f. sp.	9	70	87	157	139	—
Chironomid l. and p.	sp.	124	204	254	129	237	874
	su.	159	429	356	—	91	567
	au.	48	302	117	73	680	95

No tadpole was recorded inside a fish. Most disappeared within a few days of starting to swim, and dates on which fish were netted could easily have fallen on either side of this short period. Moreover a tadpole probably does not remain recognizable long in the digestive juices of a trout.

Deronectes assimilis was found inside fish in 1961 on 8 out of the 11 occasions when samples were examined, and many Coleoptera larvae were eaten during that summer too. The species was not taken in the tarn in 1963 or 1964 (table 2).

Cloëon dipterum. Numbers were liable to big fluctuations when there were no fish, which may indicate that the species, generally associated with rich lowland ponds, is near the limits of its tolerance. The coming of an additional adverse factor, predation, has resulted in a great diminution in abundance (table 2). Few specimens were found in fish (table 1).

Gammarus pulex was found in fish but the reduction in numbers (table 2) may have been due in part to the growth of *Littorella* over the loose stones, the place where greatest numbers occurred.

Nymphula nympheata. MACAN (1965) suggested that small catches in 1959 and 1960 could have been due to the lateness of the date, but its absence or scarcity in later years does not support this. Therefore the original decline started before the predation, but whether this factor has prevented recovery must remain conjecture; no specimens were found in fish.

Leptocerus aterrimus. As this species occurred in deeper water beyond the reach of a wading collector, no certain conclusions about it may be drawn. Numbers fell in 1959 and were low also in 1960. The fact that they never rose again after the release of the fish and that larvae were found in fish regularly each year in May and June probably indicates that total numbers were reduced by predation.

It is concluded that the decrease of all except *Gammarus* and *Nymphula* was due to predation. All in this section are among the least numerous of the abundant species. From the point of view of the effect of predation they resemble species classed as "occurring regularly but always in small numbers" more than the most numerous members of those rated abundant. It would seem possible that predation pressure has been one of the factors to which species successful, that is numerous, under conditions of this nature have adapted themselves.

Adaptation in behaviour has been important. In a tarn well stocked with fish, little life is visible to the human observer. In a tarn without them, nymphs of *Notonecta* hang everywhere from the water surface and larvae of Coleoptera and of frogs and toads can be observed swimming freely in the open water. These are the animals that are much scarcer in the presence of fish. Their behaviour is clearly inappropriate to conditions where there is a large predator.

Two species, both greatly reduced in number, belong to genera (*Deronectes* and *Cloeon*) in which a second species has been little affected. There must be something fundamentally different in the way of life of the two.

5.32 Species moderately reduced in numbers

Phryganea striata and *varia*. Numbers are fewer but no change in distribution is evident. Fair numbers have been found in fish throughout the period, particularly in the autumn. This is a period of high mortality in the absence of fish (Macan 1965 fig. 4).

Limnephilus marmoratus. The autumn totals were always variable and on the figures in table 2 there is no evidence of decline since predation started; in 1964 the total was the highest recorded. On the other hand the spring totals have been consistently low compared with those in the fish-free era. However, reduction is not great, and it is not surprising to find that few specimens are eaten; they have been found in fish on five occasions only and four of these are in 1964.

Triaenodes bicolor. There was a big reduction in numbers, and a fair consumption of larvae by fish in summer in 1961 and 1963 though not in 1964. This is the time when larvae are active and there is probably some kind of hibernation in winter.

Holocentropus dubius was found inside fish in 9 out of 10 collections between mid-April and mid-June 1964 and again in September. In other years it was less frequent but some were eaten.

Enallagma cyathigerum. The average number that reached a size where emergence the same summer was likely ranged from 6 to 7 in the four years before fish were introduced (Macan 1964 table 12). The averages since range from 5 to 9 (table 3). However there has been a change in distribution, and higher numbers in *Littorella* and lower numbers in the *Myriophyllum* have combined to produce the similar averages. Allowance must be made for this because *Myriophyllum* covers a larger area than *Littorella*. The following correction has been applied:

1. From the figures in the extreme right- and left-hand columns of table 3 are calculated an average per catch in *Carex*, *Littorella*, *Potamogeton natans* and *Myriophyllum*; *Glyceria* has been ignored because the area which it covers is very small. The figures for the shallow station between posts 6 and 7 have not been used in the calculation of the average catch in *Littorella* because *Enallagma* was scarcer at the extreme edge than in deeper water. The figures for the station between posts 18 and 20 have been omitted in the calculation of the average for the earlier period as *Littorella* grew more sparsely then.

Table 3. Hodson's tarn. Net collections in spring. Numbers of *Enallagma* large enough to emerge the same summer.

	Average of previous years	1961 April	1962 May	1963 April	1964 April	Average last 4 yrs
Carex A—C	2	1	3	1	1	1·5
14—15	2	1	1	2	0	1
4—5	1	2	1	1	0	1
Glyceria 7—9	4	3	11	2	1	4
16—17	3	1	20	0	3	6
Litt. 10—12	10	21	13	8	13	14
9—10	12	10	19	13	15	14
6—7 sh	5	9	11	10	4	8·5
6—7 dp	18	12	9	6	5	8
18—20	6	11	18	14	9	13
P. natans	3	6	3	4	6	5
Myr. 3—20	10	—	—	1	2	1·5
7—20	12	—	0	1	4	1·5
	Total specimens	77	106	63	63	
	No. of stations	11	12	13	13	
	Average	7	9	5	5	

2. These averages per catch are multiplied by a factor that gives numbers/m^2. The factor has been obtained by comparing twenty-five collections with a pond net and twenty-five collections with the sampler close together in time and space (Macan 1963 table 39). Recent collections compared in the same way have given similar ratios. The area covered by the SCS is known, and the area covered by the net is calculated from the ratio of the catches obtained by the two methods. For example, the net catches 8 nymphs of *Enallagma* to every one in the SCS. The SCS covers 375 cm^2 and the net, therefore, $375 \times 8 = 3000$ cm^2. Number per net $\times$ 3 · 3 gives, therefore, numbers/m^2.

3. Numbers/m^2 are multiplied by the area covered by the plant in which the station lay.

In this way are reached the figures in table 4, which are reasonably close to those in table 17 (Macan 1964) calculated by a slightly different method. Allowance having thus been made for the large area covered by *Myriophyllum*, the numbers of *Enallagma* reaching full size are seen to have been approximately halved.

For reasons discussed in the previous paper, *Enallagma* is more difficult to analyse than *Pyrrhosoma* and results are never as certain. When the catches of *Enallagma* in the SCS are treated in the same way as those of *Pyrrhosoma* are in table 7, a close similarity between the two species is evident.

Table 4. Hodson's Tarn. Total numbers of *Enallagma cyathigerum* large enough to emerge the same summer in the four main types of vegetation. (The calculations are made from the averages in table 3 as explained in the text. The area for each species of plant used is that given in MACAN (1965) for the pre-fish time and that given in the present paper for the period with fish.)

		before fish	with fish
Carex		3,960	1,980
Littorella		21,500	35,640
Pot. natans		5,964	6,600
Myriophyllum		79,400	9,900
	Total	110,824	54,120

Lestes sponsa. Figures for the spring collection are open to the danger that the collection was made before all the eggs had hatched, or after the nymphs had started to disperse all over the tarn, but predation is the more likely explanation of the reduction in the last three years in table 5. There was no reduction in 1961 because, almost up to the time of collection, the generation had been invulnerable in the egg stage. Unexpectedly the reduction is not as great in the summer population, though it is still marked. A notable feature of the summer catches is the absence of the species from the *Myriophyllum*, where, when there were no fish, it was sometimes abundant (fig. 1). A calculation like that made for *Enallagma* has not been made, as numbers vary so greatly from year to year.

Table 5. Hodson's Tarn. Number of *Lestes sponsa* caught with a net at 10 stations in spring (April and early May) and in summer (June and early July).

	1956	1957	1958	1959	1960	1961	1962	1963	1964
spring	30	100	250	120	160	360	9	4	13
summer	140	100	120	100	60	120	—	6	42

The eggs are laid in shallow water but the nymphs soon spread all over the tarn, particularly to the *Potamogeton natans* and *Myriophyllum* (MACAN 1964 table 19). Evidently it is the nymphs that leave the neighbourhood of their hatching place that are generally caught by fish.

The number of tiny nymphs not long out of the egg was highest in 1961 and in the third week in June numbers were still as high as in previous years (table 5). Fish, however, were preying extensively on these nymphs all the time, and some in every collection contained them. How many reached the adult stage is not known, but in the following spring only 10 specimens were collected, all in the *Carex* near the inflow. Nymphs were not found in fish again until one occurred in 1964.

Haliplus fulvus is not much affected but all the low totals in summer are after the introduction of fish. It is found occasionally inside fish throughout the period. Before fish were introduced it was a species of the shallow water especially in emergent vegetation. Afterwards it was relatively scarcer in the *Littorella* except at the one station at the extreme edge, where the highest number was caught.

Eight *Haliplus* larvae were taken in the pre-fish years and eleven afterwards, and it was not discovered where the larvae live. They appeared

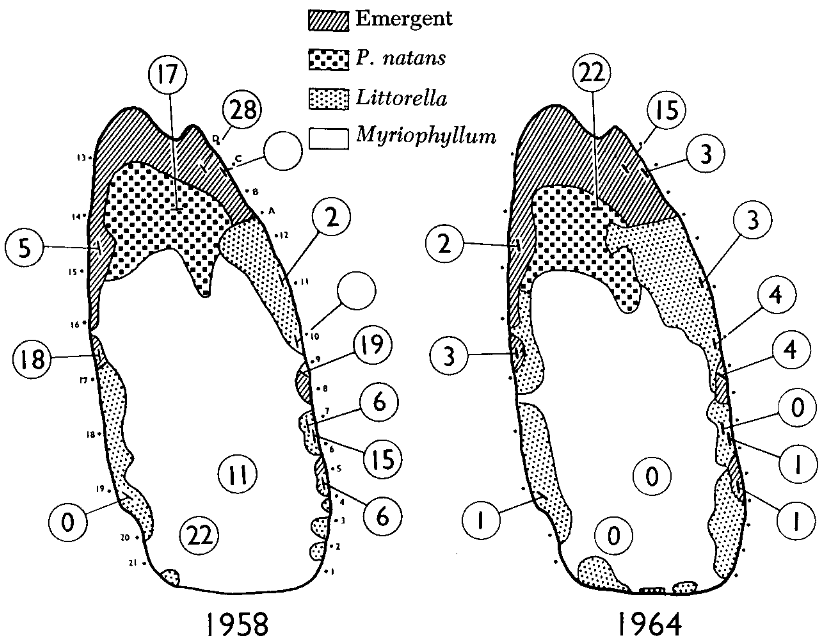

Fig. 1. Hodsons Tarn. Occurrence of the main types of vegetation (surveyed 1955 and 1964), positions of the collecting stations and the number of nymphs of *Lestes sponsa* caught at each with a net. Collections of 1—3 July 1958 andm 17—23 June 1964. The position of the numbered posts are also shown.
No collections were made in 1958 at the two stations at which no figures are shown in the circles.

to be well hidden from fish also to judge from the infrequency with which they were eaten, but two fish contained large numbers; there were 42 in one caught on 7 June 1961 and 21 in another caught on 23 July 1964. Both fish contained more than we had seen in ten years, but whether they had discovered how to find the larvae or whether they had stumbled on an exceptional concentration cannot be determined.

The reduction of the last three species has accompanied a restriction in range; the species have been reduced in numbers in places where they are not well protected from predation but maintain their numbers where they are.

The other five species, all Trichoptera, have been reduced uniformly as far as can be made out, but it is not possible to be certain on this point, as numbers are small during the later stages of the generation.

Large numbers of *Phryganea* are eaten in autumn at a time when there was a reduction in numbers in the years before fish were present (Macan 1965 fig. 4). At this time of year fish are not doing much more than remove surplus destined to perish in any case.

5.33 Species not or scarcely reduced in numbers

Leptophlebia marginata and *vespertina*. Nymphs are small enough to pass through the net in the autumn and therefore assessment of the population at that time of year must be based on collections with the SCS (table 6). Fewest specimens were taken in 1962 and not many more in 1963,

Table 6. Hodson's Tarn. SCS. *Leptophlebia* nos/m^2.

	1957	1958	1959	1960	1961	1962	1963	1964
Autumn collections								
Littorella 10—12	4640	4410	7965	2484	4096	2740	2873	8831
off 19	—	—	7290	1917	2580	1037	3751	6464
Carex	6479	9954	8370	5940	5134	2075	3884	9097
Spring collections								
Littorella 10—12	—	—	459	27	166	213	426	585
off 19	—	—	162	27	80	346	426	585
Carex	—	—	—	1215	638	1330	1303	1383
Number caught with net at 10 stations	669	1649	744	389	521	515	586	1490

but the difference between 1962 and 1960, when there were no fish, is negligible. The greatest number was taken in 1964. Admittedly the number of fish had been reduced by then, but predation was still a factor. The results suggest that it is not one which has much effect on small nymphs.

The numbers caught in spring by both methods are shown in the lower half of the table. Totals caught in the net during the first three years with fish are lower than all except one in the years before, but the total in 1964 is second highest. Nymphs are eaten by trout from about November onwards, probably being too small before then, and are consumed in greater quantities than any other organism in the early months of the year. Notwithstanding this predation, as the figures discussed above indicate, the numbers attaining maturity are only slightly reduced. An explanation is offered later.

Unexpectedly few adults and nymphs on the point of emergence were found in fish, probably because emergence, and later on oviposition, take place close to the shore.

Pyrrhosoma nymphula. Up to 1958 nymphs in *Carex* required two summers to complete development, and they emerged in their fourth year. In the winter 1958/59 the population was greatly reduced, and the 1959 year-class completed development in one summer (MACAN 1964, fig. 5) emerging in its third year. The 1960 year-class also achieved this and, after the introduction of fish there was no return to the former cycle, though some members of some year-classes took two summers to complete development. As the slower development had been attributed to overcrowding, it had been expected that it would not recur when the nymphs were subject to predation.

Table 7 shows the number caught with the SCS, the data being set out as in table 8 of MACAN (1964), which is the source of the last line. There were about half as many newly emerged nymphs as in the pre-fish years and half as many nymphs in their second summer. Third-summer nymphs are relatively fewer still, as is to be expected from what has been written in the preceding paragraph about life history. Nymphs about to emerge are more numerous, but the figures of this end of the table are small, and errors due to chance can therefore be large. However, the num-

Table 7. Hodson's Tarn. *Carex* 14—15. Numbers of *Pyrrhosoma* in 5 SCS samples.

date	newly emerged	2nd summer	3rd summer	about to emerge
Oct. 1961	22	6	0	
Sept. 1962	16	7	0	
Oct. 1963	45	2	1	
Oct. 1964	11	14	5	
Apr. 1961		1	0	2
May 1962		15	0	
Apr. 1963		9	4	2
Apr. 1964		3	1	4
Total	94	57	11	8
Number of collections	4	8	8	3
Average	23.5	7	1·4	2·7
Average 1957—1960	53	17	4	1

Table 8. Hodsons's Tarn. *Pyrrhosoma.* Average number of full-grown nymphs caught with a net in April or May. (The average has been calculated in the same way as in table 4 of MACAN, 1964.)

1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
5	7	5	6	9	7	4·6	4·6	6·2	5·2

bers of larger nymphs caught in the net can be brought in for comparative purposes, which is done in table 8. The number of full-grown nymphs is on the average very slightly lower after the introduction of fish. Net catches also confirm that numbers of specimens in their first year, after the previous year-class has emerged and before the succeeding one has hatched, tend to be lower after the release of the fish (table 2).

The result of predation seems, then, to be a smaller population at the beginning of the generation, quicker growth, lower mortality, and a final number that is only a little lower than it was before predation.

Nymphs, mainly larger ones, are eaten all through the year but especially in spring, possibly because, about to emerge, they become restless then.

No explanation is offered of the smaller number of newly emerged nymphs. Various methods of counting cast skins after emergence have not shown any marked reduction of these, and the figures in table 1 do not indicate extensive predation on adults, though Dr. W. E. Frost once recorded a large number inside a trout caught in a nearby tarn.

An explanation of subsequent events is put forward. The earlier work while there were no trout in the tarn showed that, when numbers were high, only a proportion developed at the usual rate and the rest grew little at first, though many remained alive for a long time. It was suggested that those which grew were those which were successful in obtaining a place where enough food could be obtained. Others occupied places where they could not obtain enough to eat to grow at the normal rate until good places were vacated when their more successful brothers and sisters emerged. There were probably yet others in even less satisfactory places which died of starvation after a longer or shorter period. When fish were present, there was a constant removal of larger nymphs from good places, but always a sufficient reserve of small undernourished specimens to provide a replacement to take over both situation and rate of growth. Accordingly the number of large nymphs remained the same and smaller ones were fewer.

Erpobdella octoculata was eaten regularly throughout the period of observation, though large numbers were never found inside a fish. The numbers in the tarn (table 2) and the distribution showed no change.

Cloeon simile. Numbers showed a progressive increase from 1961 when they were at their lowest to 1964 when they were at their highest by a wide margin. Of 190 specimens in autumn 1964, 104 were in *Myriophyllum*, 27 in *Potamogeton natans* and the rest were distributed among most of the remaining stations, a pattern similar to that observed before fish were present. Fluctuations in numbers were evidently little influenced by fish, which preyed on the nymphs to a slight extent only (table 1).

Triturus helveticus. Numbers collected in spring were not greatly different before and after the arrival of fish, but numbers at other times of year were a little lower after it. Few larvae were found in fish but adults were preyed on heavily in relation to their numbers.

Limnaea pereger. In 1960 the catches in spring, summer and autumn were higher than any previously. Fish were then introduced and, in the years that followed, they fed freely on *L. pereger,* which, notwithstanding, maintained high numbers until 1964. The breeding population was moderately large that year, but the catch in the autumn was the smallest ever recorded. In other words the population increased before the fish were put in, remained high when predation was greatest, and decreased suddenly

Table 9. Hodson's Tarn. Heights of *Limnaea pereger* taken by means of a net in April 1963.

Station	2 mm	3 mm	4 mm	5 mm	6 mm	7 mm	8 mm	9 mm	10 mm	11 mm	12 mm	13 mm	Total	Average length
Littorella 6—7 sh	2	1	5	11	8	7	8	1	1	1			45	6·1
6—7 dp	2		1	1		2		3					9	5·8
9—10	4	1	6	10	10	7	9	1	1				49	5·8
off 11	3	16	20	7	1	4	1	2					54	4·2
off 19	1	3	8	9	3	2	3	1					30	5·1
Eleocharis 8—9									1				1	10·0
16—17			1		1								2	5·0
Carex off C							1		1	4	4		10	11·0
14—15											1		1	12·0
4—5						1							1	7·0
Potamogeton natans												1	1	13·0
Myriophyllum 5—20													—	—
7—20											1		1	12·0
No. per length	12	21	41	38	23	23	22	8	4	5	6	1		

at a time when fish were becoming fewer; clearly there is little connexion between the two.

When *L. pereger* became numerous, unevenness in its growth at different places became apparent, and, accordingly the height of every specimen was measured during the last three years. The results obtained in April 1963 are shown in table 9. In April 1964 the total catch was about the same and the general picture similar although the winter had been much less cold. In 1962, also after a mild winter, only about half as many snails were taken, and mean, minimum and maximum size were all higher. There is here a strong suggestion that size and numbers are related, though it can be objected that the imponderable factor of climate may be involved too. HUNTER (1961 b) found that the size of *Limnaea pereger* in Loch Lomond was influenced by the severity of the winter but not by numbers. The range over which the numbers fluctuated was greater in the tarn than in the loch, as was also the range in size. Comparison of different stations in the same year, a comparison not open to this objection, supports the suggestion. It may be seen in table 9 that most of the large specimens were taken where snails were few and most of the small where they were numerous. The densest population had the smallest average length and the sparsest the greatest, though in between numbers and average size do not all fall in the same order.

The fate of the small ones was not ascertained because samples were not obtained sufficiently frequently; nor was their origin certain. HUNTER (1961 a) has shown that some specimens of *Limnaea pereger* may lay eggs in autumn. No eggs were ever found in Hodsons Tarn at this time nor did any figures such as those in table 9 show the peak on small specimens that should result from a second generation. The possibility must be borne in mind, but it is probable that specimens 2 mm long in spring derived from eggs laid during the previous summer. Subsequently they may have died, grown rapidly, or remained so small that in the summer collections they were indistinguishable from the new generation. It is unlikely that they attained a large size and, therefore, if they produced eggs at all, the number produced was probably low in comparison with the number laid by a specimen that had been large for a long time.

There is evidently some mechanism which, when the numbers of *L. pereger* are high, prevents more than a limited proportion reaching full size while permitting the survival of small ones, from which, no doubt, gaps in the ranks of larger ones can be filled. How far it is comparable to that which produces a similar result in *Pyrrhosoma* is discussed later.

Chironomid larvae and pupae. Numbers were highest in 1963 und 1964 but, as the species were not identified, the significance of this cannot be assessed.

Deronectes duodecimpustulatus was never found in *Myriophyllum* or *Potamogeton natans* and most specimens were in the *Littorella*. The biggest catches were made at the deep station between 6 and 7, both before and after the arrival of the fish, and numbers taken there in the same number of collections were identical. Elsewhere there was a small reduction when fish were present. Other air-breathing swimmers survived predation best in the shallowest water, and insufficient is known about *D. duodecimpustulatus* to explain why it differs from them.

Anisoptera. Three species of libellulids and *Aeschna juncea* have not decreased in abundance. In the fish-free years, the total number of libellulids ranged from 13—31. Bigger hauls, notably 101 at 11 stations in summer 1961 and 109 at 14 in summer 1964, were made when fish were present. The autumn catches in those two years were 3 and 1 respectively.

The numbers found inside fish (table 1) suggest that there was another cause for this spectacular drop.

Probably few of these anisopteran nymphs or newt larvae were eaten because they spent so much of their lives securely concealed in the vegetation. There is no obvious explanation of why few nymphs of *Cloeon* were found inside fish.

It is to be expected that the populations of these species would not alter when fish were introduced. It remains to discuss how some species maintained their numbers although many specimens were eaten by fish. First it is noteworthy that all were abundant species; in other words they were successful, and it has already been suggested that this was due in part to adaptation to conditions in which predation was an important factor.

If a breeding population is to remain constant in size whether or not the species is subject to predation, which takes heaviest toll of the largest specimens, there must be some mechanism whereby a reserve of small specimens is created and maintained. Any of these provided with the opportunity to take the place of a larger specimen which has perished will survive and grow; the rest will die. It is suggested that the reserve of small dragon-fly nymphs consists of those specimens that have not secured a position in the vegetation from which they could catch enough to eat. It is not difficult to picture how the success of a predator which waits till its prey comes within reach depends on gaining possession of a perch which the prey passes often and which perhaps offers possibilities of concealment. It is less easy to picture how this process can apply to a herbivore such as *Leptophlebia,* or more particularly *Limnaea pereger,* which appears incapable of any offensive act. It is necessary to suppose that a larger specimen can secure and keep for itself a large territory from which it can obtain all that it requires for growth. A smaller one is prevented from enlarging its territory and is unable to grow. An alternative is that some substance which inhibits growth is produced. The Roses (1965) have shown that larger tadpoles can prevent the growth of smaller ones in this way and cause their deaths in a short time. It is necessary to postulate that, if a secretion is produced by, for example, *Limnaea pereger,* it is milder than that produced by tadpoles since it arrests growth or slows it down without causing death in a short time, but there is nothing inherently objectionable about this postulate.

6. Discussion

Many of the inhabitants of the tarn are the larvae of insects that ultimately fly away and probably die elsewhere. Fish eat some of these either before they leave the water or as they are about to. They also catch insects that live their lives outside the tarn and which otherwise would fly away again or strand on the bank. Therefore there is more matter in circulation when fish are present than when they are not, but what effect this has on other inhabitants of the tarn was not discovered.

Salmo trutta does not disturb the vegetation in the way that some fish do. Its chief effect is as a predator that will eat any organism which exposes itself. Though this does not affect some of the commoner species, it restricts others to a smaller, sometimes a much smaller, area than they inhabited before. Where this process extends to the point of elimination is very difficult to make out, but *Notonecta* and certain dytiscids are particularly susceptible to predation and would occur in more places were it removed.

The tarn is poorer in species as a result of the introduction of fish, and no addition to the list, increase in range or increased abundance seems related to their arrival.

Specimens have been measured but not weighed and therefore no measurements of biomass have been possible. There can be no doubt that it has decreased. Production has probably gone up; some of the abundant species are producing as many mature specimens as before and in addition a large number that fall a prey to fish. It is likely that this extra production more than makes good that lost by species now less numerous at all stages. This is the conclusion reached by Hayne and Ball (1956) who, however, did not consider species individually.

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8. Summary

Hodson's Tarn is a moorland fishpond some 4000 m^2 in extent and 3 m deep. The main types of vegetation are shown in figure 1.

During the years 1955 to 1960 there were few or no fish. 500 young *Salmo trutta* were introduced in the autumn of 1960 and another 500 a year later.

Some species were greatly reduced, possibly eliminated, after the introduction of fish. Of these *Notonecta*, and the larvae of *Rana*, *Bufo* and several dytiscids lacked the behaviour appropriate in a water inhabited by a large predator. They survived, if at all, in a few marginal places where thick vegetation barred entry to fish.

Other species were moderately reduced. *Enallagma cyathigerum* showed no

diminution of numbers in the shallow water but was less abundant in the *Myriophyllum* further out. *Lestes sponsa* was less abundant everywhere and, though formerly generally numerous there, was not recorded in *Myriophyllum* after the release of the trout. *Haliplus fulvus* was less abundant, diminution of numbers being greater in *Littorella* than in emergent vegetation. Five species of Trichoptera were less abundant but no change in their distribution was evident.

The numbers completing a generation of the remaining species were similar before and after the introduction of fish. *Deronectes duodecimpustulatus* and *Cloeon simile* came into this group though *D. assimilis* and *C. dipterum* were severely affected by predation. The reason for this difference was not discovered. *Leptophlebia marginata* and *vespertina, Pyrrhosoma nymphula* and *Limnaea pereger* were among the most numerous of the larger animals living among the plants, and they were also important as food for trout, which fed mainly on large specimens. The number of these was maintained by recruitment from a reserve of smaller specimens, which probably died if this opportunity did not present itself. It is thought that a few dragonflies secure places where they can obtain enough to eat to grow, and many obtain places where the food is sufficient for no more than the maintenance of life. It is less easy to picture a snail occupying a good territory and keeping it by virtue of superior size. The possibility that large snails may inhibit the growth of small ones by means of a secretion is mentioned.

9. Zusammenfassung

Hodson's tarn ist ein Fischteich im Moorgelände. Seine Fläche umfaßt 4000 m^2, und seine Tiefe beträgt 3 m. Seine wichtigsten Vegetationstypen sind in Abb. 1 dargestellt.

Während der Jahre 1955 bis 1960 gab es dort wenige oder keine Fische. Im Herbst 1960 wurden 500 junge *Salmo trutta* eingesetzt und ein Jahr später weitere 500.

Die Folge war, daß einige Arten stark reduziert, vielleicht eliminiert wurden, darunter *Notonecta* und die Larven von *Rana, Bufo* und einige Dytisciden. Sie überlebten, wenn überhaupt, nur in wenigen Randbezirken, wo den Fischen der Eintritt durch eine dichte Vegetation verwehrt wurde. Andere Arten wurden nur mäßig reduziert. *Enallagma cyathigerum* zeigte keine Bestandsverminderung im flachen Wasser, war aber weniger zahlreich im *Myriophyllum*-Bestand weiter draußen. *Lestes sponsa* ging überall an Zahl zurück und wurde im *Myriophyllum*-Bestand nicht mehr festgestellt, obgleich diese Art hier vordem zahlreich vorhanden war. *Haliplus fulvus* wies eine stärkere Bestandsminderung zwischen *Littorella* als im Röhricht auf. Fünf Trichopteren-Arten gingen an Zahl zurück, ließen jedoch keine Änderung in ihrer Verbreitung erkennen.

Die Vermehrungsziffern der verbliebenen Arten waren vor und nach dem Fischeinsatz gleich. Auch *Deronectus duodecimpustulatus* und *Cloeon simile* gehörten zu dieser Gruppe, obgleich *D. assimilis* und *C. dipterum* stark unter dem Fischfraß litten. Jedoch war es nicht möglich, eine Erklärung hierfür zu finden. *Leptophlebia marginata* und *vespertina, Pyrrhosoma nymphula* und *Limnaea pereger* gehörten zu den zahlreichsten größeren, zwischen den Pflanzen lebenden Tieren, und sie waren alle als Nahrung für die Forelle wichtig, die sich vornehmlich an die größeren Exemplare hielt, deren Zahl sich aus der Reserve an kleineren Individuen ergänzte, die andernfalls vermutlich gestorben wären. Es wird angenommen, daß einige Libellen im Gewässer Plätze fanden, wo genügend Nahrung zur

Verfügung stand, zahlreiche aber fanden gerade so viel Nahrung, wie zur Erhaltung des Lebens notwendig war. Möglicherweise wird das Wachstum von kleinen Schnecken durch die Sekretion großer Individuen gehemmt oder unterbunden.

10. References

HAYNE, D. W., & BALL, R. C. (1956): Benthic productivity as influenced by fish predation. — Limnol. Oceanogr. **1:** 162—175.

HUNTER, W. R. (1961 a): Annual variations in growth and density in natural populations of freshwater snails in the west of Scotland. — Proc. zool. Soc. Lond. **136:** 219—253.

— (1961 b): Life cycles of four freshwater snails in limited populations in Loch Lomond, with a discussion of infraspecific variation. — Proc. zool. Soc. Lond. **137:** 135—171.

MACAN, T. T. (1963): Freshwater Ecology. — London: Longmans. X + 338.

— (1964): The Odonata of a moorland fishpond. — Int. Rev. Hydrobiol. **49:** 325—360.

— (1965): The fauna in the vegetation of a moorland fishpond. — Arch. Hydrobiol. **61:** 273—310.

ROSE, S. M., & ROSE, F. C. (1965): The control of growth and reproduction in freshwater organisms by specific products. — Mitt. int. Verh. Limnol. **13:** 21—35.

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