THE NATURAL HISTORY OF MALHAM TARN

By PAUL F. HOLMES*

MALHAM TARN lies in a small basin with steep limestone cliffs and slopes to the north, at a height of 1,229 feet above sea level. Its short inflow stream arises from springs near the base of the Great Scar Limestone, and presumably not far above the impervious Silurian "slates" which the geological map shows as underlying the southern half of the Tarn. The present outflow stream flows overland for about 500 yards before disappearing underground after crossing the North Craven fault. At some time the level of water in the Tarn must have been higher than it is today but by the Late-glacial period after the last glaciation it had assumed its present level, although the area of water must have been nearly twice as large as it is now, so as to include the whole of the area later occupied by the Tarn Moss. The latter is a typical raised bog formed in the old western half of the Tarn, and borings through the peat reach ultimately a shelly calcareous mud on top of the clay (Pigott and Pigott, 1959). The level of the Tarn was raised artificially in 1791 (when the estate was owned by Thomas Lister, who later became the first Lord Ribblesdale) by a sluice gate, slipway and embankment constructed at the southern end which seem to have raised the level about four feet. This raising has caused a rapid cutting back of the peat on the Tarn side of the raised bog, so that the west shore is now a vertical peat bank up to 15 feet above water level—an unusual feature to find by a calcareous water.

The present Tarn is 153 acres in extent and very shallow; the maximum depth recorded is 14 feet, while most of the offshore parts are between 6 and 10 feet deep. It has undoubtedly been much deeper and is now rapidly silting up with suspended matter brought down in flood and particularly with organic remains. The level of the water does not vary by more than about 6 inches, since no water escapes when the level drops below the lip of the slipway. A rough calculation of the volume of water in the Tarn came to 316,130,000 gallons, and the apparent catchment area to only 2·43 square miles, though this is bound to be guesswork in such an area of underground water courses. At times a surprising amount of atmospheric pollution reaches the Tarn from the industrial regions to the south and south-west, measurements of which are quoted by Raistrick and Gilbert (1963). On calm mornings it may show itself as a scum on the shore.

Very marked foam strips appear on the water in winds between force 3 and 5 (8 to 24 miles per hour); these do not seem to be due to diatoms or other planktonic organisms nor to detergents used at the Centre. The exact cause of the foam is not clear though it may be the result of saponification of fats washed out of the peat on the west shore, or released by decomposing vegetation.

Temperatures of the surface water have been taken at intervals of roughly ten days since 1958. In such a shallow water exposed to winds, thorough

* The late Warden of Malham Tarn Field Centre, near Settle, Yorkshire.

Aerial view of Malham Tarn, looking almost due North

Photo: by J. K. St. Joseph from the Cambridge University Collection mixing of surface and deeper water is probably usual and long calm spells in which a temperature gradient might develop are rare. Temperatures up to 67° F. (19·4° C.) have been recorded twice and in the exceptional summer of 1959 they remained above 59° F. (15° C.) for three months: the more usual summer temperatures are well below this. The Tarn freezes for varying periods most winters, often with snow on top of it, and in 1962-63 this lasted for 86 days.

The effects of high alkalinity on the flora and fauna constitute some of the most interesting aspects of the biology of the Tarn. Regular fortnightly samples were sent for three years, from 1949 to 1951, and monthly samples for the next two years, to the Freshwater Biological Association at Windermere. A summary of the results of the analyses, carried out by Mr. F. J. Mackereth, is shown in the following table, compared with similar figures for Windermere: the outstanding difference can be seen to be the high alkalinity values for the Tarn, estimated as calcium carbonate in milligrams per litre.

	Malham Tarn		Windermere	
	Max. (mg./l.)	Min. (mg./l.)	Max. (mg./l.)	Min. (mg./l.)
Silica	2·6	0·18	2·5	0·2
Nitrate nitrogen	0·36	0·01	0·40	0·04
Phosphate phosphorus ..	0·0025	0·001	0·004	0·001
Alkalinity	142	62	10	6

The concentration of calcium carbonate was found at certain times to be reduced by as much as half between the inflow and outflow streams. There is some doubt about the actual means by which the lime is "removed" from the Tarn water. Precipitation of calcium carbonate is usually brought about by the loss of dissolved carbon dioxide: this can occur through rise in temperature, and the Tarn water in summer is several degrees warmer than the inflow stream. Carbon dioxide and bicarbonate ions are also extracted by living plants (and animals); many of the aquatic plants in the Tarn have an incrustation of lime and the proportion of molluscs to other freshwater animals is high. Probably the phytoplankton too plays at least some part in the precipitation of lime which accumulates with the organic mud on the bottom.

SHORES

The shorelines vary according to the nature and gradient of the shore and to the degree of exposure to winds, though the general slope is gentle in conformity with the shallowness of the basin (Fig. 1, a–e).

(1) *North and north-east shores*

The solid limestone here has a variable depth of glacial drift and weathering debris over it, and wave action has produced a varied shore composed of stones which range from small pebbles to large boulders; these rest loosely on top of one another and provide abundant shelter for Crayfish, Bullhead and Stone-loach. Anyone collecting here soon realizes that this is far from a uniform habitat and that for a small invertebrate it is made up of a large number of different microhabitats (Fig. 2), in which the conditions for living vary enor-

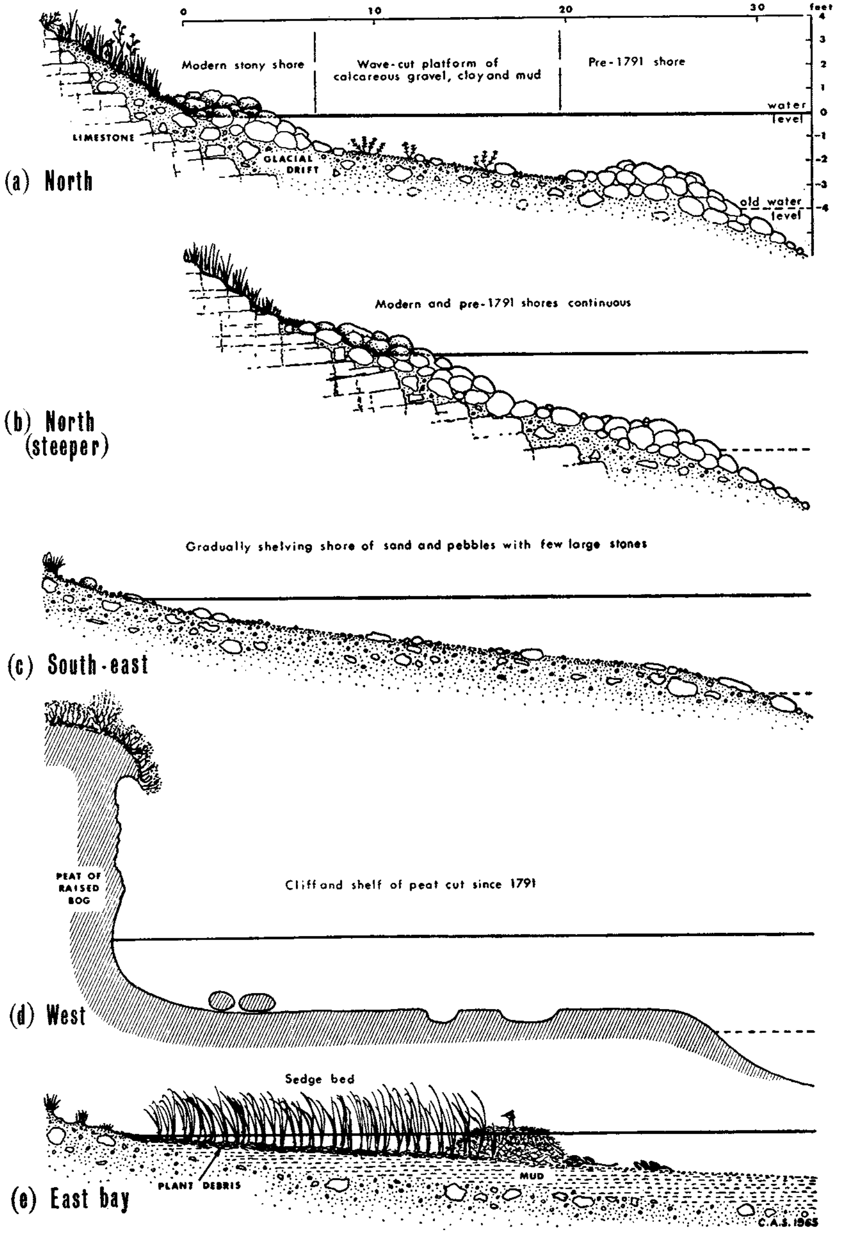

FIG. 1.

Malham Tarn: schematic shore profiles and sections.

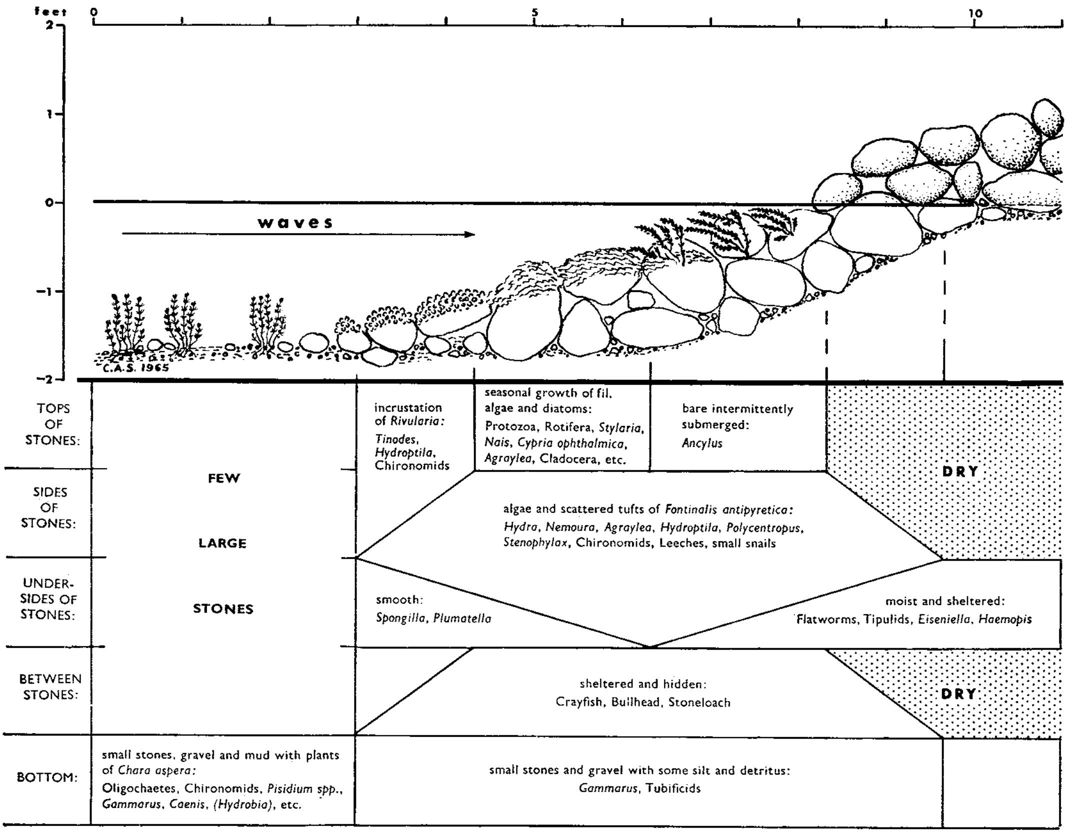

FIG. 2.

Diagram of stony shore to show characteristic range of microhabitats.

mously. One has only to compare the top and bottom of one stone to appreciate the more obvious differences in exposure to wave action and to light, of algal covering and therefore texture of the substratum.

Inshore are stones which are dry on top but have a film of water underneath where flatworms abound, and where tipulid larvae, *Eiseniella* and *Haemopis*, may occur. A little further out the upper surfaces of the stones are covered with water but may become dry when the Tarn level drops a few inches; the moss *Fontinalis* is locally common here. In windy weather *Ancylus* may be the only sizeable animal able to survive the wave action on smooth upper stone surfaces, though the more sheltered sides and under surfaces begin to have a varied fauna, most of which continues outwards: other small snails, *Hydra*, leeches, *Nemoura*, larvae of the caddises *Agraylea*, *Hydroptila*, *Polycentropus*, *Stenophylax*, and chironomid larvae. Several layers of such stones usually rest on a gravelly substratum where detritus and a little sediment settles; this is a very different microhabitat where scavengers such as *Gammarus pulex* and burrowers such as *Tubifex* live. The surface of these littoral stones becomes colonized with a rich growth of algae (Lund, 1961), starting with a great outburst of epilithic diatoms in early spring, which quickly turns the white of the limestone to a brown colour. This is followed by filamentous algae whose fresh green soon becomes dulled by growth of diatoms epiphytic on the filaments. Such algae are a primary source of food for the herbivorous members of the shore fauna. Especially under trees and in deeper water away from the breaking of the waves, this algal growth on the surface of stones may eventually become dense, while in more exposed places it may give the surface a dirty and fluffy appearance. It completely modifies the stone surface and provides conditions for an interesting microfauna of its own. A thick growth of *Cladophora cristata*, for example, contained Protozoa and rotifers, *Nais* and *Stylaria* worms twisting among the filaments, the ostracod *Cypria ophthalmica*, littoral Cladocera and harpacticids, small chironomid larvae and the early instar of the minute caddis *Agraylea*, caseless with very long setae and feeding directly on the algal filaments. Such a community of algae and associated microfauna is usually referred to by the German term "aufwuchs", since there is no English equivalent for it.

In somewhat deeper water the upper surfaces and sides of the stones become covered by growth of lime-precipitating blue-green algae, especially *Rivularia*, and this produces another microhabitat in the form of an irregular incrustation which can be several millimetres thick from the accumulation of many years (Lund, 1961, p. 10). In this, large numbers of larvae of the caddis *Tinodes waeneri* and of a small chironomid build their galleries, and the minute larvae of *Hydroptila* wedge themselves amongst the *Rivularia* cushions on the sides of the stones. A count of the population of one well encrusted stone off the north shore is given in Table 1 but the numbers are very variable. Thus a similar stone of total surface area 690 square centimetres had over 600 chironomid larvae, 67

Table 1. *Numbers of animals on one* Rivularia-*covered stone, on the north shore of Malham Tarn*, 17 April, 1953.

Fauna	Upper surface 380 sq.cm.	Under surface 320 sq.cm.	Side (a) 260 sq.cm.	Side (b) 200 sq.cm.	Side (c) 144 sq.cm.	Side (d) 208 sq.cm.	Totals 1,512 sq.cm.
Tinodes larvae	79	10	5	2	1	4	101
Hydroptila larvae		21	160	80	11	30	302
Chironomid larvae	26	9	4	2		6	47
Polycentropus larvae		1					1
Hydracarines		2					2
Ancylus fluviatilis		7				1	8
Limnaea pereger	5	4	2				11
Hydrobia jenkinsi		2					2
Spongilla fluviatilis		1					1
Erpobdella sp.		1					1
							476

Tinodes and only 2 *Hydroptila*. If the incrustation on a stone is scraped off, the surface of the limestone is often found to have a pattern of sinuous grooves on it, resembling a brain coral: these are the shape of *Tinodes* galleries and must be due to the excretory products of the larvae.

Attached to the smooth under sides of stones will be found colonies of the sponge *Spongilla fluviatilis* and the encrusting polyzoan *Plumatella repens*, both of which increase in deeper water and may become locally common. It must be emphasized that this description of the microhabitats of the shore is incomplete and artificial for the purposes of description; they merge into one another, vary considerably with the exact place and the seasons, and their subdivision could be continued indefinitely.

(2) *South and south-east shores*

These drift shores are mostly composed of smaller and more uniform stones and the basal ones are embedded in a more clayey material (Fig. 1, c). The east shore in particular bears the full force of the predominantly westerly winds. The fauna is less varied but it is an easier shore to sample quantitatively, and Table 2 gives the results of ten pairs of students each counting the numbers of selected animals in 6 one-foot-squares from the water's edge outwards, in an attempt to investigate the zonation of these species.

Table 2. *Zonation of selected species on east stony shore.* Numbers are per 10 sq. ft.—roughly per sq. metre. Combined figures from results of 10 pairs of students, 31 May, 1955.

Fauna	Distance from water's edge 0–1 feet	1–2 feet	2–3 feet	3–4 feet	4–5 feet	5–6 feet
Spongilla fluviatilis	0	1	2	20	16	26
Polycelis nigra	817	51	22	9	2	0
Hydra oligactis	71	4	8	3	14	2
Eiseniella tetrahedra	14	2	5	0	0	0
Tubificid worms	28	21	37	25	40	42
Glossiphonia complanata	1	2	3	2	2	1
Agraylea multipunctata	24	20	13	5	11	8
Hydroptila femoralis	4	21	55	48	96	87
Stenophylax sp.	19	19	24	32	43	26
Ancylus fluviatilis	91	173	206	139	115	75
Planorbis contortus	163	123	42	28	23	12

Where the drift material composing a shore is smaller in grade, shelter from waves and variety of microhabitats are proportionately less with a corresponding reduction in the fauna. Finally, in those places where the shore is composed of sand-sized particles only, there is no shelter on the surface and the fauna is reduced to a few burrowers, tubificid worms, red *Chironomus* larvae, *Pisidium* spp. and smaller animals such as rotifers and harpacticids living in the interstices between the grains.

(3) *West shore*

Most of this is a vertical peat bank resting on a fairly level platform of submerged peat, with deep pockets locally (Fig. 1, d). It is a very inhospitable place for animals when the waves beat up against it during spells of easterly winds, and at such times it may be difficult to find a single invertebrate there. Peat is not a suitable substratum for aquatic burrowing types, though *Sialis* larvae pupate there in some numbers just above the water line. During calm spells or prolonged periods of westerlies some invertebrates may migrate on to the peat and vast swarms of the minute hemipteran *Micronecta poweri* can be seen. In one place along this shore the cutting back of the raised bog, after the artificial raising of the Tarn in 1791 has exposed a small island of glacial drift. Subsequently buried beneath peat, this is now partly exposed again to give a stretch of stony shoreline with a fauna similar to that of the north shore.

(4) *Sedge beds*

The two large bays in which *Carex rostrata* swamp is established both provide totally different ecological conditions to the wave-washed shores, though they differ somewhat from each other because of their geographical position in the Tarn. That in the north-west corner shows a good plant succession from open water through *Carex* swamp to dry land which trampling could quickly destroy so that collecting there is discouraged. The east bay, on the other hand, is already trampled and manured by cattle in summer and has been frequently sampled; it forms the basis of this description (Fig. 1, e).

The substratum is soft mud derived from sediments brought down in flood and from dead material washed in from the Tarn, especially *Chara* remains. In this lives a considerable burrowing fauna (tubificids and other worms, *Chironomus* larvae, four species of *Pisidium*), animals which plough their way through the surface of the mud (*Herpetocypris reptans*, *Valvata piscinalis*), and carnivores which feed on these (*Sialis*, *Caenis*, *Tanypus*, Leeches). In the denser parts of the sedge bed the partially decayed remains of sedge plants accumulate and overlie the mud, and this is the main habitat in the Tarn for *Corixa* (*Sigara*) *dorsalis* and *Planorbis leucostoma*. Other snails occur here also (*Limnaea stagnalis*, *L. pereger*, *L. palustris*, *Physa fontinalis*, *Valvata piscinalis*, *Planorbis albus*) with larvae of *Phryganea striata*, *Limnophilus* spp., and occasionally *Centroptilum*. Calm water makes it possible for the pond-skater *Gerris asper* to live here on the surface film. On the outer edges of the bay there is often a thick accumulation of rotting plant remains in which the larvae of *Eristalis* and *Ptychoptera* may sometimes be found; here and elsewhere in the sedge bed oxygen supplies must at times be very depleted.

(5) *Wave-cut platform*

Where the slope of the ground is neither too steep nor too gentle, a wave-cut platform has been formed just offshore, and is best developed on parts of the northern side of the Tarn (Fig. 1, d). On these flat areas are small stones mixed with calcareous gravel and mud, or sometimes with clay from the drift. On the offshore side of such a platform, however, lies a wide zone of stones and boulders, which is similar to that of the present-day shore. This zone must represent the pre-1791 shoreline, before the level of the Tarn was raised, and it shelves steeply into deeper water.

The characteristic plant of the platform is the small stonewort *Chara aspera* "rooted" in the gravelly mud between pebbles. In places off the north shore this can form a continuous sward in summer, when it may be sampled conveniently with the underlying mud in 1½ feet of water. The dominant animals are oligochaete worms and six species of *Pisidium*, with others becoming common at certain seasons: chironomid larvae, young *Gammarus*, *Caenis* and various snails. Small numbers of the stony shore fauna exist on the pebbles.

Typical counts are given in Table 3. In the April counts numbers are at a minimum after the winter and before breeding. July figures show a big increase in tubificids and *Pisidium* and of *Caenis* nymphs which move inshore and were hatching out at the time. By September the young *Gammarus*, snails, caddis and chironomid larvae have swelled the population to five times that of the spring. During the years 1951–1957 *Hydrobia jenkinsi* appeared in huge numbers in this zone on parts of the north shore (up to 1,000 per square ft), but the population

Table 3. *Population counts on Wave-cut Platform north shore, Malham Tarn.* Numbers are per sq. ft., the average of 2 sq. ft. counts = roughly per 1/10 sq. metre. Figures for % of the population, to the nearest whole number, have been added for comparison with Table 4 (+ = less than 0·5%).

Fauna	14 April, 1961		13 July, 1962		2 September, 1961	
	No/ sq. ft.	% of pop.	No/ sq. ft.	% of pop.	No/ sq. ft.	% of pop.
Tubificid worms	62	22	194	28	422	26
Stylaria lacustris					10	1
Erpobdella sp.	1	+			18	1
Glossiphonia complanata					4	+
Helobdella stagnalis					8	+
Gammarus sp.			9	1	156	10
Micronecta poweri	2	1			8	+
Caenis nymphs	17	6	130	19	12	1
Deronectes sp.	1	+	23	3	4	4
Agraylea sp.			4	1	34	2
Hydroptila femoralis	1	+			16	1
Athripsodes cinereus	1	+	6	1	78	4
Limnophilid larvae	2	1			22	1
Polycentropus sp.	1	+	1	+		
Tinodes waeneri	1	+	3	+		
Chironomid larvae	51	18	12	2	424	25
Hydracarine spp.	3	1	15	2	4	+
Hydrobia jenkinsi	3	1	30	4		
Limnaea pereger	10	4	3	+	50	3
Planorbis contortus	3	1			70	4
Planorbis albus			6	+		
Planorbis crista			1	+		
Sphaerium corneum	1	+	3	+		
Pisidium spp.	121	43	252	37	226	13
Total numbers	281		692		1,566	

fluctuations of this snail are discussed later. It must be admitted that figures based on only 2 square feet as in Table 3 are unreliable and some would say useless. Many more samples have been taken but the figures show that it would be of little value to average them since so much depends on the particular season and the time of year.

Deeper water

(1) *The bottom*

Beyond the old shoreline the bottom shelves steeply down to a depth of 6–10 feet over most of the Tarn, with some deeper pockets down to 14 feet. Here the disturbing effect of waves is reduced and sediments can accumulate as they have been doing since the basin was formed. Continuous samples have been taken through 3 metres of these bottom deposits down to sediments dating to Pollen Zone VII. Although attempts to get a complete core have failed, samples from deeper levels show that early Post-glacial and Late-glacial deposits are present (Pigott and Pigott, 1959). The surface 3–5 inches are a rather flocculent black mud, rich in organic debris derived from decaying plants and animals, mixed with shell fragments. This changes to a cream-coloured marl predominantly composed of lime, with occasional dark brown bands. The marl changes near the bottom of the basin to Late-glacial clay, such as is found at the base of the Tarn Moss deposits.

The bare mud away from weed beds has a limited fauna, mainly tubificid worms, *Pisidium* spp., chironomid larvae and pupae, *Gammarus lacustris*, *Herpetocypris reptans*, and *Valvata piscinalis*. Quantitative samples from the middle of the Tarn made with a Petersen grab gave total populations varying between 445 and 1,335 animals per square metre, whereas sampling with a Gilson sampler has given figures up to 3,000 per square metre. More extensive sampling is obviously needed. Muds under the large weed beds may differ considerably from the above and there are indications that mud under *Chara* is unsuitable for most animals except *Chironomus* larvae.

(2) *Weed beds*

Rooted in the mud are various plants forming extensive weed beds, which provide contrasting animal habitats. The most important of these is *Chara delicatula* (Fig. 3a), a large stonewort which forms a dense sward 1½ to 2 feet high covering between a quarter and a third of the bottom of the Tarn. During a long calm and hot spell in 1959 so much gas was trapped in this sward off the north shore that great quantities of *Chara* were brought to the surface and a boat could only be rowed through it with difficulty.

There are large patches of the emergent *Potamogeton lucens* (Fig. 3c), which seems to have increased considerably in the last 60 years, and other *Potamogeton* species occur in smaller quantities: *P. perfoliatus* in one or two deep-water beds, the hybrid *P. x nitens* in the inflow bay, and *P. berchtoldii*. This latter species was scarce in 1955, occurring only thinly on the outer edge of the shelf beyond the old shoreline, but in 1962 there were several thick beds of it, possibly where the *Chara* had been uprooted in 1959. There are a few patches of *Myriophyllum spicatum* (Fig. 3b) and isolated plants may be found anywhere since pieces root readily. Except after mild winters, all the previous season's growth of *P. lucens*

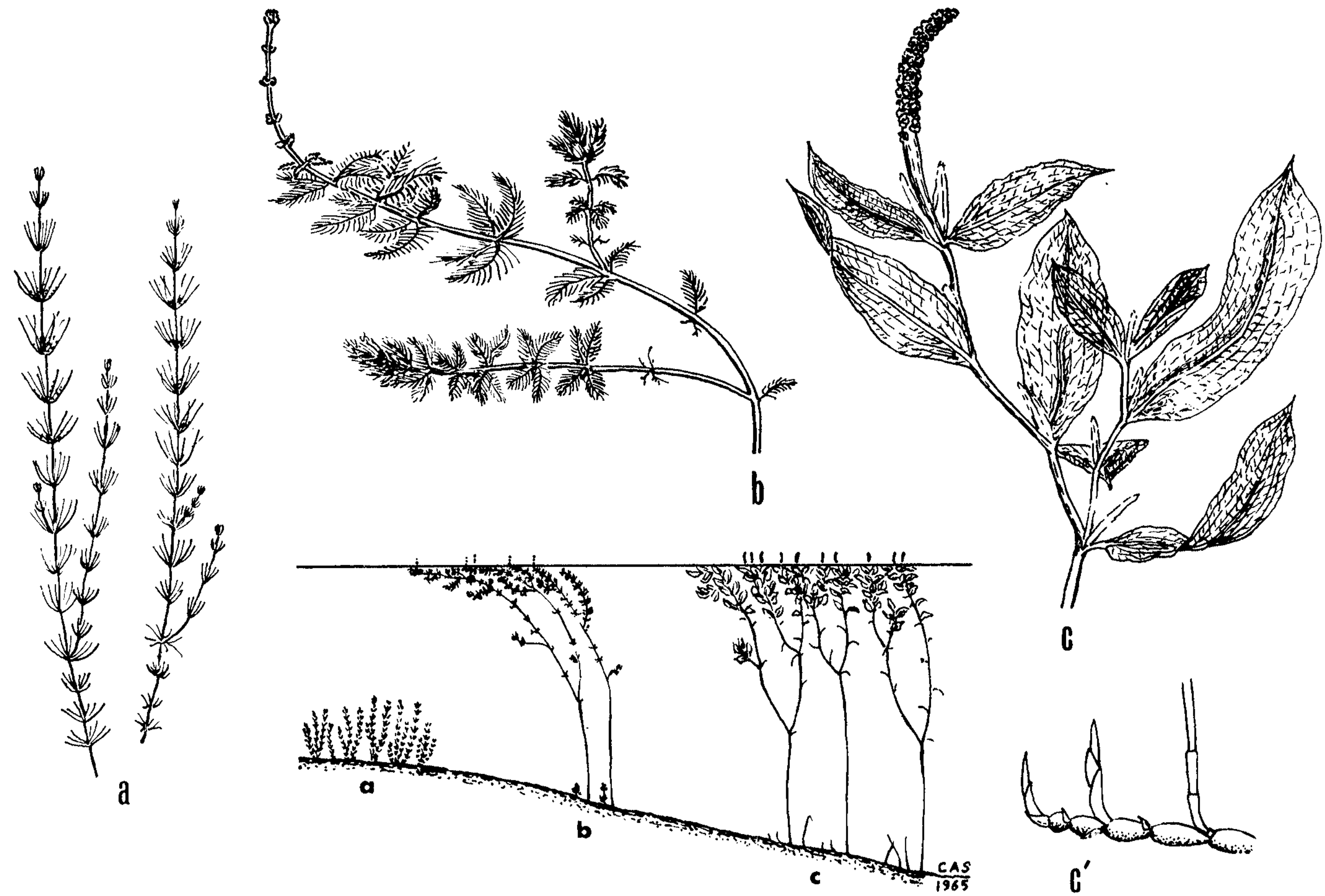

Fig. 3.

Weed bed species: (*a*) *Chara delicatula*, (*b*) *Myriophyllum spicatum*, (*c*) *Potamogeton lucens* (c^1 rhizome).
Larger drawings $\times \frac{1}{4}$, inset habit drawings $\times 1/100$.

and *Myriophyllum* has disappeared by April, and new growth starts from the rhizomes, so that the flowering spikes do not usually break the surface until August. Autumn winds detach and uproot great quantities of weed which are washed up on the shore, and the surprising variation in the position of the beds from year to year is presumably a result of this. Scattered specimens of the moss *Fontinalis antipyretica* are found at all depths wherever there are suitable stones for attachment.

The Canadian Pondweed, *Elodea canadensis*, appeared as a small patch outside the west boathouse in July, 1962, probably introduced by chance from the collecting net of a visiting student, and a year later this had become a patch of roughly 13 feet by 15 feet. It will be interesting to watch the spread of this species which has invaded so many British waters but whose vigour as an invader seems to have subsided (Elton, 1958).

Quantitative sampling of the weed beds in terms of numbers of animals per unit area seems impossible: how can one sample the 9-ft.-tall plant of *Potamogeton* to make it comparable to a sample of *Chara* or a square foot of shore or mud? A useful idea of the composition of the fauna and the relative abundance of animals in different weed beds can, however, be gained by obtaining a large quantity of the weed with a plant grapnel, counting all the animals in the sample and expressing the numbers as a percentage of the total animals found. This has frequently been done with parties of students for the three most important weeds, *Chara delicatula*, *Potamogeton lucens*, and *Myriophyllum spicatum*, usually 200 to 300 yards out from the west boathouse. There is considerable variation of course, from month to month and year to year, but an average picture can be obtained from Table 4, in which the percentage composition of 9 samples of *Chara* and 6 each of *Potamogeton* and *Myriophyllum* are given. The two latter cannot be sampled satisfactorily until they have grown up about mid-July, and these weed beds must be repopulated each summer, in contrast to the *Chara* which does not die right back. There are some striking differences in the faunas of the three habitats which are partly correlated with the different structure and growth form of each plant (Fig. 3 a, b, c).

The *Chara* provides a rather dense habitat, away from wave action, in which molluscs are dominant, comprising 85 per cent of the fauna. The commonest species is the bivalve *Sphaerium corneum* (27 per cent) which is able to climb in the *Chara* with its long foot. *Planorbis contortus* is even commoner than on the stony shores, and in late summer when the young have hatched it may become commoner than *Sphaerium*. *Limnaea stagnalis* and *L. pereger* attain their maximum size and numbers here. The larvae of two caddis flies which make their cases of the *Chara*, *Phryganea obsoleta* and *Limnophilus politus*, are often numerous, with occasional larvae of the rare *Agrypnetes*.

The stems of *Myriophyllum*, which may be up to 9 feet long, bear whorls of leaves with numerous small linear segments and a dense bed of this plant provides a fairly sheltered habitat. Molluscs are again the dominant group (52 per cent), but with differences in the dominant species: *Sphaerium* is rare, *Planorbis contortus* is absent and its place is taken by *Planorbis albus*, and *Physa* attains 11 per cent. Chironomid larvae become abundant in late summer and in some years *Hydra*.

Potamogeton lucens provides a much more open and exposed habitat than the

Table 4. *The average % composition, to the nearest whole number, of the faunas of the weed beds*, 1958–62. Combined figures from 3 samples in July and 3 in September from all three weed beds, plus 3 in early May from *Chara*. (+ = less than 0·5 %.)

Fauna	*Chara delicatula*	*Myriophyllum spicatum*	*Potamogeton lucens*
Hydra oligactis	+	10	2
Stylaria lacustris	+	+	
Lumbriculus variegatus	+		
Erpobdella spp.	+	+	4
Glossiphonia complanata	1	+	1
Glossiphonia heteroclita	+	1	+
Gammarus lacustris	1	7	44
Micronecta poweri	+		
Deronectes sp.	+	+	+
Haliplus sp.	+		
Eubrichius sp.	+	+	
Macroplea appendiculata			+
Phryganea obsoleta	3	+	+
Agrypnetes crassicornis	+		
Limnophilus politus	2		
Cyrnus sp.		+	+
Agraylea sp.	1	1	16
Chironomid larvae	1	19	6
Hydracarines	4	3	2
Limnaea stagnalis	14	8	3
Limnaea pereger	9	8	9
Physa fontinalis	+	11	1
Planorbis albus	7	25	9
Planorbis contortus	21		+
Planorbis crista	2	+	1
Valvata piscinalis	2	+	1
Valvata cristata	3	+	
Bithynia tentaculata	+	+	+
Hydrobia jenkinsi	+		
Sphaerium corneum	27	+	+
(*Limnaea stagnalis* to *Sphaerium corneum*, bracketed)	85% Molluscs	52% Molluscs	24% Molluscs
Total animals counted	8,152	4,486	4,817

other two, with widely spaced leaves and branches on long stems. Molluscs are no longer dominant (24 per cent); the two species of *Limnaea* are scarce in July but commoner when the young of the year have appeared in September. The dominant animal is *Gammarus lacustris* (44 per cent) which unlike most of this fauna can swim back if detached. *Cyrnus* makes use of the large leaves to build its silk net for catching prey, in a similar way to *Polycentropus* on the stones of the shore, and chironomid larvae build tubes attached to the leaves. There are two animals adapted for special modes of life on the *Potamogeton*: the beetle *Macroplea* whose grub-like larva lives on the rhizomes and penetrates the intercellular air-space for its oxygen, and the larva of the leaf-mining fly, *Hydrellia*. These last two species are exceptional in feeding directly on the host plant. The gastropods are predominantly herbivores browsing on epiphytic algae, and *Sphaerium* feeds on organic particles suspended in the water. *Hydra* and hydracarines catch planktonic organisms, while *Gammarus* and the chironomids are mainly detritus feeders. Of the caddises, *Phryganea* is partly carnivorous, *Limnophilus* and *Agraylea* feed on algae: and the leeches prey on the molluscs.

The fauna*

Protozoa

Little work has been done on the Protozoa but one unusual species calls for comment. Abundant colonies of the ciliate *Ophrydium versatile* appear each year towards the end of May as small greenish blobs of jelly attached to stones in about 1 to 2 feet of water, particularly along the gently shelving parts of the east shore. The green colour is due to zoochlorellae in the individuals, and the colonies grow through the summer; sometimes to the size of a penny, and then in August they are detached from the stones during strong winds and large numbers are washed inshore. Here zoospores appear to be liberated and the blobs of jelly persist for some time, looking like jellyfish.

Coelenterata

Hydra oligactis appears irregularly but often in large numbers in *Myriophyllum* beds, and also under stones close inshore where over 1,000 per square foot have been recorded. The average of 21 foot-square samples on the north shore, 4 June, 1962, was 547 *Hydra*. These shore populations probably originate from the quantities of *Myriophyllum* washed inshore in autumn since a wave-washed shore can hardly be the ideal habitat for *Hydra*. It is also taken in plankton hauls in spring and autumn.

Platyhelminthes

The only common flatworm is *Polycelis nigra*, very varied in colour from black and grey to reddish-brown, living under stones close inshore (Table 2), though *Planaria alpina* is occasionally found with it near to where trickles from cold springs emerge. *P. hepta* and *P. tenuis* were found by Reynoldson (1956) to be absent, and *Bdellocephala punctata* occurs mostly in weed beds in deeper water.

Annelida

(1) OLIGOCHAETA. Two families which are well represented in the Tarn are the Naididae and the Tubificidae. The muds of the two sedge beds and the calcareous gravel of the wave-cut platform each support an abundant fauna of these worms, and some 11 species have been recorded. Two other oligochaetes often found are *Eiseniella tetrahedra*, a large species superficially similar to some terrestrial worms, and *Lumbriculus variegatus*, of much smaller size. The former is commonly found amongst stones on the north shore and in wet moss by the outflow. The latter is numerous under stones in 0–1 foot of water.

(2) HIRUDINEA. Of the 7 species of leech to be found in the Tarn 5 are numerous and well distributed on the stony shores. *Haemopis sanguisuga* is not infrequently found but *Theromyzon tessulatum*, the parasite of water fowl, is only occasionally

* Many of the species to be found in the Tarn are mentioned; detailed faunal (and floral) lists may be consulted at the Centre.

taken. A common feature of the under sides of stones is the large number of elliptically-shaped cocoons of the two species of *Erpobdella*, *E. octoculata* and *E. testacea*.

ARTHROPODA

(1) CRUSTACEA. Malham Tarn is one of the few waters in England where *Gammarus lacustris* occurs, though it is present in numbers of lakes in western Ireland, north-west Scotland, and north-west Wales (Hynes, 1955). The widespread *Gammarus pulex* is also present and in the Tarn there seems to be a definite ecological separation of the two species (Fryer, 1953). *Gammarus pulex* is mostly confined to the stony wave-washed shores, while *G. lacustris* lives in more sheltered places, where organic sediments accumulate: the two sedge beds, offshore weed beds, and on mud in deeper water. *Gammarus* is an important item in the diet of Tarn trout and medium-sized perch, as shown by the stomach of a 5 lb. trout caught on 22 May, 1961, which contained 1,117 *Gammarus* specimens. Unfortunately, the two species cannot be quickly told apart but out of 81 examined from the stomach of a 1 lb. perch, 79 were *G. lacustris* and I think most of those preyed on by perch and trout are this species. It might well be more profitable for anglers to introduce this into certain waters as potential fish food instead of *G. pulex*.

Crayfish were apparently introduced into the Dales in the 16th century from the south of England and they are now plentiful on stony exposed shores. They attain a good size; the remains of one specimen found had a chela measuring 57 by 25 millimetres. Large numbers of crayfish remains have been noted around the edges of the Tarn when otter have been recorded in the area, and crayfish may well form part of this mammal's diet. A detailed analysis of the stomach contents of 20 crayfish showed insect larvae and bones of small fish, as well as plant remains, to be the principal constituents.

The smaller Crustacea are mentioned in the section on the plankton in the Tarn.

(2) INSECTA. An investigation of the insects of the Malham Tarn area, including those of the Tarn, has been carried out by members of the Entomological Section of the Yorkshire Naturalists' Union (Flint *et al.*, 1962).

Small stonefly nymphs (Plecoptera), are common under stones on wave-washed shores, particularly species of *Nemoura*. The only common mayfly (Ephemeroptera), is the small *Caenis horaria* which emerges in vast numbers on suitably calm evenings in July and early August. Anyone standing near the edge of the water at these times will leave covered with their empty sub-imago skins. The other species occurring in the Tarn are decidedly rare: *Ecdyonurus dispar* on stony shores, *Centroptilum pennulatum* and *Cloeon simile* in the sheltered sedge beds.

Only one dragonfly (Odonata) breeds on the Tarn, *Enallagama cyathigerum*, whose nymphs are occasionally taken in the offshore *Chara* beds, though eggs are likely to be laid on *Myriophyllum* or *Potamogeton*. Larvae of *Sialis lutaria* (Megaloptera) are common in muddy habitats and where detritus has accumulated.

The Hemiptera are represented by only 4 species of which the minute

Micronecta poweri is easily the most numerous. It seems to winter in deeper water and may appear on stony shores towards the end of April, the exact time depending on the temperature, and on calm days the nymphs can be seen there swarming in huge numbers. The water-cricket *Velia caprai* also occurs in the sheltered corners of wave-washed shores. *Corixa* (*Sigara*) *dorsalis* is common in the two sedge beds though occasionally found elsewhere, and *Gerris lateralis* is confined to these.

Caddis flies (Trichoptera) are a great feature of Malham Tarn and the numbers of a few species such as *Tinodes*, *Agraylea*, *Hydroptila* and *Polycentropus* are enormous. The adults of 71 species have been taken within half a mile of the Tarn and of these I consider 39 may breed in it, though this is partly conjecture with the present state of knowledge of their larvae. The adults emerge between May and October and the flight periods of the commoner species are shown in Fig. 4, which is compiled from many records over the last 14 years. There is a number of uncommon species but the most interesting is *Agrypnetes crassicornis*, found nowhere else in Britain and known elsewhere only in Finland, and north-west Mongolia (Kimmins, 1952). Its larvae live in the *Chara* beds.

Of the beetles (Coleoptera) in the Tarn, *Platambus maculatus* found on stony shores is conspicuous by its large size and colour. The amount of yellow pattern on the otherwise dark elytra is very variable but shows a definite tendency to be reduced and so is typical of the northern end of this beetle's distribution.

Members of the midge family (Chironomidae, Diptera) are a dominant feature of the weed beds especially in the mud below the offshore *Chara*. An indication of the number and success of these midge species may be gained at dusk on a calm evening in late May when enormous numbers of *Chironomus* pupae emerge and give rise to clouds of adult flies.

It is perhaps of interest to record something of the very different insect fauna of a few acid peat pools which are only 300 yards away from the west shore of the Tarn, on the surface of the raised bog. Beetles are well represented and include occasionally the large *Dytiscus marginalis*. Nymphs of the dragonfly *Aeshna juncea* can also be found; and by careful searching the larva of *Phalacrocera replicata* can be picked out from amongst the *Sphagnum* moss which it so closely resembles. These acid peat pools are very small in size and, though of great interest, would be quickly depleted if collection were not severely restricted.

Mollusca

A recent account of the mollusca of the Malham area has been given by Stratton (1956), and as might be expected in the calcareous water of the Tarn there are many species: 13 water snails and 9 small bivalves. Eight out of the 16 British species of pea-mussels (*Pisidium*) occur, 6 of them together in the muddy gravel of the wave-cut platform. It is the highest locality in Britain for a number of species shown in Table 5, which also gives the 6 species whose shells have been identified from the marl below the raised bog when this was open water in Preboreal time, *circa* 8,000 B.C. (Pigott and Pigott, 1959). *Valvata cristata* is the only species common to both columns of this table.

A recent colonizer is *Hydrobia jenkinsi* which was first recorded at the end of May, 1950 when it was common round the mouth of the inflow stream and in

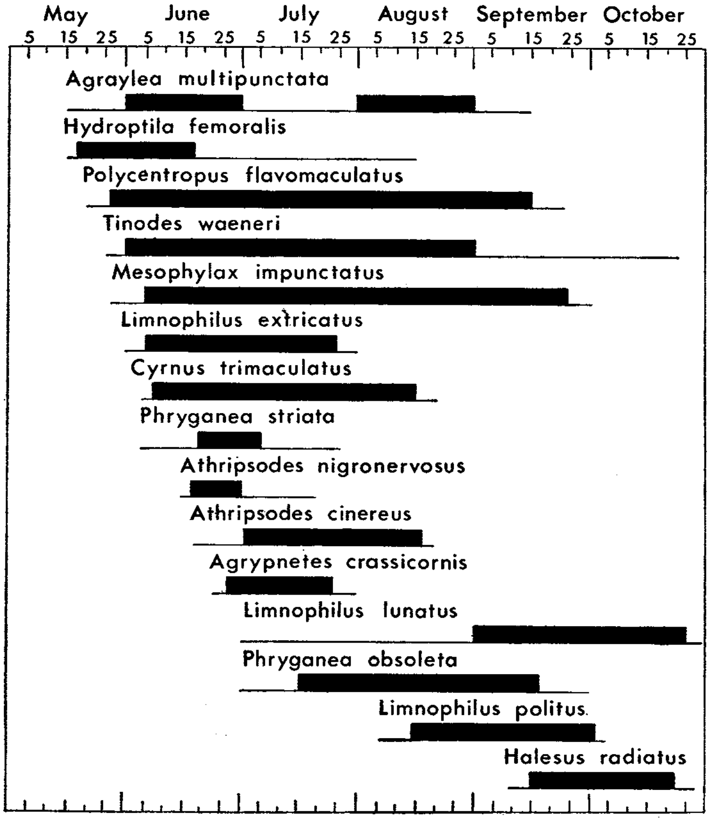

FIG. 4.

The flight periods of the 15 most frequently recorded species of Tarn caddis flies. The length of the single base line indicates the time over which each species is likely to be found in flight; the ends of these lines are the extreme dates at which adult caddis have been taken, and the thickened sections represent times when species have been observed to be especially abundant.

In general, the time of noticeable abundance of the adults lies about the middle of the total flight period, though *Hydroptila femoralis* and *Limnophilus lunatus* are evidently exceptions to this rule. Some species have a long spell of abundance, e.g. *Polycentropus flavomaculatus*, while others such as *Phryganea striata* are much more restricted. *Agraylea multipunctata* shows two quite separate periods of abundance which may indicate two generations of this species in the Tarn each year.

In all but 3 cases the records from which the extreme dates have been drawn have been made on the actual shore-lines: 3 captures were made by the lit window of the Study at Tarn House. The diagram incorporates all records available in the card index at the Centre, and the information given by Holmes (1963) in the Trichoptera section of the Insects of the Malham Tarn area. The figure is compiled from observations over the last 14 years but future records may require some revision to be made.

the North-west sedge bed. Dr. T. T. Macan did not collect it during a reconnaissance in 1947 which included the inflow bay (personal communication), nor did I find it during the first two years of the Field Centre in 1948 and 1949. Its arrival coincides with the arrival of many freshwater biology students and

Table 5. *Molluscs* (a) *whose highest British locality is Malham Tarn, and* (b) *which have been identified from Preboreal marl deposits of Tarn Moss.*

Species	Highest locality in Britain	Present in Marl of Tarn Moss
Hydrobia jenkinsi	+	
Limnaea pereger		+
Limnaea stagnalis	+	
Planorbis crista	+	
Planorbis leucostoma	+	
Planorbis contortus		+
Planorbis albus		+
Physa fontinalis	+	
Valvata piscinalis	+	
Valvata cristata	+	+
Bithynia tentaculata	+	
Sphaerium corneum		+
Pisidium amnicum	+	
Pisidium obtusale		+

it was probably introduced by chance in those years. It quickly spread along the north shore to the bay below the house where it became the dominant animal from 1952–1957, particularly on the wave-cut platform where its numbers reached up to 1,550 per square foot in July, 1957. During the following winter it suffered a disastrous "crash" and not a single living *Hydrobia* was found on the shores of the Tarn in 1958 and 1959; 5 only were collected in those years in *Chara delicatula*. Since then there has been a slow increase and recolonization of the wave-cut platform, very different to the initial explosion, 30 in one square foot being recorded in July, 1962. The cause of the spectacular crash in numbers is completely unknown.

The size of some snails varies greatly according to the habitat and the particular year. *Limnaea stagnalis* on the exposed shores is dwarf in comparison with the same species in the sheltered *Chara* or sedge beds, and this is probably a question of food supply. The great variation in average size from year to year in the weed beds may be connected with the water temperatures during the growing season; this may also be the cause of the peculiar variety which is still found in the Tarn but in certain years only (Stratton, 1956). This variety has a small delicate shell, with banding transverse to the whorls which Taylor (1895) considered to be due to growth checks.

Normally Tarn temperatures are low enough for the pulmonate snails to obtain all the oxygen they need from solution in the water; but during occasional hot and calm spells *L. stagnalis* and *L. pereger* may be seen coming to the surface from the *Chara* and other weed beds to fill their lungs.

Fish

Fish are an important part of the fauna and as in other calcareous waters they mostly attain a large size, though the reasons for this are still not understood.

Bullhead (*Cottus gobio*) and stoneloach (*Nemacheilus barbatula*) are common under stones on exposed shores, particularly on the north shore where stones are larger and lie loosely on top of one another. Smyly (1957) collected 43 bullhead from the Tarn between March and May and, estimating their age from the otoliths, gives the following figures of length from age, below which are his figures from Windermere for comparison.

	Males Year of life				Females Year of life			
	1	2	3	4	1	2	3	4
Malham Tarn (cms.) ..	5·2	7·2	8·2	9·1	4·8	6·6	8·0	8·2
Windermere (cms.) ..	4·7	6·0	6·7	6·8	4·2	5·3	5·9	6·4

Frequent collections of these two species have been made with students using torches at night when the fish leave their hiding-places to feed, and analyses of their food carried out from the stomach contents. The results from 3 such collections in May, July, and September are given in Fig. 5 in which the per cent by bulk of each food category is shown, using the points system as used by Smyly (1955). Such an analysis is not of course adequate to give a comprehensive picture, but it does indicate that these two fish, living in the same habitat, are not competing markedly. Bullheads have large mouths, feed only on moving animals and have very catholic tastes, taking advantage of what is most available. Thus on 16 July, 1959 all but one of 20 fish examined had been feeding on young crayfish which formed 69 per cent by bulk of their stomach contents. Stoneloach have small mouths, apparently feed by scent and rely largely on chironomid larvae and littoral Cladocera and Copepoda.

The three-spined stickleback (*Gasterosteus aculeatus*) is extremely common in some years when shoals of perhaps several thousand are seen, but in other years they may be quite scarce. Males guarding nests have been observed just offshore on the wave-cut platform and if this is the main breeding area success must be chancy. A high proportion of sticklebacks are infested with plerocercoid stages of cestodes in the body cavity including *Schistocephalus solidus* which probably prevents breeding (75 per cent in a sample of 24 in July, 1963). The stickleback is an important part of the diet of larger perch and Great Crested grebe. The minnow (*Phoxinus phoxinus*) is comparatively scarce though shoals of 20–30 fish may be seen. They reach a length of up to 9·8 centimetres.

The only two large species of fish in the Tarn are perch and trout which have probably been there since the 12th century, when "Malewater and the fishing thereof" was granted to the monks of Fountains Abbey by William de Percy; his daughter, Matilda, Countess of Warwick, confirmed in 1175 that "they may fish in Malhewater". It is difficult to see how these fish could have colonized the Tarn naturally with the impassable barriers of Malham Cove and Gordale Falls, so that they must have been introduced by man at some distant time.

Perch up to 2¾ lb. have been caught, and their numbers have fluctuated markedly over the last 100 years as can be seen from the records in the old game books of the numbers of fish caught between 1858 and 1929, shown in Fig. 6. For the first 62 years of this period the estate was in the hands of one owner, Walter Morrison, who is likely to have allowed the same amount of fishing so that numbers probably have some meaning. In 1911 ten rods caught 821 perch in one day and 3,357 were caught in that year, yet only a single fish

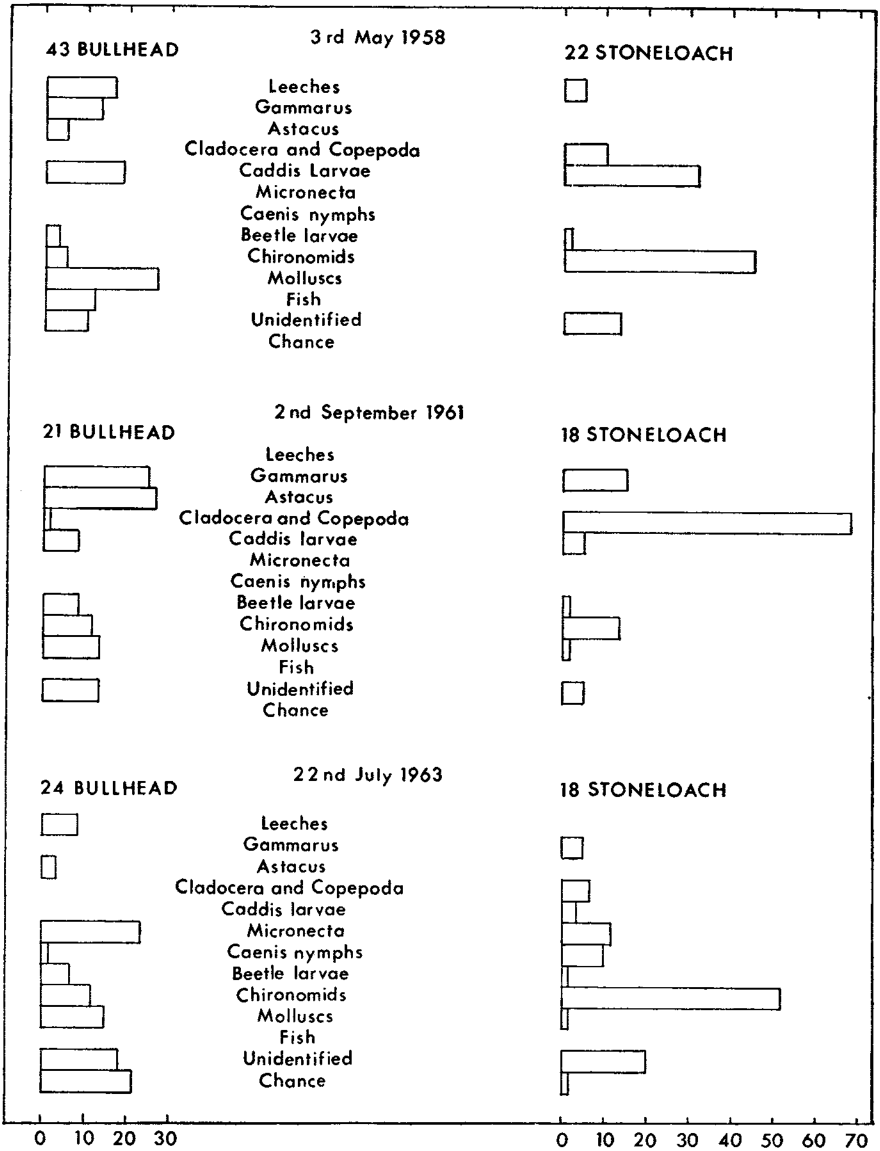

FIG. 5.

A comparison of the food found in the stomachs of Tarn bullhead (*Cottus gobio*) and stoneloach (*Nemacheilus barbatula*). The % by bulk of each food category is shown.

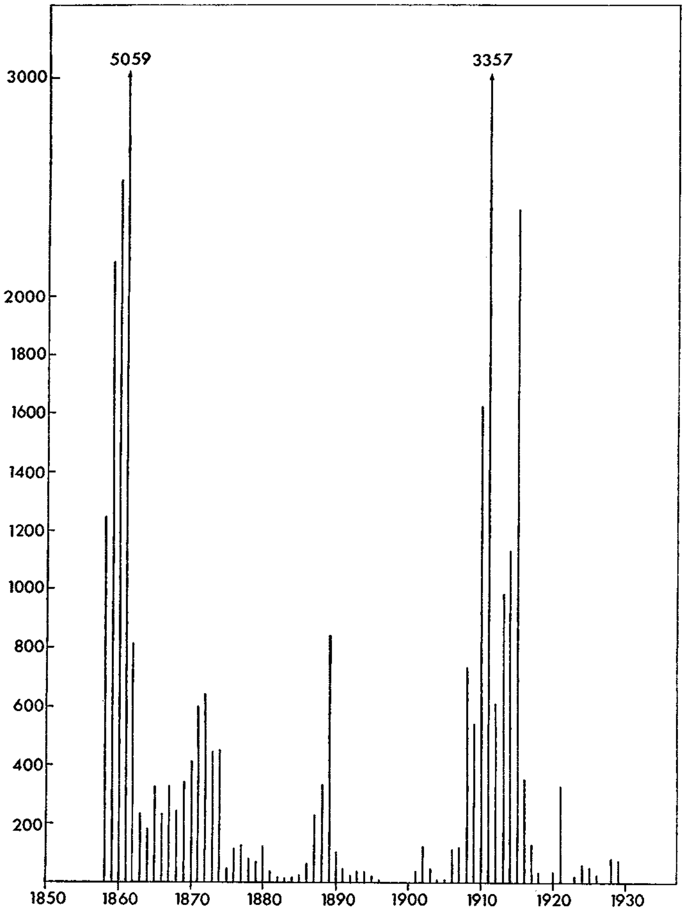

FIG. 6.

Numbers of perch caught at Malham Tarn 1858–1929 as recorded in the Game Books.

is recorded for 1905 and none in 1919. Similar fluctuations have occurred since 1948 when the populations were very low after the severe spring of 1947 which is said to have killed large numbers. But about 700 were quickly caught in 4 traps in May, 1953 and most of them were found by Mr. Le Cren to belong to one age-group, probably 2 year olds, indicating a successful breeding in 1951. In August, 1957 vast shoals of fry, which I estimated at "tens of thousands", were seen along the east shore and I prophesied that the Tarn would soon be overrun with perch. Yet from 1961 onwards hardly any perch have been caught. A discussion of such variation in success from year to year in Windermere and other lakes is given by Le Cren (1955). The food of the Tarn perch is a complicated matter depending on availability. The fry feed on zooplankton and soon graduate to bottom invertebrates such as *Gammarus*, chironomid larvae and snails, when 2–3 years old. They also start taking sticklebacks, and become predominantly fish eaters if sufficient are available. At times, however, fish up to 1 lb. have been found feeding mainly on *Gammarus lacustris* which may indicate a lack of fish prey.

In the past the Tarn was extensively stocked with brown trout, but none had been added for at least 15 years before 1948, which was the year in which they were first investigated. The 70 trout whose age and growth have been determined were caught between 1948 and 1957 and thus were all part of a population recruited from natural spawning.

Sixty-two of the 70 trout examined for age and growth were caught by fly fishing, between May and September, 4 were seined in March, 2 were caught by hand net in April and 2 were captured when spawning. All the fish were measured in centimetres from snout to fork of tail, weighed in pounds and ounces, and samples of scales taken. As the sex and gonad condition was not noted for all fish, no distinction of sex is made when giving results obtained from the age and growth investigation.

The age of each of the 70 fish was determined from the scales and the length at the end of each year of life back-calculated from them. The results are shown graphically in Fig. 7, in which the growth of brown trout from 2 Irish loughs, Lough Derg and Lough Atorick, is also given (Southern, 1935) for comparison with growth in Malham Tarn. Lough Derg (Co. Tipperary) is a limestone water rich in calcium and thus somewhat similar to Malham Tarn, while Lough Atorick (Co. Clare) contrasts markedly, being a non-limestone water with very low calcium content. Fig. 7 shows that the Tarn trout grow as rapidly as those of Lough Derg for the first 3 years of life, and though thereafter not quite so quickly they continue to grow at a rate comparable with that of the trout in the Irish limestone lough. On the other hand, at no time do the Tarn trout grow as slowly as the trout from the non-limestone Lough Atorick.

Though not as numerous as they once were, Tarn trout still attain a good size, e.g. one fish of 5 lb. in May, 1961 and another of $5\frac{3}{4}$ lb. late in the season of 1963. The largest fish landed was one of $6\frac{1}{2}$ lb. in 1924.

The food of Tarn trout has been investigated by analysing the stomach contents (and to some extent those of the intestine) of all fish caught by fly fishing from 1948–1957 inclusive and of 12 fish caught in March in a seine. The stomach contents were all dealt with on a points system, and the percentage composition based on this for the different months is given in Table 6. The number of fish in all months except August is small and thus can give only a very incomplete picture of the diet of the trout, especially as nearly all the fish were caught in the evenings from dusk onwards.

Table 6 shows that in March the dominant food is *Gammarus*: this is *Gammarus lacustris* typically found in deeper water offshore, and according to Hynes (1955) has only one breeding season, in spring. Thus in March there will be a large quantity of shrimps available as food, and this number will decrease later in the year as the adults die off and the young of the new generation are still small.

The results in Table 6 are important in showing the large contribution which the fauna of the weed beds, especially *Chara delicatula*, makes to the diet of the

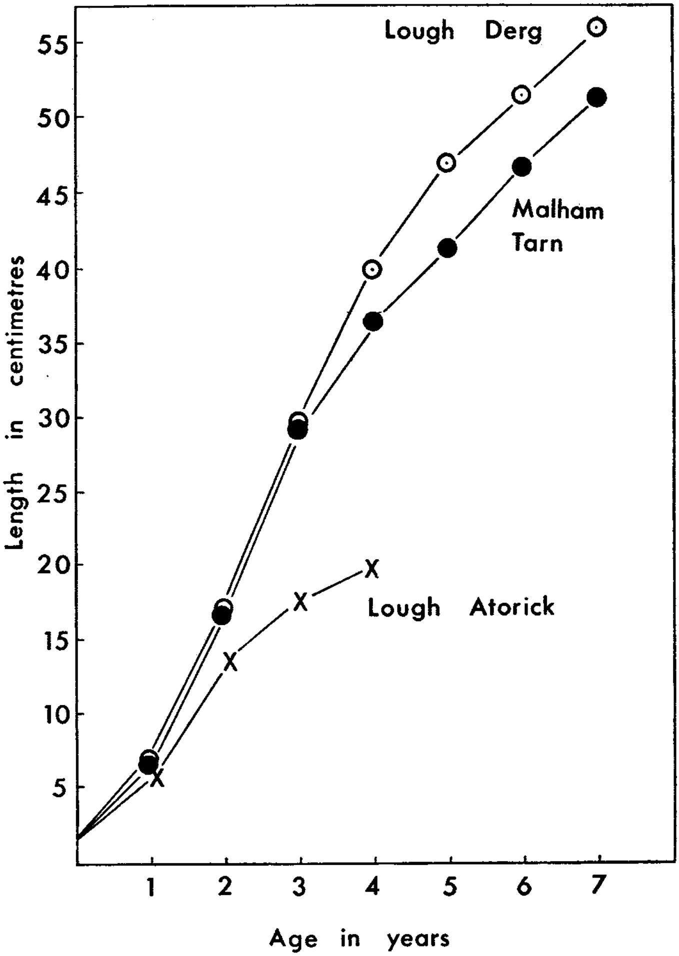

FIG. 7.
Growth of brown trout in Malham Tarn compared with that in two Irish Loughs.

trout, for example: species of *Phryganea* and *Limnophilus* in March, of *Chironomus* in May, and both caddis and midge species in June and July. In May and June snails which are found browsing on *Chara* also appear to be important, e.g. *Valvata spp.* In August and September although there is a notable variation in the diet, caddises still dominate the picture. The hatching adults of *Phryganea obsoleta* are taken for 5 or 6 weeks from the last week in July to early September in most years, and the swimming pupae of *Limnophilus politus* as they move to the shoreline to emerge to the adult form.

Table 6. *The food of Trout in Malham Tarn.* The % composition of stomach contents, estimated on a points system.

	March	May	June	July	Aug.	Sept.
Leeches	—	—	—	—	1·3	1·9
Gammarus	84·6	29·3	0·8	4·1	13·0	0·9
Astacus	—	—	—	—	—	25·2
Phryganea adult or emerging	—	—	—	28·2	60·0	4·3
Phryganea and *Limnophilus* larvae	2·5	9·3	30·4	25·5	0·1	0·3
Limnophilus, emerging pupae	—	—	—	—	0·6	40·0
Chironomid larvae	—	0·3	—	—	3·1	8·7
Chironomid emerging pupae or adults	—	44·0	54·6	26·0	6·5	—
Miscellaneous terrestrial adults Diptera	—	—	2·6	0·5	0·1	5·9
Water beetles larvae and adults	—	1·0	1·6	—	0·6	1·6
Sialis larvae	1·0	0·2	—	—	—	—
Caenis nymphs	—	—	—	—	1·3	—
Flying ants	—	—	—	—	—	9·0
Antler moth	—	—	—	—	0·3	—
Sphaerium	1·5	1·5	0·3	0·5	1·7	0·6
Pisidium	1·5	1·7	0·3	—	0·5	—
Limnaea	—	0·1	1·0	—	0·3	—
Valvata	6·9	2·7	7·8	—	1·3	1·6
Fish	—	8·3	—	15·2	1·5	—
Aphanocapsa (algae)	2·0	0·5	—	—	0·4	—
Unidentified organisms	—	1·1	0·6	—	7·4	—
Number of fish examined containing food	4	7	5	6	32	6
Empty stomachs additional to above	—	—	2	—	5	1

Other items of food which have been recorded during September are crayfish, flying ants, various casual insects such as terrestrial Diptera and ichneumon flies, and the larvae of *Chironomus* together with several small leeches (*Helobdella*). After the middle of September I suspect that the trout return mainly to feeding on the bottom and weed bed fauna, predominantly on *Gammarus* and molluscs. There is little evidence of regular fish-eating in the larger fish; only 3 out of 68 trout examined contained fish remains, these being of young perch.

Like the perch in the Tarn, the trout are also commonly infected by tapeworm parasites. Heavy infestations with the plerocercoid cysts of *Diphyllobothrium norvegicum* can result in death of trout either directly or by exposing them to infections with the fungus *Saprolegnia ferax* (Vik, 1957). A very high proportion of Tarn trout are also infected by an adult tapeworm, *Eubothrium crassum.* Fuller details of these parasites and of the natural history of the Tarn trout may be found in Holmes (1960).

Plankton

A general discussion of the phytoplankton and a more detailed comparison of the periodicity of the diatom *Asterionella formosa* in the Tarn and in the south basin of Lake Windermere is contained in Lund (1961). This comparison is made with particular reference to the concentrations of silica (SiO_2), nitrogen ($N.NO_3$) and phosphate phosphorus ($P.PO_4$). The species in the plankton are those which suggest a rather eutrophic body of water though the quantity is more typical of a Tarn lacking in dissolved nutrients. Lund comments that the shallow water allows large weeds such as *Chara*, *Potamogeton*, and *Myriophyllum* to compete effectively against the phytoplankton for essential nutrients and this is one reason for its scarcity.

In general it may be said that the zooplankton species which occur in the Tarn are common in most alkaline lakes whatever their altitude (A. L. Galliford, personal communication). He has found that the majority of the zooplankton is either bottom-living or littoral. Amongst the few definite planktonts, those which are dominant are the copepod *Diaptomus gracilis*, the Cladocera *Daphnia hyalina* and *Bosmina longirostris*, and the Rotifera *Asplanchna priodonta* and *Keratella cochlearis*.

Mr. Galliford has also found from the Centre's samples that in 1962, 1963 and 1964 the copepod *Cyclops vicinus* was abundant in the plankton. This had not been previously recorded or found in preserved material prior to 1956. The Tarn trout are infected with a parasite which is said to have an intermediate stage in the copepod, *Cyclops strenuus*. This species has not yet been found in the Tarn, but *C. vicinus* is a closely related species and may therefore also be an intermediate host of the parasite. The apparently sudden arrival of *C. vicinus* in the plankton may reflect some recent changes in the Tarn environment, such as increasing pollution. The appearance of *Hydrobia jenkinsi* in 1950 and of *Elodea canadensis* in 1962 has already been noted. In both cases visiting students are very likely to have been instrumental in these introductions. The large numbers of biology students and those interested especially in freshwater life may well have had other effects on the environment.

In particular the shorelines of the Tarn suffer intensive collection and disturbance every year and it is essential that every care should be taken, as in the past, to reduce the depletion of the fauna to a minimum. The majority of animal life should continue to be returned to its point of collection; after examination, stones should be carefully replaced in their original positions, and the numbers of animals removed from the Tarn should be quite strictly limited. Some restraint must also be observed in the actual numbers of students in any one year who work on the shorelines, or the natural replenishment of the fauna will be curtailed.

ACKNOWLEDGEMENTS

It had been the intention of Paul Holmes to revise and expand his first paper on the biology of the Tarn (Holmes, 1955), and had not his most untimely and tragic death intervened in December, 1964 he would certainly have published this himself. The paper now presented is very largely his work and the result of his meticulous and painstaking observation over the period of sixteen years when he was Warden of Malham Tarn. However, I am sure he would have wished me to thank sincerely all those people who have contributed to the paper, including the students of those years who were always adding to the knowledge of the Tarn which is now available.

I should like to thank particularly the following for their willing assistance in the final preparation of the paper: A. L. Galliford for his communication about the zooplankton, Charles Sinker for producing the fine drawings in

Figures 1, 2 and 3 (1 and 2 based on Paul Holmes' original pencil sketches), Keith Clayton and his staff for the completion of the remaining figures. I am also grateful to John Barrett, Donald Pigott, Charles Sinker and Deirdre Williams for correcting the typescript and for making helpful suggestions.

In conclusion I have learnt a great deal about the natural history of Malham Tarn and have gained an insight into Paul Holmes as the kind and first-class naturalist he was, and for this I am deeply grateful.

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Warden, Malham Tarn Field Centre.

REFERENCES

Elton, C. S. (1958). *The Ecology of Invasions by Animals and Plants.* London

Flint, J. H., *et al.* (1963). The Insects of the Malham Tarn Area. *Proc. Leeds. phil. lit. Soc.*, Sci. Sect., **9** (2), 15–91.

Fryer, G. (1953). The occurrence of *Gammarus lacustris* G.O. Sars, and *Gammarus pulex* (L.) in Malham Tarn, and a note on their morphological differences. *Naturalist, Hull,* No. 847, 155–156.

Holmes, P. F. (1955). Malham Tarn: a Background for Freshwater Biologists. *Ann. Rep. Fld. Stud. Coun.*, **1954–55**, 48–57.

Holmes, P. F. (1960). The Brown Trout of Malham Tarn, Yorkshire. *Salm. Trout Mag.*, **159**, 127–145.

Hynes, H. B. N. (1955). Distribution of some freshwater Amphipoda in Britain. *Mitt. int. Verein. theor. angew. Limnol.*, **12**, 620–628.

Kimmins, D. E. (1952). *Agrypnetes crassicornis* McLachlan (Fam. Phryganeidae), a caddis fly new to Britain. *Ann. Mag. nat. Hist.*, **5**, 1039.

Le Cren, E. D. (1955). Year to year variation in the year-class strength of *Perca fluviatilis. Mitt. int. Verein. theor angew. Limnol.*, **12**, 187–192.

Lund, J. W. G. (1961). The Algae of the Malham Tarn District. *Field Studies*, **1** (3), 85–119.

Pigott, M. E. and C. D. (1959). Stratigraphy and pollen analysis of Malham Tarn and Tarn Moss. *Field Studies*, **1** (1), 84–101.

Raistrick, A. and Gilbert, O. L. (1963). Malham Tarn House: its Building Materials, their Weathering and Colonization by Plants. *Field Studies*, **1** (5), 89–115.

Reynoldson, T. B. (1956). Some Records of Freshwater Triclads in Yorkshire. *Naturalist, Hull,* No. 856, 9–11.

Southern, R. (1935). The food and growth of Brown Trout from Lough Derg and the River Shannon. *Proc. R. Ir. Acad.*, **42**, 87–172.

Smyly, W. J. P. (1955). On the Biology of the Stone-loach *Nemacheilus barbatula* (L.). *J. anim. Ecol.*, **24**, 167–186.

Smyly, W. J. P. (1957). The life-history of the Bullhead or Miller's Thumb (*Cottus gobio* L.). *Proc. zool. Soc. Lond.*, **128** (3), 431–453.

Stratton, L. W. (1956). The Mollusca of the Malham Area. *J. Conch., Lond.*, **24** (4), 111–138.

Taylor, J. W. (1895). *Monogr. of the Land and Freshwater Mollusca of the British Isles.* Vol. 1, Pt. 2. Leeds.

Vik, R. (1957). Studies of the Helminth fauna of Norway. I. *Nytt Mat. Zool.*, **5**, 25–93.