Aspects of the Ecology of The Northern Pennines

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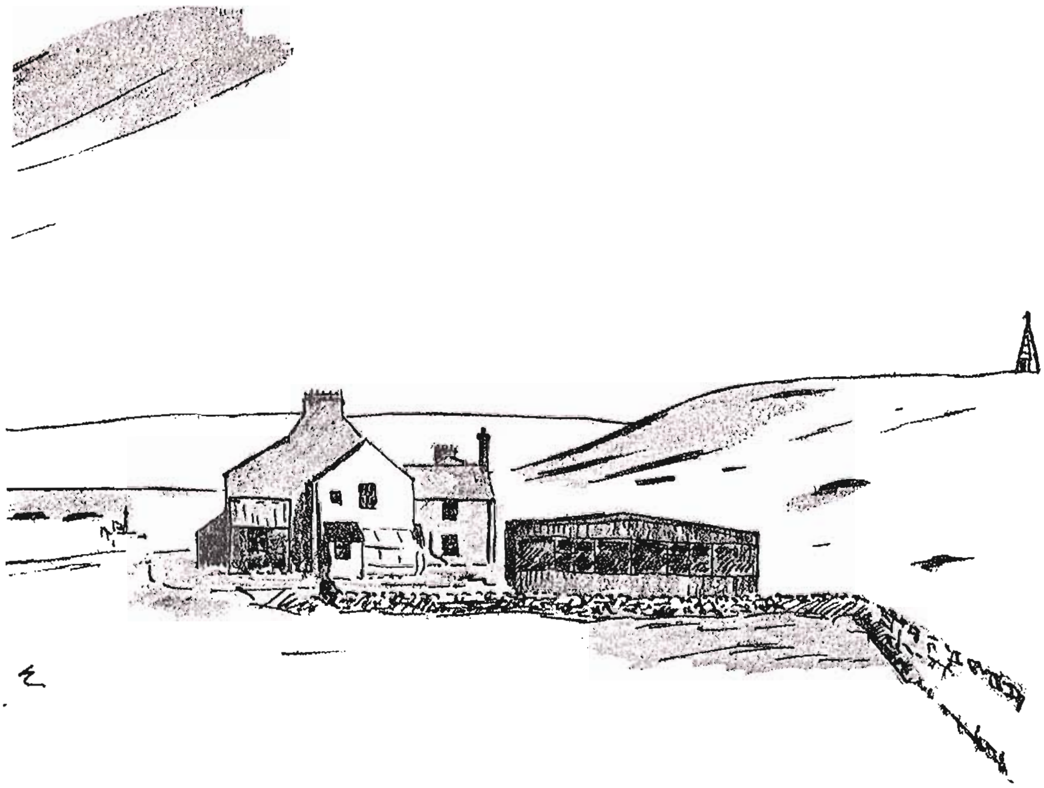

MOOR HOUSE

Aspects of the Ecology of the northern Pennines

11. Fish Populations

by

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Introduction

Moor House Occasional Paper No. 5 (1973) gave a brief summary of preliminary studies on fish by Crisp (1963). Since then, more intensive studies have been made of fish populations in tributaries of the River Tees (Crisp et. al. 1975) and of the River Eden (Crisp & Cubby, 1978).

In the first part of this account the information from these papers is brought together, augmented by some unpublished data, and compared with data from fish populations at Cow Green (Crisp et. al. 1974). The second part brings together miscellaneous information on the stomach contents and feeding of fish. Most of these data have not been published but, despite the rather speculative nature of this section, it seems worthwhile to put the results on record.

I. Population Studies

a). Distribution and movement

Figure I shows the known distribution of brown trout (Salmo trutta L.) and bullhead (Cottus gobio L.) within the Reserve and in some adjacent streams. Note that the minnow (Phoxinus phoxinus (L.)) was recorded (Crisp et. al. 1974) within the original boundary of the Reserve (R. Tees at NY/788311) before construction of the Cow Green reservoir.

The trout is widespread in the streams of the Reserve up to at least 648 m O.D., though in some of the smaller headwaters within and around the Reserve it is absent upstream of natural waterfalls or man-made obstructions (eg.s. Lodgegill Sike, Rowantree Sike, Rough Sike, Force Burn, Swindale Beck). The bullhead was not found within the Reserve boundaries in either of the two Eden tributaries studied. In the Tees system it is abundant in the main river, and present in at least the lowest reaches of most tributaries. Its upstream limit does not appear to depend solely on altitude for it occurs at higher altitudes in large streams than in small streams. For instance, it was not recorded at 543 m O.D. in Great Dodgen Pot Sike (0.04 m^3s^{-1} annual mean discharge) though its highest recorded occurrences in Nether Hearth Sike (0.15 m^3s^{-1}), Trout Beck (0.57 m^3s^{-1}) and the River Tees (0.75 m^3s^{-1}) were 544, 628 and 600 m O.D. respectively.

Crisp et. al. (1974) suggested that, within the Cow Green reservoir basin, recruitment to the trout population in the main river was largely a result of movement of young trout from the nearby tributaries. They also suggest that many of the fish from the main river returned to the tributaries to spawn. Subsequent observations on tagged reservoir trout indicate that large numbers of reservoir fish do spawn in adjacent tributaries and often return to the same beck on each spawning occasion.

It has also become clear that some reservoir fish ascend the Tees to at least 580 m O.D. during their spawning run. Therefore, it is probable that the trout of the upper Tees system have always shown some spawning migrations, if only on a modest scale, though the Trout Beck population appears to be isolated by the metering weir and the falls at Trout Beck Bridge. In contrast, the trout population in Knock Ore Gill is known to receive a substantial input of spawners either from the River Eden (10 Km away) or from the lowland reaches of Knock Ore Gill itself.

b) Age and growth

The trout of the Moor House National Nature Reserve have rather slow growth rates but show considerable variation in their lengths at any given age. Therefore, in order to clarify the growth pattern obtained by reading scales from the older fish, it is necessary to smooth the data by means of Walford plots (Ricker 1958). The values of l_∞ and k for the Walford plots used for the trout populations on and around the Nature Reserve are given in Table 1.

Table 1 Estimated values of the asymptotic length (l_∞) and the gradient (k) which describe the Walford plots used to smooth the observed length-for-age data for brown trout.

	l_∞ (cm)	k
Trout Beck system	22.5	0.722
Great Dodgen Pot Sike	21.5	0.824
River Tees and tributaries at Cow Green	39.0	0.860
Knock Ore Gill (beck fish)	30.8	0.800
Knock Ore Gill (Eden fish)	44.4	0.720

A summary of the smoothed mean lengths-for-age of brown trout is shown in Table 2.

Table 2 Smoothed mean lengths-for-age of brown trout in October for the Trout Beck system and Great Dodgen Pot Sike (Moor House), for the River Tees and tributaries at Cow Green, and for two tributaries of the River Eden within the Moor House National Nature Reserve. Based on data from Crisp et. al. (1974, 1975) and Crisp & Cubby (1978).

Mean length (cm)

Age Group	Tees tributaries-Moor House: Trout Beck System	Tees tributaries-Moor House: Great Dodgen Pot Sike	Tees system-Cow Green: Durham tributaries	Tees system-Cow Green: Westmorland tributaries	Tees system-Cow Green: River Tees	Eden tributaries: Knock Ore Gill	Eden tributaries: Swindale Beck
0	5.6	5.2	5.2	5.9	6.9	6.1	5.4
I	10.2	8.0	9.6	10.4	11.3	10.2	9.9
II	13.6	10.3	13.4	14.4	15.1	14.2	14.1
III	16.1	12.2	16.8	17.8	18.4	17.5	17.5
IV	17.9	13.8	19.7	20.7	21.2	20.1	20.0
V	19.2	15.1	22.3	23.2	23.6	22.2	22.2
VI	20.1	16.2	24.5	25.4	25.7	-	-
VII	20.8	17.0	26.4	27.3	27.5	-	-
VIII	21.3	17.8	28.1	28.9	29.0	-	-

The most rapid growth occurred in the River Tees at Cow Green before impoundment, and in the tributaries within the Cow Green basin, though Crisp et. al. (1974) showed that these growth rates were very much slower than those observed in streams in southern England. The observed lengths-for-age in the two Eden tributaries were similar to those at Cow Green. In contrast, the lengths-for-age of fish in Trout Beck were similar to those in the Eden tributaries up to age I, but smaller in older age-groups. Thus, on average, a Trout Beck fish reached 20 cm at age VI whereas a Knock Ore Gill fish reached the same length at age IV. The most striking difference between streams, however, was the one between Great Dodgen Pot Sike and the Trout Beck system. The growth of the Dodgen Pot trout was very slow and, on average, they reach 16 cm at age VI, compared with age III in Trout Beck.

A summary of observed mean lengths-for-age of bullheads at three sites is given in Table 3.

Table 3 Observed mean lengths-for-age (± 95% confidence limits) of bullheads in August for the Trout Beck system, for the River Tees at Tees Bridge, and for the River Tees at Cow Green.

	mean length (cm)		
Age Group	Trout Beck System	River Tees at Tees Bridge	River Tees at Cow Green
0	2.6 ± 0.06	1.5 ± 0.16	2.2 ± 0.05
I	5.8 ± 0.25	5.3 ± 0.19	4.8 ± 0.20
II	7.4 ± 0.38	6.5 ± 0.13	6.3 ± 0.19
III	8.6 ± 0.63	7.4 ± 0.21	7.6 ± 0.35
IV	10.2 ± 0.88	7.7 ± 1.00	8.4
V	-	8.5	8.6
VI	-	-	8.9

The bullheads of the upper Tees have a smaller length-for-age in the August of their first year of life than in southern chalk streams (Mann, 1971) or in the Lake District (Smyly, 1957). However, the growth rates of older bullheads at Tees Bridge and in Trout Beck is faster than in the Lake District and similar to that in the chalk streams. Within the upper Tees area, the growth and longevity of bullheads is greater in places such as Trout Beck where the fish are at a low population density, than in the Tees and other places where they are more numerous (see Tables 3 and 5).

c) Population estimates and movement

Table 4 summarises the estimates of population density and biomass of the trout. The first part of the Table shows data from fish census reaches and the second part shows data from surveys of whole streams. The census stations within the Moor House National Nature Reserve gave population estimates of 0.04 - 0.28 fish m^{-2} and biomasses of 1.14 - 5.54 g m^{-2}. The results from the more 'flashy' Cow Green becks fell into the same range, but in the more calcareous streams at Cow Green (eg. Dubby Sike, Weelhead Sike) there were population densities of 0.25 - 0.89 fish m^{-2} and biomasses of 2.11 - 8.94 g m^{-2}. In contrast, Station 1 of Knock Ore Gill had 0.83 fish m^{-2} (4.96 g m^{-2}) whilst Station 1 of Swindale Beck had a similar biomass (c. 6.13 g m^{-2}) but its population density (c. 0.25 fish m^{-2}) was more like that in Trout Beck (0.16 fish m^{-2}). The data from whole-stream surveys show a similar pattern. The River Tees at Cow Green had a much lower population density and biomass of trout than its tributaries, and contained a sparse population of older fish. Many of these older fish spawned in the afferent tributaries which were the main source of recruits to the Tees population.

Table 4. Mean population densities and biomass of brown trout at three times of the year in a series of marked census reaches and in four whole-stream surveys. The data under (A) are means of 5 years' data (1967-1971), those under (B) are means of 3 years' data (August or October 1967 to May 1970 inclusive) and those under (C) are for 1975 (Knock Ore Gill) and August 1973 (Swindale Beck).

Marked census reaches	Population density (fish m^{-2})			Biomass (g m^{-2})		
(A)	May	Aug.	Oct.	May	Aug.	Oct.
Tees tributaries (MHNNR)						
Moss Burn	0.07	0.12	0.11	1.19	2.00	1.87
Nether Hearth Sike	0.04	0.08	0.05	1.14	2.62	2.02
Trout Beck	0.05	0.13	0.06	1.45	3.97	1.47
Great Dodgen Pot Sike A	0.22	0.25	0.28	4.55	5.54	5.41
Great Dodgen Pot Sike B	0.05	0.10	0.10	1.85	3.77	3.88
(B)						
Tees tributaries, Cow Green						
Lodgegill Sike	0.05	0.06	0.10	0.92	0.42	3.28
Mattergill Sike	0.08	0.15	0.13	1.28	3.18	7.49
Dubby Sike	0.25	0.66	0.38	2.22	4.39	4.40
Weelhead Sike	0.40	0.89	0.59	2.11	3.69	8.94
(C)						
Eden tributaries (MHNNR)						
Knock Ore Gill St. 1	0.53	1.23	0.74	4.25	7.31	3.31
Swindale Beck St. 1	-	0.25	-	-	6.13	-
Whole-stream surveys						
Trout Beck	0.13	0.22	0.12	2.50	3.17	2.00
Cow Green tributaries	0.17	0.33	0.24	2.80	3.83	4.70
Cow Green, R. Tees	0.02	0.02	0.02	1.37	0.91	0.71
Knock Ore Gill	0.45	0.92	0.58	8.46	10.99	6.58

Information on the population densities of bullheads at three sites is given in Table 5. These values are low compared to estimates from other streams (Mann, 1971; Le Cren, 1969). The bullhead population in Trout Beck and its tributaries is very sparse, probably because years of good recruitment are infrequent. There was good recruitment in Nether Hearth Sike in 1967 when the population density (chiefly fry) was estimated as 0.46 fish m^{-2}. Large numbers of 0 group bullheads were not seen again in Nether Hearth Sike until 1972.

Table 5 Estimates of population density and biomass of bullheads based on electro-fishing and, at Tees Bridge, on tray samples

	Population density (fish m^{-2})			Biomass (g m^{-2})		
	Aug.	Oct.	May	Aug.	Oct.	May
Trout Beck System	0.04	0.04	0.04	-	-	-
R. Tees, Tees Bridge	7.80	5.30	2.50	-	-	-
R. Tees, Cow Green	0.47	0.65	0.47	0.74	0.49	0.46
R. Tees, Moor House NNR	0.25	0.18	0.18	0.87	0.48	0.57

Estimates of population density at Tees Bridge by electro-fishing in 1970-71 gave values of 1.1-2.4 fish m^{-2}, which are a little higher than those in the Tees at Cow Green (0.47 - 0.65 fish m^{-2}). However, electro-fishing is not a very effective method of sampling bullheads, in the upper Tees. The data in Table 5 for Tees Bridge, which are based on tray samples, show that electro-fishing may lead to the population density being underestimated by a factor of about three. Though there is some year-to-year variation in recruitment success in the River Tees, bullhead fry are present in most years and the population has a more stable age structure than that in Trout Beck.

d) Instantaneous mortality rates

Despite the considerable year-to-year variation in recruitment of trout which occurs in some streams (Table 6), a combined cohort method can be used (Crisp et. al. 1975, Crisp & Cubby, 1978) to estimate mean instantaneous mortality rates (M) from data obtained in whole-stream surveys. Table 7 gives estimates of M and of the corresponding annual survival rates (S). For the Trout Beck system, which can be regarded as a closed population, M is 0.66 $year^{-1}$. The tributaries and River Tees at Cow Green give values of 0.90 and 0.29 respectively. Clearly there is an interchange of trout between these last two areas which form parts of the same biological population. Combining the data from the Tees and its tributaries gives an estimate of M of 0.57 $year^{-1}$, which is reasonably close to the value for Trout Beck.

Table 6 % number of fry in the total population of trout in fish census reaches during August in various years.

Census reach	% number of fry 1967	1968	1969	1970	1971	1973	1975
Moss Burn	0	0	33.0	25.8	79.8	-	-
Nether Hearth Sike	0	6.9	54.3	0	23.3	-	-
Trout Beck	3.4	0	13.9	6.4	13.3	-	-
Great Dodgen Pot Sike A	0	0	38.8	4.8	34.9	-	-
Great Dodgen Pot Sike B	0	0	0	0	15.2	-	-
Lodgegill Sike	-	0	67.0	-	-	-	-
Mattergill Sike	5.3	43.8	55.8	-	-	-	-
Dubby Sike	-	4.0	79.3	-	-	-	-
Weelhead Sike	46.4	65.4	82.6	-	-	-	-
Swindale Beck, St. 1	-	-	-	-	-	33.5	0
Knock Ore Gill St. 1	-	-	-	-	-	22.5	68.7

Table 7 Instantaneous mortality rates (M) and survival rates (S) per year for trout and bullheads at Cow Green and on the Moor House National Nature Reserve

Stream	M	S
Trout		
Trout Beck system	0.658	0.52
Tees tributaries, Cow Green	0.905	0.40
R. Tees, Cow Green	0.289	0.75
R. Tees & tributaries, Cow Green	0.567	0.57
Knock Ore Gill	0.970	0.38
Bullhead		
R. Tees, Tees Bridge	1.190	0.30
R. Tees, Cow Green	1.100	0.33

The Knock Ore Gill trout must be regarded as only a part of a population which includes fish in the downstream reaches and part of the River Eden. The estimated mortality rate of 0.97 year^{-1} is similar to the rate estimated for the tributaries of the Tees at Cow Green.

Table 7 includes an estimate of M for the bullheads at Tees Bridge and all the values in the Table are low compared to those for populations studied in southern England. In southern streams values of M of 2.35 year^{-1} or more have been estimated for trout, and 4.00 or more for bullheads.

(e) Reproduction

Table 8 is a summary of information on sex ratios, age at first sexual maturity, fecundity and mean weight per ripe egg.

Table 8 Summary of information on sex ratio, age at first sexual maturity, fecundity and mean weight per ripe egg for bullheads and trout.
+ In this stream there was no correlation between length of female trout and egg number. The mean number of eggs per ripe female was 65, but in any given year about 30% of sexually mature females did not ripen any eggs.

Trout	Sex ratio (% males)	% females sexually mature at age:- I	II	III	IV	V	VI	Fecundity a	b	Mean weight /ripe egg (g)
Trout Beck system	50	0	16	88	96	100	100	0.440	2.037	0.048
+ Great Dodgen Pot Sike	50	0	17	67	84	91	-			0.054
Tees tributaries, Cow Green	50	0	26	85	100	100	100	0.082	2.642	0.062
R. Tees, Cow Green	50	0	0	25	83	100	100	0.082	2.642	
Knock Ore Gill (beck fish)	67	0	40	100	100	100	100	0.921	1.890	0.041
Knock Ore Gill (Eden fish)	27	-	-	-	-	-	-	0.065	2.691	
Bullhead										
Trout Beck system	50	0	80	100	100	100	100	1.944	2.354	-
R. Tees, Tees Bridge	50	0	80	100	100	100	100	0.981	2.518	-
R. Tees, Cow Green	50	33	100	100	100	100	100	1.134	1.570	0.004

The sex ratio of trout in the Tees and its tributaries is approximately 1:1. In contrast, there is a preponderance of males amongst the beck trout in Knock Ore Gill at spawning time, whereas the Eden fish spawning in the same study area show a preponderance of females. This suggests that young female trout move downstream from the nursery areas more readily and, perhaps, for longer distances than do the males.

Sexual maturity is attained at similar ages in the Trout Beck system and in the becks at Cow Green, whilst fish in the main river take, on average, one year longer. The resident trout in Knock Ore Gill reach sexual maturity rather earlier than those of Trout Beck.

Most bullheads (30%) in the Trout Beck system and in the Tees at Tees Bridge reached sexual maturity by age II and none were mature at age I. However, in the Tees at Cow Green, 33% reached sexual maturity at age I and virtually all were mature at age II. There was a 1:1 sex ratio at all three sites.

The reproductive performance of the trout in Great Dodgen Pot Sike is unusual: the fish are relatively slow to become sexually mature, the mature females do not spawn every year, and the eggs laid are few and large. These points are discussed at length by Crisp et. al. (1975).

The trout in the study area spawn during late October and early November, and alevins usually appear from late April to mid-May, though they may appear earlier in some calcareous becks at Cow Green. The bullheads in the study area spawn in late April and early May, and fry of 1.1 - 1.5 cm length can be found in mid-July.

In both species there was considerable year-to-year variation in the numbers of 0 group fish present in August. In the bullhead this was more noticeable in the tributaries than in the main river; in the trout it was more striking in the 'flashy' becks than in the calcareous becks. The latter point is shown in Table 6 where the numbers of trout fry are expressed as a percentage of the total numbers of trout in August. The two most calcareous and least 'flashy' streams used in the table are Knock Ore Gill and Weelhead Sike. This variation in recruitment is likely to reflect variation in survival between the time of oviposition and the time when fry first become vulnerable to electro-fishing.

(f) Production

Wide variation in numbers of 0 group fish from year to year, and movements of these young fish within the streams, cause some problems in estimating population production. This subject is discussed in detail by Crisp et. al. (1975). The problems can be reduced by combining data collected over a period of years from whole-stream (or stream system) surveys. This approach was used to construct Table 9. Le Cren (1969) found a range of values of 3-12 g m^{-2} (fresh weight) for trout production in a wide variety of small streams in Britain. The results from the Tees tributaries lie towards the bottom end of this range, but the estimate from the main river was much lower. In contrast, the estimated production for Knock Ore Gill trout was higher than most other published estimates for trout in small streams.

Table 9 Estimates of trout production (fresh weight) from whole-stream surveys.

Stream	Period	Mean Production g $m^{-2}year^{-1}$
Trout Beck system	1971-72	2.33
Tees tributaries, Cow Green	1969-70	4.40
R. Tees, Cow Green	1969-70	0.70
R. Tees + tributaries, Cow Green	1969-70	1.20
Knock Ore Gill	1975	13.89

Table 10 gives estimates of the mean, fresh weight production in eight census reaches. The values for the Moor House streams are maxima, though minimum estimates (based on the assumption that all recruitment is by immigration) are given in parentheses. The result from the first five stations (Moor House streams) agree closely with the estimates for Trout Beck in Table 9. Similarly the values for the last three stations in Table 10 are reasonably close to the estimated production in all tributaries at Cow Green (Table 9).

Table 10 Estimates of trout production (fresh weight) from the census stations. Minimum estimates, based on the assumption that all recruitment is by immigration, are in parentheses.

Stream	Period	Mean production g m^{-2}year^{-1}	
Moss Burn	1967-71	2.25	(1.64)
Nether Hearth Sike	1967-71	2.10	(1.64)
Trout Beck	1967-71	2.16	(1.55)
Great Dodgen Pot Sike (A)	1967-71	3.50	(1.99)
Great Dodgen Pot Sike (B)	1967-71	1.02	(0.54)
Mattergill Sike	1967-70	5.91	
Dubby Sike	1967-70	5.96	
Weelhead Sike	1967-70	8.55	

The reliability of the estimates of bullhead production depends upon the precision of the population estimates upon which they are based. The estimate for the Tees at Cow Green in Table 11 is based on electro-fished samples and is low relative to the estimates of trout production in Tables 9 and 10. However, the result from Tees Bridge is based on tray sampling and is high relative to trout production in most tributaries. We must, therefore, conclude that the bullhead contributes a very small proportion to the total fish production in the tributaries, but may make a substantial contribution (possibly 50% or more) in the main river.

Table 11 Estimates of bullhead production (fresh weight). μ - based on tray samples. + - production estimate for a good year; in most years production at this site, and in the whole Trout Beck system, will be much less.

Stream	Period	Mean Production g m^{-2}year^{-1}
R. Tees, Tees Bridge	1970-71	7.43 μ
R. Tees, Cow Green	1967-68	1.07
Nether Hearth Sike	1967	0.49 +

II. Stomach contents and feeding

The study of the food and feeding of fish raises a complex problem. The main difficulty is that estimates of the production of potential food organisms are not available, and comparisons of estimated food requirements with the standing crop of potential food organisms are of little value. This account is not an attempt to resolve the problem, it simply brings together unpublished data relating to three aspects of the food and feeding of fish in the streams on the Moor House National Nature Reserve.

(a) Composition of stomach contents

A large number of fish stomachs have been examined but the sampling has been rather patchy. However, satisfactory data are available for several sites and these form the basis of the comparisons which follow.

Samples of about 30 bullheads (excluding 0 group fish) were taken at monthly intervals from the Tees at Tees Bridge (NY/760338) from July 1969 to July 1970. The results, in terms of major taxa, are summarised in Figure 2. Over the whole year, three taxa formed about 76% of the number of prey items found in the stomachs (Ephemeroptera 37.6%, Trichoptera 15.5%, Mollusca 22.8%). The Ephemeroptera consisted of 9.4%, Baetidae nymphs and 90.6% Ecdyonuridae nymphs, and the Mollusca were composed of 66.5% Ancylastrum fluviatilis Müller and 33.5% Lymnaea peregra (Müller). Ephemeroptera and Mollusca together formed numerically between 43% and 95% (mean 60%) of the stomach contents each month. The relative proportions of the two groups showed considerable month-to-month variation, probably as a result of fluctuations in the population density of Mollusca within the sampling area. Casual observations suggest that, in periods of dry summer weather, the population density of Mollusca in pools in the Tees increases but that sudden spates rapidly reduce the population density. Figure 3 shows monthly changes in the percentage number of Mollusca in bullhead stomachs and in the mean discharge in Trout Beck. The figure suggests that the contribution of Mollusca to the stomach contents increases during relatively dry, spate-free periods, and decreases during spates.

One hypothesis which fits these observations is that Mollusca are a preferred food of the bullheads in this reach of the Tees but, when Mollusca are scarce, the bullheads take more of other foods, especially Ephemeroptera nymphs. Certainly these two groups are complementary in the stomach contents of Tees Bridge bullheads. Figure 4 is a plot of Ephemeroptera against Mollusca in terms of the percentage contribution of each group to the total number of prey items in the bullhead stomachs. A log:log plot gives a linear relationship between the two groups, with a correlation coefficient of $r = 0.7285$ ($P<0.01$).

Figure 5 summarises the stomach contents of samples of trout taken at three times of the year in Knock Ore Gill and Nether Hearth Sike, the latter station being typical of the Trout Beck system. The Knock Ore Gill data show a contrast between the stomach contents of 0 group and older trout. The May sample of 0 group trout consisted of alevins whose stomach contents had only three components; Ostracoda, small Baetidae nymphs and small Chironomidae larvae. By August a wider variety of food types was present in the stomachs but Baetidae nymphs still formed the bulk of the contents (nearly 60% by number). In contrast, 50% of the stomach contents in older fish in August were Plecoptera nymphs. The October stomachs of 0 group trout had similar contents to those of older fish, though Ostracoda were present only in the former. In addition, these 0 group stomachs contained smaller proportions of Plecoptera and Gammarus compared to the stomachs of older fish. This suggests that the 0 group trout probably have difficulty in taking the larger invertebrates such as Gammarus and Perlodidae nymphs.

There were considerable differences between the stomach contents of older trout in Knock Ore Gill and those from Nether Hearth Sike. These probably reflect differences in the composition of the benthos at the two sites, though there are no analyses of the benthos in Knock Ore Gill to confirm this. Gammarus contributes about 10% of the stomach contents in Knock Ore Gill throughout the year. In Nether Hearth Sike Gammarus is scarce and forms a negligible component of the stomach contents. During August and October, Trichoptera formed a large component (c. 50%) in Nether Hearth Sike but contributed very little in Knock Ore Gill. However, the differences between the two sites become more evident if the major taxa in the stomach contents are subdivided. Table 12 shows subdivisions of the Ephemeroptera, Plecoptera and Diptera. There is little difference in the Ephemeroptera in stomach samples, with Baetidae forming about 80% of the total at each site. Ecdyonuridae and Ephemerella ignita each make a minor contribution, but their relative importance differs between the sites. However, major differences are seen in the Plecoptera and Diptera. Perlodidae formed 76% of all Plecoptera in stomachs from Knock Ore Gill, whereas in Nether Hearth Sike they were replaced by Leuctridae (64%) and Taeniopteryx nebulosa (25%). Similarly, Chironomidae formed the bulk (87%) of Diptera in stomachs from Knock Ore Gill, but Simuliidae (69%) were more important in Nether Hearth Sike.

Table 12 Percentage numerical composition of each of three taxa within the stomach contents of trout in Nether Hearth Sike and Knock Ore Gill.

Ephemeroptera	Nether Hearth Sike	Knock Ore Gill
Baetidae	82	79
Ecdyonuridae	16	5
Ephemerella ignita Poda	2	16
Plecoptera		
Leuctridae	64	19
Perlodidae	6	76
Nemouridae	5	5
Taeniopteryx nebulosa (Linne)	25	0
Diptera		
Chironomidae	13	87
Simuliidae	68	13
Others	19	0

(b) Calculated food requirements

Winberg (1960) gives equations to estimate the food required by fish for growth using data on fish production and the food required for metabolism. The metabolic requirements can be estimated from the water temperature and the population density and weight-frequency distribution of the fish population. The data necessary for this process are now available for trout in the Tees and in a number of its tributaries.

The following assumptions are inherent in the Winberg method:

(i) 1 g fresh food ≡ the production of 1 g fish flesh (fresh weight)

(ii) The energy of the ration = 1.25 (energy of metabolism + energy of weight increase)

(iii) For salmonid fishes, resting metabolism (ml O_2 hour^{-1} at 20°C) = $0.498\ W^{0.76}$, where W = fresh weight of fish (g).

(iv) To correct for field temperature divide by q, a divisor given by Winberg and based on Krogh's 'normal' curve.

(v) 1 mg O_2 consumption ≡ expenditure of 1 mg dry matter of 5 mg fresh matter (for fish or food).

(vi) Active metabolism = 2 x resting metabolism.

Table 13 Food requirements, mean biomass, annual production and P/B ratio of trout populations on the Moor House National Nature Reserve and at Cow Green. The results are based on two whole-stream surveys and on data from two census reached in Great Dodgen Pot Sike. Temperature data from the actual sites have been used for Great Dodgen Pot Sike, but approximate temperatures based on records from stream sites on the Moor House National Nature Reserve have been used elsewhere. The annual maintenance ration for trout in the Tees tributaries at Cow Green was estimated as 19.4 g m^{-2} (fresh weight) from the equation of Elliott (1975) (cf. the Winberg estimate of 18.8 g m^{-2}).

	Food requirement (g m^{-2} year^{-1} fresh weight)				Mean biomass (g m^{-2})	Production (g m^{-2} year^{-1})	P/B
	Metabolism	Growth	Egested	Total			
Trout Beck system	7.1	2.3	2.4	11.8	2.6	2.3	0.9
R. Tees, Cow Green	5.9	0.7	1.7	8.3	1.2	0.7	0.6
Tees tributaries - Cow Green	18.8	4.4	5.8	29.0	3.5	4.4	1.3
R. Tees & tributaries- Cow Green	7.4	1.2	2.2	10.8	1.5	1.2	0.8
Great Dodgen Pot Sike 'A'	30.9	3.5-1.5	8.6-8.1	43.0-40.5	5.7	3.5-1.5	0.61-.26
Great Dodgen Pot Sike 'B'	15.8	1.0-0.5	4.2-4.1	21.0-20.4	3.3	1.0-0.5	0.30-0.15

Table 13 gives estimates of the food required by trout, which are based on smoothed population data from whole-stream surveys (Trout Beck and the Cow Green sites) and two census reaches (Great Dodgen Pot Sike). The estimates are approximate, but are a good general guide to quantities. Where the fish population consists mainly of young and relatively fast-growing trout (eg. tributaries at Cow Green), the total food requirement and the P/B ratio are larger than in populations composed mainly of older fish (eg. River Tees). The trout population in Great Dodgen Pot Sike is composed largely of old, slow-growing fish at a relatively high density and this results in a high mean biomass (B), low P/B ratio and a large food requirement.

Table 14 shows the approximate distribution, between months and between age groups, of maintenance rations for trout in the Tees tributaries at Cow Green. These estimates are based on equations given by Elliott (1975). Table 14 A shows that most of the food required for population metabolism is utilised by the I, II and III age groups. The ratio of the food required for metabolism to biomass decreases with age. Table 14 B shows that about 78% of the annual maintenance ration is required during the five months, May - September.

(c) Surface foods

The stomachs of trout from the Moor House streams contain a substantial proportion of prey taken at the water surface, particularly during the summer. Nelson (1965) and Crisp (1966) described simple sticky traps for sampling insects close to stream surfaces. This account brings together information from both these papers, together with some unpublished data, in a preliminary exploration of the interrelationships between temperature available prey at the water surface, and the food requirements of trout.

Nelson compared traps, set with their sticky surface about 2.5 cm above the water surface, with traps on the stream banks. He found differences (in terms of broad taxonomic groups) between catches over the stream and catches over the bank. Diptera formed 96% of the total catch and three times as many flies were caught over the stream as on the bank. This difference was chiefly a result of larger catches of Chironomidae (species listed by Birkett 1976) and Empididae (Nelson 1971). The water-surface catches were dominated numerically by Chironomidae (48%) and Empididae (39%). In terms of biomass, Empididae (31.5%), Muscidae (17.7%), Tipulidae (9.4%) and Chironomidae (6.3%) were the main components.

Estimated annual catches on these traps are 260800 individuals $m^{-2}year^{-1}$ (Nelson 1965) and 213400 indi'viduals $m^{-2}year^{-1}$ (Crisp 1966). The approximate 95% confidence interval on the latter estimate is $\pm$ 64000. These values correspond to an annual biomass of about 80g $m^{-2}year^{-1}$ (dry weight).

Nelson (1965) noted that there was a good agreement between weekly catch size and weekly average maximum screen air temperature. A plot of approximate values taken from Nelson's Figure 1 is shown in Figure 6. The plot approximates to a straight line; there is a significant correlation (r = 0.8534, P 0.001), and the catch (y) can be related to the weekly average maximum screen air temperature (x) by the calculated regression $\log_{10} y = 0.26\,x - 0.60$. The data used by Crisp (1966) from a set of similar traps were re-examined in terms of the catch $m^{-2}day^{-1}$ during six-day trapping periods (y) and mean air temperature in the vegetation layer on the stream bank during each trapping period (x°C). The relationship y = 0.3198 x 2.6052 (Figure 7) gave the best fit to the data (r = 0.9509, P 0.001).

Parallel trials were made to test the effect of frequency of cleaning the trap surfaces. The comparisons were between traps cleaned at hourly intervals for 9 hours and traps cleaned once every 9 hours (ie. 9 x 1 hour and 1 x 9 hours), traps cleaned daily for three days and once every three days (3 x 1 day and 1 x 3 days), and traps cleaned daily for 5 days and once every five days (5 x 1 day and 1 x 5 days). In each trial the total catch was increased by more frequent cleaning of the traps and chi-squared tests showed that the differences were significant (P 0.001). This suggests that the results from the six-day operations may have led to the total availability of flying insects at the water surface being underestimated. However, it is reasonable to assume that the results from the traps represent:

a) An index of changes in availability throughout the season.

b) An estimate of, at least, the order of magnitude of food available to trout at or near the water surface.

Table 14 A) Distribution of biomass and population maintenance ration between age-groups of trout in Tees tributaries at Cow Green.

B) Distribution of annual maintenance ration of trout between months for Tees tributaries at Cow Green.

A) Age Group	0	I	II	III	IV	V	VI	VII & older
% total annual maintenance ration	9.3	23.2	23.1	17.8	12.1	7.3	3.8	3.4
% total biomass	6.4	18.1	21.4	19.5	15.2	9.5	5.2	4.7

B) Month	Jan.	Feb.	Mar.	Apr.	May	Jun.
% annual maintenance ration	0	0	0	5.5	10.6	15.3
	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
	18.7	19.1	14.7	11.2	4.9	0

As the food requirements of fish can be related to water temperature and because both water temperature and trap catches can be related to air temperature, there should be some agreement between seasonal variation in food requirements and the availability of insects at or near the water surface. A comparison of the trap catches and the annual maintenance ration for trout (from Elliott 1975) (Figure 8) supports this conclusion. The estimated availability of insects at the water surface (80 g $m^{-2}year^{-1}$ dry weight) is high relative to the estimated food requirements of the trout (8 - 43 g $m^{-2}year^{-1}$ fresh weight - see Table 13).

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Figure Legends

Fig 1. Maps of Moor House National Nature Reserve (a = western half of Reserve, b = eastern half of Reserve) and surrounding area to show known distribution of fish species (excluding changes of distribution caused by Cow Green Reservoir). O = Trout and bullhead present, O = Trout present, ⊛ = Trout, bullhead and minnow present, • = spot heights in m O.D.

Fig 2. Percentage numerical composition of major taxa in the stomach contents of bullheads at Tees Bridge between July 1969 and July 1970. n = number of stomachs examined, n_1 = number of prey organisms found, n_2 = number of empty stomachs.

Fig 3. Number of Mollusca expressed as a percentage of all prey items in bullhead stomachs at Tees Bridge (O), and monthly mean discharge (m^3s^{-1}) in Trout Beck (histograms), between July 1969 and July 1970.

Fig 4. Relationship between mollusca (x) and Ephemeroptera (y) in terms of percentage contribution of each group to the total number of prey organisms in bullhead stomachs, between July 1969 and July 1970. $r = 0.7285$, $P < 0.01$ and $y = 172.2\ x^{-0.55}$.

Fig 5. Percentage numerical composition of the stomach contents of trout in May, August and October at (A) Nether Hearth Sike (older trout 1967-8) (B) Knock Ore Gill (older trout, 1975) and (C) Knock Ore Gill (fry, 1975). Definitions of n, n_1 and n_2 as in legend of Fig 2.

Fig 6. Relationship between the catches on sticky traps at the water surface ($\log_{10}$ number of flies $week^{-1} = y$) and average screen maximum air temperature ($^{o}C = x$). $r = 0.3534$, P 0.001 and $y = 0.26\ x^{-0.06}$. Developed from data given by Nelson (1965).

Fig 7. Relationship between catches on sticky traps (number caught in $m^{-2}dry^{-1} = y$) and mean air temperature in the vegetation layer of the stream bank ($^{o}C = x$). From Crisp (1966) and unpublished data. $r = 0.9509$, P 0.001 and $y = 0.3198\bar{x}^{2.61}$.

Fig 8. Monthly catches on sticky traps (O) and the monthly food needs of trout for maintenance expressed as a percentage of the annual need (histograms) calculated from observed water temperatures and equations given by Elliott (1975).

FIG. 1a.

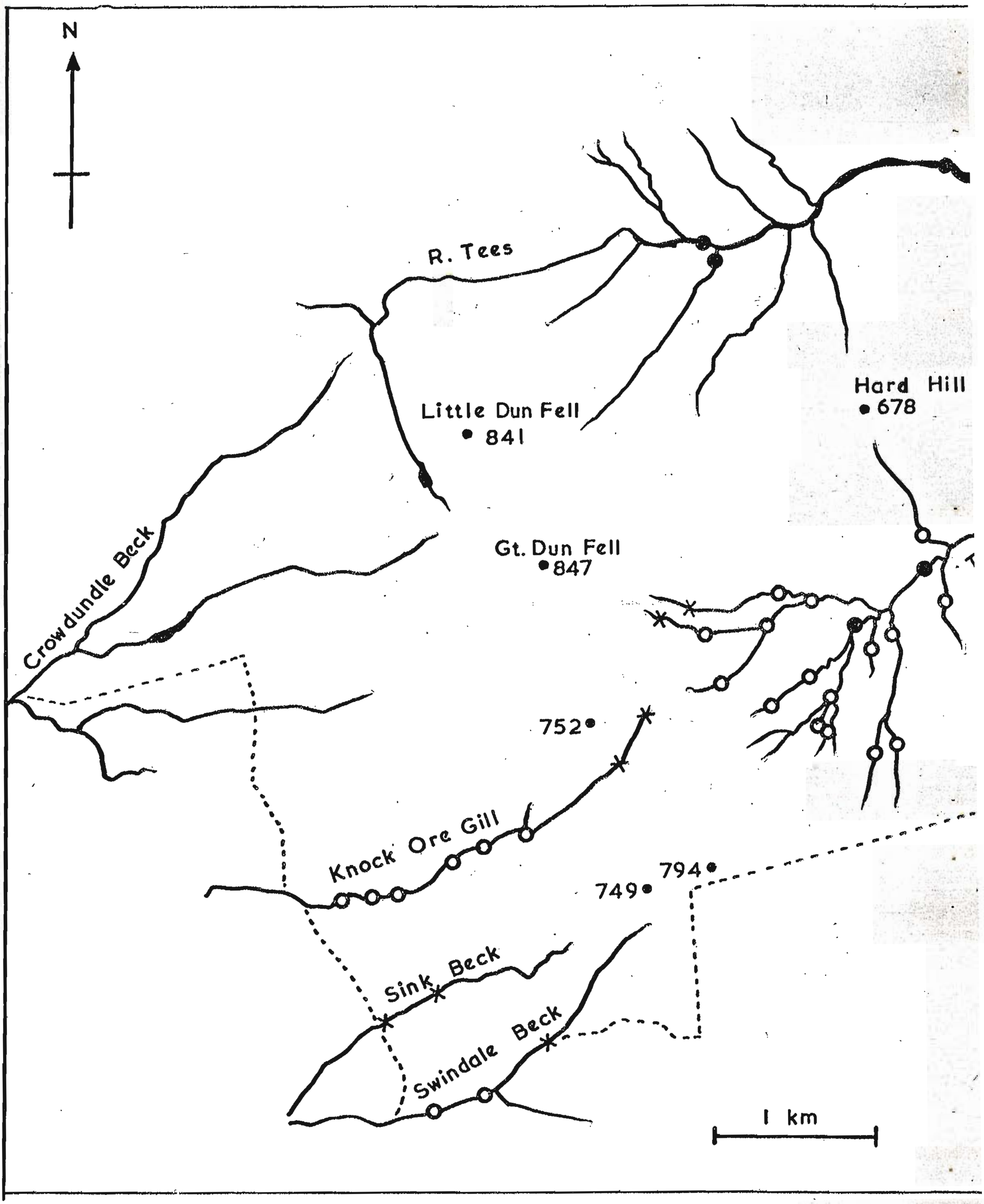
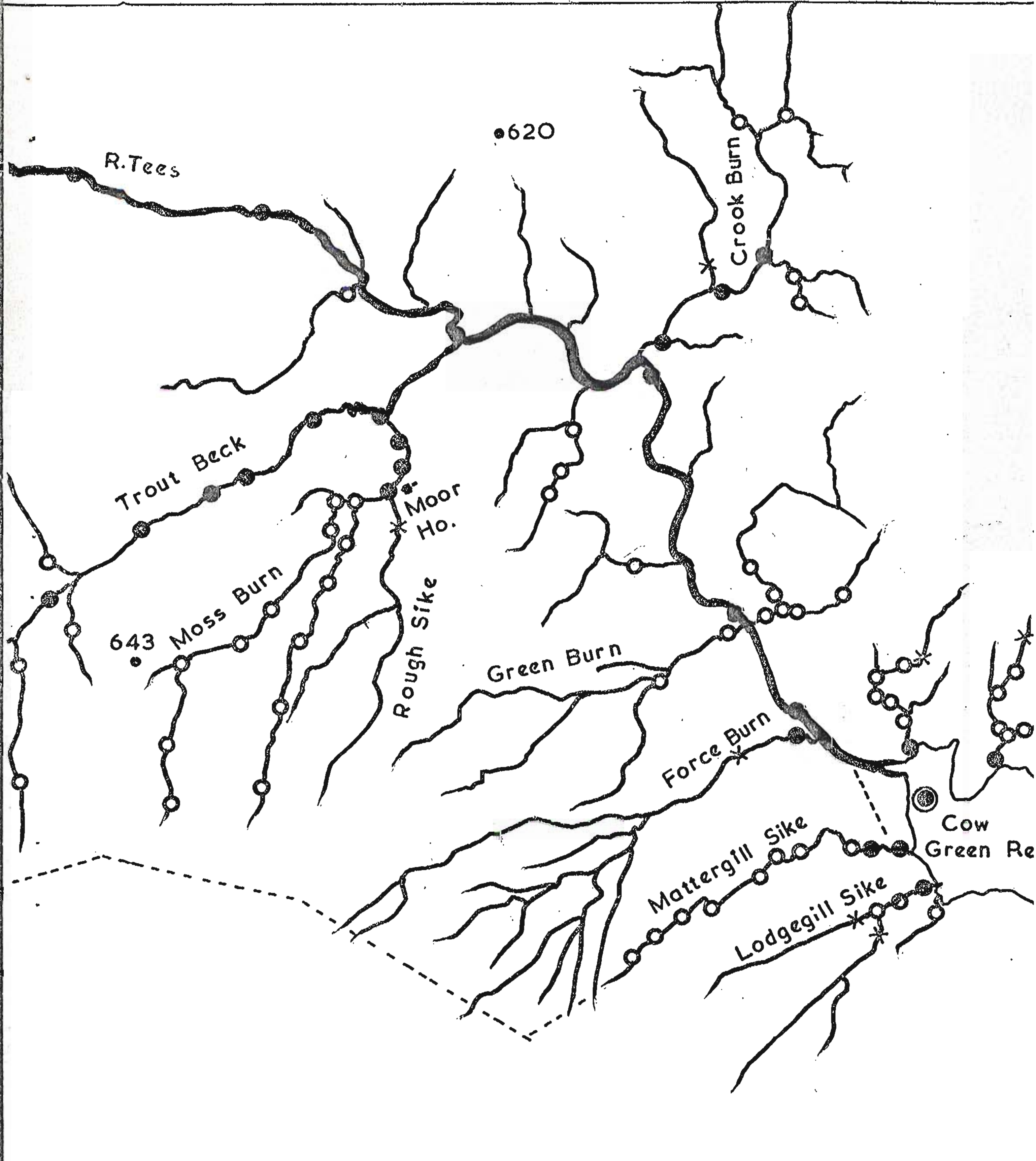
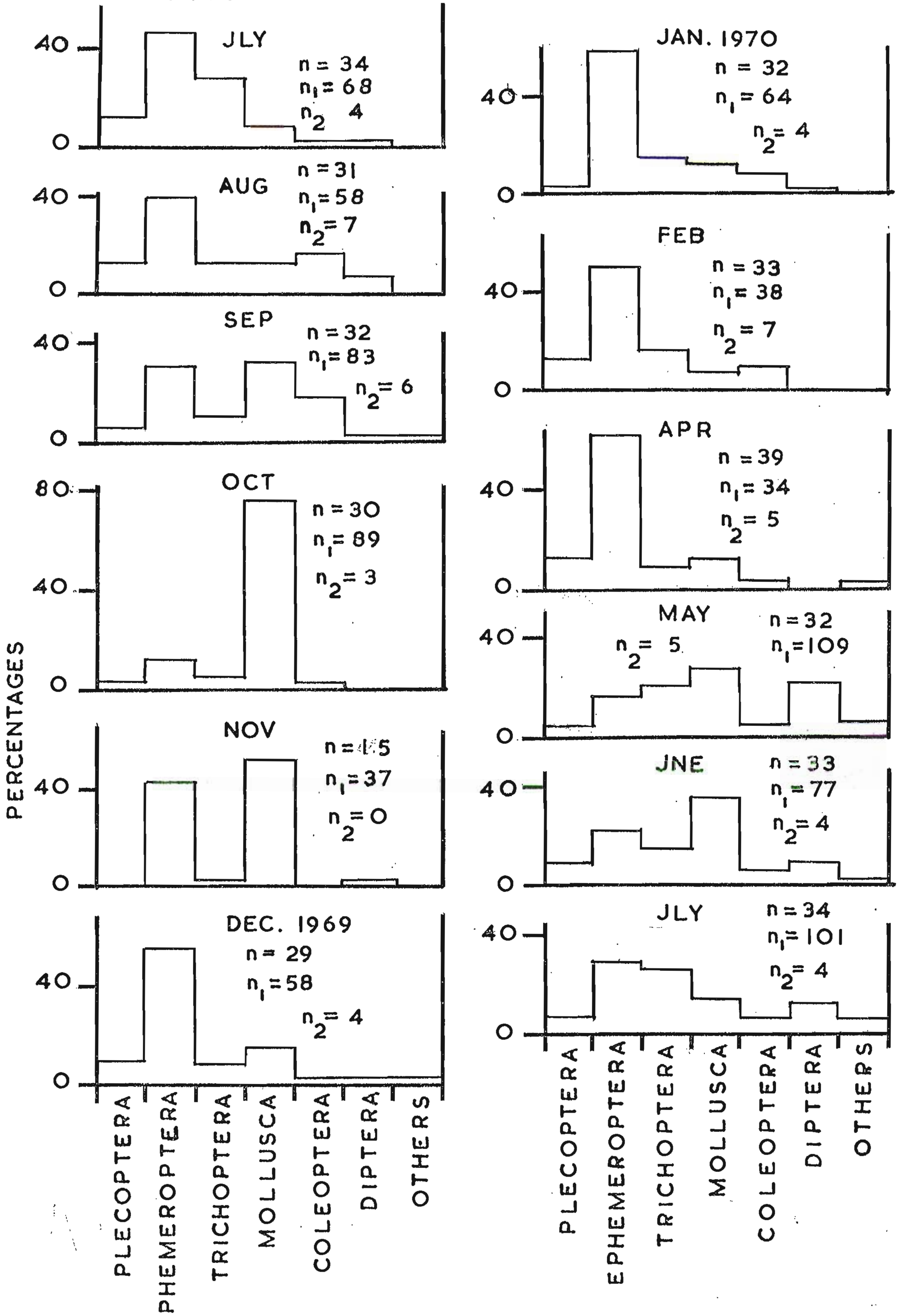

N
R. Tees
Little Dun Fell
841
Hard Hill
678
Gt. Dun Fell
847
Crowdundle Beck
752
Knock Ore Gill
794
749
Sink Beck
Swindale Beck
1 km

FIG.1b.



R.Tees
620
Crook Burn
Trout Beck
Moor Ho.
Moss Burn
643
Rough Sike
Green Burn
Force Burn
Cow Green Re
Mattergill Sike
Lodgegill Sike

FIG. 2.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SEP
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OCT
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NOV
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n_2 = 0
DEC. 1969
n = 29
n_1 = 58
n_2 = 4
JAN. 1970
n = 32
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n_2 = 4
FEB
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n_1 = 38
n_2 = 7
APR
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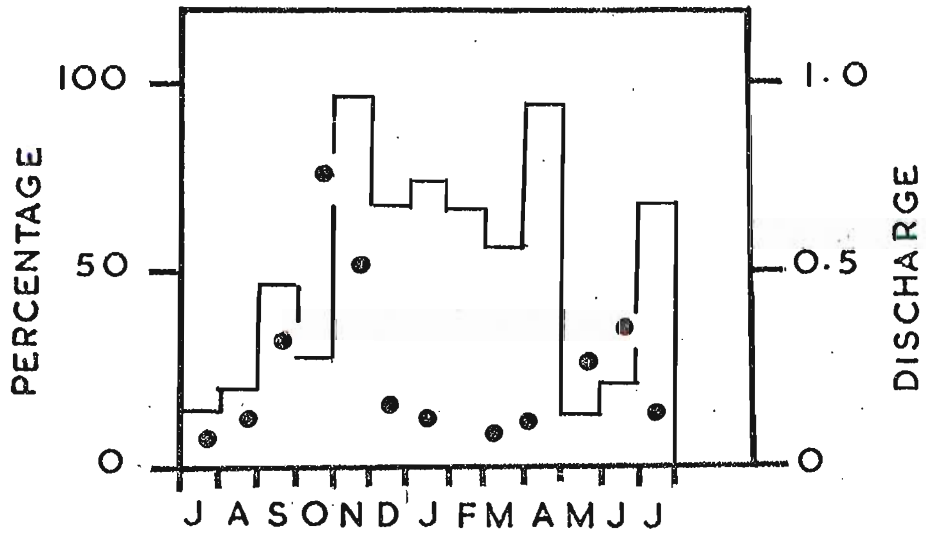
n_1 = 34
n_2 = 5
MAY
n = 32
n_1 = 109
n_2 = 5
JNE
n = 33
n_1 = 77
n_2 = 4
JLY
n = 34
n_1 = 101
n_2 = 4
PERCENTAGES
0
40
80
PLECOPTERA
EPHEMEROPTERA
TRICHOPTERA
MOLLUSCA
COLEOPTERA
DIPTERA
OTHERS

FIG. 3.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50
0
PERCENTAGE
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0.5
0
DISCHARGE
J A S O N D J F M A M J J

FIG. 4.

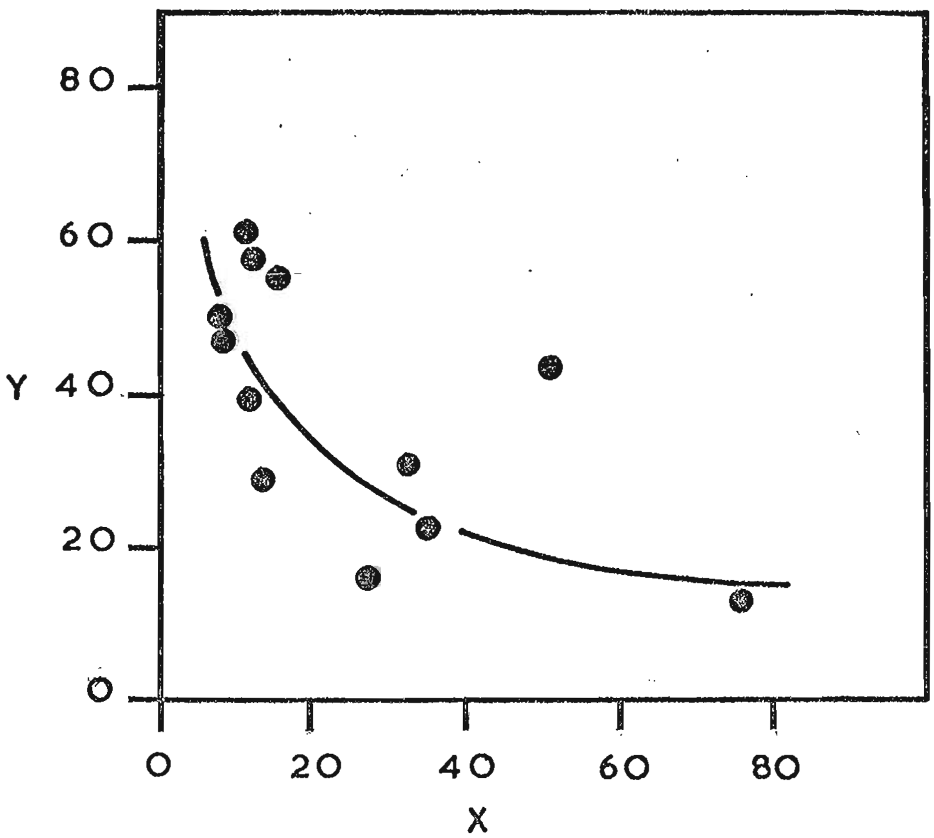
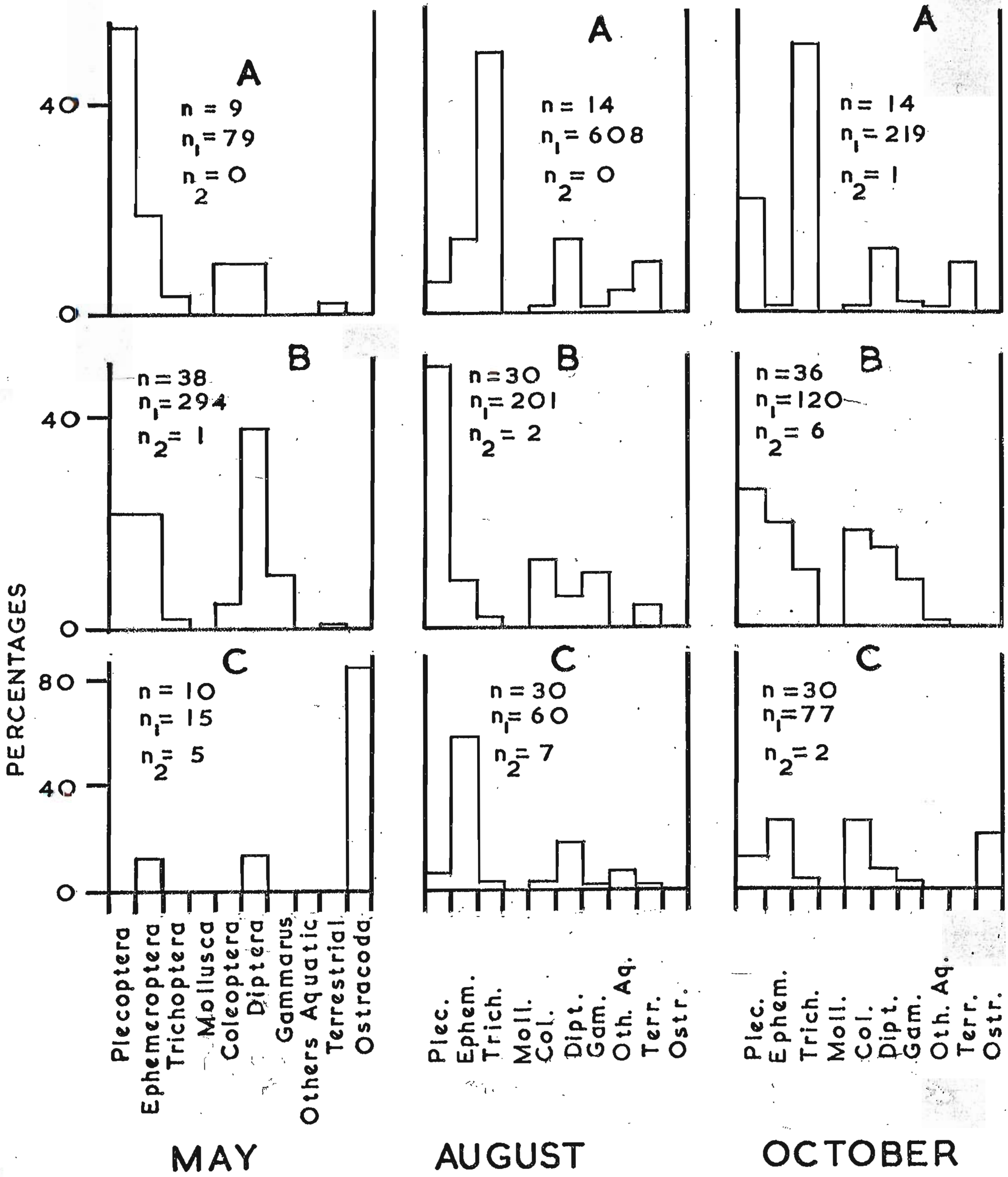

80
60
Y 40
20
0
0 20 40 60 80
X

FIG. 5


PERCENTAGES
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n2 = 0
A
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n1 = 608
n2 = 0
A
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n1 = 219
n2 = 1
B
n = 38
n1 = 294
n2 = 1
B
n = 30
n1 = 201
n2 = 2
B
n = 36
n1 = 120
n2 = 6
C
n = 10
n1 = 15
n2 = 5
C
n = 30
n1 = 60
n2 = 7
C
n = 30
n1 = 77
n2 = 2
0
40
80
Plecoptera
Ephemeroptera
Trichoptera
Mollusca
Coleoptera
Diptera
Gammarus
Others Aquatic
Terrestrial
Ostracoda
Plec.
Ephem.
Trich.
Moll.
Col.
Dipt.
Gam.
Oth. Aq.
Terr.
Ostr.
MAY
AUGUST
OCTOBER

FIG.6

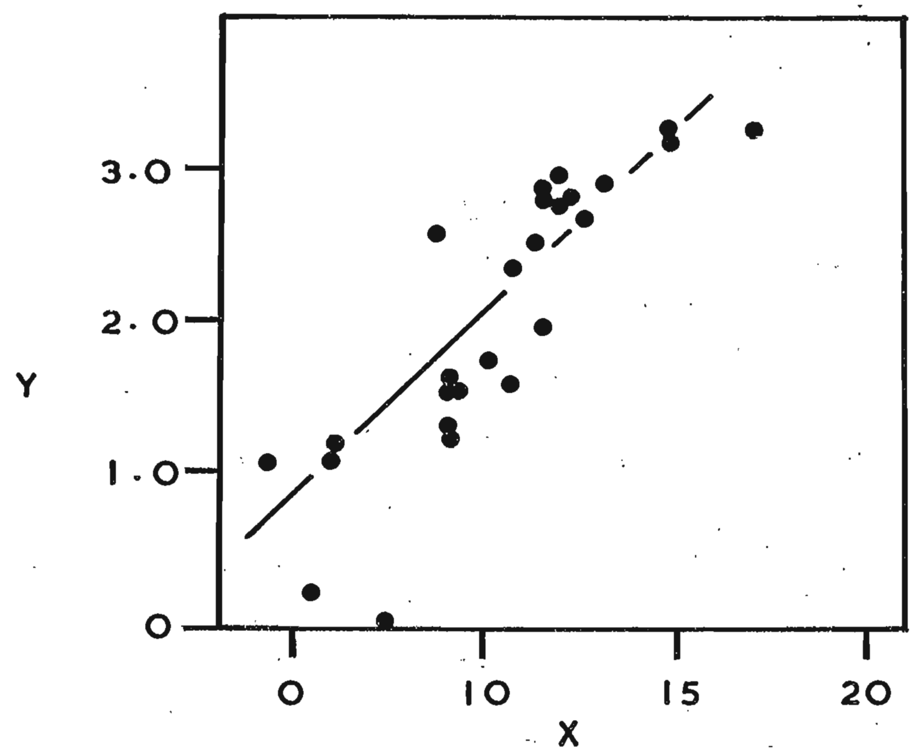


FIG.7

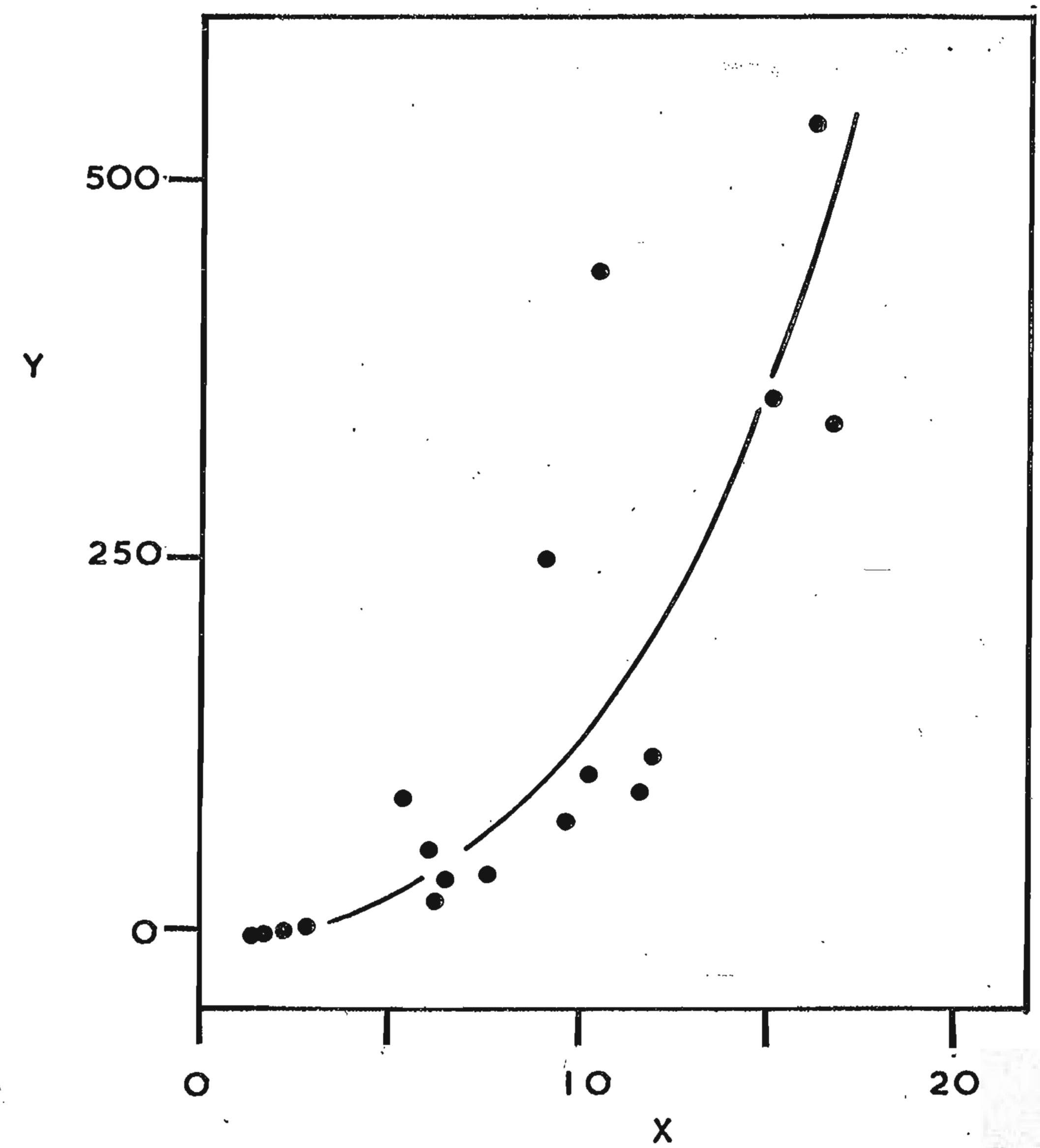
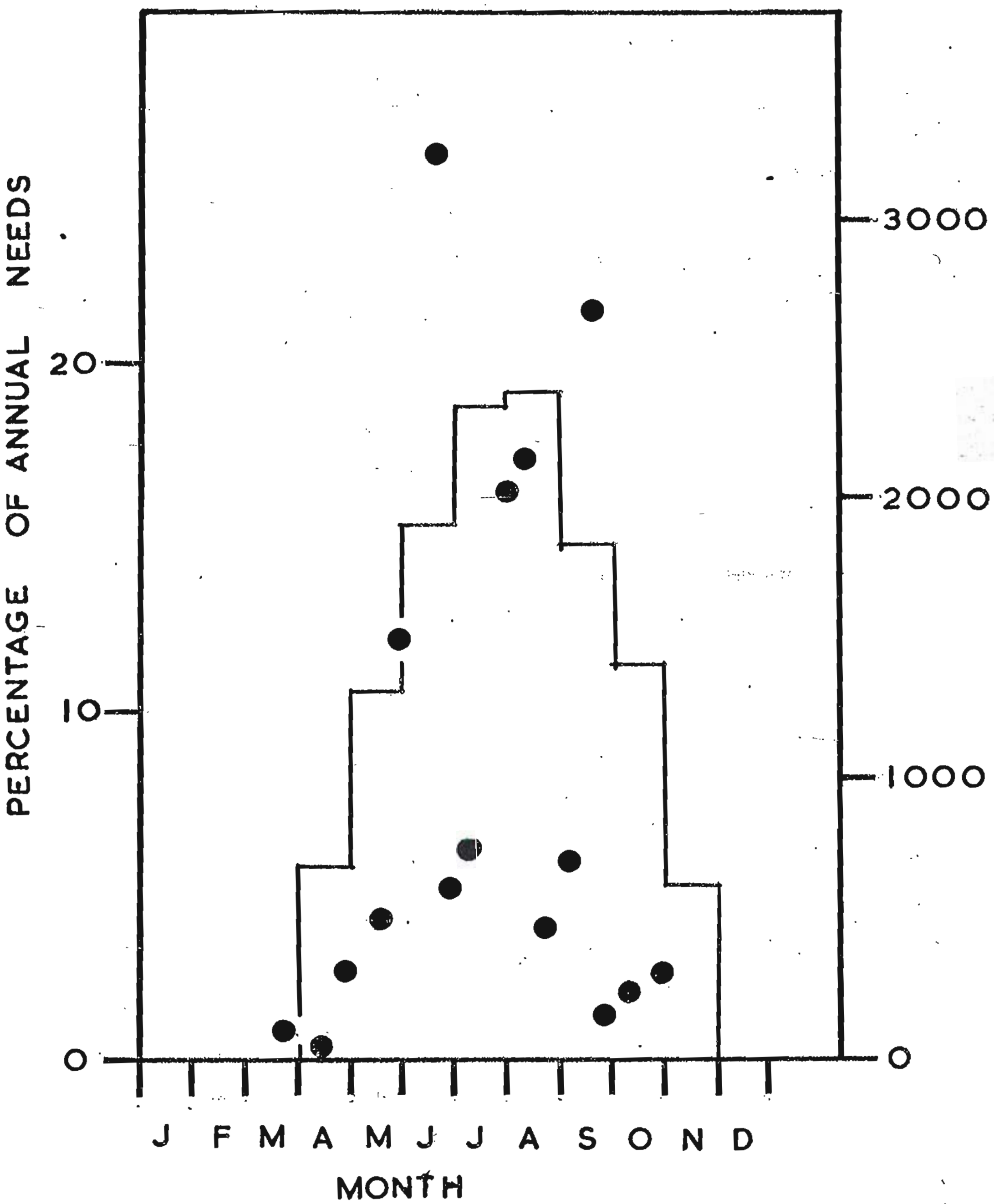


FIG. 8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10
0
3000
2000
1000
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NUMBER OF FLIES
J F M A M J J A S O N D
MONTH