A twenty-year study of the fauna in the vegetation of a moorland fishpond

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With 1 figure and 1 table in the text

Abstract

The fauna in the vegetation of a moorland fishpond was sampled during 20 years. Fish *(Salmo trutta)* were removed and then added. After most of the big population added had been caught, cover provided by vegetation declined. There were few changes in the list of species during the 20 years. Most diminished in number after the fish had been introduced but recovered as these were removed. Some were more affected by the decline in the vegetation than by predation. Among these were two odonate larvae whose reduction was followed by a great increase in the numbers of *Gammarus*. The community is discussed in terms of stability, and in relation to THIENEMANN's basic principles.

Key words: Fishpond, predation, plant cover, stability, community, artificial substrate, Plecoptera, Ephemeroptera, Odonata, Megaloptera, Lepidoptera, Coleoptera, Diptera, Amphibia, Crustacea, Mollusca, Hirudinea.

Introduction

The original objective was to study the effect of predation by *Salmo trutta* LINN. on the numbers of its prey. Later, attention was turned to sampling by means of artificial vegetation. Preliminary trials having proved satisfactory, regular samples were taken by this method. The outcome of these two lines of investigation is a record of the numbers of the species studied over a period of twenty years, and the purpose now is to discuss the fluctuations observed and to relate them to changes in the tarn. Some of the relations recorded may be fortuitous, and if one species declines while another increases the changes are not necessarily connected. However, if the reverse process can be observed, the likelihood of a relationship is greater. In the two decades, predation by fish was reduced to nothing, then greatly increased, and finally reduced again, while much of the vegetation declined and recovered; therefore there are data about both phases of any relationship.

Previous publications

All are by the present author, except where the names of co-authors are quoted. An account of the Odonata (1964), notably their life histories and num-

bers in different parts of the tarn at different times of year, was followed (1965 a) by an account of the fauna as a whole from 1955 to 1960, when fish were introduced. The effect of five years of predation was described in two papers (1965 b, 1966 a), the Hemiptera being treated separately from the rest. The growth of fish in relation to numbers, and the question of how prey organisms maintained constant populations were discussed (1966 b). Temperature was measured with a recording thermometer during the seven years from 1956 to 1964 (MACAN & MAUDSLEY, 1966). MACAN, McCORMACK & MAUDSLEY (1966/67) discussed survival, numbers and growth of fish, and revert to their food, dwelling on seasonal changes rather than on total numbers eaten as was done in the 1966 a paper. MACAN & KITCHING (1972) described the artificial vegetation and the results of preliminary trials with it. The work on Odonata was taken up to 1971 and the numbers caught by different methods presented (1974 b). An account of some of the changes in 20 years and of some of the results of sampling with artificial *Littorella* was given (1975). MACAN & KITCHING (1976) record what was found on various substrates hung in midwater. The changes in the Heteroptera were described (1976) and an account of the changes in the vegetation has been accepted by the Journal of Ecology. An account of the fauna as revealed by regular collecting with artificial vegetation is planned.

Changes in the environment

Hodsons Tarn is an artificial fishpond, just under half a hectare in extent, lying in a drainage area some thirty times greater. Beside the tarn steep slopes supported plantations of *Picea* and *Larix* at the start of the work, but higher up the plantations were only a few years old. The growth of these recent plantations has been the only obvious change in the drainage area.

When the work started, there was rooted vegetation in nearly all of the tarn, four species occurring in thick continuous stands.

Myriophyllum alterniflorum DC occupied the deepest parts, which extended down to about 3 m. The shallower marginal zones were covered with swards of *Littorella uniflora* (L.) ASCHERS. At the shallow end, where the one small stream flowed in, *Potamogeton natans* L. occupied the centre, and *Carex rostrata* STOKES the marginal zone. Soon after observations started, in 1955, the *Carex* was observed to be thinning in the middle, and by 1961 much of the centre of the bed was devoid of vegetation. Recovery started in about 1965, and by 1971 the *Carex* was thick and continuous, and the margins were a little further into the middle of the tarn. The *Potamogeton natans* has moved slowly away from the inflow end of the tarn and advanced towards the dam. *Myriophyllum* began to decline soon after the first survey and by 1961 there was little left. It recovered completely, however, to become as thick as formerly. A second decline during the next three or four years left most of the deeper parts of the tarn without vegetation, and the *Myriophyllum* was so scarce that the plants could be counted individually. There was some colonization of the

bare areas by *Potamogeton alpinus* BALB. but its growth has never been luxuriant. *Littorella* was growing with great vigour up to 1964, colonizing new ground in all possible directions. A sudden decline started in 1965 and by 1967 living plants were scarcely to be found in water deeper than about 30 cm, though in that zone the plants appeared healthy. A slow recovery then set in, and by 1975 the area occupied was a little less than in 1964, but the plants were smaller and further apart.

It is thought that these declines were related to changes in the soil as plant remains accumulated, but there is no firm evidence.

In 1948 the tarn was drained and all the fish removed, or so it was thought. In fact a few survived and the last one was netted in 1957. In 1960, after the collections had been made, 500 *Salmo trutta*, hatched earlier in the year, were introduced. Another 500 were put in a year later, but it is thought that few of these survived. Fish were caught with gill-nets so that the source of their food might be studied, and, by 1965, 434 had been caught. This was probably the end of the introduced fish, but a small population of unknown origin has persisted ever since in spite of annual netting.

The collections

Methods

Three methods were employed. The chief was standard sweeping with a net of coarse mesh (10 strands/cm). The net brings in many specimens without harming the vegetation or gathering excessive amounts of debris which hamper sorting. Its disadvantages are that it is selective (MACAN, 1974 a, p. 290) and that it is not quantitative.

A quantitative sampler worked well and provided figures from which the area covered by the net could be calculated. Its disadvantages were that, removing substratum as well as vegetation, it altered the environment and produced a sample whose examination took a long time.

The artificial *Littorella* had four advantages: it was a means of sampling in deep water; it did not alter the environment; it provided samples strictly comparable with each other; it yielded the smallest specimens, because it could be brought up inside a net of mesh so fine that it would have clogged if used for sweeping. Its disadvantage is that it was not natural, and in fact generally harboured more animals than the same area of real vegetation.

The program

In the early years collections were made with a net at ten, eleven or twelve stations and this was repeated once a month. When, after a few years, sufficient data had been obtained in this way to discern certain unknown life histories, collections were made only in spring, summer and autumn. In 1964 and 1965 collections were made at fourteen stations, but thereafter the numbers declined, sometimes down to eight, because the vegetation had disappeared. In 1970, 1971 and 1972, when time was devoted to experimenting with artificial vegetation, the net collections were reduced to three or four. They were raised again to about 10 in the last three years but not at all the seasons.

In 1969 experiments with artificial vegetation started. It was necessary to discover the optimum area of a mat, the time necessary for colonization, the variation from mat to mat, and the effect of different numbers of strands per unit area. Gradually a standard technique evolved. During 1971 five mats were laid at each of nine, later ten, stations, and one mat from each station was lifted at each visit. All were numbered so that the mats could be lifted in turn. Each was raised gently off the bottom and then surrounded by a net. The mats were lifted from a boat in order that there should be no trampling of the substratum. Two people were, therefore, required, and this led to some irregularity during a period of six months at the beginning of 1972 when, in my absence, my assistant, Miss ANNETTE KITCHING was not always able to obtain help on a specified day. On my return in the autumn we started regular sampling once a fortnight and reduced it to once a month after a year and then to three times a year.

Presentation of results

Collections in 1955 are omitted because the sampling program was not identical with that of subsequent years.

The purpose of the figures in Table 1 and Figure 1 is to present as clear a picture as possible of the numbers each year. They are generally the numbers at the end of a generation. Numbers at the beginning can vary enormously from year to year and bear little relation to numbers later on.

The numbers are generally those at 10 stations where collections were made with a net. During the last three years net collections and artificial-vegetation collections were made at the same time, and from a comparison it was possible to calculate from the catches in artificial vegetation what would have been caught in a net. Figures for 1972, spring 1973 and autumn 1974 were obtained in this way. The figures for 1970 and early 1971 are least accurate because neither method of collection covered the full range of stations. Inevitably some error creeps in when numbers are calculated but it is believed that, even in 1970, they are not great enough to mislead.

If the numbers of a species in the *Myriophyllum*, which disappeared during the period of the investigation, were above or below the average for all stations, the number per 10 stations does not include any of the collections in *Myriophyllum*. The figures for those species which were numerous in one species of plant and scarce in others are based on the collections in that species of plant only. Figures for different species (Table 1) are, therefore, not all comparable one with another without further arithmetic.

The collections are roughly quantitative but the net is selective. An approximate idea of the number per unit area can be gained from the ratios quoted by MACAN (1974 a, p. 290).

Changes in the species list

Certain groups, listed by MACAN (1974 a), being hard to identify and generally poorly represented, have been omitted.

Most of the additions to earlier lists have been due to advances in taxonomy or more expert collecting. The publication of EDINGTON's (1964) key revealed that there were three, not one, species of polycentropodid in the tarn, and collecting of adult leptocerids beside the tarn after larvae had become more abundant also yielded three species where only one had been recognized before. The list now reads:

Cyrnus	*Athripsodes aterrimus* (STEPH.)
flavidus McL.	*Mystacides*
trimaculatus (CURT.)	*longicornis* (LINN.)
Holocentropus dubius (RAMBUR)	*azurea* (LINN.)

Larvae in an unfamiliar case were found in the tarn in 1973 and 1974 but it was not possible to name them. In 1975 some members of the Societas internationalis Odonatologica caught *Leucorrhinia dubia* (VAN DER LIND.) beside Hodson's Tarn, and this species may breed in it.

The one newcomer that may be so designated with confidence in view of the extensive collecting in previous years is a species of *Polycelis*, either *P. nigra* (O. F. MÜLLER) or *P. tenuis* IJIMA. Six specimens were found in a square of artificial *Littorella* off post 20 in March 1973. Another was taken there in May, and then none until November, after which specimens were taken in nine out of ten successive samples, the greatest number being 23 in April 1974. Occurrence was more sporadic after that date. In December 1974 one specimen was found on the other side of the tarn and another at a deep station, and since then *Polycelis* has been recorded at seven of the ten stations, but numbers have remained low.

One species numerous in the early years has died out. *Nymphula nympheata* (LINN.) was not recorded after 1968 and had been scarce from 1959 onwards.

Changes in numbers

MACAN (1974 a, Table 5) lists the species in four categories according to numbers caught, but this arrangement must be modified for the present analysis, partly because a different approach requires a different treatment and partly for other reasons set out below. The next few paragraphs are concerned with species about which there is not much to be written because they were never numerous. They include all the species designated "casual", most of those designated "taken regularly but almost always

in small numbers", and some of those designated "less numerous species". Hemiptera are omitted because they have been treated separately (MACAN, 1976).

Hirudinea. The net has been shown to be an unreliable method of collecting leeches. *Glossiphonia complanata* (LINN.) and *Theromyzon tessulatum* (MÜLL.) occurred regularly in the artificial *Littorella* in small numbers, and were clearly not "casuals" as the net collections apparently showed them to be. They may have been regular members of the fauna throughout the period of investigation, but nothing more can be said about them in the present context.

Coleoptera. *Hydroporus gyllenhalii* SCHIÖDTE (1956), *H. palustris* (LINN.) (1955, 1974), *H. umbrosus* (GYLLENHAL) (1975), *Agabus affinis* PAYKULL (1965), were taken in the years indicated, only one or two (*H. palustris* 1974) being captured. These are true casuals. *Agabus sturmi* (GYLL.) occurred in five of the seven years between 1964 and 1970. *Acilius sulcatus* (LINN.) occurred in four successive years until fish were introduced, and has not been seen since, except in 1974 when two larvae were found in an enclosure floating at the surface and containing a mat of artificial *Littorella*. Larvae of *Dytiscus* reappeared in 1965 after a period of absence when predation was most intense, and have been recorded regularly since. Adults of *D. semisulcatus* (O. F. M.) were recorded in 1955, 1956, 1959 and 1975, and a single *D. marginalis* LINN. was seen in 1965. There were no adults of *Rantus exsoletus* (FORST.) during three years of heavy predation but since then, small numbers, never exceeding 10 at ten stations, have been taken almost every year, as they were before fish were lodged in the tarn.

Odonata. *Cordulia aenea* (LINN.), *Libellula quadrimaculata* (LINN.) and *Sympetrum scoticum* (LEACH) are regular members of the fauna. Numbers of small ones have sometimes reached about 100 in 10 stations in the summer collections but have been scarce at other times. These small nymphs are hard to identify and generally no attempt to name them was made. Therefore nothing can be stated about fluctuations in numbers. As noted, it is possible that *Leucorrhinia dubia* should be added to this list.

Plecoptera. *Nemoura cinerea* was listed among the casual species on the strength of its sporadic occurrence up to the end of 1968, but its numbers since then warrant its inclusion in the next section.

Numbers of the remaining species, and of three which are discussed in the text only, are presented in Table 1, where they are grouped according to whether fluctuations are slight, or larger and apparently inexplicable or explicable.

Species whose numbers have fluctuated explicably

Pyrrhosoma nymphula. During the years 1955 to 1965 inclusive, the numbers of full-grown nymphs in spring, that is at the end of the generation, ranged between 46 and 93, the latter being the result of the exceptionally large year-class of 1957 (MACAN, 1974 b, Table 3 a, 1975, Fig. 5). This period includes the years of the experiment on the effect of predation, and the effect was clearly slight. In 1966 the total was down to 19 and in 1967 to 5, after which numbers remained well below those reached in the earlier years. This decline coincided with the death of much of the *Littorella,* and the obvious deduction is that the amount of cover is a more important factor regulating numbers than the numbers of *Salmo trutta.*

Pyrrhosoma eggs hatch in late summer or autumn, but the nymphs scarcely grow at all until the following spring. They have reached full size by the autumn when numbers are not excessive, but a high proportion require a further full summer to complete development when a generation is large. Adults emerge early in the following summer (MACAN, 1974, Figs. 4 & 5, 1974 b, Fig. 1). *Pyrrhosoma* is one of the main carnivores, and therefore the important number is that during the summer, the main feeding time. The figures in Table 1 and Fig. 1 are those at the end of this period, and they include all the nymphs except those of the new generation just appearing. The range is much greater than that of the mature nymphs in spring, which is expected, because, when numbers are high, many of the nymphs will not emerge in the following year. Moreover there is mortality during the winter, which appears to be greater when nymphs are plentiful. These figures, like those for the mature nymphs, show clearly the reduction in numbers in 1966 and the following years and some recovery in 1975, by which time *Littorella* has regained much lost ground.

Enallagma cyathigerum. As were those of the preceding species, numbers were scarcely affected by predation and reduced when the vegetation disappeared. Recovery, however, started earlier and the autumn total in 1975 was similar to those in the early years.

Leptophlebia marginata (LINN.) and *vespertina* (LINN.). Numbers were lowest during the years of intense predation by trout (1961, 1962, 1963) but they quickly recovered as the fish population was reduced. A slight fall after 1966 could have been related to the decline of *Littorella.* It is possible that predation by nymphs of Zygoptera also affected the numbers of *Leptophlebia,* for these were high towards the end of the period, when dragon-fly nymphs were still scarce after the loss of so much cover when *Littorella* died. Moreover, during the first four years, numbers

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56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75

Predation by trout

Myriophyllum and
Potamogeton alpinus

Littorella

Enallagma
cyathigerum

200

100

Pyrrhosoma nymphula

715

200

100

Leptophlebia spp.

2000

1000

Gammarus pulex

500 500 582

200

100

Lestes sponsa

100
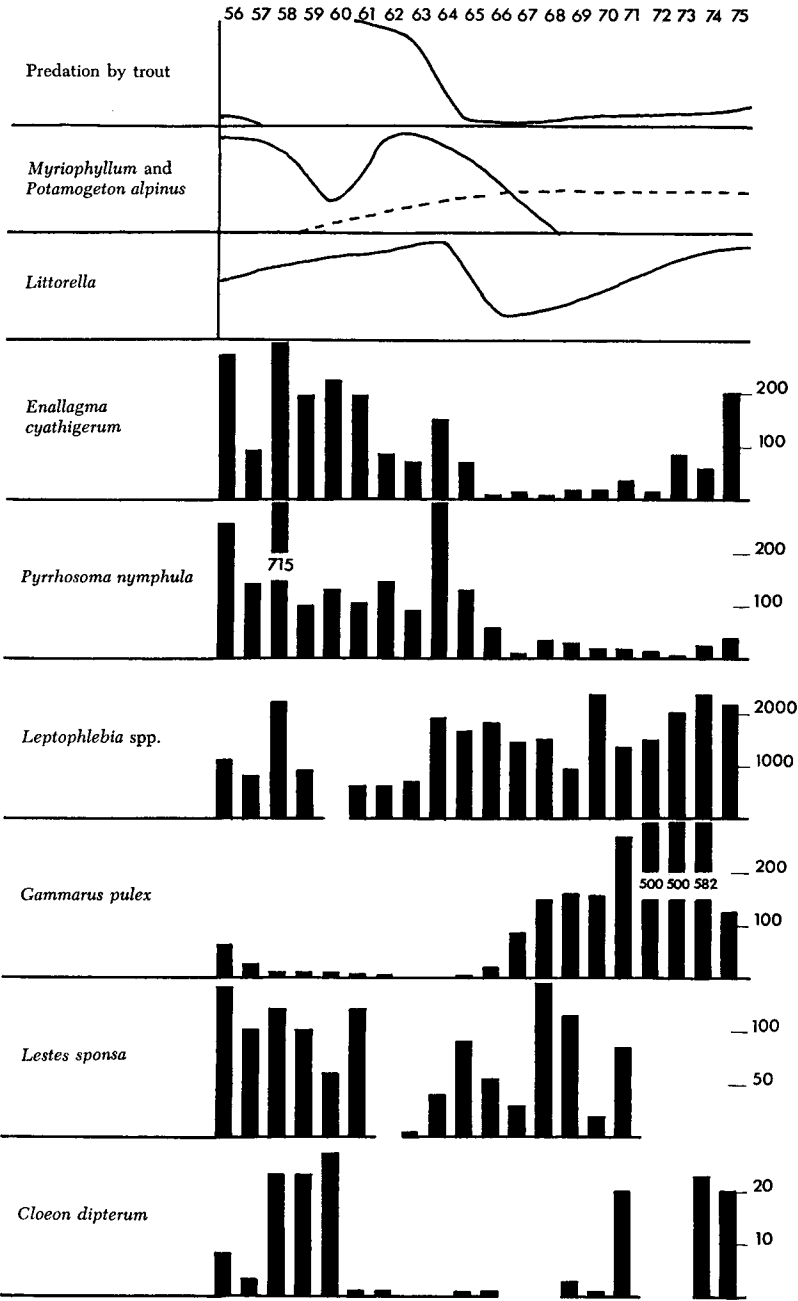
50
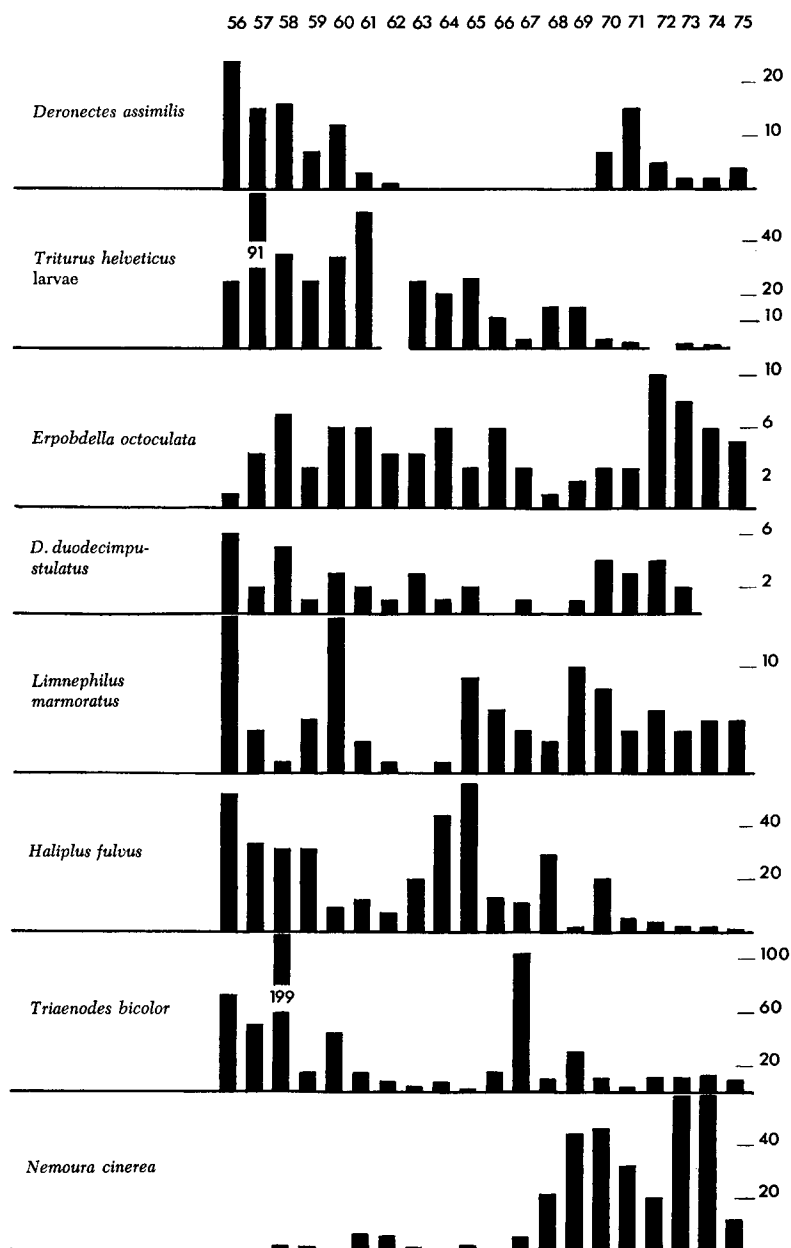
Cloeon dipterum

20

10

Fig. 1a

Fig. 1b

Fig. 1. Hodson's Tarn; Three environmental variables and the numbers of various species in twenty successive years. The second and third graphs and the last part of the first are based on visual assessments, not on quantitative data.

of dragon-fly nymphs were high, low and high, and the numbers of *Leptophlebia* in the springs following were low, high and low.

Gammarus pulex (see also MACAN, 1975, Fig. 6). This species appears to be sensitive to predation. Its numbers were at their lowest when fish were most abundant, and increased enormously when the number of Zygoptera nymphs decreased as their cover diminished. In 1975 there was a partial recovery by the Zygoptera, and the expected drop in the numbers of *Gammarus* was well-marked.

Lestes sponsa (see also MACAN, 1966 b, Fig. 5). In the summer catch of 1961 nymphs were numerous. This species overwinters as an egg and grows rapidly, and it is suggested that there had not been much predation because the nymphs had only recently reached a size likely to be eaten by fish. It was, however, noticed that there were no nymphs in *Myriophyllum*, where usually they were plentiful, and this was thought to be due to capture by fish of nymphs migrating from the shallow water where the eggs are laid. There was no summer collection in 1962, and in 1963 nymphs were few, but numbers rose again as predation eased. The absence of collections with a net in summer after 1970 makes it impossible to co-ordinate catches by that method and catches with the artificial vegetation.

Holocentropus dubius and *Cyrnus flavidus* were not distinguishable in the early days. Moreover, they were most numerous in the *Myriophyllum* (MACAN, 1965, Fig. 9), which ceased to exist as a continuous stand. The figures in Table 1 are, therefore, combined for the two species and must also include *C. trimaculatus* which is rare; they also exclude the catches in the *Myriophyllum*, a compromise which though regrettable is inevitable. As expected, numbers decline with the *Myriophyllum* and are also low during the years of intense predation.

Phryganea striata (LINN.) and *P. varia* (FABR.) were scarce during the years of heavy predation, more numerous before and after. Numbers have been low since *Myriophyllum* declined.

Cloëon dipterum was severely affected by predation, and numbers did not recover for several years after it ceased to be intense. This species was found mainly in *Potamogeton natans* and the deeper parts of the *Carex*, and the recovery evident in 1971 may have been partly related to the regeneration of the central parts of the *Carex* bed.

Deronectes assimilis was also greatly reduced by predation, and the continuing low numbers after the fish population had been reduced was probably related to the scarcity of *Littorella*, the main haunt of the species. It never regained the abundance of the early years, when there were no fish, possibly because *Littorella* was not as thick during the years when it was recolonizing the area formerly occupied.

Triturus helveticus. Adults were reduced in number by predation but larvae were not, which is in accord with the numbers eaten by fish (MACAN, 1966 a, Table 1). Larvae were probably secure in thick vegetation, and were less numerous from 1966 onwards because the *Littorella* was no longer thick.

Rana temporaria (LINN.) and *Bufo bufo* (LINN.). The tadpoles, which were not distinguished, tend to aggregate, which makes quantitative collection impossible. It is necessary, therefore, to rely on observation (MACAN, 1965 a). Only a few survived, in sheltered places, when fish were numerous. In 1964 they were observed once more in the open water, and from 1966 onwards they were numerous. Frogs spawned in *Carex*. Absence of spawn was noted in 1966, 1971 and 1974. There were positive records only in 1968, when the egg-masses were stranded by a drop in water level, and in 1975. *Rana* has become less abundant. Toads spawn in deeper water, sometimes on the nets set to catch fish. Adults were seen in the tarn in 1966, and from 1969 onwards numbers were generally high. There has probably been an increase in abundance, but it must be pointed out that up to 1966 or 1967 toads in the thick *Myriophyllum* could not have been seen.

Chaoborus spp. were not mentioned in the earlier papers because they are not strictly members of the community in the vegetation, but they are included here because their disappearance is so striking. It was not possible in the time available to identify every specimen, but in a collection from *Potamogeton natans* in September 1958 the following were recognized: 42 *C. crystallinus* (DE GEER), 23 *C. obscuripes* (VAN DER WULP) and 5 *C. flavicans* (MEIGEN). In 1957 what was believed to be the last surviving trout in the tarn was caught. Numbers of *Chaoborus* thereupon increased enormously, and the figure in 1960 would have been higher had not the *Myriophyllum* died to an extent that made collecting in it impossible. With the re-introduction of fish *Chaoborus* disappeared. It reappeared when predation was less but died out again, possibly as a result of the final disappearance of the stand of *Myriophyllum*, the only species providing thick cover in the central part of the tarn. Only one pupa was found in a fish (MACAN 1966 a, Table 1), but fish were not examined until they had been in the tarn for a whole winter, and the large population of small fish could have eliminated the larvae during the course of it.

The numbers of all the species in this group were reduced by the predation of *Salmo trutta* but most recovered as it lessened. *Chaoborus*, not strictly a member of the weed fauna, did not, and the numbers of *Rana* visiting the tarn to lay eggs have remained lower than formerly though spawn is still plentiful in nearby pools. Fewer species were affected

Table 1. Hodson's Tarn. Number of specimens caught with a net at 10 stations un-

			1956	57	58	59	60	61
Pyrrhosoma nymphula (SULZER)	O	au	253	140	715	101	128	104
Enallagma cyathigerum (CHARP.)	O	au	270	88	298	195	226	195
Leptophlebia spp.	E	sp	1210	847	2191	900	—	575
Gammarus pulex (LINN.)	Cr	sp	60	23	10	10	10	4
Lestes sponsa (HANSEM.)	O	su	140	100	120	100	60	120
polycentropodid larvae	T	sp	14	3	24	4	8	3
Phryganea spp.	T	sp	13	5	21	24	7	2
Cloeon dipterum (LINN.)	E	sp	8	3	23	23	27	1
Deronectes assimilis (PAYK.)	Co	au	24	15	16	7	12	3
Triturus helveticus (RAZ.) ad.	A	sp	4	2	1	1	2	2
Triturus helveticus (RAZ.) l.		su	25	91	35	25	34	51
Chaoborus spp.	D	au	17	75	440	861	422	0
Erpobdella octoculata (LINN.)	H	sp	1	4	7	3	6	6
Aeshna juncea (LINN.)	O	sp	3	9	2	2	4	1
Haliplus confinis STEPH.	Co	sp	2	1	1	1	1	0
		au	4	3	5	0	0	1
Deronectes duodecimpustulatus OLIV.	Co	au	6	2	5	1	3	2
Limnephilus marmoratus CURT.	T	sp	16	4	1	5	17	3
Haliplus fulvus FAB.	Co	au	52	33	31	31	9	12
Triaenodes bicolor (CURT.)	T	sp	74	52	199	16	44	16
leptocerid larvae	T	sp	9	2	6	0	0	3
Lymnaea peregra (MÜLL.)	M	sp	9	22	22	28	70	90
Nemoura cinerea (RETZ.)	P	sp	0	0	2	1	0	6
Caenis horaria (LINN.)	E	au	0	0	0	3	24	0
Sialis lutaria (LINN.)	Mg	sp	5	3	2	0	4	4
		au	4	0	0	5	11	4

A = Amphibia, Co = Coleoptera, Cr = Crustacea, D = Diptera, E = Epheme-
roptera, H = Hirudinea, M = Mollusca, Mg = Megaloptera, O = Odonata, P =
Plecoptera, T = Trichoptera; au = autumn, sp = spring, su = summer; ad. =
adult, l. = larva.
(1) Senior generation only.
(2) Catches in *Myriophyllum* omitted.
(3) *Carex* and *Potamogetan natans* only. Figures are numbers at one station based
    on an average.
(4) *Littorella* only. Figures are totals at 5 stations.
(5) *Carex* only. Figure are totals at 3 stations.

by the deterioration of the cover provided by the vegetation, though it
must be reiterated that this analysis does not take account of numbers in
the whole tarn; the total numbers of many species must have been affected
by the disappearance of the stand of *Myriophyllum*. The decline of the
plant cover has had far-reaching indirect effects because the inhabitants
most affected were *Pyrrhosoma* and *Enallagma*, which, when cover was

less otherwise stated.

62	63	64	65	66	67	68	69	70	71	72	73	74	75	
144	91	303	132	60	10	36	28	20	20	17	5	26	41	(1)
83	70	150	70	10	17	8	20	20	37	16	84	60	200	(1)
620	692	1912	1634	1738	1464	1482	949	2358	1366	1500	2000	2333	2157	(2)
1	0	0	1	19	83	144	162	157	263	500	500	582	125	
—	6	42	89	56	32	145	116	22	83	—	—	—	—	
1	0	7	13	15	11	1	4	7	9	6	6	3	1	(2)
0	1	4	15	30	21	17	0	8	0	—	—	0	1	
1	0	0	1	1	0	0	3	1	20	—	—	23	20	(3)
1	0	0	0	0	0	0	0	7	15	5	2	2	4	(4)
1	1	0	0	0	0	0	2	2	3	1	2	2	3	
—	25	20	26	11	3	15	15	3	2	—	2	1	—	
0	0	4	84	7	0	0	0	0	0	3	0	—	0	
4	4	6	3	6	3	1	2	3	3	10	8	6	5	
0	0	1	1	1	1	1	1	1	1	2	3	3	0	(5)
0	0	0	1	1	1	1	6	1	0	—	—	0	1	(2)
1	2	3	24	4	5	10	2	46	3	0	4	5	5	(2)
1	3	1	2	0	1	0	1	4	3	4	2	—	—	(4)
1	0	1	9	6	4	3	10	8	4	6	4	5	5	
7	20	44	56	13	11	29	2	20	5	4	2	2	1	(2)
8	4	6	1	16	104	11	32	10	3	12	12	13	8	
0	0	2	1	0	1	0	0	1	3	7	15	15	15	
87	157	139	11	6	2	0	2	—	—	—	—	1	1	
5	1	0	2	0	5	21	44	46	32	20	60	65	12	(5)
0	0	0	1	0	3	73	96	0	3	0	0	—	2	(5)
3	3	6	2	5	4	14	8	65	33	—	—	12	12	
0	3	5	19	9	7	11	34	48	32	17	12	—	4	

thick and extensive, contributed a large proportion to the total population. Both are carnivorous, and it is likely that the great increase in the numbers of *Gammarus* and the slighter increase in the numbers of *Leptophlebia* was related to their reduced numbers.

Species whose numbers have fluctuated little

Erpobdella octoculata. The net does not capture all the leeches present in the area which it traverses, presumably because some resist dislodgement by clinging firmly to the vegetation. However, collections with the quantitative sampler confirm that numbers of *Erpobdella* changed little during the twenty years.

Aeschna juncea. In August 1956 69 specimens were taken at thirteen stations. Numbers declined in successive months but were still as high as 26 at eleven stations in the following June. The figure of 9 in April

quoted in the table is, therefore, unexpectedly low. This was the only generation to reach this size throughout the period, and in other years numbers caught rarely exceeded double figures.

Haliplus confinis. The numbers are relatively high in the autumns of 1965 and 1970, presumably representing a successful generation, but by the following spring the total has sunk to the uniformly low level of other years.

Deronectes duodecimpustulatus was little affected by predation but its numbers were at their lowest when *Littorella* was least extensive. The contrast between this species and *D. assimilis*, in the previous section, is marked but inexplicable.

Limnephilus marmoratus. Hundreds of larvae were sometimes captured in the autumn at the start of the generation, but numbers after the winter were consistently uniformly low.

The numbers of *Pyrrhosoma* at the end of a generation were not greatly affected by predation, though nymphs were eaten by fish. The explanation put forward is that the numbers reaching maturity are determined by the establishment of territories of some kind, and that those unsuccessful in the struggle for a good place form a reserve from which any good place left vacant by the death of the incumbent can be filled (MACAN, 1966 a). Some such process of self-regulation, but survival for a fairly long time of those unsuccessful at the start, must account for the steady population of the species in this group, some of which, notably *Erpobdella*, were eaten fairly often by fish.

Aeschna, with its one generation more successful than all the rest, might, perhaps, more properly have been considered in the next section.

Species whose numbers have fluctuated inexplicably

Haliplus fulvus was unlike *H. confinis* in that high numbers in autumn were generally followed by high numbers in spring. Totals caught recovered rapidly after some reduction during the period of intense predation, but fell inexplicably to a low level in the last five years when the cover provided by both *Littorella* and *Carex* was increasing.

Triaenodes bicolor. The occasional total in spring far above the general average depended on survival during the winter, not on the numbers present during the previous autumn. For example, the small numbers in the spring of 1959 followed an autumn total exceeded only once in the previous three years (MACAN, 1965 a, table 6). Numbers were low when predation was intense, and the steady level of the last six years, well below that during the period before fish were introduced, is probably related to the absence of continuous *Myriophyllum. Triaenodes* larvae,

which swim, are taken freely by fish and are likely to be affected adversely by the absence of cover.

Leptocerid larvae. As noted by MACAN (1966 a), the net is an unreliable method of catching these larvae. On the other hand they appeared to be attracted by the artificial *Littorella*, and large numbers of cases from which adults had emerged were found attached to the strands. That numbers were higher during the last three years than in any of the previous seventeen was shown clearly by the artificial-vegetation collections.

Lymnaea peregra. The high numbers of this species when predation was at its height, although fish were feeding on it, and the subsequent crash remain one of the most inexplicable features of this investigation. HIGLER (1968) records the sudden disappearance of this species from a locality where it had previously been numerous.

Cloëon simile has two generations a year, the overwintering one emerging in late May and early June, the quick summer one in late August and early September (MACAN, 1965 a). Some of the summer and autumn collections, therefore, fell between two generations and gave a misleading impression of low numbers. Furthermore *C. simile* occurs in the deeper water, and on some occasions most of the specimens were taken in *Myriophyllum* when that plant was still present as a continuous stand. Few were found in the mats of artificial *Littorella*, and MACAN & KITCHING (1972) record large numbers on artificial *Carex* when the ropes were 45 cm long but few when the ropes were 8 cm long. Therefore collections in the deeper water were unsatisfactory after the *Myriophyllum* stand disappeared, and accordingly no figures are quoted.

Up to 1964 it was scarce, numbers never exceeding 20 at ten stations (MACAN, 1966 a, table 2). In the spring of 1964 there were 38 specimens, in autumn of that year 190, and in the spring of 1965 179, all at 14 stations. This was the only successful overwintering generation recorded, and numbers in spring never reached double figures again, though there were good summer generations in 1968, 1969, and 1970. It is unexpected that these should have occurred after the *Myriophyllum* had disappeared.

Nemoura cinerea. Some preliminary experiments by Miss LUCINDA HAGGAS indicated that this species fell a prey to *Phryganea* more readily than most, and 1968, the year in which numbers were first distinctly higher than previously, was also the year in which the decline of *Phryganea* started. However, stronger evidence is required before *Nemoura* can be moved from the category of species whose change in numbers is inexplicable.

Caenis horaria is a species of the mud rather than the weed fauna, but it was taken regularly in the net. Numbers were small, generally below 10, until the autumn of 1968. Forty-nine were taken in the spring of 1969, and the large autumn total of that year shown in the table was

followed by a spring catch of 158. In the autumn of 1970 no specimens were taken. There were, therefore, two extremely successful generations and an abrupt return to scarcity.

Sialis too is a species that generally dwells in the mud, but the samples with the quantitative sampler, which brings up the soil as well as the plants, shows a rise in numbers similar to that shown by the net. A surprising feature of both sets of figures is that all remain uniform throughout the year, and there are no large totals soon after the eggs hatch such as are typical of other species.

Of the eight species in this group, *Lymnaea*, *Haliplus fulvus* and *Nemoura* have each changed in abundance in a unique way. *Triaenodes*, *Cloëon simile*, *Caenis* and *Sialis* are all species in which occasional exceptionally good survival of a generation, sometimes two or more consecutive generations, has produced big fluctuations in numbers. The leptocerid larvae may be similar but this must remain in doubt because the rise came in the last years of the observations.

Stability

There is dispute about what constitutes stability. When the subject was discussed at the British Ecological Society's winter meeting in 1974, some defined a stable community as one whose constituent species varied little in abundance from year to year. Others attached more importance to absence of change when some unusually large variation in the environment occurred. The idea that a community in which numbers oscillated was stable, provided that the amplitude of the oscillations did not vary greatly, appeared to be new to some of those present. However defined, stability is relative, not absolute, and no general assertion can be made about Hodson's Tarn until comparable figures for other communities are available.

The nature of the rooted vegetation is of paramount importance to the animals considered here. It is not apparently a source of food until it is dead and decaying; if it were not there, allochthonous matter would probably provide the food required by the animal community. How important it is as a substratum for epiphytes which animals eat is not known. On the other hand, if it were not there, many species of animal would not be there either because, in the absence of cover, predators would eliminate them.

The vegetation cover has not remained constant. Of the four species extending over a large area of the tarn, only *Potamogeton natans* has produced a uniform canopy year after year. *Littorella* disappeared from a large part of the area once covered and has since been slowly recolonizing

it. *Carex* died in the centre of the bed and then recovered. The most farreaching change has been the disappearance of the continuous stand of *Myriophyllum*, which once occupied half the tarn. Comparison with other tarns suggests that this last change is permanent. Whether the changes in *Carex* and *Littorella* are oscillations could not be established in the time available.

The fauna has been exposed to predation in varying degrees by these changes in the protecting cover, and, in addition, the predation itself has been altered experimentally. It is believed that there were no fish in the tarn from the summer of 1957 to the autumn of 1960, when 500 small trout were introduced. Predation suddenly became intense, but fell steadily in subsequent years as the fish were netted. Some fish persisted to the end of the observations.

Chaoborus, a planktonic species, which, however, makes use of cover, disappeared. So did the lepidopterous larva feeding on the leaves of *Potamogeton natans*, though for reasons unlikely to be associated with the two factors described because the *P. natans* has changed little, and the decline had started before fish were introduced. One species of caddis certainly established itself during the two decades, but this, unfortunately, is a group in which many species can still not be identified in the larval stage, and there remains uncertainty about the extent of the changes. A planarian grained a foothold but the work of DAVIES (1969) indicates that it may not be able to maintain a population as the numbers of Zygoptera nymphs recover, which they appear to be doing.

Of the Heteroptera, *Sigara scotti* and *Hesperocorixa castanea*, the species characteristic of places like Hodson's Tarn, were, as expected, present throughout the period, with numbers fluctuating according to the state of plant cover and the abundance of predators. *S. distincta* occurred regularly in the early years, but only in small numbers before the spring of 1969, since when it has been plentiful. *Cymatia bonsdorffi* appeared in 1970 and has maintained a moderate population since then. The success of these two species, not previously found in abundance in tarns of this type, may be due to the low rate of predation that has prevailed in Hodson's Tarn during the last decade (MACAN, 1976). These moorland fishponds generally hold a big population of trout.

Of the species in Table 1, eight have been less abundant during the last few years than during the first few. *Lymnaea peregra* remains an enigma, but the reduction of the rest could well be due to the diminished cover rendering them more exposed to predation. Three are more numerous, particularly *Gammarus*. This species appears to afford the one example of a secondary change, its increase being made possible by the reduction of predators occasioned by the decline of plant cover. Whether the increase

in the other two, leptocerid larvae and *Nemoura cinerea*, can be explained in the same way is less certain.

The numbers of thirteen species were little different at the start and the end, though most were lower during the period of intense predation.

Stability is to be judged on the species that breed in the tarn and particularly on their numbers at the end of a generation. Predators reduced the numbers of casual visitors recorded by the human collector, evidently because the fish caught them first (MACAN, 1976). Predation greatly reduced certain species on the fringe of this community, *Notonecta* which hunts at the surface, beetles whose larvae hunt in the open water, and tadpoles which make little attempt to conceal themselves.

Of the significance of the sudden and outstanding success of the occasional generation of some species (for example, *Triaenodes* in 1967) it will be possible to say little until more is known about the reason for this success.

With the exceptions just mentioned, numbers of each species have not been widely different from year to year. A major change in the environment, the introduction of fish, led to a great reduction of certain species not adapted to survive this kind of predation, but otherwise modified the structure of the community only slightly. Decline of the vegetation was more important but caused no changes in the components of the community and affected only their relative numbers. In the absence of comparable data, the community appears to be stable. MACAN (1975) discusses possible reasons. The tarn, sufficiently well supplied with water to maintain a constant volume, and not productive enough to suffer deoxygenation, provides stable physico-chemical conditions. The abundant small predators regulate their own numbers, are sessile, take a year or more to complete development and feed extensively on small Crustacea, which appear suddenly, reproduce so rapidly that predation cannot depress their numbers seriously, and then form resting eggs when conditions become unfavourable.

Thienemann's basic principles

1. The more variable the conditions in a biotope, the greater is the number of species inhabiting it.

2. The more conditions in a biotope depart from the normal and from the optimum for most organisms, the poorer it will be in species, the more characteristic will the community be, and the greater will be the numbers of those species that do occur (THIENEMANN, 1950, pp. 43, 44).

These two must be taken together and may be illustrated by reference to certain groups only, particularly those with large numbers of species.

The Corixidae are notable because each species is found in a restricted range of conditions. *Sigara scotti* and *Hesperocorixa castanea* occur on

organic soils where the decomposition of vegetable remains is slow, *H. castanea* occupying the regions where cover is thick. They are the only species generally abundant in places of the Hodson's Tarn type. In this tarn there are patches of sandy-gravelly soil with a low content of organic matter, but they are small. In the nearby much larger Wise Een Tarn such patches are of sufficient extent to permit the occurrence of species typical of this substratum. In Windermere, larger still, sandy substrata are extensive owing to wave action, but, in deeply indented bays, organic matter accumulates and decomposes slowly or rapidly according to the extent to which the bay becomes isolated and stagnant. These varied conditions provide the habitat for a larger number of species (MACAN, 1938). The group illustrates the first principle clearly. If the explanation above of the abundance of two unusual species in Hodson's Tarn is correct, this is an example of the second principle. Heavy predation, typical of these moorland tarns, is an unfavourable factor, a departure from the optimum, and one which keeps the number of species low.

BOYCOTT (1936) writes that "With a few exceptions, the needs of the species are so similar that habitats can be classed as good or bad for Mollusca as a whole". The soft water and the unproductive condition that go with it are the main features that make Hodson's Tarn unsuitable for snails. It may be deduced from the extensive records quoted by BOYCOTT that, if these two features were favourable, it might contain 8 species or more. With only one, *Lymnaea peregra*, it is similar to many tarns in the Lake District, and affords a clear illustration of the second principle; the short species list is related to a departure from the optimum represented by the low calcium concentration, though the exact nature of the relation remains obscure.

Though larger in size and relatively less deep, some of the Dutch polders, calcareous and productive, afford a useful comparison with Hodson's Tarn because the necessary faunistic work has been done. The much longer lists, particularly in the groups that are not insects, are striking, and among the polycentropodids, the two species of *Holocentropus* and three of *Cyrnus* recorded by HIGLER (1969) and HIGLER & BRANTJES (1970) contrast with the one and two, the second being rare, respectively in Hodson's Tarn.

THIENEMANN's (1954) third principle states that: "The more continuously the conditions in a locality have developed, and the longer the environment has been similar, the more species in the community and the greater their balance and stability."

GODWIN (1923) investigated a number of ponds which had been excavated at known dates, and found that the number of species of rooted plants increased with the age. Nothing comparable has been observed in Lake District tarns, but this may be because the soil is unfavourable and

only a few species are able to colonize it; it is usual to find that extensive areas are bare, as in Hodson's Tarn latterly.

The principle is applicable mainly to lakes of great age, such as Baikal, Ohrid and some of the African lakes. Shallow tarns are transitory, and, moreover, it is hard to decide whether the establishment of a newcomer is due to changing conditions as the tarn evolves and fills up. A further point is that many of the species are insects, which, having a winged stage, colonize new places rapidly. However, if *Polycelis* succeeds in establishing itself in Hodson's Tarn, it will be an example of the third principle. *Asellus aquaticus* has recently been found by Professor W. D. WILLIAMS (personal communication) in some nearby tarns in which it had not been taken previously. Twenty years is probably not long enough to discover whether the third principle applies to bodies of water of this type.

Production

Production by any one species can be calculated if total numbers in the place under investigation at various stages of the life history are known. In the present study an attempt was made to investigate all the larger species dwelling in the vegetation, and it was, therefore, impossible to time the collections to coincide with critical stages in the life history of every species. Furthermore any one method of collecting will yield optimum numbers of a few species only. The rest will, in the eyes of the statistician, be more numerous than is necessary or too scarce.

Collections by means of artificial vegetation (MACAN & KITCHING, 1972) showed that the numbers of species in apparently identical areas varied widely. The numbers of *Gammarus* in swards of *Littorella* in different parts of the tarn were dissimilar, though no great difference in the swards could be detected (MACAN, 1975). Numbers of *Enallagma* nymphs, which do not move far, depended on the suitability of the neighbourhood for oviposition. Figures on which a reasonably accurate calculation of production could have been based would, therefore, have required a sampling program far beyond the powers of the team of two persons, with additional help in the vacations. *Leptophlebia*, however, was both more numerous and more evenly distributed than any other species and it is hoped to publish calculations of the production by that genus.

Summary

Fish were removed from Hodson's Tarn, a small moorland fishpond, and the rest of the fauna was studied for five years. In 1960 the tarn was heavily stocked with *Salmo trutta* which were netted over the next five years (Fig. 1). After this experiments with artificial vegetation started. In 1965 *Littorella* was declining rapidly, *Myriophyllum* more slowly. The former recolonized lost

ground, the latter did not (Fig. 1). Of the other common plants, *Carex* deteriorat-
ed in the middle of the bed soon after observations started, but *Potamogeton
natans* changed little.

During the twenty years of observations the species list has not changed
greatly. *Nymphula nympheata* disappeared for reasons unknown and *Chaoborus*
spp. was eliminated by predation. A planarian entered the tarn but its numbers
have remained small. Another addition was a trichopteran larva which could not
be named. Casual species were taken less often while fish were numerous. Of the
first 11 species in table 1, all were affected by predation by fish. *Chaoborus* spp.
were eliminated. *Cloëon dipterum* was greatly reduced in numbers, but eventu-
ally recovered. The two zygopteran odonates and larvae of *Triturus* were affected
more by the decline of the vegetation than by predation. The small numbers of
Gammarus in the early years are attributed to predation both by odonate nymphs
and by fish. When most of the fish had been caught and odonate nymphs had
become scarce owing to the reduced plant cover the numbers of *Gammarus* in-
creased enormously.

The numbers of *Erpobdella* changed little throughout the period, although
it did not escape predation by fish. The numbers of the next 4 species in table 1
were lowest when fish were most abundant but otherwise changed little during
the twenty years. There is evidence that numbers of large specimens of *Pyrrho-
soma* are maintained at a relatively steady level during predation by the establish-
ment of some kind of territory and a reserve of small specimens which take the
place of large specimens caught by fish and are consequently able to grow. It is
suggested that other species may be able to maintain their numbers in a similar
way.

No explanation is offered of the fluctuations in numbers of the last 7 species
in table 1. *Haliplus fulvus* became scarce towards the end of the period, lepto-
cerid larvae and *Nemoura* more abundant. *Lymnaea* was the only species to in-
crease its numbers when fish were preying on it, but when fish were few it be-
came scarce. An occasional generation, sometimes two or three in succession, of
Triaenodes, Caenis and *Sialis* and also *Cloëon simile* was far more successful
than the rest.

The community in the vegetation of Hodson's Tarn appears to be stable,
though stability is a relative term which can be measured only when extensive
comparative data are available. All but a few species, *Notonecta*, certain Coleop-
tera larvae, and tadpoles, avoid excessive predation by fish by remaining in the
cover provided by vegetation. Within this cover the self-regulation of numbers,
and the feeding by the common predators extensively on small Crustacea, which
are present only in summer when they reproduce rapidly, contribute to stability.
Physico-chemical conditions are stable. Low concentration of calcium and con-
sequent low productivity, and predation by fish are two "departures from the
normal and from the optimum for most organisms" which lead to a paucity of
species in accordance with THIENEMANN's second basic principle.

Zusammenfassung

Aus dem Hodson's Tarn, einem kleinen Fischteich, der sich in einem Moor-
gebiet befindet, wurden alle Fische herausgefangen und während fünf Jahren
wurde die verbleibende Fauna studiert. Im Jahre 1960 wurde der Teich dicht mit

Salmo trutta besetzt und die Fische wurden in den fünf folgenden Jahren mit Netzen gefangen (Abb. 1). Anschließend wurden Experimente mit künstlicher eingesetzter Vegetation (*Littorella* etc.) begonnen.

1965 zeigte *Littorella*, die ihre alten Gebiete neu kolonisierte, eine schnelle, *Myriophyllum*, nicht in den ehemaligen Bereichen wachsend, eine langsamere Abnahme (Abb. 1). Von den übrigen häufigen Pflanzenarten zeigte die *Carex*-kolonie kurz nach Beginn der Beobachtungen eine Abnahme im Zentrum, *Potamogeton natans* veränderte sich wenig.

Im Laufe der 20 Jahre hat sich die Artenliste nur wenig verändert. *Nymphula nymphaeata* verschwand aus unbekannten Gründen und *Chaoborus* wurde gefressen. Ein Strudelwurm trat neu auf, aber seine Population ist im Teich gering geblieben. Ein anderer Einwanderer war eine Köcherfliegenlarve, die aber nicht identifiziert werden konnte. Zufällige Arten wurden seltener gefangen, wenn die Fische zahlreich wurden.

Die ersten 11 Arten in Tabelle 1 wurden durch Fischfraß beeinflußt. *Chaoborus* wurde vernichtet. *Cloëon dipterum* zeigte eine große Abnahme, aber erholte sich schließlich wieder. Die zwei Zygopterenarten und die Molchlarven wurden mehr von der Vegetationsabnahme als vom Fischfraß beeinflußt. Man glaubte zunächst, daß die Zahl von *Gammarus* in den ersten Jahren durch Fraß von Odonatenlarven und Fischen klein blieb. Nachdem man fast alle Fische gefangen hatte und die Odonatenlarven durch die reduzierte Pflanzendecke selten geworden waren, nahm die Zahl von *Gammarus* ungeheuer zu.

Die Zahl von *Erpobdella* änderte sich wenig, obgleich sie auch von Fischen gefressen wurde. Die Zahl der folgenden 4 Arten in Tabelle 1 waren am niedrigsten, wenn Fische am häufigsten waren, aber zeigten sonst wenig Veränderungen während der 20 Jahre. Es liegen Beweise dafür vor, daß die Zahl großer *Pyrrhosoma*larven trotz Fischfraß verhältnismäßig gleich bleibt, und zwar durch die Errichtung einer Art Revier und durch eine Reserve kleiner Individuen, die die Stelle der gefangenen Großen übernahmen und auf diese Weise groß werden konnten. Es wird angenommen, daß andere Arten auf eine ähnliche Weise eine konstante Populationsdichte erreichen.

Es wird keine Erklärung dafür gegeben, warum die Zahl der letzten 7 Arten in Tabelle 1 schwankte. *Haliplus fulvus* wurde selten am Ende der Experimentzeit, Leptoceridlarven und *Nemoura cinerea* wurden häufiger. *Lymnaea peregra* war die einzige Art, die eine Zunahme zeigte, wenn die Fische zahlreich wurden; wenn aber Fische selten waren, wurde *Lymnaea* auch selten. Eine gelegentliche Generation, bisweilen 2 bis 3 in der Sukzession von *Triaenodes*, *Caenis* und *Sialis* und auch *Cloëon simile* waren viel erfolgreicher als die anderen.

Die Lebensgemeinschaft der Vegetation des Hodson's Tarn scheint stabil zu sein; aber Stabilität ist ein Beziehungswort, das nur dann realen Wert erlangt, wenn weit ausgedehnte vergleichbare Daten vorhanden sind. Mit Ausnahme von *Notonecta*, einiger Coleopterenlarven und Kaulquappen, entgingen die anderen Arten dem Fischfraß durch Verbleiben im Schutz der Vegetation. Innerhalb dieses Schutzes tragen die Selbstregulation der Organismendichte, der ausgedehnte Fraß durch die häufigsten Raubtiere, kleine Crustaceen, die nur im Sommer anwesend sind und in dieser Zeit eine große Vermehrungsfähigkeit zeigen, zur Stabilität bei. Die physikalischen und chemischen Verhältnisse sind stabil.

Ein niedriger Ca-Gehalt und demgemäß eine niedrige Produktivität sowie der Fischfraß bedeuten zwei Abweichungen vom Normalen und für die meisten

Organismen Optimalen, die nach dem Zweiten Biozönotischen Grundprinzip THIENEMANNS zu einer artenarmen Bioconöse führen.

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