Studies on the ecological energetics of damselfly larvae (Odonata: Zygoptera)

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Chapter 9

THE ENERGY ASSIMILATED (A)

Assimilated energy was defined as that part of the food energy absorbed from the alimentary canal (see appendix 1).

Thus:- $A = C - F$

A great deal of information on assimilation in aquatic organisms suitable for use in an energetics study is now accumulating. Conover (1964) summarised the information on planktonic crustacea but, with the possible exception of the fisheries literature on assimilation reviewed by Ricker (1946), no pattern or accurate predictive theory has yet emerged. The wide variability in the results obtained by different workers on the same or similar species (e.g. Conover 1964) has added to this difficulty and measurements of assimilation must still be made by any investigator wishing to construct energy budgets for any given species.

In the present study, as many variables as possible likely to affect assimilation were investigated. These were:-

a) Prey type

b) Feeding rate

c) Larval size

d) Temperature

e) Final instar diapause and metamorphosis.

9.1 METHODS

9.1a General

The basis of the method used to measure assimilation lay in being

able to estimate the dry weight of food eaten by Pyrrhosoma in a given time and in measuring the dry weight of faeces produced from this food; percentage assimilation on a dry weight basis or in terms of calories (using data presented in chapter 3) could then be calculated according to the formula:-

$$\text{Percentage assimilation} = \frac{C - F}{C} \times 100$$

where C and F are expressed as dry weights or calories food eaten (C) and faeces produced (F).

9.1b The Prey Types Utilised

Four prey types, representative of the range of species taken by Pyrrhosoma in the field were used. These were:-

Chironomid larvae of an unidentified species obtained from mud dredged from the River Wear, Durham City. Chironomids formed about 75 percent by dry weight of the food eaten in the field (see chapter 8). These were used in feeding rate experiments only (see below).

Daphnia obtusa obtained from laboratory cultures maintained on yeast and dried milk. Daphnia were typical of the entomostracan prey taken in the field. Because chironomid larvae could not be obtained in large quantities, Daphnia were utilised in the experiments on the effects of feeding rate, temperature, larval size, diapause and metamorphosis on assimilation.

Cleon dipterum larvae (Ephemeroptera: Baetidae) collected from the study area. Cloeon was regarded as typical of the wide range of larger

none dipterous insect larvae captured in the field.

Asellus aquaticus (Isopoda) collected from the study area where they were extremely common but rarely taken by Pyrrhosoma (see chapter 8). Assimilation with Asellus prey was examined to see if the absence of Asellus in the diet of Pyrrhosoma was in any way correlated with poor utilisation (low percentage assimilation) in Pyrrhosoma.

Estimation of the Dry Weights of Food Consumed from Measurements of Living Prey

The relationship between wet weight and dry weight was obtained for chironomid larvae and the relationship between length and dry weight for the other prey species. Thus estimates of the dry weight of food presented to and eaten by Pyrrhosoma could be made from measurements of living prey. All dry weights on which figures 14 to 16 are based were made on a Cahn Electrobalance (model M-10) with material dried in a vacuum oven at 60°C on preweighed foil trays.

Daphnia obtusa

Individuals were classed as either non-reproductive (empty brood pouches) or as reproductive (eggs or young in the brood pouch). Lengths were measured with a micrometer eye-piece from the top of the head to the base of the tail spine. Figure 14 shows the graph of length (mm) against individual dry weight (mg) from which regressions were calculated for the three categories:-

i) Non-reproductive < 1.0 mm long

$$y = 0.0184x - 0.0102$$

ii) Non-reproductive > 1.0 mm long

$$y = 0.0447x - 0.0370$$

iii) Reproductive (always > 1.0 mm long)

$$y = 0.0961x - 0.1090$$

Where x = length of *Daphnia* in mm

y = dry weight per individual (mg)

Chironomid Larvae

Freshly collected larvae were washed and dried with filter paper to remove excess surface moisture before wet weights were measured on a Mettler balance (model H-16) or the Cahn Electrobalance. The relationship between wet weight (mg) and dry weight (mg) is shown in figure 15a. Two regressions were calculated:-

i) For Chironomids < 4.0 mg Wet Weight

$$y = 0.146x + 0.059$$

ii) For Chironomids > 4.0 mg Wet Weight

$$y = 0.293x + 0.541$$

where x = wet weight (mg)

y = dry weight (mg)

Cloeon dipterum

Freshly collected larvae were measured from the front edge of the head to the tip of the last abdominal segment by means of a micrometer eye-piece. The relationship between length (mm) and dry weight (mg) on a log: log scale is shown in figure 16. For the purpose of calculating the regression, dry weights were multiplied by 100 to eliminate negative logs. The regression obtained was:-

$$y = 2.897x - 0.344$$

where y = log (dry weight x 100) (mg)

x = log length (mm)

Asellus aquaticus

Lengths were measured (either with a micrometer eye-piece or with callipers) from the front of the head at the base of the antennae to the mid point at the end of the abdomen. No distinction was made between the sexes or between reproductive and non-reproductive stages. Figure 16 shows the relationship between length (mm) and dry weight (mg) on a log: log scale. The regression obtained was:-

$$y = 2.698x + 0.176$$

where y = log (dry weight x 100) (mg)

x = log length (mm)

9.1c The Correlation of Food Eaten with Faeces Produced: "Marker" Foods

In pilot experiments a marker food (Phillipson 1960a, b) was employed. Daphnia placed in a suspension of carmine or chlorazol black E (B.D.H. Standard Stain) rapidly filled their guts with red or black particles. Pyrrhosoma larvae fed with these "marker" Daphnia produced either bright red or dark, black faeces which were quite distinct from the normal brown pellets. The "marker" Daphnia were fed, followed by normal prey. The experiment was terminated by a final feeding of "marker" Daphnia. The food eaten between the two "marker" feeds and the normal brown faeces produced between the coloured faeces were used to give an estimate of percentage assimilation with the normal Daphnia.

In all later experiments "marker" prey were not used. A period of 24 to 48 hours was allowed to elapse so that guts were cleared of all food. Larvae were then fed for several days and the faeces collected daily. Following this, larvae were starved for a further 1-2 days to ensure that the guts were again empty and the remaining faeces produced added to those previously collected. All the faeces produced by a known quantity of food were therefore obtained and percentage assimilation could be calculated.

Comparison of the two methods showed that the results obtained were virtually identical (see table 32).

9.1d Details of Experimental Procedure

Larvae were placed individually in small containers with dechlorinated tap water and a small twig on which they could cling. Though no experiments were continued for longer than one week, larvae kept like this for several months moulted through a number of instars and emerged without suffering any ill effects.

All experiments, except those concerned with temperature effects, were carried out at 15°C ± 0.5°C. A light regime (controlled by a time clock) that was as close as possible to the natural photoperiod at the time of the experiment was maintained. The experiments to investigate temperature effects were carried out at 4°C ± 0.1°C and at 10°C ± 0.1°C. Freshly collected larvae were allowed to acclimatise to the experimental temperature for 24 to 48 hours before each set of measurements.

Following the initial period of starvation (see 9.1c) and acclimatisation, fresh prey were added and uneaten food and faeces removed every day. The following procedure was adopted with each prey type.

Daphnia

Daphnia of uniform size were obtained by passing them through graded sieves. 50 individuals from each "uniform" batch were measured and the number of reproductive and non-reproductive individuals counted. A known number of Daphnia from the batch were then fed to each Pyrrhosoma and the average size and proportion of reproductive to non-reproductive individuals assumed to be the same as in the 50 measured initially.

Before adding fresh Daphnia, uneaten prey from the previous day was carefully collected and counted. The number, size and reproductive condition of Daphnia eaten by each larvae over the preceding 24 hours could be estimated and hence the dry weight of food (and ultimately calories).

Chironomids, Asellus and Cloeon

Chironomids were sorted into similar sized individuals by eye and wet weighed in groups. Asellus and Cloeon were measured individually. From these measurements, the dry weight and calories of food presented were calculated. Uneaten and partially eaten prey left from the previous day were collected and dried in a vacuum oven at 60°C on preweighed foil trays, material from each larva being kept separate. The dry weight of the uneaten food was used to correct the total weight of food presented to the weight actually eaten.

Faeces Collection

Faeces were collected every day, the pellets from each animal being grouped separately on preweighed foil trays and dried in a Vacuum oven at 60°C immediately after collection. Faeces dry weights were measured on the Cahn Balance at the end of the experiment.

9.1e Specimen Calculations

Example 1 Percentage assimilation on a dry weight basis: Daphnia as prey

Table 33 shows data obtained for one larva in a typical experiment with final instars at 15°C.

The dry weights of reproductive and non-reproductive Daphnia eaten, shown in column 5, were calculated as follows:-

Take day 1 as an example.

From regression equation section 9.1b.

Dry weight of a reproductive Daphnia of length 1.499 mm

= 0.0351 mg

Dry weight of a non-reproductive Daphnia of same length

= 0.0300 mg

On average, of the 21 Daphnia eaten on day 1, 30.77 percent were reproductive and 69.23 percent non-reproductive.

Therefore, the total dry weight of reproductive Daphnia eaten on day 1 is given by:-

$$\frac{0.0351 \times 21 \times 30.77}{100} = 0.227 \text{ mg}$$

and of non-reproductive Daphnia by:-

$$\frac{0.0300 \times 21 \times 69.23}{100} = 0.436 \text{ mg}$$

Therefore the total dry weight of Daphnia eaten on day 1 was

0.663 mg

Then

TOTAL DRY WEIGHT EATEN (C) = 3.708 mg

TOTAL FAECES PRODUCED (F) = 0.551 mg

TOTAL ASSIMILATION (C - F) = 3.157 mg

PERCENTAGE ASSIMILATION = $\frac{3.157}{3.708} \times 100 = 85.1$ percent

Example 2 Percentage assimilation on a dry weight basis: chironomids as prey

Table 34 shows data obtained for one larva in a typical experiment with final instars at 15°C

Then

TOTAL DRY WEIGHT EATEN (C) = (6.806 - 1.804) = 5.002 mg

TOTAL DRY WEIGHT FAECES (F) = 0.790 mg

PERCENTAGE ASSIMILATION = $\frac{(5.002 - 0.790)}{5.002} \times 100$

= 84.2 percent

Calculations in terms of calories were made by multiplying the dry weights of food eaten and faeces produced by the calorific values of food and faeces given in chapter 3. Percentage assimilation was then calculated in the usual way from the calories consumed and calories assimilated by each larva.

Experiment	Instar	Method	% assimilation on a dry weight basis
1	final	"marker" food	85.49
2	final		81.16
3	final	without "marker" food	85.10
4	final		83.33

Table 32 Comparison of the two methods of carrying out assimilation measurements using Daphnia as prey.

Day	Mean length of Daphnia (mm) 2	Percentage reproductive and non-reproductive in batch 3	Total number eaten in 24 hours 4	Calculated dry weight eaten (mg) a) reproductive b) non-reproductive 5	Total dry weight eaten (mg) reproductive and non-reproductive 6
1	1.499	R 30.77 NR 69.23	21	0.277 0.436	0.663
2	1.715	R 67.27 NR 32.73	13	0.488 0.169	0.657
3	1.596	R 42.31 NR 57.69	19	0.357 0.376	0.733
4	1.518	R 33.33 NR 66.67	20	0.246 0.412	0.658
5	1.580	R 29.41 NR 70.59	14	0.177 0.332	0.509
6	1.532	R 14.75 NR 85.25	15	0.085 0.403	0.488

a) TOTAL DRY WEIGHT OF DAPHNIA EATEN, days 1-6 (total of column 6)

C = 3.708 mg

b) TOTAL DRY WEIGHT OF FAECES PRODUCED from this food, (from direct weighting)

F = 0.551 mg

Table 33 Typical Daphnia assimilation experiment results.

Day	Number presented	Wet weights of Chironomids added each day (mg)	Calculated dry weights added (mg)
1	2	1.381 0.900	0.261 0.191
2	3	3.521 1.514 1.514	0.573 0.280 0.280
3	2	4.545 2.778	0.792 0.465
4	2	2.700 5.892	0.453 1.187
5	1	9.770	2.324

TOTAL DRY WEIGHT PRESENTED (total of column 4) days 1-5

= 6.806 mg

TOTAL DRY WEIGHT PRESENTED but not eaten (from direct weighing of uneaten food)

= 1.804 mg

TOTAL DRY WEIGHT OF FAECES PRODUCED from this food (from direct weighings)

F =0.790 mg

Table 34 Typical chironomid assimilation experiment results.

9.2 RESULTS

Calculations on a dry weight basis were sufficient to illustrate the effects of most variables on assimilation. The data were converted to calories only when this was necessary for subsequent energy budget calculations.

9.2a Assimilation on a Dry Weight Basis

i) The Effect of Feeding Rate on Assimilation

All experiments were carried out at 15°C with final instar larvae.

The mean dry weight eaten per larva per day over the experimental period, plotted against the calculated percentage assimilation for the four prey types is shown in figures 17 and 18 (Dotted lines show the 95 percent confidence limits.) With three prey species there was slight positive correlation between percentage assimilation and feeding rate and one negative correlation.

Daphnia	$r = +0.174$
Chironomids	$r = +0.293$
Asellus	$r = +0.543$
Cloeon	$r = -0.185$

It is clear that the effect of feeding rate is not great and can be effectively ignored.

ii) The Effect of Prey Type on Assimilation

All experiments were carried out at 15°C with final instar larvae.

Since feeding rate had such a small effect, a mean percentage assimilation figure was calculated for each of the prey types Cloeon, Asellus and Chironomids. A number of independent estimates of assimila-

tion were made for final instars with Daphnia as prey and a range of typical results is presented in table 35, together with the estimates for the other prey species.

From table 35, it is clear that prey type did influence percentage assimilation. The majority of Daphnia results were in the 84 - 86 percent region; chironomids were similar but assimilation with Cloeon was much higher (90.6 percent) and with Asellus much lower (76.9 percent).

Though variable between prey types, the high values for assimilation with the four foods tested is marked.

iii) The effect of Larval Size on Assimilation

All experiments were carried out at 15°C with Daphnia as prey

Figure 19b shows the mean percentage assimilation, ± 2 standard errors, in Pyrrhosoma larvae of different sizes; the regression was fitted by eye. A steady decline in percentage assimilation with increasing size is apparent, ranging from a mean of 92.9 percent in larvae of length 3.97 mm, to about 85 - 86 percent in final instars (13 - 14 mm long).

Using the methods described in section 8.1d, it was impossible to measure assimilation in larvae below a length of about 3.5 mm: attempts were made with animals smaller than this, but handling both food and faeces was found to be impossible. The assimilation of small larvae was estimated by extrapolation (figure 19b) and suggests that instar 2 larvae (mean length 1.3 mm) assimilate about 95 percent of the prey which they consume. This is not an unreasonable figure in view of the nature of the prey taken by these small forms (chapter 8).

iv) The Effect of Temperature on Assimilation

Two sets of experiments were carried out with final instars and Daphnia as prey, one at 4°C ± 0.1°C and the other at 10°C ± 0.1°C. Table 36 shows the results.

The results at 10°C and 4°C lie well within the range of values found at 15°C shown in table 35 and show that temperature did not influence percentage assimilation in Pyrrhosoma.

v) The Effect of Diapause and Metamorphosis on Assimilation

All experiments were carried out at 15°C with Daphnia as prey.

a) Diapause

Monthly estimates of assimilation were made during the winter of 1967-68 and these are shown in table 37. Data are presented in chapter 13 indicating the nature and duration of the diapause stage in the final instar: from table 37 it is clear that there is no obvious change in results obtained through the winter and it is reasonable to conclude that assimilation is unaffected by diapause.

b) Metamorphosis

The stages of metamorphosis were described in chapter 2. Assimilation measurements were made on larvae prior to and just entering stage 2 metamorphosis until feeding stopped on entering stage 3. The results are presented in table 28 and do not differ from the range of values found for non-metamorphosing final instars given in table 35.

9.2b Assimilation in Terms of Calories

Measurements on a dry weight basis for final instars with Daphnia

Prey type	Mean % assimilation	1 S.E.	Number of larvae in sample (n)
Daphnia	87.2 maximum	0.24	16
	86.5	0.57	10
	86.3	0.30	10
	85.8	0.89	10
	85.5	0.74	10
	84.9	0.60	16
	84.3	0.70	19
	81.2 minimum	0.70	10
Chironomids	84.0	1.04	38
Asellus	76.9	1.40	19
Cloeon	90.6	0.51	18

Table 35 Percentage assimilation on a dry weight basis in final instar Pyrrhosoma larvae at 15°C with different prey types.

Temperature	Mean % assimilation	1 S.E.	Number of larvae in sample (n)
4°C	85.2	0.30	16
10°C	86.2	0.36	15

Table 36 The effect of temperature on assimilation (on a dry weight basis) in final instar Pyrrhosoma larvae with Daphnia as prey

as prey showed that percentage assimilation was unaffected by feeding rate, temperature, metamorphosis or diapause. Consequently, all "Daphnia" faeces produced by final instars were pooled and provided ample material from which to determine calorific values of "Daphnia" faeces produced by final instars.

"Chironomid", "Cloeon" and "Asellus" faeces were obtained by feeding final instars at 10°C. Feeding was continued until sufficient material for two calorific value determinations with each type was obtained. With 20 Pyrrhosoma larvae for each prey type, this took approximately two weeks. Clearly, to obtain sufficient faeces from larvae smaller than final instars would have involved such long periods of time and so many small larvae that it would very doubtful have repaid the labour involved in increased accuracy. Despite the fact that assimilation on a dry weight basis was known to increase with decreasing larval size, it was necessary to assume that all faeces had the same calorific value as final instar faeces.

Calorific values of food and faeces are presented in chapter 3, table 5 and 6.

Dry weight estimates suggested that only larval size and prey type influenced percentage assimilation in Pyrrhosoma. Data on the effects of prey type and larval size were therefore recalculated in terms of calories for use in subsequent energy budget calculations.

Table 39 shows the data presented in table 35 treated in this way. Only three typical Daphnia results were recalculated. All the results were slightly higher than when calculated on a dry weight basis but

Date of larval collection	Mean % assimilation measured over following week	1 S.E.	Number of larvae in sample (n)	Probable diapause condition
20/10/67	86.9	0.31	30	diapause
18/11/67	85.1	0.39	15	
12/12/67	87.2	0.24	16	
15/ 1/68	86.3	0.30	10	post diapause
27/ 2/68	87.2	0.31	15	

Table 37 The effect of diapause on percentage assimilation of Daphnia by final instar Pyrrhosoma at 15°C. (Calculated on a dry weight basis.)

Experiment	Mean % assimilation	1 S.E.	n	Metamorphosis condition
1	85.0	0.45	17	immediately prior to and very early stage 2.
2	86.5	0.60	11	stage 2 until feeding stopped in stage 3

Table 38 The effect of metamorphosis on percentage assimilation of Daphnia by final instar Pyrrhosoma at 15°C Calculated on a dry weight basis.)

Prey type	% mean assimilation in terms of calories	1 S.E.	Number of larvae in sample	% mean assimilation in terms of dry weight
Daphnia	86.8	0.70	10	85.5
Daphnia	87.7	0.44	10	86.5
Daphnia	86.2	0.55	16	84.9
Chironomids	86.8	0.86	38	84.0
Cloeon	91.3	0.46	18	90.6
Asellus	82.8	1.05	19	76.9

Table 39 Assimilation in terms of calories in final instar Pyrrhosoma at 15°C.

their relative order remains the same.

Figure 19a shows the results of the effects of larval size on percentage assimilation from figure 19b recalculated in terms of calories. The same decline in assimilation with increasing larval size is apparent. The regression was fitted by eye and extrapolated back for larvae below 3.5 mm.

9.3 APPLICATION OF ASSIMILATION DATA TO THE FIELD

Although Pyrrhosoma took a wide range of prey types in the field, chironomids (including the Tanypodinae) formed at least 75 percent of the food eaten on a dry weight basis. Percentage assimilation of chironomid and Daphnia prey by Pyrrhosoma in the laboratory was virtually identical and although only two other prey types were tested (Cloeon and Asellus), percentage assimilation was higher with the former and

lower with the latter than with Daphnia. This suggests that assimilation with these types of prey may approximate to the values found for Daphnia and chironomids.

In view of these points, percentage assimilation estimates were applied to the field population by reading the appropriate values for larvae of different sizes directly from figures 19a, which relates larval length to percentage assimilation in terms of calories using Daphnia as prey. Since the maximum and minimum values for percentage assimilation with different prey types (measured in terms of calories with final instars) differed by only 8.5 percent (91.3 percent - 82.9 percent), the maximum error likely to arise from the use of Daphnia data alone was probably small.

Faeces produced by larvae after collection but before being fed in the laboratory were collected and dried exactly as described for laboratory faeces. However, the calorific value of these field faeces was only 2,794 cal per g. in contrast to 4,500 - 5,000 cal. per g. found for laboratory faeces produced by larvae fed on typical prey (e.g. Daphnia, chironomids and Cloeon) (see table 5, chapter 3). The value for field faeces was close to that for laboratory "Asellus" faeces (2,565 cal. per g.) although Asellus was rarely taken as prey.

The most likely explanation for the discrepancy can probably be found in the suggestion in chapter 8 that, unlike laboratory larvae in clean experimental containers, larvae in the field accidentally consumed quite large quantities of detritus. This lowered the calorific value and raised the ash content of field faeces.

9.4 DISCUSSION

Assimilation has been measured by a number of workers using methods similar to those in the present study. Dry weights of food and faeces have been measured by Corner (1961) (Calanus), Gerking (1955) (Lepomis), Hubbel et al. (1965)(Armadillidium) and Phillipson (1960a, b) (Mitopus). Calorific values of food and faeces, together with dry weights, were used by Brocksen et al. (1968) (Acroneuria, Cottus and Salmo), (Davies (1963, 1964) (Carassius) and Paine (1965) (Navanax).

The possible errors inherent in the methods used in the present study are as follows:-

i) Overestimation of consumption: percentage assimilation too high

a) Appreciable weight loss by the food item during the experiment would tend to overestimate consumption. However, weight change by starved Daphnia pulex over the first 24 hours was negligible (Richman 1958) and data shown in figure 15b suggests that there was no measureable weight loss over 24 hours in chironomids.

b) During prey capture, some loss of body fluid is inevitable (see Conover 1966a). However, during the capture of Chironomus sp., the loss of red body fluid was readily observed and after initial capture careful manipulation of the prey by Pyrrhosoma reduced fluid loss to a minimum. Small prey items like Daphnia were consumed whole with great rapidity and body fluid loss was probably minimal.

ii) Underestimation of faeces production: percentage assimilation too high

a) Soluble unassimilated material could be released by some aquatic invertebrates (Johannes and Satomi 1967) so that collecting only solid

faeces will overestimate assimilation efficiency. In Odonata, tests for non-nitrogenous compounds do not appear to have been made, the only reported soluble release products being excretory ammonia and small quantities of uric acid (Staddon 1959). The release of significant quantities of soluble, non-nitrogenous faecal material was a possible, though improbable source of error.

b) Failure to collect all the solid faeces is a major source of error in experiments with small crustacea (Conover 1964). None of the large readily observed faeces produced by Pyrrhosoma were left uncollected.

c) Bacterial action may cause significant changes to take place in the faeces composition within a short time of production (Johannes and Satomi 1966 Newell 1965). In the present study all faeces produced were collected within 24 hours and bacterial action was therefore reduced to a minimum.

iii) Overestimation of faeces production: percentage assimilation too low

a) Faeces obviously contain material other than that derived from the food. In aquatic invertebrates, solid excretory products can probably be ignored; but intestinal secretions and, perhaps by weight the most significant contribution, peritrophic membrane may be present in sufficient quantities to influence the results. Since starving Pyrrhosoma continued to produce transparent faeces made up almost entirely of peritrophic membrane, its production appeared to be relatively independent of food consumption. Therefore, the lowest estimates for assimilation might be expected at low feeding rates where the contribution of material derived from the gut to the faeces is probably proportionally greater. The

slight positive correlation between percentage assimilation and feeding rate noted with three prey species could perhaps be explained in this way, but the effect is so small that it can be effectively ignored.

Most of these errors tend to overestimate assimilation efficiency but, for the reasons stated, the total error is probably small.

A larger number of alternative techniques are available for measuring assimilation, each with different sources and magnitudes of error and these are probably the cause of some of the variation in reported results (see Conover 1964). Comparison with other work is made more difficult by the use of different parameters in making the measurements (e.g. dry weight, calories or organic carbon). However, percentage assimilation in fish computed from either dry weight, calorific value or protein nitrogen data is very similar (Winberg 1956), as were the calorific value and dry weight estimates in the present study. (Clearly the two methods will not give identical results unless the calorific values of food and faeces are identical.) On the assumption that the percentage assimilation results obtained by different methods do not vary markedly, the following comparisons were made.

Table 40 shows percentage assimilation values for invertebrate carnivores and table 41 those for vertebrate carnivores (mainly fish). Most of the results are very similar or slightly higher than those obtained for Pyrrhosoma. It should be pointed out, however, that the two basic methods employed in making these estimates (quantitative measurements of consumption and faeces production, or radiotracer techniques) are both prone to overestimate the actual value of assimilation, the former

for reasons already given, the latter owing to exchange of labelled food compounds with unlabelled compounds in the gut wall (Johannes and Satomi 1967). The magnitude of the possible errors involved is not known with certainty, though in the present study it was probably small. With this qualification, however, percentage assimilation in carnivores seems to be high, nearly always above 70 percent and mostly between 80 percent and 90 percent so that the high value for percentage assimilation in Pyrrhosoma was clearly typical of many other carnivore species.

It is therefore unfortunate that the only other data on percentage assimilation in zygopteran larvae (those of Fischer 1966, 1967a for Lestes sponsa) are much lower than any of the other carnivore species shown in tables 40 and 41. Assimilation in Lestes was estimated by Fischer from the difference between consumption and respiration plus growth. Larvae were maintained at 20°C in the laboratory and completed development in approximately 40 days: prey consisted of Daphnia magna for the first month, after which they were given Tubifex tubifex. Not only are the results obtained at variance with most other carnivore data, but they do not agree in the two papers. Fischer (1966) indicated that percentage assimilation increased with increasing larval size, being very low for the first two weeks (about 20 percent) rising to 30 percent for the majority of larval life. Fischer (1967a) suggested that small larvae have a higher assimilation efficiency (45 - 50 percent), but that this falls to between 30 percent and 40 percent in larger larvae. Both papers agree in reporting a sudden increase in assimilation to over 80 percent for about five days prior to metamorphosis followed by a decline

Species	Group	Mean percentage assimilation	Units	How measured and prey type	Author
Acroneuria pacifica and A. californica (larvae)	Plecoptera	82.8	calories	quantitative estimates of food eaten and faeces produced: fed aquatic midge larvae	Brocksen et al. (1968)
Melanotus rufipes (larvae)	Coleoptera	90.3	calories	Ditto: fed soft bodied dipterous larvae	R. Dutton pers. comm (1968)
Mitopus morio final instar small instars	Phalangida	40-50 74	dry weight	Ditto: fed a variety of insect prey	Phillipson (1960a, b)
Navanax inermis	Mollusca opistho-branchiata	62	calories	Ditto: fed Haminoea virescens	Paine (1965)
Euphausia pacifica	Crustacea	84	organic carbon	C_{14} radiotracer technique: fed Artemia nauplii	Lasker (1966)
Stalia major	Nabidae	83	dry weight	calculated from gross growth efficiency and % utilisation of assimilation energy for P+R: fed Coleoptera larvae	Pewkes (1960)
Lestes sponsa	Odonata Zygoptera	mainly 20-40	calories	calculated from C and R+P (see text)	Fischer (1966, 1967a)

Table 40 Percentage assimilation in other invertebrate carnivores.

Species	Percentage assimilation	Units	How measured and prey type	Author
Abramis brama Bream	75-80	organic carbon	C_{14} radiotracers fed Bosmina	Sorokin and Panov (1966)
Carassius auratus Goldfish	maximum 92-94 minimum 60-70	calories	quantitative estimates of food eaten and faeces produced fed Enchytraeus albidus	Davies (1963, 1964)
Cottus perplexus Sculpin	81.9	calories	Ditto fed "herbivorous midge larvae"	Brocksen et al. (1968)
Salmo clarki Trout	85.5			
Lepomis Blue gill sunfish	97 94.4	protein N. dry weight	Ditto	Gerking (1955)
Mirror carp	89	calories	-	Ivlev (1939b)
General fish carnivores	76-96 mean 85	dry weight and calories	-	Winberg (1956)
General fish carnivores	80-90	dry weight and calories	-	Ricker (1946)
Oryzomys Rice Rat	88-95	calories	quantitative estimates of food eaten and faeces produced: fed eggs and young of marsh wren	Sharp (1967)
Parus sp. Tits	67-82	calories	Ditto fed seeds, mealworms and mixed insects	Gibb (1957)
Parus major Great Tit	82.2-86.6	calories	Ditto: fed mealworms only	C. Lachlan (1968) pers. comm

Table 41 Percentage assimilation in vertebrate carnivores.

to a very low level again before emergence.

Because of the confliction data on Lestes, the influence of larval size cannot be compared with the Pyrrhosoma data. However, the generally low value of the Lestes results and the marked influence of metamorphosis were quite different to the situation observed in the present study. How much of this difference can be attributed to the very different methods employed cannot be evaluated but in view of the contrasting life histories of Pyrrhosoma and Lestes, the low percentage assimilation reported for Lestes is surprising; indeed, it would appear to be a considerable disadvantage in a life history where very rapid development is essential (see chapter 7 , section 7.3).

The influence of feeding rate on assimilation is interesting and obviously of importance in any attempt to apply laboratory measurements of assimilation to the field. Three possible responses were recognised in the present study.

In a type A response, percentage assimilation remains constant over a wide range of feeding rates. Pyrrhosoma appears to be in this category which includes several other examples e.g. Conover (1964) for many Crustacea and Conover (1966b) for Calanus; Ivlev (1939b) for Mirror carp and Gerking (1955) the sunfish (Lepomis).

In a type B response percentage assimilation decreases with increasing feeding rate. Many fish appear to show this type of response e.g. Brown (1946), Dawes (1930, 1931), Karzinkin (1935) (in Ricker 1945) and Kinne (1960). Ursin (1967) regarded this as theoretically "typical" of fish. Several invertebrates also show a type B response e.g.

Daphnia spp. (Richman 1958, Monakov and Sorokin 1961, Schindler 1968), Artemia (Sushchenya 1962) and Armadillidium (Hubbel et al. 1965). A type B response may be partially explained by "over feeding" at high food levels, causing defecation before digestion is complete (Barrington 1957).

In a type C response, percentage assimilation increases with increasing feeding rate. This response is rare and has only been reported by Davies (1963, 1964) for Carassius, where it is suggested that low food intake provided only sub-optimal stimulation of the digestive tract. It is possible that a type C response was shown by Navanax (Paine 1965) though this is not considered by the author.

Only with a type A response can laboratory estimates of assimilation be applied to the field without prior knowledge of field feeding rates, so that the presence of a type A response in Pyrrhosoma was fortunate.

Few studies take into account the influence of size or developmental stage on assimilation. In Pyrrhosoma, assimilation efficiency decreased with increasing size, a situation similar to that shown by Phillipson (1960a, b) in Mitopus; Schindler (1968) in Daphnia magna and Qasrawi (1966) in the grasshopper Chorthippus. The conflicting results reported by Fischer (1966 and 1967a) have been noted. Wiegert (1964) reported an increasing assimilation efficiency with increasing size in Philaenus, whilst Sorokin and Panov (1966) showed that assimilation was unaffected by size in Bream. Clearly, all types of response are possible. The results obtained for Mitopus and Pyrrhosoma may eventually be shown to be typical of carnivores where softer bodied, more easily digested prey

are taken by the smaller individuals.

Temperature might be expected to influence percentage assimilation in a poikilotherm, though because temperature also influences feeding rate, which can itself affect percentage assimilation, the response need not necessarily be simple. In both Pyrrhosoma and Calanus (Conover 1966b) percentage assimilation was unaffected by temperature and was also unaffected by feeding rate. In Daphnia magna increasing temperatures lead to increased assimilation efficiency, despite the fact that percentage assimilation was lower at higher feeding rates: this was probably due to the fact that feeding rate itself did not increase with temperature (Schindler 1968). Percentage assimilation has been shown to be affected by temperature in four species of fish, increasing with temperature in two (Arnoldi and Fortunatova 1937 and Karzinkin 1935, both in Ricker 1946) and decreasing with temperature in one (Davies 1964). In the Cichlid, percentage assimilation first increased with rising temperatures between 20 and 28°C and then fell between 28 and 36°C (Warren and Davis 1967). In view of the complex interaction possible between temperature, feeding rate and assimilation, it is clear that great care must be exercised in any assimilation study to elucidate the nature of these interactions.

Conover (1966b) found a negative correlation between percentage ash content of various diatoms and percentage assimilation in Calanus. Schindler (1968) reported a strong increase in percentage assimilation of Daphnia magna with increasing calorific value of the food between 2,200 and 5,300 cals. per g., followed by a steady decline with foods

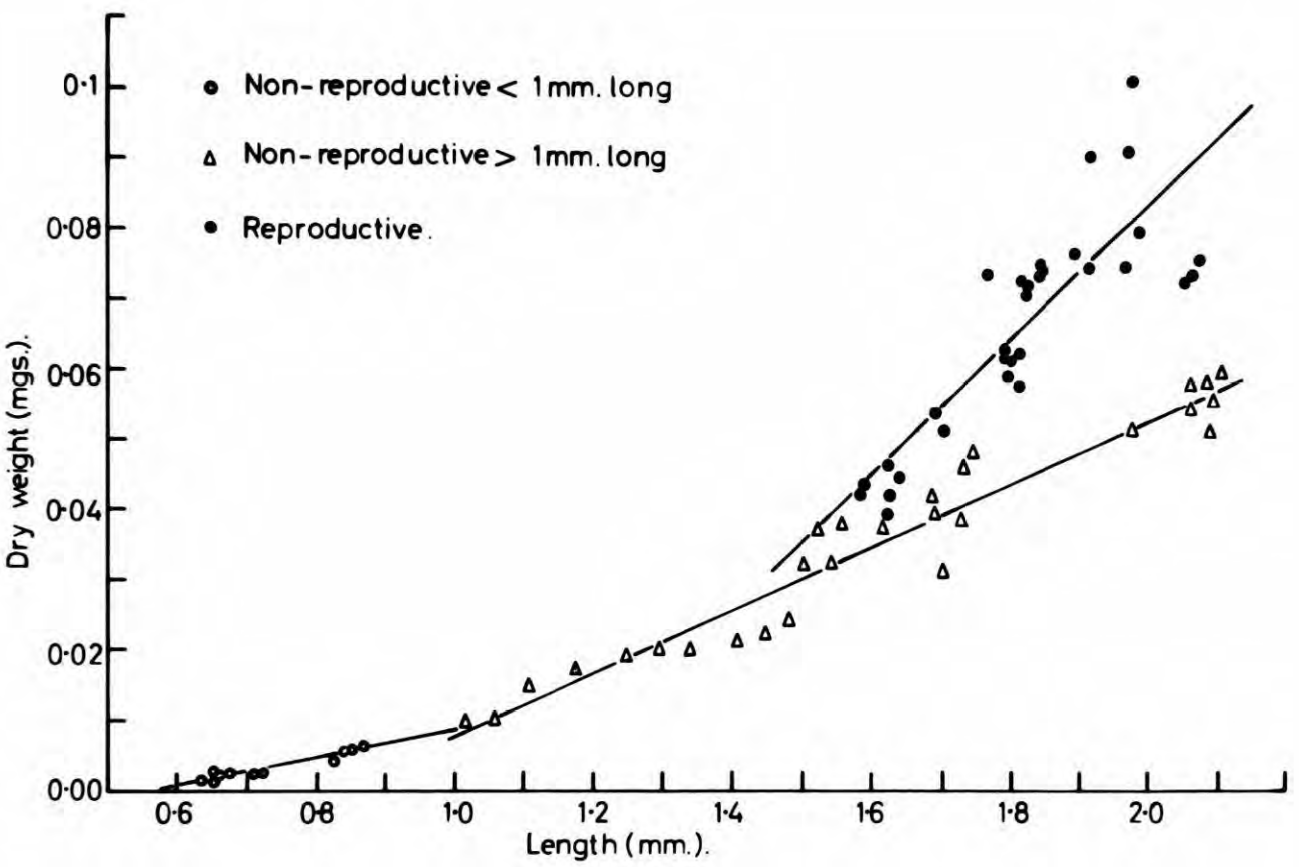
of calorific value between 5,300 and 7,300 cals. per g. In Pyrrhosoma, percentage assimilation was not obviously correlated with either the ash content or the calorific value of prey.

Few generalisations about percentage assimilation appear to be justified until more detailed information is available. Pyrrhosoma appears to be typical of most carnivores in showing a high assimilation efficiency; 80 percent and above being the rule rather than the exception. Nor does there appear to be any difference between vartebrates and invertebrates or homoiotherms and poikilotherms (see tables 40 and 41). This is interesting in view of the observation by Treherne (1967) that insects and mammals at least, rely on quite different processes for assimilation of food from the lumen of the gut. Ecologically, the differences are much less than the physiological or biochemical differences might suggest.

In this respect, carnivores are an exception to the comment by Engelmann (1966) that "poikilotherms are at most 30 percent efficient in digesting food, whereas most homiotherms are around 70 percent efficient". It is doubtful whether this remark is really applicable to herbivores either. Many herbivorous homoiotherms do appear to have a high assimilation efficiency (Connell 1959, Golley 1959, 1960), but many invertebrate herbivores and litter feeders appear to be equally high (e.g. Conover 1966b, Corner 1961, Hubbel et al. 1965, Schindler 1968). However invertebrate herbivores (including litter feeders) as a group include many species where percentage assimilation is much lower than in the great majority of invertebrate and vertebrate carni-

vores. Therefore, as far as assimilation efficiency is concerned, a more satisfactory ecological division than Engelmann's might be into carnivores and herbivores and to further subdivide the latter into a high percentage assimilation group (most vertebrates and some invertebrates) and a low percentage assimilation group (mainly invertebrates). This is still crude, since assimilation efficiency in many species is also influenced by feeding rate and temperature, which cannot yet be rationalised into a detailed scheme.

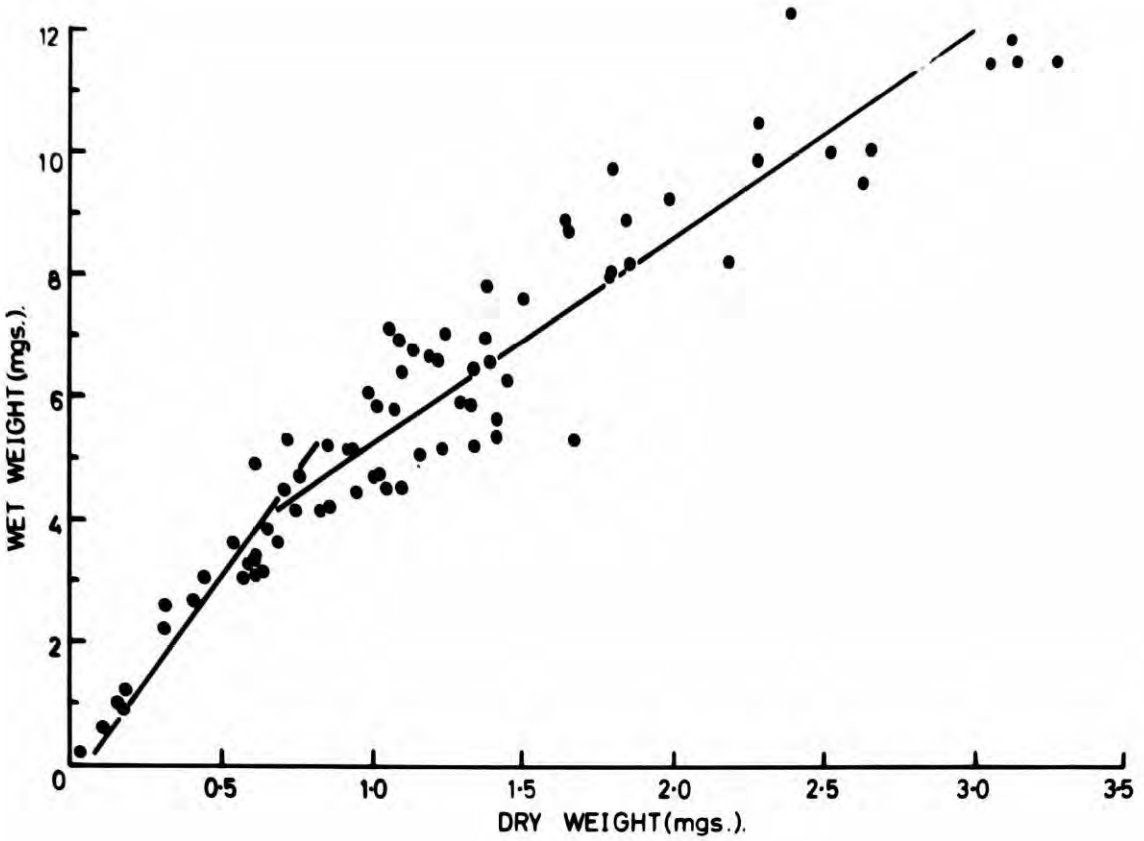
Fig. 14. Length: dry weight relationship in Daphnia obtusa, used in feeding and assimilation experiments with Pyrrhosoma. The calculated regressions are presented in section 9.1b.



Length: Dry weight relationships in Daphnia obtusa according to size and reproductive condition.

Fig. 15a. Dry weight: wet weight relationship in the chironomid larvae used in assimilation experiments with Pyrrhosoma. The calculated regressions are presented in section 9.1b.

Fig. 15b. Initial wet weight of individual chironomid larvae, plotted against their change in wet weight after 24h. in experimental containers without food, to show that there was no appreciable change in weight during this time.


WET WEIGHT (mgs.).
DRY WEIGHT (mgs.).
0
2
4
6
8
10
12
0·5
1·0
1·5
2·0
2·5
3·0
3·5

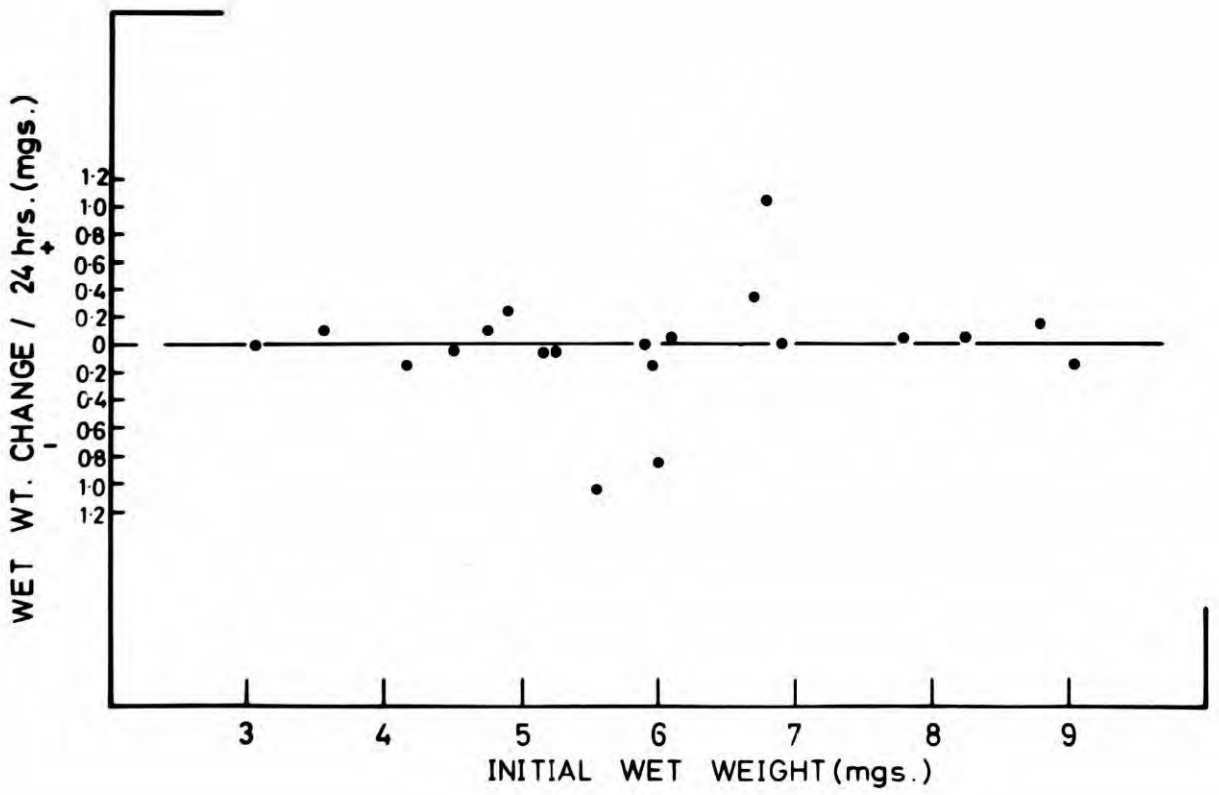

WET WT. CHANGE / 24 hrs. (mgs.)
1·2
1·0
0·8
0·6
0·4
0·2
0
0·2
0·4
0·6
0·8
1·0
1·2
3
4
5
6
7
8
9
INITIAL WET WEIGHT (mgs.)

Fig. 16. Length: dry weight relationships in *Asellus aquaticus* and *Cloeon dipterum* larvae, used in assimilation experiments with *Pyrrhosoma*. The calculated regressions are presented in section 9.1b.

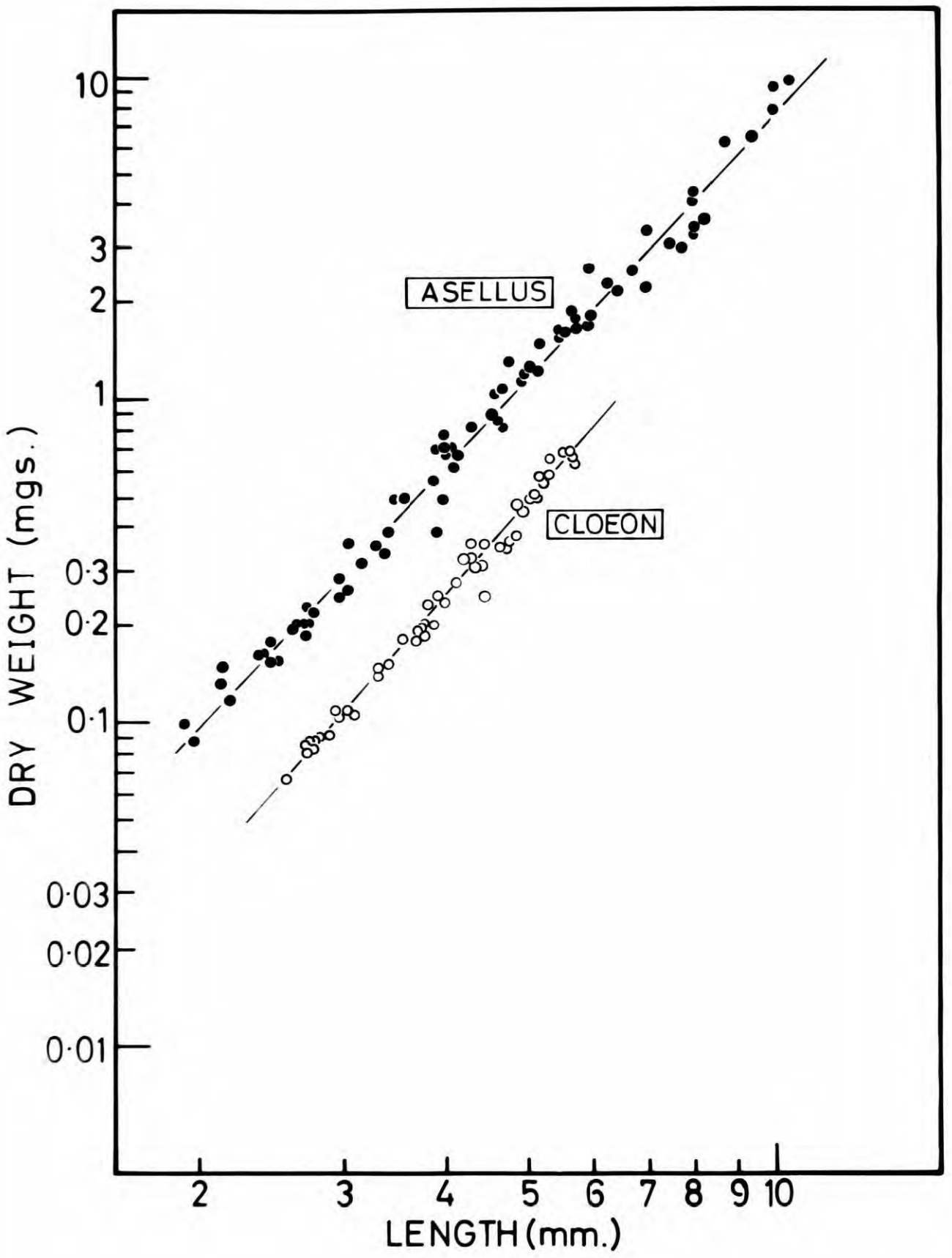
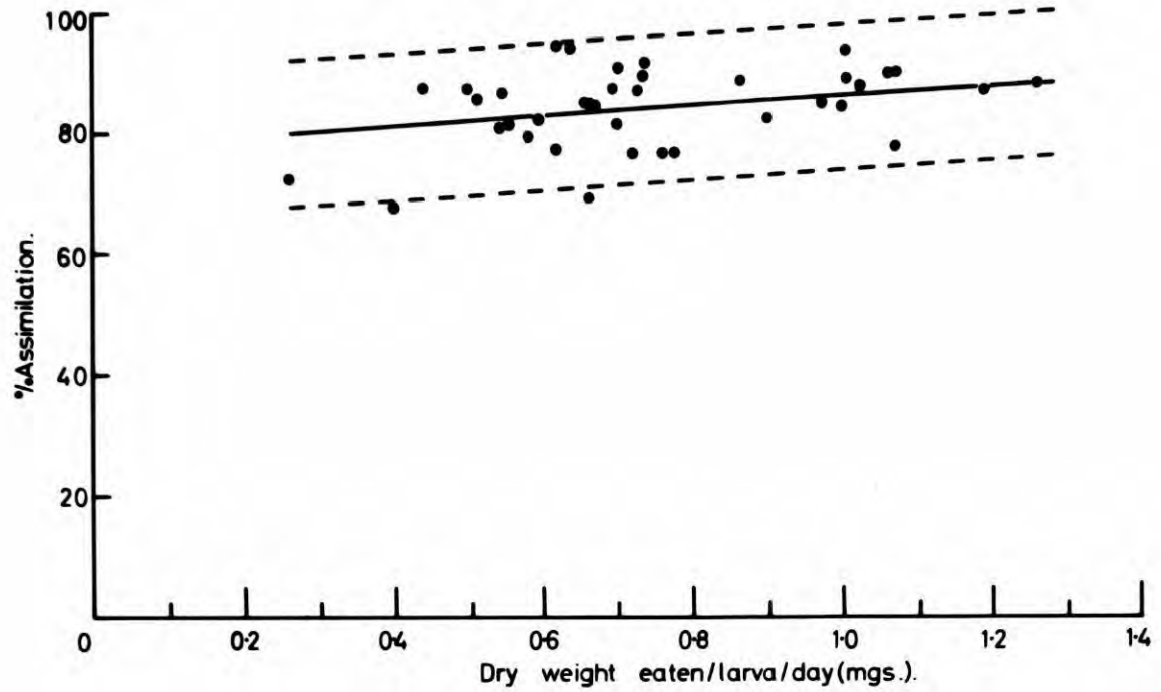

10
3
2
1
0·3
0·2
0·1
0·03
0·02
0·01
DRY WEIGHT (mgs.)
ASELLUS
CLOEON
2
3
4
5
6
7
8
9
10
LENGTH (mm.)

Fig. 17a. The effect of feeding rate on percentage assimilation in final instar Pyrrhosoma, with chironomid larvae as prey, calculated on a dry weight basis. The figure shows the calculated regression and 95 percent confidence limits.

Fig. 17b. The effect of feeding rate on percentage assimilation in final instar Pyrrhosoma, with Daphnia as prey, calculated on a dry weight basis. The figure shows the calculated regression and 95 percent confidence limits.


100
80
60
40
20
% Assimilation.
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
Dry weight eaten/larva/day (mgs.).

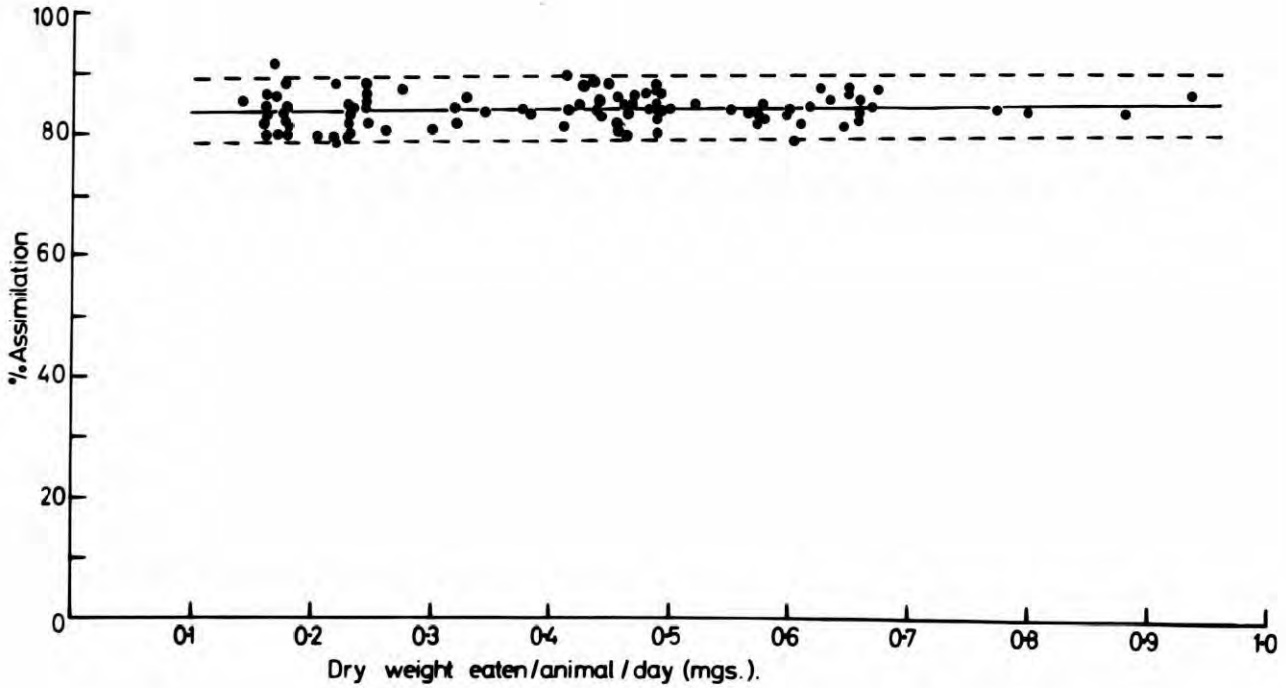

100
80
60
40
20
0
% Assimilation
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
Dry weight eaten/animal/day (mgs.).

Fig. 18a. The effect of feeding rate on percentage assimilation in final instar Pyrrhosoma, with Cloeon as prey, calculated on a dry weight basis. The figure shows the calculated regression and 95 percent confidence limits.

Fig. 18b. The effect of feeding rate on percentage assimilation in final instar Pyrrhosoma, with Asellus as prey, calculated on a dry weight basis. The figure shows the calculated regression and 95 percent confidence limits.

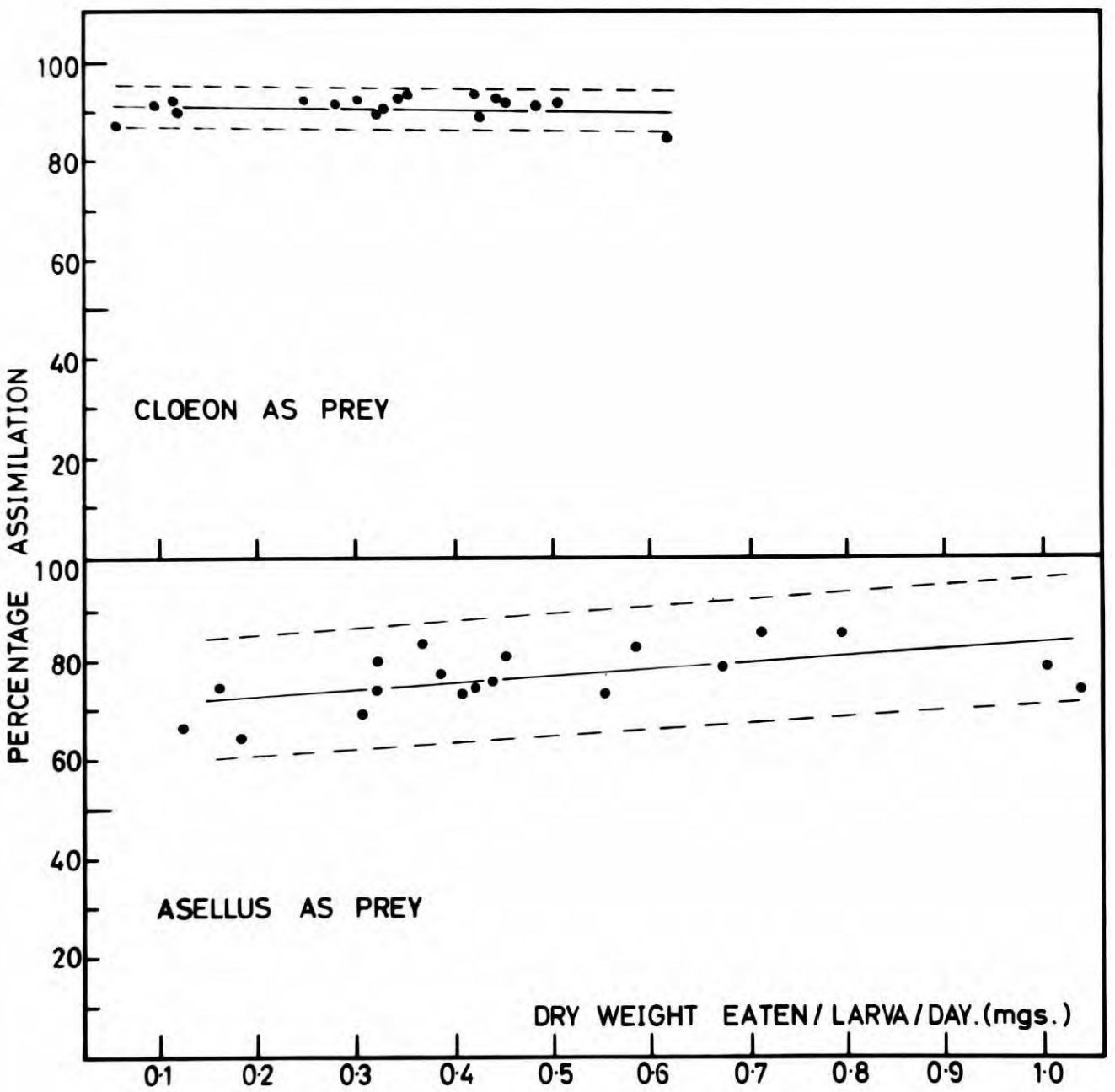
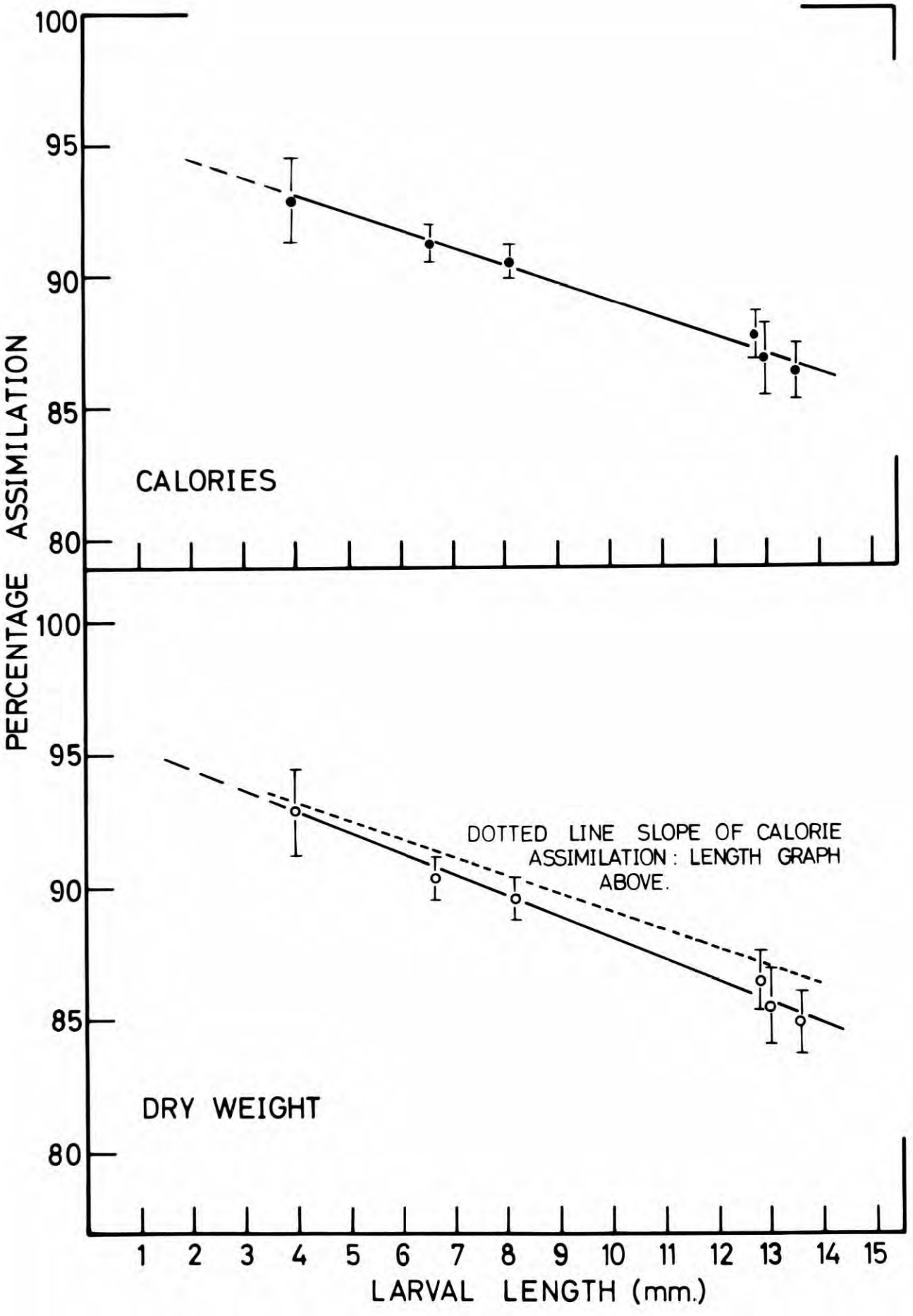

PERCENTAGE ASSIMILATION
100
80
60
40
20
CLOEON AS PREY
100
80
60
40
20
ASELLUS AS PREY
DRY WEIGHT EATEN / LARVA / DAY. (mgs.)
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0

Fig. 19a. The effect of larval size on percentage assimilation in Pyrrhosoma, calculated in terms of calories: vertical lines are ± 2 standard errors. (Daphnia as prey at 15°C) Regression drawn by eye.

Fig. 19b. The effect of larval size on percentage assimilation in Pyrrhosoma, calculated in terms of dry weight: vertical lines are ± 2 standard errors. (Daphnia as prey at 15°C). Regression drawn by eye.


PERCENTAGE ASSIMILATION
100
95
90
85
80
CALORIES
100
95
90
85
80
DOTTED LINE SLOPE OF CALORIE ASSIMILATION : LENGTH GRAPH ABOVE.
DRY WEIGHT
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
LARVAL LENGTH (mm.)

Chapter 10

RESPIRATION (R)

10.1 METABOLIC ACCLIMATISATION IN PYRRHOSOMA

10.1a Pilot Experiments on Metabolic Acclimatisation

The problem of respiratory acclimatisation to temperature in poikilotherms (see Bullock 1955, Prosser and Brown 1961, Teal 1959) presents greater methodological and theoretical difficulties than almost any other aspect of ecological energetics.

Before conducting detailed respirometory, experiments were carried out to determine whether or not Pyrrhosoma showed metabolic acclimatisation to temperature. Measurements were made in a Warburg Respirometer, following the standard procedure (Umbreit et al. 1964) for measuring oxygen uptake.

Seventy larvae, approximately one year old, were collected in July 1966 (when pond temperatures were approximately 15°C) and were divided into a control group of 30 larvae kept at 15°C ± 0.5°C and an experimental group of 40 kept at 5°C ± 0.1°C for a period of 10 days. During this time they were fed with excess Daphnia and experienced natural photoperiod. After 10 days all the larvae were run in the Warburg at 15°C with five similar sized individuals in each flask. Approximately one hour elapsed between removing the larvae from the 5°C and 15°C constant temperature rooms and running them at 15°C. The Warburg run was then continued for a further two hours.

Figure 20 shows the respiratory rates (µl per larva per hour) plotted against the mean wet weight (mg) for the larvae in each group.

If Pyrrhosoma had shown acclimatisation the respiratory rates of the larvae maintained at 5°C and run at 15°C should have been higher than larvae of the same size maintained and run at 15°C. It is obvious from figure 20 that this was not the case.

It was concluded that respiratory rate in Pyrrhosoma stabilised very rapidly after changes in temperature and that Pyrrhosoma either showed no metabolic acclimatisation or very rapid partial acclimatisation of the type discussed by Bullock (1955).

10.1b Treatment of Larvae Prior to Making Main Respiratory Measurements

Although the pilot experiments indicated that Pyrrhosoma showed a rapid stabilization in its respiratory rate after changes in temperature, all larvae were kept for 24 - 48 hours after collection at the temperature at which the respiration rate was to be measured. This was done for two reasons.

i) If Pyrrhosoma showed rapid rather than no acclimatisation, it was possible that this would proceed more slowly at lower metabolic rates per mg i.e. in larger larvae and at lower temperatures (K. Bowler pers. comm. 1967). A short period of exposure to the temperature at which measurements were to be made would ensure that all sizes of larvae were given the opportunity to acclimatise.

ii) Larvae taken from the field and quickly placed at laboratory temperatures higher than those at which collection was made, frequently showed signs of stress; activity increased, larvae took up positions at the water surface and even attempted to climb out of the container. These are all signs of stress arising from sudden reductions in oxygen

tension (Corbet 1962). However, they were always observed to disappear within a period of less than 24 hours. (Oxygen stress was not observed in the pilot experiments using the Warburg, presumably due to the small quantity of water in each flask (2 ml) and the large air-water interface.)

During the short "acclimatisation" period, larvae were placed in large tanks of water containing pond weed, leaves and twigs and were fed Daphnia. It is extremely unlikely that this affected the metabolic rate in any way other than to ensure that the larvae had become accustomed to the experimental temperature.

10.2 BASIC METHODS USED IN THE MAIN RESPIRATION MEASUREMENTS

Respiration rates were measured at 5, 10 and 16°C on most sizes of larvae using a Winkler technique. This could not be used for very small larvae and respiration rates in these were measured at 16°C with a Cartesian Diver apparatus.

10.2a The Cartesian Diver

Plate 4 shows the Cartesian Diver apparatus used to measure respiration rates of larvae from hatching up to instar 4 or 5. Zeuthen's stoppered Cartesian Divers were used, the methods followed being those of Zeuthen (1950) and Klekowski (see Klekowski 1967, Klekowski and Duncan 1967, Klekowski and Shushkina 1966a and 1966b). Details and techniques were taught by Klekowski and Duncan at Royal Holloway College, London (September 1966) and by Klekowski at the Nenski Institute of Experimental Biology, Warsaw, Poland (April 1967).

Cartesian divers are constant volume, variable pressure respirometers. After being charged with a fixed volume of gas (different for each and termed the "diver constant" Vg) the divers float neutrally bouyant in the flotation medium (0.1 N NaOH). The diver stoppers are constructed so that pressure changes in the flotation chamber are transmitted to the gas bubble, but prevent diffusion of gas between the bubble and the medium. Increasing the pressure on the diver causes the bubble to decrease in size and the diver to sink (and vice-versa).

The experimental animal is placed in the water filled head of the diver (see plate 5). Next is the gas bubble and finally NaOH in the stem of the diver above the stopper. The NaOH is continuous as a thin film, between the stopper and stem of the diver, with the NaOH of the flotation medium. Oxygen is withdrawn by the animal from the bubble in respiration and CO_2 is returned; this is absorbed by the NaOH, the gas bubble decreases in volume and the diver sinks. To refloat the diver to a constant point the pressure in the flotation chamber must be decreased and the bubble expanded. This is done with a manometer containing Brodies fluid and the change in pressure necessary to refloat the diver noted, By taking a series of readings from each diver and noting the time, a graph similar to that shown in figure 21 can be constructed. This shows the increasing pressure difference (Δh as mm of Brodies fluid) necessary to refloat the diver plotted against the time of reading. A line was drawn through the points by eye, from which respiration rate in μl per individual per hour could be calculated. It is clear that the equation is identical to that used to determine O_2 uptake in a Warburg manometer.

$$\Delta VO_2 = \frac{Vg \cdot \Delta h}{P_o} \cdot \frac{273}{T}$$

where ΔVO_2 = volume of O_2 consumed as l per individual per hour.

Vg = Diver Constant: the volume of the gas bubble (μl).

Δh = Pressure change as mm per hour

P_o = Normal pressure for system

10,000 mm of Brodies fluid.

T = Absolute temperature of system.

The diver apparatus was operated in a 15°C constant temperature room and the water bath controlled at 16°C with an accuracy greater than 0.05°C by using an electric lamp bulb as a heater and a Gallenkamp Jumo thermostat with a Sunvic F 103/4 control. A maximum of eight divers could be run in each experiment.

Measurements were made for approximately two hours with each individual and the O_2 uptake calculated for the central one hour period. During the run, larvae usually remained quietly on the side of the diver (see plate 5) occasionally walking slowly round inside the "head". On completion of the run they were removed, starved for twelve hours to empty the gut and then wet weighed.

All divers were siliconised inside to prevent break-down of the bubble meniscus or "creep" of the NaOH into the water containing the larva. A 5 percent solution of Dichloro-dimethyl-silane $(CH_3)_2SiCl_2$ in carbon-tetrachloride was placed inside the diver which was then heated for 24 hours at 100°C, leaving a film of silicone inside. Before use, the diver was thoroughly rinsed in distilled water. No sign of

any toxic effects due to the silicone were noted: indeed, following experimentation many moulted successfully to the next instar.

10.2b The Winkler Measurements

Dissolved oxygen was measured with the micro-Winkler method described by Fox and Wingfield (1938). The standard syringe manufactured by Philip Harris Ltd., Birmingham was used throughout the study, with a grade A microburette (Technico) reading to 0.005 ml.

Carpenter (1965a and b) and Carrit and Carpenter (1966) pointed out a number of errors in the Winkler technique and their recommendations were followed as closely as possible.

Respiration rates were measured by determining the dissolved oxygen concentration in closed bottles at the beginning and end of an experimental period. As long ago as 1934 Allee and Oesting pointed out that errors in absolute oxygen concentration determination "can be tolerated if there is assurance that the absolute, not the relative, error in the same for samples taken at the two ends of the respiration period." Therefore, the precautions taken were those designed to eliminate the more serious random errors, particularly the loss of volatile iodine during titration.

The following solutions were prepared:-

$MnCl_2$ - 60 g per 100 ml.

Alkaline KI - 320 g per litre NaOH

200 g per litre KI.

Orthophosphoric acid - concentrated acid S.G. 1.75 diluted with an equal volume of distilled water.

Starch indicator - 1 g per 100 ml of saturated salt solution and filtered.

$\frac{N}{50}$ $Na_2S_2O_3$ - from B.D.H. concentrated ampouls.

$\frac{N}{40}$ KIO_3 - from analar, oven dried (60°C) KIO_3 (used in standardising and checking of $Na_2S_2O_3$).

Solutions that were too viscous to enter the syringe easily were made more dilute than Carrit and Carpenter suggested but all were more concentrated than those recommended by Fox and Wingfield (1938).

In making oxygen determinations, the syringe dead space was filled with $MnCl_2$ and then the water sample taken (11.33 ml). Four complete turns of the head screw were used to draw in the alkaline KI and six complete turns for the orthophosphoric acid. The syringe was rinsed out twice with distilled water. The pH of the sample was tested on a number of occasions and found to lie between 1.8 and 2.1 with most of the readings about pH 1.9 - 2.0. Carpenter (1965a) recommended a pH of 2.

Respiration measurements were made in individually numbered ground glass stoppered bottles containing lengths of ground glass rod on which the larvae could cling. Three different sizes of bottle (approximately 33, 67 and 128 ml.) were used, depending on the size of the larvae being studied: the volume of all bottles including the ground glass rod were determined individually and recorded.

Before making measurements the water was allowed to stand for 48 hours at the experimental temperature. Durham tap water was used throughout. The bottles were filled and closed carefully to ensure

that no air bubbles were trapped and the time of closing each bottle noted. For each set of measurements two initial control bottles were filled and titrated immediately. Hence the oxygen tension at the beginning of the experimental period could be calculated. For every four bottles containing Pyrrhosoma larvae, one final control bottle without larvae was also set up. All experiments were run for approximately 24 hours. At the end of this experimental period, the bottles containing larvae and the final control bottles were titrated. The difference between the oxygen in the final control bottles and in the bottles containing Pyrrhosoma gave the oxygen uptake over that period. The change in oxygen tension between initial and final controls was also calculated; if the difference was greater than 10 percent the run was discarded (this was necessary on only two occasions).

With large larvae one or two individuals were placed in each bottle whereas with small larvae up to ten individuals were necessary, particularly at lower temperatures. In each case, the numbers used were estimated to give a fall in oxygen concentration of between 5 and 10 percent.

Experiments at 5 and 10°C were conducted in constant temperature rooms held at ± 0.1°C and experiments at 16°C in a large water bath also held at ± 0.1°C. Natural photoperiod was experienced throughout. At the end of the experiment larvae were allowed to empty their guts and were wet weighed.

The calculation of the amount of dissolved oxygen in each sample is given in detail by Fox and Wingfield (1938).

10.3 RESPIRATION RESULTS

Using the two basic techniques described, information was obtained on four aspects of respiration in Pyrrhosoma

i) The effect of size and temperature on respiratory rate.

ii) The change in monthly respiratory rates of final instars and the effects of metamorphosis.

iii) The effects of oxygen tension on respiratory rate.

iv) Sexual difference in respiratory rate.

10.3a The Effect of Size and Temperature on Respiratory Rate

Data were collected between July 1967 and May 1968. The results are presented in figure 22, which shows the respiration rates (µl per larva per hour) plotted against wet weights (mg) on a log: log scale for the three temperatures. In this instance, only final instar measurements made between October and December were included.

The expected straight line relationship between wet weight and respiration rate on a log:log plot was obtained at all three temperatures. The Cartesian diver results (open circles) at 16°C fitted extremely well onto the Winkler results obtained for larger larvae (solid dots) at 16°C. Three separate regressions were calculated, which were as follows:-

5°C $y = 0.903x - 1.099$

10°C $y = 0.891x - 0.899$

16°C $y = 0.848x - 0.486$

where y = log (respiration rate x 100) (µl per larva per hour)

x = log (wet weight x 100) (mg)

The lines shown in figure 22 were calculated from these equations and the 16°C and 5°C slopes drawn on the 10°C graph for comparison. However, these equations were not those used in subsequent energy budget calculations.

A t test (Mather 1964) showed that there was no significant difference between the slopes: these were therefore pooled and a common regression coefficient of b = 0.867 obtained (Snedecor 1962). Three new regression lines were calculated using this common slope according to the formula

$$y = \bar{y} + b(x - \bar{x})$$

given by Davies and Walkey (1966)

where $\bar{y}$ = mean of all the y values

$\bar{x}$ = mean of all the x values

b = common regression coefficient.

The new regression equations (used in all subsequent energy budget calculations) were:-

5°C	y =	0.867x - 1.002
10°C	y =	0.867x - 0.832
16°C	y =	0.867x - 0.535

Since b was a constant, it is clear that temperature affected all sizes of larvae equally. Figure 23 shows that a graph of log R: temperature was not linear (where R = respiration rate in µl per larva per hour) and several transformations failed to give a linear relationship. Therefore, a multiple regression analysis (e.g. Comita 1968) could not be used to calculate respiration rates of larvae at intermediate temperatures

(i.e. temperatures other than 5, 10 and 16°C). The lack of linearity is shown in figure 23 where the calculated respiratory rate on a log scale is plotted against temperature for two sizes of larvae. The dotted line does not presuppose that it is the 16°C point which is "out", but simply illustrates the extent of the non-linearity.

The relationship of log R: temperature was probably curvilinear, but the error in assuming that the 5, 10 and 16°C points were joined by straight lines was assumed negligible and the assumption greatly simplified calculation. Changes in log (respiration rate x 100) per °C were calculated as follows:-

16 - 10°C change in log (R x 100)/°C = 0.0494

10 - 5°C change in log (R x 100)/°C = 0.0341

Log (R x 100) could then be calculated at any temperature for any size of larva by calculating it for the nearest regression line (i.e. 5, 10 or 16°C) and adding or subtracting the appropriate correction factor worked out from the change in log (R x 100)/°C. For example:- Calculate log (R x 100) for a larva at 12°C.

1. First calculate log (R x 100) at 10°C
2. To this answer add (2 x 0.0494)
3. This gives log (R x 100) at 12°C.

(Alternatively calculate log (R x 100) at 16°C and take off 4 x 0.0494.)

Therefore using the three regression equations recalculated with a common regression coefficient and the calculated changes in log (R x 100)/°C, the respiration rates of larvae of any size at any temperature could be found (with the exception of some final instar stages,

see 10.3b).

For the purpose of comparing the effects of temperature on respiratory metabolism with the effects of temperature on feeding rate (see chapter 12) respiration rates at 5 and 10°C were calculated as percentages of the rates at 15°C. The results were as follows:-

Respiration rate at 10°C = 71.32 percent of rate at 15°C

Respiration rate at 5°C = 48.13 percent of rate at 15°C.

Q_{10} values were also calculated:-

Between 5 and 10°C Q_{10} = 2.20

Between 10 and 16°C Q_{10} = 3.12

10.3b Respiration in Final Instars

Non-metamorphosing final instar respiration rates were measured at 16°C monthly from October 1967 until April 1968: stage 2 metamorphosis larvae were also measured.

Table 42 (p 197) shows the mean wet weights and respiration rates of the larvae used in these experiments. The table also shows the respiration rates of the experimental larvae predicted from the 16°C regression relating log wet weight to log respiration rate (section 10.3a). Finally, the mean wet weights per individual of final instars in pond B, over the same period, (estimated from the growth curve in figure 12 chapter 7) are included, together with their predicted respiratory rate at 16°C.

The mean weights of larvae used for respiration measurements were not always very close to the mean monthly larval weights in pond B.

The discrepancies were probably due to the fact that the larvae for respiration measurements were taken from other ponds in the study area, where growth patterns may have been slightly different.

Although the regression equations given in section 10.3a were calculated incorporating final instar data for October-December only, it is clear that the predicted and observed value for R shown in table 42 are in close agreement up to February 1968. From March onwards, an obvious change took place and the observed values lie consistently above the predicted values, being 1.5 times higher in non-metamorphosing March and April larvae and nearly twice as high in stage 2 metamorphosis larvae. The increase in March and April is probably associated with metamorphosis before external changes become visible.

10.3c Effect of Oxygen Tension on Respiratory Rate

Water of different oxygen tensions was prepared by bubbling nitrogen through a large reservoir. Winkler respiration measurements were carried out in the usual way except that larvae were kept in the bottles for about 5 hours only. Figure 24 shows the respiratory rate of each larva plotted against the mean percentage oxygen saturation of the water. Saturation values were taken from Carpenter (1966)

It is clear that respiratory rate in Pyrrhosoma was affected by changes in oxygen tension. Between 100 and 50 percent saturation the effect was small, whereas below 50 percent the effect was much greater.

These results do not invalidate the Winkler technique used for routine measurement of metabolic rate, since oxygen saturated water was

always used and the number of larvae and bottle sizes were adjusted to ensure that oxygen tension never fell below 80 percent saturation. The Cartesian Diver also measured the respiratory rate of Pyrrhosoma in oxygen saturated water.

The results present difficulties however, in extrapolating between the laboratory measurements of respiration rate in oxygen saturated water and the field, where oxygen tensions may vary markedly. The behaviour of the larvae is significant here. During normal measurement in saturated water, larvae occasionally walked slowly round the bottle but usually remained on the ground glass rod near the bottom. At reduced oxygen tensions, larvae attempted to climb up the rod to reach the "surface" and frequently hung upside down from the bottom of the ground glass stopper. Periods of rapid swimming were common and when sitting the lamellae were widely spread, and the abdomen waved strongly from side to side. In the field, these are all devices which would increase the supply of oxygen to the larvae and suggest that they probably rarely experienced a greatly reduced metabolic rate in small weedy ponds were the surface could be easily reached.

10.3d Sexual Difference in Respiratory Rate

Sexual differences in respiratory rate were most likely to be apparent in the final instar, Since it was desirable to compare individuals of identical wet weight, all final instar respiratory data obtained at 16°C between October 1967 and February 1968 were corrected to a wet weight of 47 mg, using the common regression coefficient of 0.867. 47 mg was chosen as being the approximate mean weight of larvae over this period.

Mean respiratory rates (±2 standard errors) obtained were:-

4.57 µl per larva per hour (±0.206)

4.43 µl per larva per hour (±0.311)

These means are not significantly different and there would appear to be no difference in the respiratory rates of male and female larvae.

10.4 DISCUSSION

The present work appears to be the first time that Cartesian Diver and Winkler measurements of respiration rate have been made on one species under comparative conditions. Despite the fact that the principles behind the two techniques differ markedly, as do the main sources of error, the observed agreement between the results obtained by them at 16°C was extremely good and provided a useful check on the accuracy of the methods used.

The present work is also the first detailed study of respiration rate in Odonata larvae where the effects of size and temperature throughout development have been examined. The value of 0.867 obtained for b, the common regression coefficient of log R: log wet weight, is typical of many arthropods (Reichle 1968, Keister and Buck 1964, Zeuthen 1953). Since b was constant at all temperatures, respiration rate increased by a constant percentage per degree centigrade rise for all sizes of larvae: this is not the most typical situation (Prosser and Brown 1961 p.245). The lack of linearity in the temperature: log R graph was also less typical than the linear response shown by many organisms (loc.cit.p.239). However, Q_{10} values were normal.

Respiration rates in Pyrrhosoma stabilised very rapidly after temperature changes so that acclimatisation was either absent or was of the "immediate type" discussed by Bullock (1955). If present, it was obviously only partial. Fresh-water poikilotherms (Bullock 1955) and indeed insects in general (Keister and Buck 1964) often show little ability to compensate for environmental temperature. However, Bayle (1928 a and b) found that large Aeshna nymphs took 72 hours to acclimatise almost completely to rising temperatures and rather longer to falling temperatures; whilst Pattée (1955) was able to demonstrate short acclimatisation times in Libellula spp. In this case, with both falling and rising temperatures acclimatisation was complete after 15 or 20 hours and, in another series of experiments, after only 5 hours. He also mentions that acclimatisation may take place in Pyrrhosoma but the details of the experiment are not reported. It is therefore possible that small Zygoptera like Pyrrhosoma show rapid partial acclimatisation to temperature and that this is complete within a matter of hours. In the initial Marburg experiments carried out in the present study, about one hour elapsed between raising the temperature of the larvae and measuring respiratory rate and if any acclimatisation occurred, most of it probably took place within this hour.

From the point of view of methodology, the absence of any acclimatisation and rapid acclimatisation are essentially similar because in both cases respiration rates stabilise very quickly after changes in environmental temperature. Under these circumstances, respiration

rates measured in the laboratory (at a series of constant temperatures) can probably be extrapolated to the field (where temperatures are changing continually) without a great deal of error.

Unfortunately, it has not been the practice to date in ecological energetics to determine the nature of the acclimatisation response in the species being studied. Those species likely to present the greatest difficulties will show acclimatisation extending over a matter of days. Under these circumstances, with habitat temperatures changing continually, acclimatisation may never be complete: alternatively animals may acclimatise to the mean daily, weekly or monthly temperatures, though at the moment it is not known which, if any, of these possibilities are correct. It is clear however, that the uncritical use of acute Rate - Temperature data (i.e. respiration rates measured without prior acclimatisation, Bullock 1955) of the type used in many energetics studies (Menhinick 1967, Wiegert 1965, Phillipson and Watson 1965) could lead to serious errors if the species being studied shows slow acclimatisation. Alternatively, if some acclimatisation is to be given at what temperature should this be? Further extensive work is required on these problems.

It was fortunate for the purposes of the present study that Pyrrhosoma did not show long acclimatisation times.

Many fish have a metabolic rate under active field conditions that is approximately twice that of the resting metabolism measured in a respirometer (Edwards 1967, Mann 1965, Winberg 1956), whilst Odum et al. (1962) used a similar relationship for several vertebrate and invertebrate

components of an old field ecosystem. On the basis of the work by Odum et al., other authors (though by no means all) have also doubled their laboratory measurements of respiration for small arthropods before applying them to the field e.g. Menhinick (1967), Saito (1967). Provided that the animals in the respirometer are not unduly restricted however, there would appear to be little justification for this procedure without a great deal more information than is at present available for most species. (For a discussion of this problem with particular reference to Cartesian Diver respirometry see Nielsen 1961). One of the reasons for chosing Odonata larvae in the present study was that they appeared to avoid such methodological difficulties by normally remaining still for long periods so that behaviour in the field and in the respirometer were similar. The extra energy expended in movement by small aquatic animals may in any case be much less than that used by fish or terrestrial species (Winberg 1956). Laboratory measurements of the respiration rate of Pyrrhosoma were therefore applied directly to the field and were not doubled.

An alternative model to the resting versus free existence metabolic rate has been proposed for fish by Ursin (1967), Warren and Davis (in Gerking 1967 and in Ricker 1968) and Krueger et al. (1968). Total metabolic rate in the field is considered as (starvation, resting metabolism) plus (energy released by activity) plus (energy cost of feeding or Specific Dynamic Action S.D.A.). This approach appears to be theoretically more satisfactory than a simple "laboratory resting/field active" approach but, for Odonata at least, it is doubtful whether attempts to

measure these components separately would give more accurate results. Sayle (1928a), for example, found that the metabolic rate of starving Aeshna larvae never stabilised so that measurement of a constant starvation resting metabolic rate would probably be impossible.

However, the S.D.A. approach clearly emphasises the effects of food intake on metabolism. As more food is consumed, the energy cost of utilising it increases so that total metabolic rate rises with increasing food intake, independent of changes in locomotive activity. Depending on the quantity and quality of the food, and on the initial metabolic state, S.D.A. may account for 5 - 40 percent of the energy value of the food consumed by fish (Warren and Davis 1967) but the problem has received little detailed attention from invertebrate ecologists. Burlacu et.al. (1967) estimated that S.D.A. in the Silkworm Bombyx accounted for only 1.5% of the ingested energy, but this was considered to be unusually low. In the present study, animals were fed before being placed in the respirometer following Mann's (1965) procedure. Since most Pyrrhosoma taken in the field had food in the gut (chapter 12 table 54) this was considered more reasonable than to run them under starvation conditions in the respirometer. However, food levels could not be matched exactly with those in the field and it is clear that because of the metabolic effects of feeding or starvation most respirometry will be subject to some error in extrapolation to the field.

Respiration rates in Mayfly larvae were minimal on substrates of "preferred" particle size; substrate also affected the response to

changing oxygen tension (Eriksen 1964). Nautier and Patée (1955), also working with Mayfly larvae, demonstrated that unsuitable substrate conditions markedly affected Q_{10} results. Evidence for substrate particle size selection in Odonata was presented by Keetch and Moran (1966) but is considered rare, though the nature of the substrate is important in that many species, including Pyrrhosoma, are strongly thigmotactic (Corbet 1962). Small Pyrrhosoma remained motionless on the sides of the Cartesian Divers for long periods, but in the Winkler bottles, larger larvae walked about continually unless provided with a ground glass rod on which they could cling. It is clear that unless these precautions to simulate natural conditions had been taken, respiration results may have been quite different.

Oxygen tension in small shallow ponds normally varies markedly, both diurnally and seasonally (Bamforth 1962, Welch 1952, Whitney 1942 etc.) so much so that to obtain any meaningful picture of oxygen tension changes requires numerous observation over 24 hours throughout the year (Macan 1963, Whitney 1942). Measurements of this type were beyond the scope of the present work. Many pond invertebrates appear to have respiration rates that are independent of falling oxygen tensions down to very low levels (Macan 1961, Jonasson 1964, Berg 1961) so that the dependent pattern of respiration shown by Pyrrhosoma was surprising, even though a very similar response was demonstrated in Anax imperator by E. Kanler (pers. comm. 1967). Zygoptera, however, show strong behavioural responses to falling oxygen tension (Corbet 1962) using

strong side to side movements of the lamellae to move fresh water over the body surface and, at lower oxygen levels, climbing to the surface. None of these responses can be effective in a closed respirometer and it is highly probable that respiration rates in Pyrrhosoma were maintained in the field in the face of falling oxygen levels by these well developed behavioural responses.

Edmondson (1961) and Phillipson (1962, 1963) have stressed the importance of allowing for seasonal and daily rhythms in respiration studies. Daily feeding and respiratory rhythms were demonstrated in Aeshna grandis by Berezina (1959) and followed each other closely. Odonata showing daily rhythms appear to be the more highly evolved forms in which the eyes have become increasingly important for prey detection (Corbet 1962) so that this excludes most of the Zygoptera, including Pyrrhosoma. Experiments demonstrating the lack of any obvious periodicity in food intake in Pyrrhosoma are reported in chapter 12, whilst the similarity between the Cartesian Diver respiration measurements made over a restricted period (usually two hours in the morning or early afternoon) and the Winkler measurements made over 24 hours, suggests that there was no daily periodicity in the respiration rate of Pyrrhosoma. There was little change in metabolic rate with season when larvae were compared at one temperature, except in final instars prior to metamorphosis. There was no evidence to indicate that changing photoperiod had an effect on metabolic rate in the way that Lutz and Jenner (1960) found for some species of Odonata.

Fischer's work (1966, 1967a) on Lestes is the only published study in which the respiration rate of a dragonfly has been measured throughout development. Unfortunately, the data are not presented in a way that can be compared with the present study. Other studies on Odonata respiration are of an extremely fragmentary nature in which respiration rates have been measured at one (rarely more) temperature and usually with larvae of unspecified size (Edwards 1946, Harnisch 1958, Sitaramaiah 1967). Again legitimate comparison is impossible.

The effects of metamorphosis on respiration have been dealt with more thoroughly. Lutz and Jenner (1960) found that metabolic rate increased markedly during metamorphosis in Tetragoneuria and Fischer (1967a) found a similar increase in Lestes just prior to and during metamorphosis. The work with Pyrrhosoma confirms this rise in respiratory rate, though it is interesting to observe that in Pyrrhosoma the metabolic rate increased some considerable time before morphological signs of metamorphosis were visible.

An attempt by Kormondy (1965) to measure metabolic rates in larvae of the dragonfly Plathemis lydia with Zinc - 65, based on the metabolic activity meter concept of Odum and Golley (1963) was unsuccessful because the larvae absorbed most of the zinc onto their body surface. Successful application of this technique might have yielded extremely valuable information about many of the methodological problems encountered during the present study.

10.5 APPLICATION OF RESPIRATORY DATA TO FIELD POPULATIONS

10.5a Oxycaloric Coefficient

An oxycaloric coefficient of 4.825 k.calories per litre was used to calculate the heat energy lost in respiration. This corresponds to an R.Q. of 0.82, which Brody (1945) described as the simplest and perhaps the most accurate figure to use. It is also the average R.Q. of many resting insects. (Edwards 1953). As Brody (1945) pointed out, the range of oxycaloric coefficients is relatively narrow, differing from the mean figure used at an R.Q. of 0.82 by only plus or minus 3.5 percent. Since Pyrrhosoma was a carnivore, its R.Q. was almost certainly less than 1, but greater than 0.7, so that the use of the average oxycaloric coefficient was probably within 1 or 2 percent of the "actual" value.

10.5b Respiration Energy Lost Per Larva Per Month

The mean monthly wet weights per individual used in the respiration calculations were calculated from tables 20 - 23 (chapter 7). Wet weights on the first on the month and on the first of the next month were added together and divided by two. The metamorphosis stage and hatching dates were those given in chapter 6.

Respiration rates were calculated as μl per larva per month using the mean monthly temperatures given in table 7 (chapter 4) and converted to calories using the oxycalorific equivalent of 4.825 k.cals. per litre. In detail the procedure was to multiply hourly rates by 24 and then by the number of days in the month. At the hatch and during metamorphosis,

respiration had to be calculated for periods shorter than one month: in these cases, mean pond temperatures for the shorter periods were used and daily respiration rates were multiplied by the appropriate number of days.

The equations and methods given in section 10.3a were used to calculate data for all larvae except final instars in March, April and May. During this period metamorphosis increased the metabolic rate above that predicted by the regression equations (see section 10.3b). Prior to entering visible metamorphosis in March and April, respiration rates calculated from the regressions were multiplied by 1.5 (see section 10.3b). Data for stage 2 metamorphosis larvae were taken directly from the figure of 10.40 μl per larva per hour at 16°C obtained for this stage, corrected for temperature. For stage 3 metamorphosis, the average caloric loss was taken as being equal to the calories respired i.e. 80.218 - 72.078 cals per larva or 8.140 calories (see chapters 2 and 7).

The results are presented in tables 43 - 46. From these figures of total respiration expressed as calories per larva per month, it was possible to calculate total population respiration per square meter and also to evaluate the proportion of ingested energy lost in respiration each month. These are calculated in chapter 14.

Month or larval condition	Number of larvae in monthly respiration sample	mg		μl per larva per hour			
		Actual mean wet weight of larvae in samples	Estimated mean wet weight of larvae in pond B	Predicted R from actual weight	Predicted R from mean size of final instars in	Actual R from monthly samples	±2 standard errors on actual R
Oct 67	22	42.1	45.2	4.06	4.31	4.23	4.48-3.98
Nov 67	21	45.7	46.7	4.35	4.44	4.78	5.20-4.36
Dec 67	19	44.7	47.2	4.27	4.48	4.04	4.43-3.66
Jan 68	17	51.8	47.5	4.86	4.50	5.82	6.33-5.30
Feb 68	20	53.2	48.1	4.97	4.55	4.31	4.74-3.87
Mar 68 Pre met.	21	55.9	49.7	5.18	4.69	7.60	8.16-7.03
April 68 Pre met.	23	56.6	Nearly all in met. not calculated	5.24	-	7.90	8.57-7.24
May 68 stage 2 met.	17	65.9	60.6	5.98	5.56	10.40	11.19-9.61

Table 42 Monthly changes in actual and predicted respiratory rates of final instar Pyrrhosoma; October 1967 to April 1968: all at 16°C.

Month or specified shorter time interval	Year	Life history stage	Mean wet weight (mg)	Calories respired/ larva (in specified time interval)
July 7th-31st		Hatch	0.121	0.063
Aug.			0.304	0.169
Sept.	1966		0.646	0.237
Oct.			0.932	0.261
Nov.		First winter	1.003	0.215
Dec.			1.003	0.175
Jan.			1.003	0.164
Feb.			1.003	0.174
March			1.034	0.219
April			1.311	0.266
May		Second summer's	1.975	0.515
June	1967	growth starts	3.671	1.281
July			7.895	3.149
Aug.			15.74	5.363
Sept.			30.65	7.031
Oct.			43.52	6.656
Nov.			46.72	5.197
Dec.			47.16	4.638
Jan.		Premetamorphosis	47.50	4.660
Feb.		rise in	48.06	5.141
March	1968	respiration	49.74	8.844
April 1st-16th		Stage 2 met.	49.74	4.864
April 17th-30th			-	7.456
May 1st-22nd			-	14.649
May 23rd-30th		Stage 3 met.	-	8.140

Table 43 Calculated calories respired per individual larva during time intervals shown: 1966 year class in pond B.

Month or specified shorter time interval	year	Life history stage	Mean wet weight (mg)	Calories respired/larva (in specified time interval)
July	1966	Second summer	7.476	2.917
Aug			15.45	5.108
Sept			30.47	6.719
Oct		Entry to final instar	42.82	7.208
Nov			45.59	5.903
Dec			46.71	4.879
Jan	1967		47.83	4.681
Feb			49.63	5.146
March		Premetamorphosis rise in respiration	51.93	9.762
April 1st-9th			51.93	2.685
April 10th-30th			-	10.177
May 1st-24th		Stage 2 met.	-	14.744
May 25th-31st		Stage 3 met.	-	8.140

Table 44 Calculated calories respired per individual larva during time intervals shown: 1965 year class in pond B.

Month or specified shorter time interval	Year	Life history stage	Mean wet weight (mg)	Calories respired/larva (in specified time interval)
July 15th-31st	1967	Hatch	0.099	0.037
Aug.			0.271	0.159
Sept.			0.634	0.244
Oct.			0.937	0.238
Nov.		First winter	1.013	0.187
Dec.			1.013	0.166
Jan.	1968		1.013	0.166
Feb.			1.013	0.159
March			1.047	0.211
April			1.238	0.230
May		Start of second summer's growth	1.931	0.540
June			4.916	2.030

Table 45 Calculated calories respired per individual larva during time intervals shown: 1967 year class in pond B.

Month or specified shorter time interval	Year	Life history stage	Mean wet weight (mg)	Calories respired/larva (in specified time interval)
July 15th-31st		Hatch	0.099	0.032
Aug.			0.260	0.142
Sept.	1967		0.551	0.195
Oct.			0.849	0.211
Nov.		First winter	0.979	0.171
Dec.			0.979	0.159
Jan.			0.979	0.162
Feb.	1968		0.979	0.150
March			0.979	0.182
April			1.066	0.216
May		Second summer's	1.471	0.368
June		growth starts	3.803	1.175
July	1967		11.02	3.690
Aug			20.43	6.257
Sept			32.97	6.734
Oct		Entry to	43.85	6.472
Nov		final instar	47.19	4.933
Dec			48.35	4.667
Jan.			48.80	4.818
Feb.			49.09	4.480
March		Premetamorphosis	49.74	8.184
April 1st-19th	1968	rise in respira-	49.74	5.373
April 20th-30th		tion	-	5.290
May 1st-24th		Stage 2 met.	-	13.792
May 25th-31st		Stage 3 met.	-	8.140

Table 46 Calculated calories respired per individual larva during time intervals shown: "composite" life cycle made up of 1966 and 1967 year classes in pond F.

Plate 4. The Cartesian Diver apparatus. In the centre of the photograph is the water bath, with eight floatation chambers; in front of the water bath is the binocular microscope used to view the divers in operation; on the extreme right is part of the large manometer, and manometer adjusting screw.

Plate 5. Pyrrhosoma nymphula in a Cartesian Diver. The head of the diver and part of the stem and stopper only are shown. X15 approx.

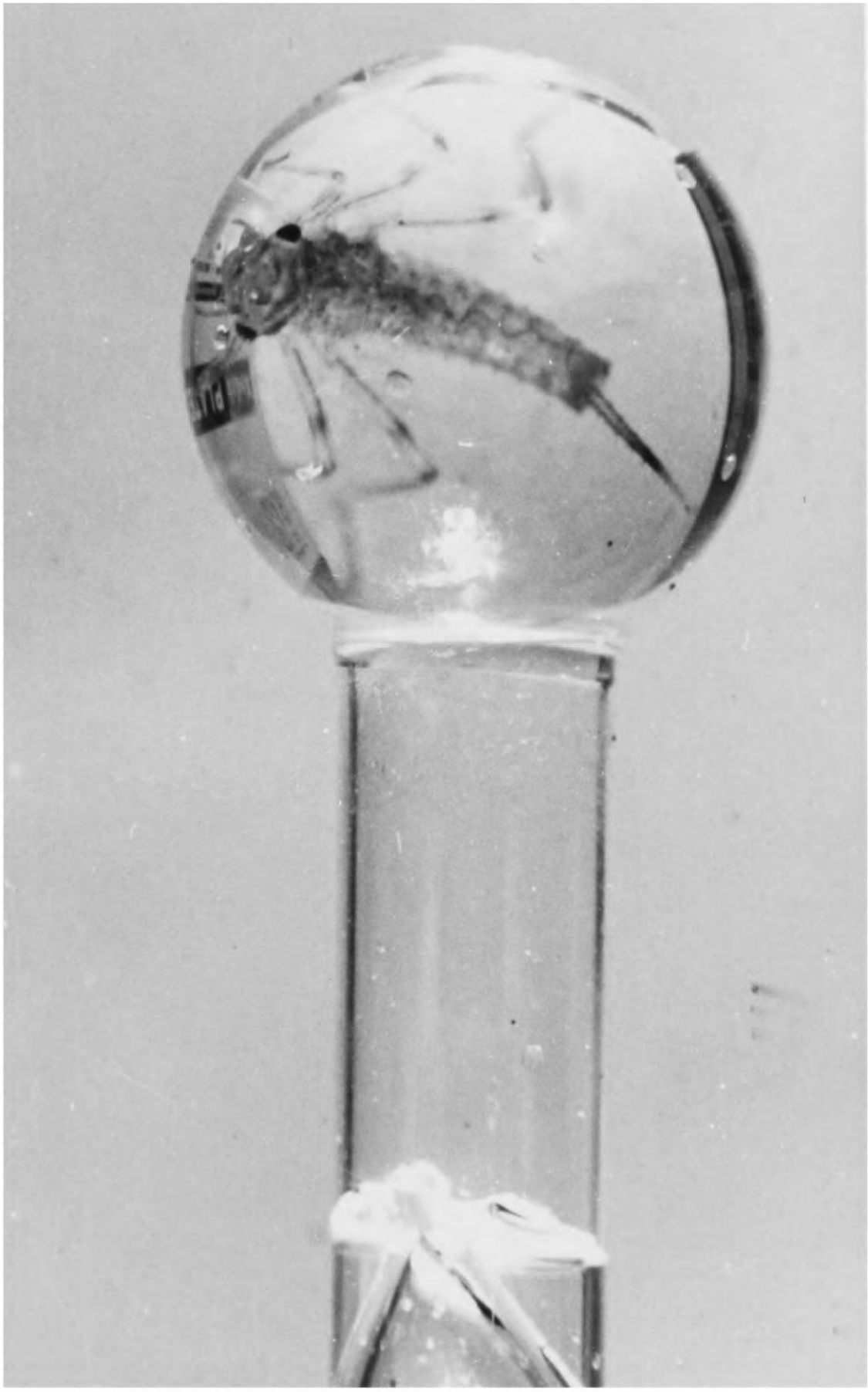


Fig. 20. Results of an experiment to test whether Pyrrhosoma showed metabolic acclimatisation to temperature. See text for details (section 10.1a.)

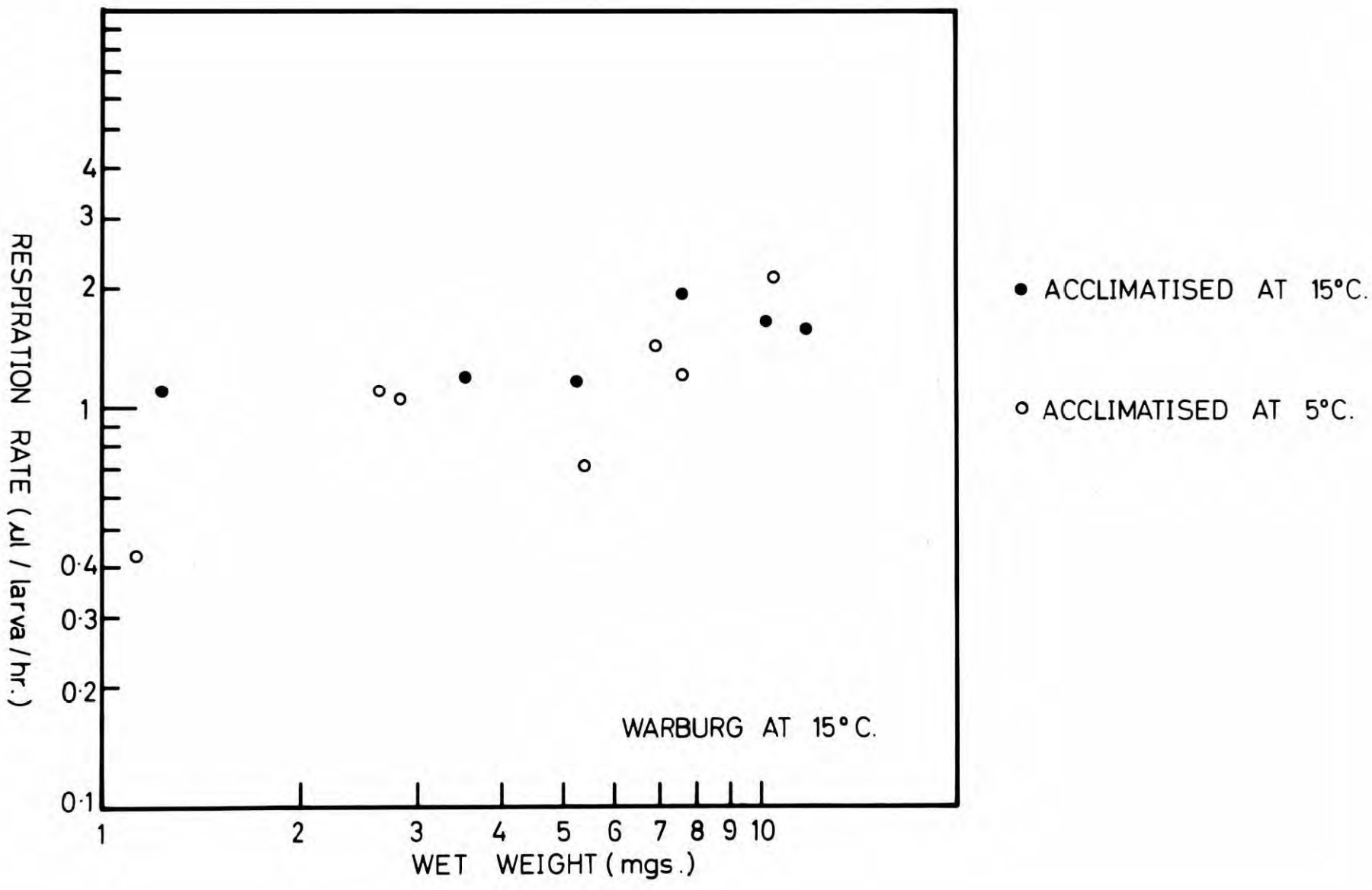

RESPIRATION RATE (µl / larva / hr.)
4
3
2
1
0·4
0·3
0·2
0·1
1
2
3
4
5
6
7
8
9
10
WET WEIGHT (mgs.)
WARBURG AT 15° C.
● ACCLIMATISED AT 15°C.
○ ACCLIMATISED AT 5°C.

Fig. 21. Typical readings obtained from one Cartesian Diver, and a calculation of oxygen uptake by Pyrrhosoma from these readings.

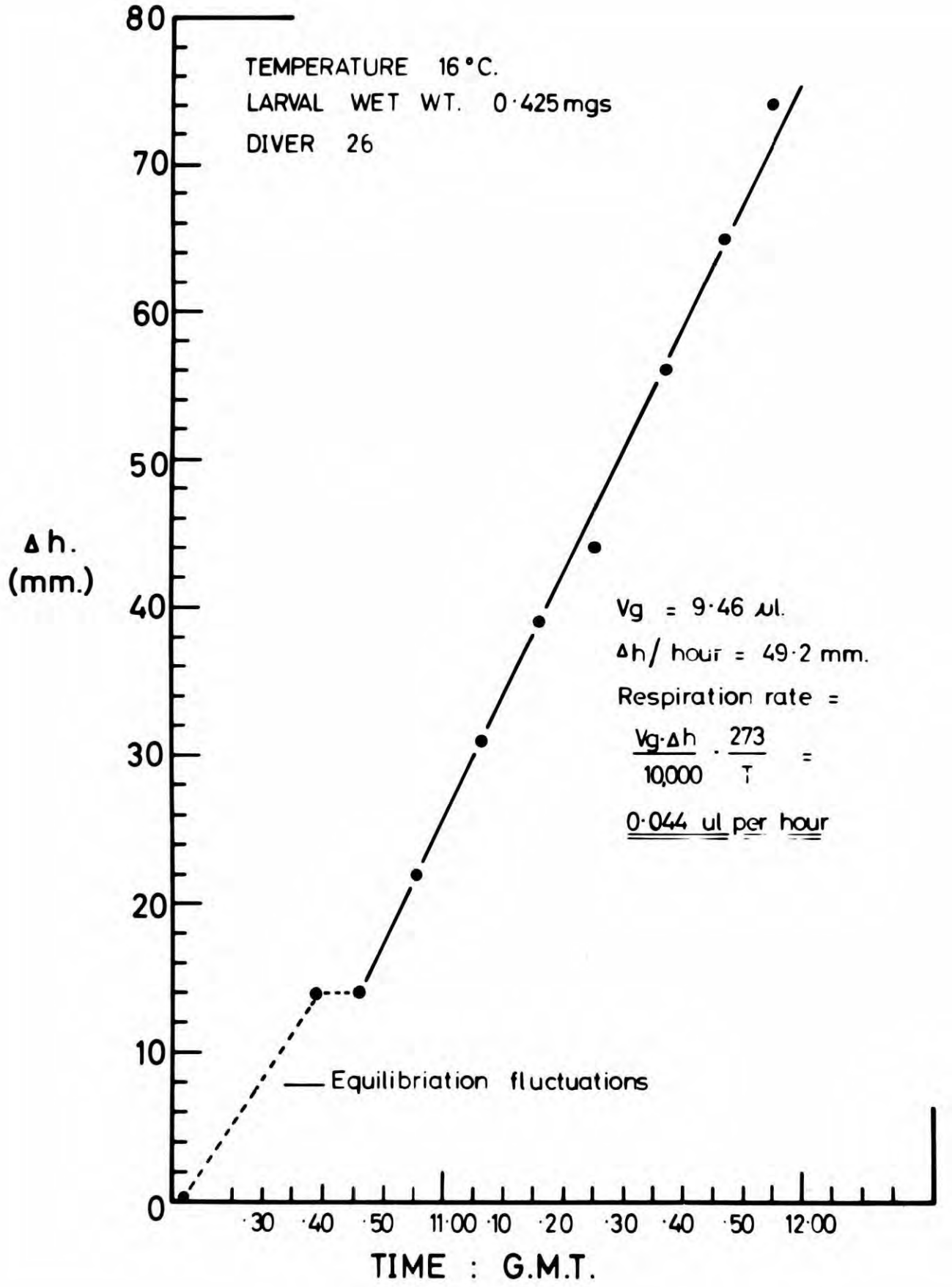

TEMPERATURE 16 °C.
LARVAL WET WT. 0·425 mgs
DIVER 26
Δ h. (mm.)
80
70
60
50
40
30
20
10
0
Vg = 9·46 ul.
Δh/ hour = 49·2 mm.
Respiration rate =
Vg·Δh / 10,000 · 273/T =
0·044 ul per hour
Equilibriation fluctuations
·30 ·40 ·50 11·00 ·10 ·20 ·30 ·40 ·50 12·00
TIME : G.M.T.

Fig. 22. The effect of larval size on the respiration rate of Pyrrhosoma at 5, 10 and 16°C. The calculated regressions are presented in section 10.3a.

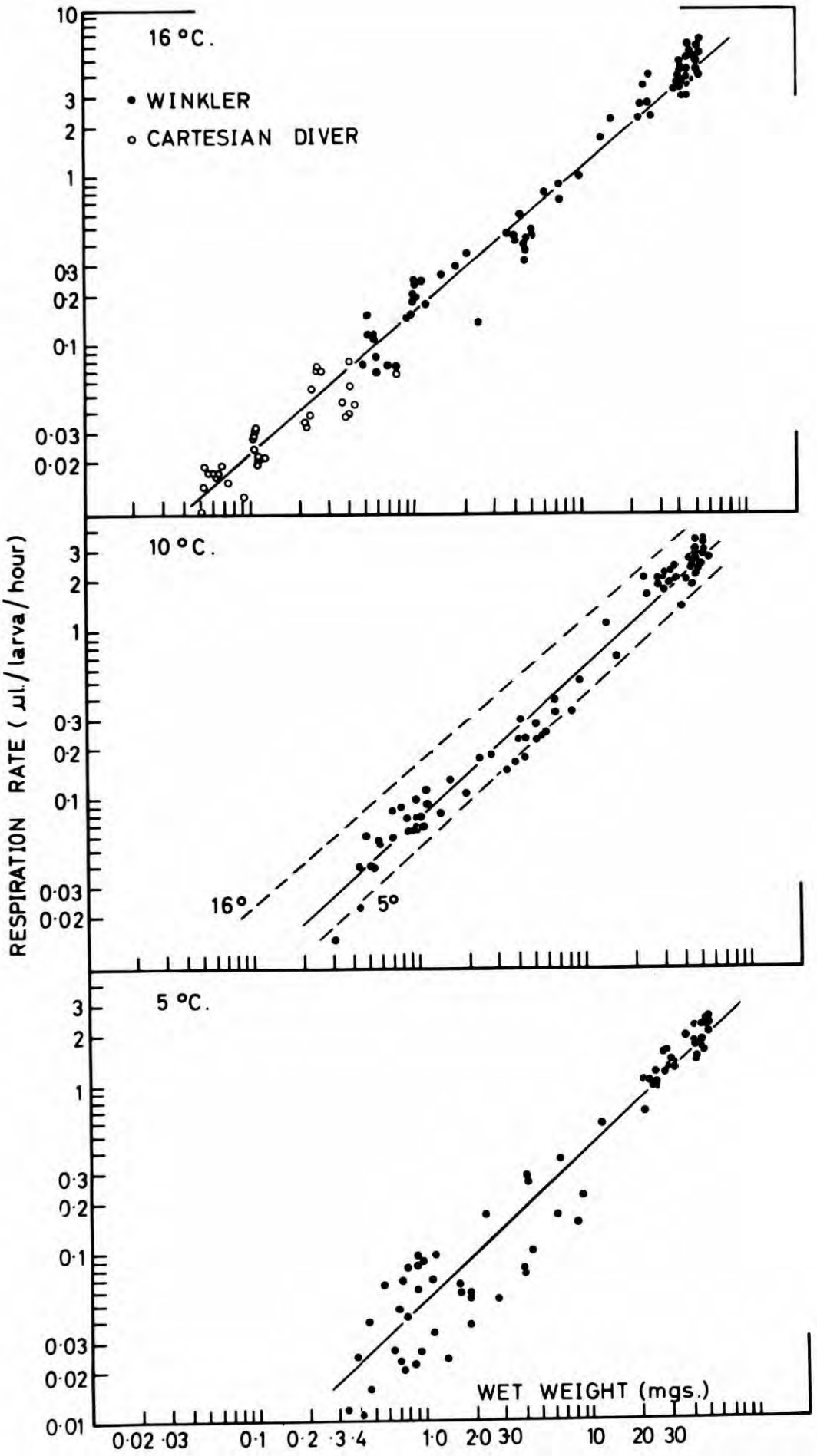

16 °C.
• WINKLER
○ CARTESIAN DIVER
10 °C.
16°
5°
5 °C.
RESPIRATION RATE (µl./larva/hour)
WET WEIGHT (mgs.)
10
3
2
1
0·3
0·2
0·1
0·03
0·02
0·01
0·02 ·03
0·1 0·2 ·3 ·4
1·0 2·0 3·0
10 20 30

Fig. 23. The effect of temperature on the respiration rate of Pyrrhosoma larvae, to show the extent of the non-linearity in a plot of log. R against temperature. (Respiration rates for the two sizes of larvae calculated from the regressions given in section 10.3a).

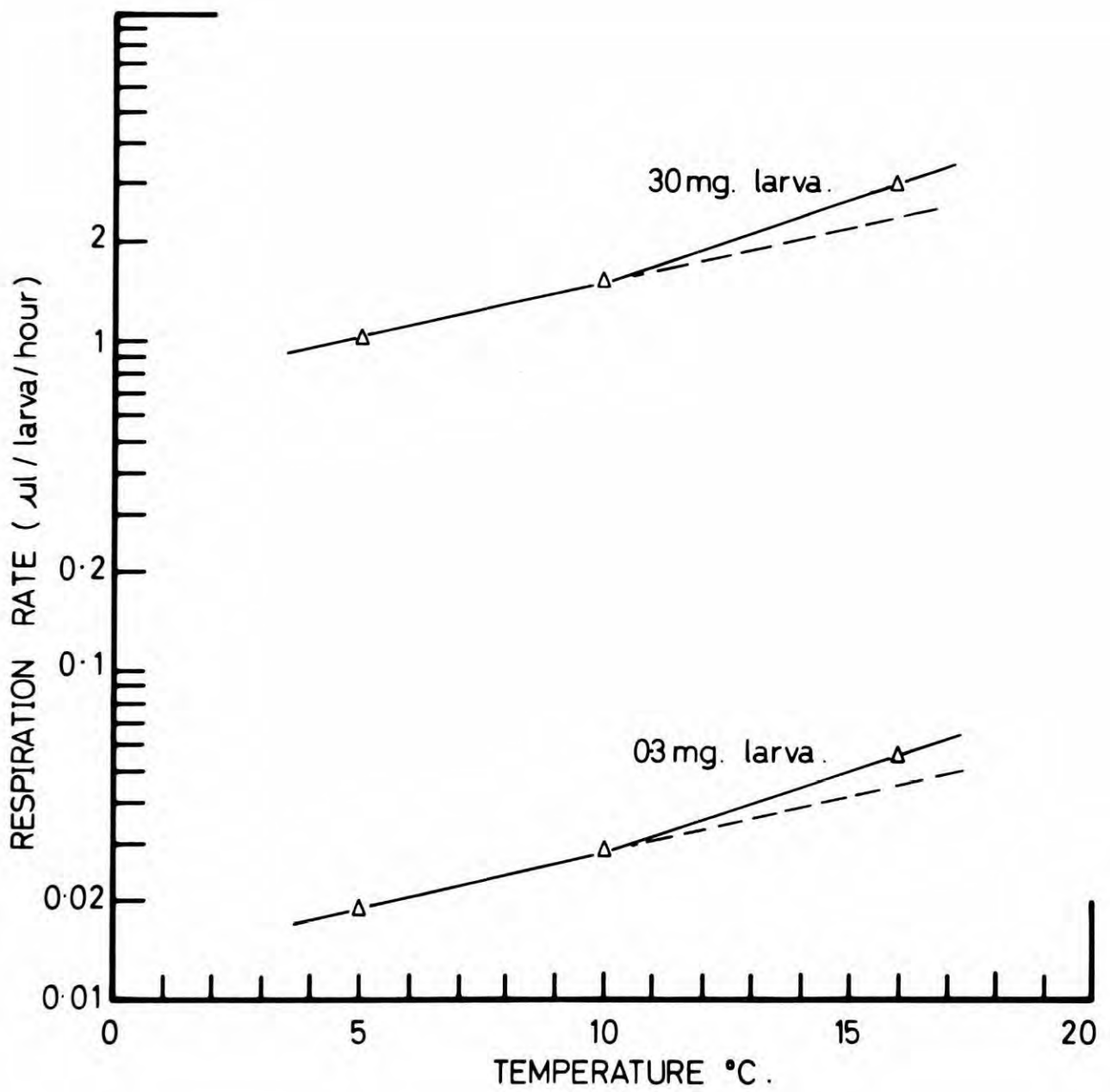
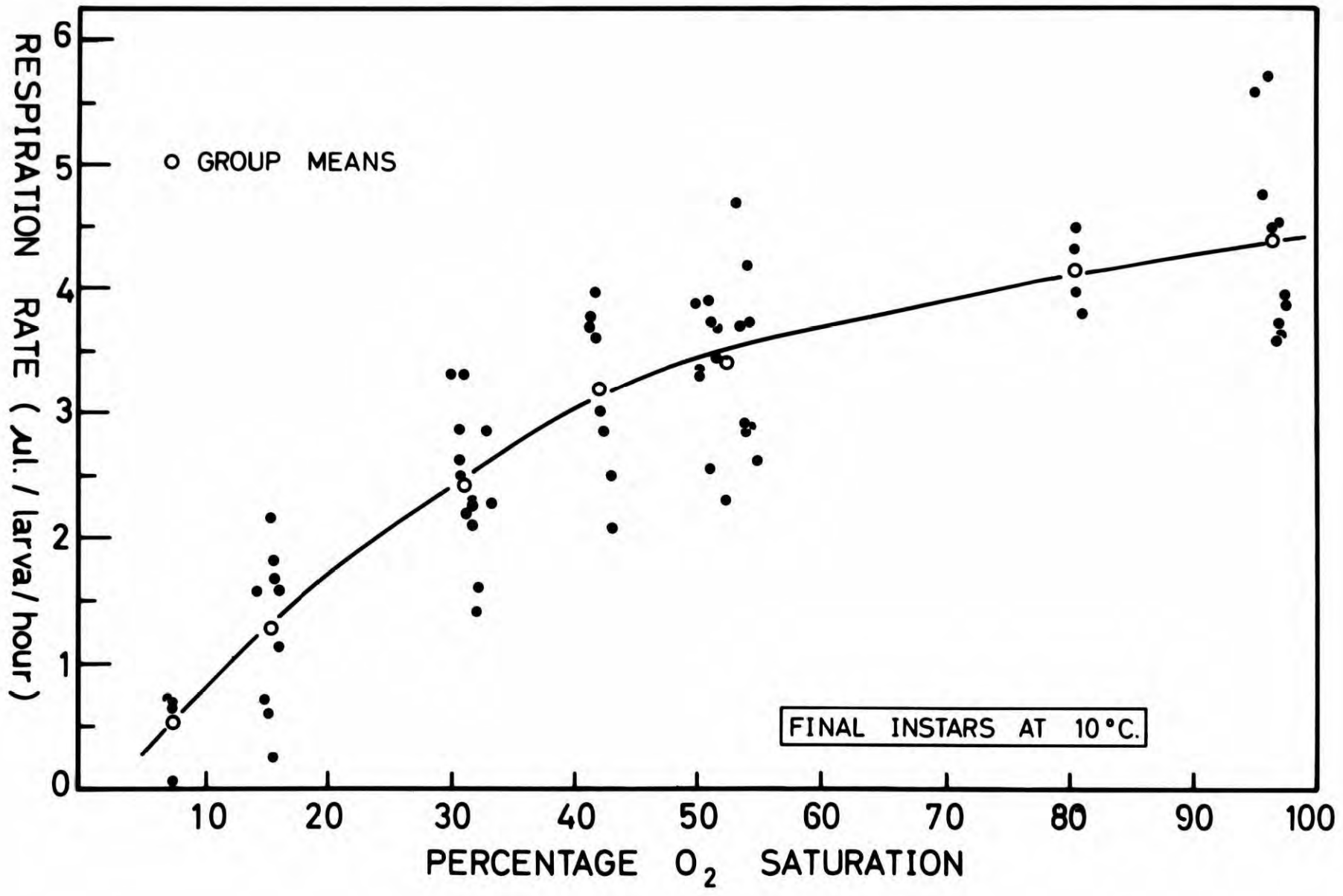

30 mg. larva.
03 mg. larva.
RESPIRATION RATE (µl / larva / hour)
2
1
0·2
0·1
0·02
0·01
0
5
10
15
20
TEMPERATURE °C.

Fig. 24. The effect of oxygen tension on the respiration rate of final instar Pyrrhosoma larvae at 10°C.


RESPIRATION RATE (µl. / larva / hour)
0
1
2
3
4
5
6
o GROUP MEANS
FINAL INSTARS AT 10 °C.
10
20
30
40
50
60
70
80
90
100
PERCENTAGE O_2 SATURATION

Chapter 11

MINOR COMPONENTS OF THE ENERGY BUDGET: Excretion and Exuvium Production

11.1 EXCRETION (U)

Staddon (1959) showed that Aeshna cyanea larvae excreted soluble nitrogenous urine. In starved larvae, 74 percent of the nitrogen excreted was in the form of Ammonia and only 8 percent as Uric Acid: 18 percent was made up of undetermined nitrogenous compounds. After feeding on protein (egg albumin), total nitrogen excretion increased and the proportion of Ammonia in the urine rose to 87 percent; excretion of Uric Acid and other components did not increase. With 24 - 48 hours of feeding, 60 percent or more of the nitrogen absorbed was excreted. This appears to be the only work on nitrogen excretion in Odonata larvae (Bursell 1967).

Tests for excretion of Ammonia were made with Pyrrhosoma kept in acetate buffer (Staddon pers. comm. 1967) using Nessler's solution. The experiments confirmed that Pyrrhosoma excreted Ammonia, though, on a colorimetric basis, the quantities were much less than in Sialis larvae of a similar size run for comparison. In view of the low metabolic rate of Pyrrhosoma, this was to be expected and it is probable that Ammonia formed the main excretory product as in Aeshna.

Winberg (1956) argued that where Ammonia is the chief excretory end product it can be ignored in final energy budget calculations. Krueger et al. (1968) independently discuss this problem and their work suggests that a number of Winberg's points require correction but without substantially altering his conclusions.

It is reasonable to assume that most of the protein nitrogen excreted in Odonata appears in the form of Ammonia, in which case, 14.2 percent of assimilated protein energy will be excreted in the urine (Krueger et al 1968) and not 28 percent as stated by Winberg. Prey in Pyrrhosoma is not 100 percent protein: the results of analyses carried out by Blažka (1966) showed that Chironomid larvae were on average 64 percent protein (mean of samples 51.-64 in Blazka's table 4). Therefore, approximately $\frac{14.2 \times 64}{100}$ or 9 percent of the total food energy assimilated will be lost in the urine. Since on average only 90 percent of the food consumed is assimilated, $\frac{9 \times 90}{100}$ or 8 percent of the total energy ingested will be excreted as Ammonia by Pyrrhosoma. This is a maximum figure assuming that none of the protein nitrogen is utilised for growth. The proportion of ingested energy incorporated in growth varied throughout development, but, except in winter (when total energy consumption was low anyway), growth usually accounted for over 40 percent of the energy ingested (see figure 33, chapter 14). It was therefore reasonable to assume that for most of development less than 5 percent of the ingested energy was lost in the urine.

Since excretory energy loss was apparently such a small proportion of the total energy consumption, no attempt was made to estimate it for Pyrrhosoma in the energy budget calculations.

11.2 EXUVIUM PRODUCTION (Ev.)

Larval head widths were measured shortly after moulting and the exuvia collected, washed to remove loose detritus and dried in a vacuum

oven at 60°C. Exuvia were placed on preweighed foil trays and the relationship between larval head width and the dry weight of the exuvium (produced in the moult to that instar) obtained. The exuvium produced by the moult from pronymph to instar 2 was not collected and was ignored in the calculations.

It was shown in chapter 2 that typically Pyrrhosoma passed through twelve instars and moulted ten times between instar 2 and entering the final instar. Larvae spend their first winter in about instar 6 (the mean head width of junior age class larvae collected between November and March was 1.1 mm) so that four moults take place between hatching in July and the end of the first summers growth in early November and the remaining six moults between resuming growth again in April and entering the final instar in early October. Moults were therefore conveniently assigned one per month as follows:-

Moult between instars 2 - 3 July, after hatch

3 - 4 August

4 - 5 September

5 - 6 October

No growth between November and March

6 - 7 April

7 - 8 May

8 - 9 June

9 - 10 July

10 - 11 August

11 - final September

Calorific values of exuvia were obtained in the usual way and are presented in chapter 3. All exuvia were grouped together except those produced at emergence by the moult to the imago. In calculating exuvium production of larvae in the pond the final instar exuvium at emergence was not, of course, included in the analysis.

The relationship between exuvium dry weight (mg) and head width (mm) of the larva after the moult which produced the exuvium is shown in figure 25. The relationship was linear on a log: log plot and the calculated regression gave

$$y = 2.664x - 1.553$$

where y = log (dry weight of exuvium x 1000)

x = log (head width of next instar x 10)

Using this regression, exuvium dry weights for the model head widths shown in fig 3a (chapter 2) were calculated and the results presented in table 47, which also shows the calories lost per exuvium estimated from the calorific value data in table 5 (sample 19).

The total calories lost in exuvium production throughout development were only 4.516 calories per larva. The total calories incorporated into final instar tissue were 80.16 cals (for an average stage 2 metamorphosis larva) so that growth plus exuvia amounted to a total tissue production of 84.7 cals. Exuvium production accounted therefore, for just over 5 percent of the total production per larva.

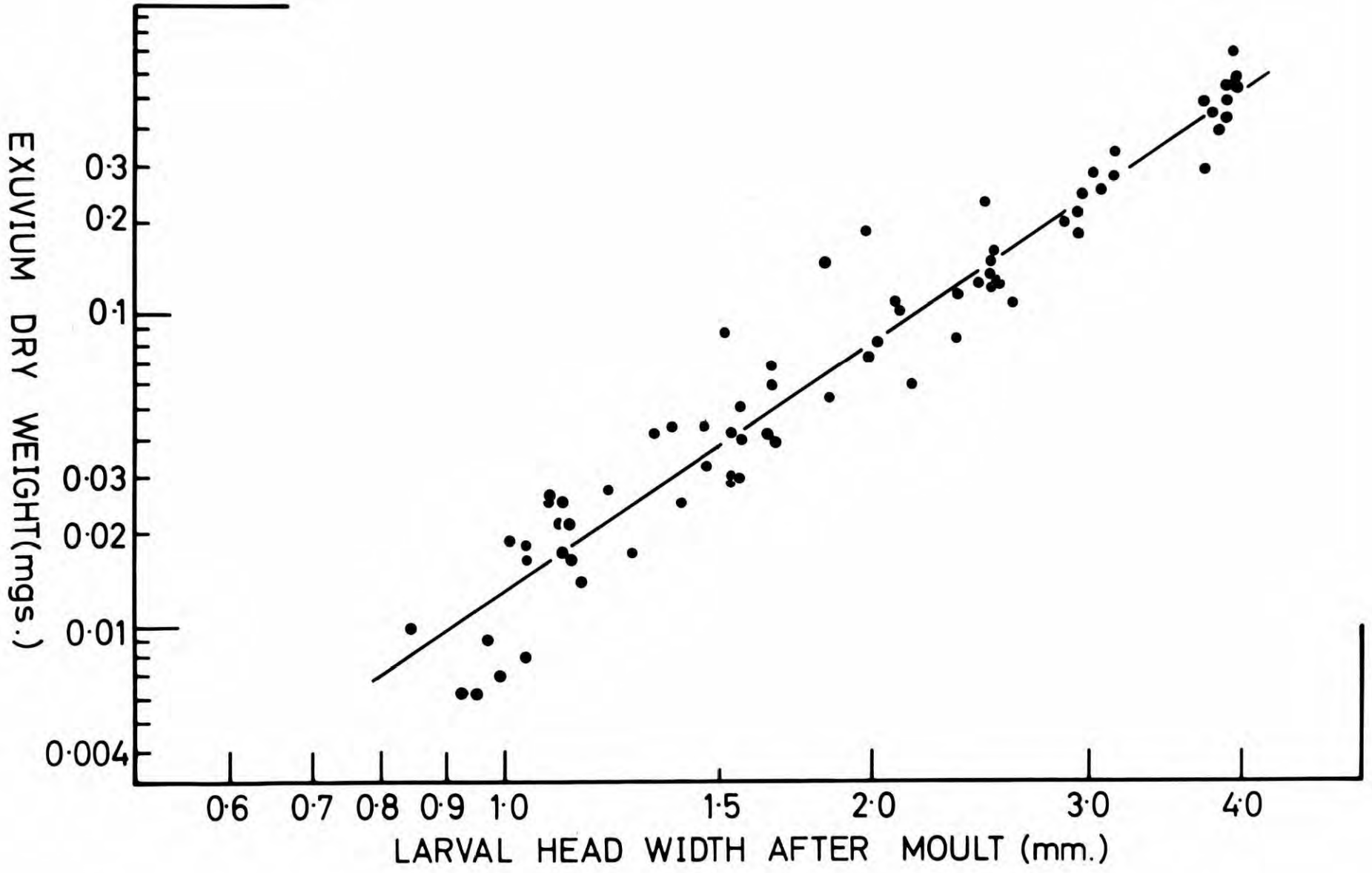
The proportion of ingested energy lost as exuvia each month throughout development is shown in figure 33 (chapter 14).

It is clear from these results that for Pyrrhosoma the energy lost as exuvia was relatively unimportant in the total energy budget, a result similar to that implied or demonstrated in nearly all other energetics studies. The largest figure appears to be that reported by Lasker (1966) for Euphausia pacifica where one third of the net growth is lost as cast exoskeleton, but this is quite exceptional. In almost all other species, exuvium production accounts for only a few percent of the total energy budget. In Anatopynia (chironomid larvae), exuvia represented about 3 percent of total ingestion (Teal 1957); in Asellus they were about 3 percent of total assimilated energy (Fitzpatrick 1968) and less than 1 percent in Calanus finmarchicus (Corner et al. 1967).

Moult between instars	Month in which moult occured	Head width (mm) of larva after moult	Calculated dry weight exuvium produced (mg)	Calories/ exuvium
2 - 3	July	0.525	0.002	0.010
3 - 4	Aug.	0.675	0.005	0.020
4 - 5	Sept.	0.825	0.008	0.035
5 - 6	Oct.	1.025	0.014	0.063
6 - 7	April.	1.250	0.023	0.106
7 - 8	May	1.550	0.042	0.188
8 - 9	June	1.850	0.067	0.302
9 - 10	July	2.350	0.126	0.571
10 - 11	Aug.	3.000	0.241	1.094
11-final	Sept.	3.850	0.469	2.127

Table 47 Dry weight and calories lost per exuvium in moult of Pyrrhosoma throughout development. Larval head widths are taken from model values presented in fig 3a, chapter 2.

Fig. 25. Exuvium dry weight in Pyrrhosoma, as a function of larval head width after moulting. The calculated regression is presented in section 11.2.


EXUVIUM DRY WEIGHT(mgs.)
0·3
0·2
0·1
0·03
0·02
0·01
0·004
0·6
0·7
0·8
0·9
1·0
1·5
2·0
3·0
4·0
LARVAL HEAD WIDTH AFTER MOULT (mm.)

Chapter 12

FEEDING AND THE ESTIMATION OF CONSUMPTION (C)

12.1 GENERAL INTRODUCTION

12.1a The Functional Response

Feeding rates in most invertebrate carnivores are not species specific but increase with increasing prey density to a sustained maximum rate, the so called functional response of Holling (1965, 1966).

Pyrrhosoma had a strong functional response (see fig 26). This particular example shows the mean number of Daphnia captured in one hour (±2 standard errors) in 6 groups (10 larvae per group) of final instars that had been starved for 48 hours at 15°C prior to the experiment, and then fed at the different prey densities indicated with similar sized Daphnia. The containers had a diameter of 5 cm and a water depth of 4 cm; one Pyrrhosoma larva was placed in each.

With the prey densities used, maximum feeding rates were not reached due to the larvae having been starved. With less hungry larvae, the response levelled out to a sustained maximum feeding rate independent of any further increase in prey density.

The strong functional response in Pyrrhosoma meant that field feeding rates could not be measured directly in the laboratory because of the almost impossible task of reproducing the complex patterns of prey density and distribution that existed under natural conditions.

12.1b Periodicity in Feeding Behaviour

Before designing feeding experiments, it was also desirable to

show whether or not Pyrrhosoma had a diurnal feeding or defaecation rhythm.

	Length (mm) or instar	Light n	Dark n	Mean number of Daphnia eaten/larva/day ±2 S.E.		
				In light	In dark	
1	3.40	10	10	5.9±1.7	7.4±2.0	not significant
2	10.00	12	13	9.6±0.5	9.9±0.5	not significant
3	final instar	10	10	10.2±0.7	10.0±0.4	not significant

Table 48 Results of experiments to test the ability of three sizes of Pyrrhosoma to capture prey (Daphnia) in the light or dark. (Different sizes of Daphnia were given to the three size groups).

Table 48 shows that there was no obvious difference in the ability of Pyrrhosoma larvae of any size to capture prey when kept in permanent daylight or permanent darkness for 24 hours.

Collecting time in field (B.S.T.)	n	Mean number of hours to produce first faeces in laboratory after collection	1 S.E.
06.00	19	5.15	1.14
12.25	18	5.38	1.07
18.05	12	6.71	2.07
24.00	16	7.14	0.98

Table 49 Mean time (hours) for larvae to produce faeces after collection: senior age class larvae (mean length 8.6mm) collected from pond B 8/8/66.

Table 49 shows that there was probably no difference in the pattern of defaecation throughout 24 hours. Larvae of a similar size (all approximately instar 10) were collected from the field every six hours, and the time taken to produce the first faecal pellets recorded for each individual. The rather longer time apparently taken by the larvae collected at 24.00 h. was unfortunately due to inadequate observation: the first examination was made at 01.00h on 9/8/66, but the second not until 06.45 h. by which time most of the larvae had produced faeces.

Time interval (G.S.T.)	Number of larvae defaecating in each 6 hour period	Number not defaecating	
18.00 - 24.00	26	24	χ^2 = 0.978
24.00 - 06.00	25	25	p = 0.9-0.8
06.00 - 12.00	20	30	No significant difference in faeces production in any six hour period.
12.00 - 18.00	22	28	

Table 50 Number of larvae defaecating in each six hour period in the laboratory. Larvae one year old (mean length 6.8 mm) experiencing natural photoperiod at 15°C.

The lack of a defaecation pattern was confirmed by the results shown in table 50. Fifty larvae (all approximately instar 9) were maintained in the laboratory for one week at 15°C with natural photoperiod and were fed excess Daphnia as prey. On 12/7/67 and 13/7/67 they were examined every six hours and the number defaecating in the preceeding six hours noted. χ^2 analysis showed that there was no significant

difference in the defaecation pattern throughout the 24 hour period.

These three experiments show that Pyrrhosoma has no diurnal periodicity in any part of its feeding behaviour.

12.2 MAXIMUM FEEDING RATES IN THE LABORATORY

12.2a Methods

Information was obtained on the maximum feeding rates likely to be achieved under natural conditions. In conducting maximum feeding rate experiments, larvae, after collection, were kept at the experimental temperature without food for 24 - 48 hours. The experiment then began and ran for about one week.

Daphnia obtusa from the same lab. culture used in the assimilation experiments were used throughout the study. Maximum feeding rates were measured initially as mg dry weight of Daphnia consumed per larva per day and the procedure followed was identical to that used in the assimilation experiments (see chapter 9). Larvae were fed a known number of Daphnia, greatly in excess of their requirements: the mean size and reproductive condition of the Daphnia were known and by counting the Daphnia left after each 24 hour period, the dry weight consumed per larva per day could be calculated. Fresh Daphnia were added and all the previous days prey removed daily.

All larvae were kept in individual containers (which varied in size according to the larva) and were provided with a twig to which they could cling. Photoperiod was controlled by time clocks and was as close as possible to that in the field at the time of measurement.

The size of Daphnia added to the containers varied depending on the size of the larvae. For very small individuals, all counting was carried out under a binocular microscope.

The results of maximum feeding rate experiments designed to test the effects of larval size, temperature and final instar diapause on metamorphosis are presented below.

12.2b Duration of the Experiment and the Difference Between Numbers of Daphnia and Dry Weight of Daphnia Consumed.

Figures 27a and 27b show the results of typical maximum feeding rate experiments at 15°C carried out for 11 days with final instars. Data from two groups of larvae (solid and dotted lines) are included; in the upper figure 27a, results are expressed as mean number of Daphnia eaten per larva per day, and in the bottom figure 27b, as mean dry weight eaten per larva per day.

The numbers eaten fluctuated widely, depending on prey size, but the total dry weight eaten was remarkably constant from day 4 to day 11 and it is clear that the limiting factor was not the number of prey consumed but rather its bulk (i.e. dry weight), a phenomenon noted by Holling (1966) and Salt (1967) for other carnivores.

It is clear that the sustained maximum feeding rate between days 4 and 11 was rather less than the initial rate on day 2 (and perhaps day 3). This initial high rate, followed by a decline to the sustained maximum feeding rate was probably due to larvae filling up their empty guts at the start of the experiment; once the gut was

full, the feeding rates settled down to sustained maximum levels. All calculations were therefore based on the sustainable rates and omitted the initial high rates.

12.2c Effects of Larval Size on Maximum Feeding Rate

Measurements were made at 15°C ± 0.5°C, for all sizes of larvae; the results presented in fig 28b show the maximum feeding rate (mg dry weight consumed per larva per day) as a function of larval length in mm. The relationship was linear on a log:log plot and the calculated regression was

$$y = 2.428x - 0.948$$

where $y = \text{Log}(\text{M.F.R.} \times 100)$

$x = \text{Log}(\text{larval length})$

Larval length measurements were also converted to wet weights (mg) and a regression coefficient of b = 0.924 calculated for log wet weight:log maximum feeding rate. A t test (Mather 1965) showed that this did not differ significantly from the slopes of the log wet weight versus log respiration rate regressions obtained in chapter 10. It may therefore be concluded that increasing larval size affected maximum feeding rate in the same way as it influenced respiration rate.

12.2d Effect of Temperature on Maximum Feeding Rate

Experiments were carried out with final instar larvae at 10°C and 4°C (both ±0.1°C) and with small larvae at 5°C (±0.1°C). 15 larvae were run at each temperature. The results are presented in table 51 and in fig 28a.

Temperature	Mean length of larvae (mm)	Actual maximum feeding rate mg/larva/day	Calculated M.F.R. at 15°C from regression equation 12.2c.	Actual rates as mean %s of rates at 15°C	1 S.E. of mean %s
10°C	13.50	0.442	0.626	70.6	2.27
5°C	3.25	0.0081	0.0197	41.0	4.11
4°C	13.76	0.200	0.656	33.9	1.53

Table 51 Effect of temperature on sustained maximum feeding rate in Pyrrhosoma.

Maximum feeding rates at 10, 5 and 4°C were calculated as percentages of the rates at 15°C from the individual dry weights eaten per larva per day using the regression given in section 12.2c. One standard error of the mean is shown in table 51 and ±two standard errors in fig 28a.

Since data from larvae of different sizes could be fitted easily onto one line (drawn by eye in fig 28a), it is reasonable to suggest that temperature influenced maximum feeding rate equally (i.e. there was a constant percentage change per °C) in all sizes of larvae. This was identical to the more thoroughly analysed situation for metabolic rate, where b was constant at all temperatures (see chapter 10).

From the slope of the line in fig 28a, a change of 6.2 percent per °C was calculated for maximum feeding rate with temperature. The maximum feeding rate for any size of larvae at any temperature could therefore be found from the rate at 15°C and the percentage change in this rate per °C.

The effect of temperature on metabolic rate appears to differ from its effect on maximum feeding rate below 10°C. This is made clear from the following comparison. Metabolic rate data are taken from chapter 10.

	Percentage of rate at 15°C in:-	
	Respiration	Maximum feeding rate
10°C	71.3 percent	69 percent
5°C	48.1 percent	38 percent

At 10°C agreement was fairly good, but at 5°C low temperatures depressed maximum feeding rate more than metabolic rate so that the relationship between metabolic rate and temperature was not linear (see chapter 10), but the relationship between maximum feeding rate and temperature was.

Also shown in fig 28a is a curve in which the change in maximum feeding rate was predicted from the effect of temperature on gut clearance time. Measurements of gut clearance time are described in section 12.3 below and for the present it is sufficient to note that the effect of temperature on maximum feeding rate was assumed to be the reciprocal of the effect of temperature on gut clearance time i.e. if gut clearance time was doubled, maximum feeding rate was halved, etc.

It is clear from fig 28a that the depression of maximum feeding rate with falling temperature, predicted from the change in gut clearance time, followed fairly closely the observed depression of metabolic rate with temperature shown above: in other words, temperature affected gut activity and total metabolism in much the same way, which might have been expected. It is also apparent, however, that as with total metabolic rate, below 10°C maximum feeding rate was actually depressed more by temperature than was predicted from the gut clearance data.

The variable effects of temperature on these different components below 10°C is discussed further in section 12.6.

12.2e Changes in Maximum Feeding Rate in Final Instars.

Maximum feeding rates in final instars at 15°C were measured monthly between October 1967 and February 1968. From February onwards, larvae rapidly entered metamorphosis on being brought into the laboratory at 15°C and maximum feeding rates could not be measured. However, there was no reason to believe that before entering metamorphosis, rates in March and April were any different to those of premetamorphosis February larvae of similar size. The effects of metamorphosis on maximum feeding rate were also investigated. The results of both experiments are presented in tables 52 and 53.

The monthly mean maximum feeding rates increased between mid-December and mid-January, at about the time when larval diapause was presumed to have ended (see chapter 13). The increased may have been associated with the termination of diapause and is discussed further in chapter 13. However, all pre and post diapause final instar data fitted the regression line shown in fig 28b so that maximum feeding rates of final instars were calculated directly from this regression, regardless of their probable diapause condition.

The effects of metamorphosis were more pronounced. Maximum feeding rates of larvae in metamorphosis were measured until feeding ceased, prior to entering stage 3. The data were arranged so that the first day on which no feeding occurred was designated day 0 and the days previous to this day -1, -2 etc.

Collecting date	Mean larval length (mm)	n	Mean maximum feeding rate mg/larva/day	1 S.E.	Probable diapause condition
20/10/67	13.00	154	0.603	0.014	diapause larvae
18/11/67	13.10	60	0.638	0.029	
12/13/67	13.35	64	0.693	0.023	
15/ 1/68	13.54	80	1.007	0.023	post diapause larvae
27/ 2/68	13.79	60	0.957	0.030	

Table 52 Change in maximum sustained feeding rate of final instar Pyrrhosoma through winter: n is the number of larval-days, i.e. total observations on the dry weight eaten by each larva each day.

Days from stopping feeding	Mean maximum feeding rate mg/larva/day	Metamorphosis stage
-6	0.879	Early stage 2 metamorphosis
-5	0.535	
-4	0.412	
-3	0.367	
-2	0.269	
-1	0.138	Late stage 2 metamorphosis
0	0	Stage 2-3 border line: labial muscles start to atrophy.
+1	0	Stage 3 metamorphosis: atrophy of labial muscles complete.

Table 53 Change in maximum feeding rate during metamorphosis in Pyrrhosoma at 15°C.

About one week before feeding stopped (day -6) maximum feeding rates of early stage 2 larvae were slightly less than in the post diapause larvae shown in table 52: feeding rates then progressively declined as shown in table 53.

Maximum feeding rates of field larvae were not calculated after March, once the population had entered metamorphosis, because of the difficulty in extrapolating between the timing of the laboratory decline in maximum feeding rate at 15°C and the much longer time spent in metamorphosis in the field; but it is probable that potential maximum feeding rates did decline throughout metamorphosis in the field, as in the laboratory though over a longer period of time.

12.3 ESTIMATION OF FIELD FEEDING RATES FROM GUT CLEARANCE TIME

Since it was impossible to estimate field feeding rates directly, an indirect method had to be used based on the often used technique of measuring the quantity of material in the gut and gut clearance time.

12.3a Gut Clearance Times

The time in hours for prey to pass through the gut from consumption to defaecation was designated the gut clearance time. Because of the lack of periodicity in feeding and defaecation, this figure, divided into 24, gave the number of times in a day that the gut contents turned over, or were replaced.

Using Daphnia as prey, gut clearance times were estimated for different sizes of larvae at 5, 10, 15 and 22°C. After defaecation,

larvae were kept without food for 24 - 48 hours at the experimental temperature and allowed to clear their guts. They were fed for 10 minutes after which time all Daphnia were removed and the mid-point of this feeding period taken as the average time at which consumption occurred. Larvae were examined every hour and average faeces production times were taken as the point midway between the last observation before faeces were produced and the first on which faeces were observed.

Chironomids could not be obtained in sufficient quantities to repeat the experiment in detail and gut clearance time with Chironomids was only measured for final instars at 15°C, following the procedure outlined for Daphnia.

Two further checks on gut clearance times were made. During the assimilation experiments with Chironomids and Daphnia carried out at 15°C (see chapter 9), the number of faecal pellets produced each day by each final instar was recorded. All faeces were approximately the same size, and the number of pellets produced per larva per day from the two types of food presumably bore the same relationship to one another as the total gut clearance times. The Chironomid data were compared with Daphnia data obtained with similar sized larvae at the same time of the year (January).

Finally, gut clearance times of field larvae were checked from the experiment described in section 12.1b, the collections made every six hours on 8/8/66, but instead of taking the mean time of first faeces production, the mean time for complete gut clearance (i.e. last

faeces production) was calculated. Pond temperatures in early August averaged 15°C so that by bringing larvae into the laboratory as soon as possible after collection and placing them in the 15°C constant temperature room, disturbance was minimal. They were then visited regularly and the time of production of the last faecal pellet containing food remains taken from the time half way between two visits, as in the laboratory Daphnia experiments. The data obtained in the 24.00 h collection were excluded from the analysis because of the long time elapsing between the first and second visits.

The results of the laboratory gut clearance experiments with Daphnia are presented in figs 29a and b. The upper graph shows the effect of larval size on gut clearance at 15°C (head width, rather than length, was found to give a better correlation with clearance time: the reason for this is not known). The equation of the line is:-

$$y = 3.268x + 2.640$$

where y = gut clearance time in hours

x = larval head width in mm.

The lower figure shows the gut clearance times at 5, 10 and 22°C expressed as percentages of the time at 15°C. Larvae of all sizes were used and their actual clearance time at these temperatures expressed as percentages of their calculated clearance time at 15°C. Fig 29b shows the mean percentages ± two standard errors. Between 5 and 15°C. gut clearance times increased by 10.6 percent per °C fall in temperature, and between 15 and 22°C decreased by 3.5 percent per

°C rise in temperature.

From the equation for gut clearance times at 15°C, and the percentage changes per °C, gut clearance times with Daphnia for any size of larva at any temperature could be obtained.

The gut clearance time in the laboratory of 14 final instar larvae fed with Chironomids at 15°C was found to be 28.92 hours (± 7.48 hours). This was 1.9 times longer than the calculated time of 15.2 hours for final instars with Daphnia.

The mean number of faecal pellets produced per day by final instar larvae at 15°C, when fed Chironomids was obtained from data on 20 larvae over a period of 14 days. Each larva produced 0.89 (±0.099) pellets per day; (so that most larvae had at least one day when no pellets were produced, even though feeding was continuous). 26 final instars fed on Daphnia produced, on average, 1.95 (±0.168) pellets per day for 7 days, so that the rate of faeces production with Daphnia was about 2.2 times that with Chironomids.

The mean time taken to clear the gut completely after collection by the small larvae taken on 8/8/66, at 15°C, was 10.27 ± 2.25 hours (n = 49). This figure may be interpreted in a number of ways. It was unrealistic to assume that all the larvae had just fed before capture so the mean figure was not the total gut clearance time as in the laboratory experiments. Observation supported the more likely interpretation that larvae on capture were in all stages of gut clearance, from individuals just about to produce a pellet and clear

the gut completely (so that total clearance time in the laboratory was zero), to larvae with full guts from which maximum gut clearance times would be obtained. The mean figure represented a point half way between these two extremes and was, therefore, half the total clearance time for these August larvae: the total gut clearance time was therefore 20.54 hours. The calculated gut clearance time with Daphnia for larvae of this size (mean head width 2.4 mm) was 10.48 hours, so that if the above interpretation is correct, field gut clearance times were 1.96 longer than those estimated with Daphnia in the laboratory. Since Chironomids formed at least 75 percent by dry weight of the food eaten by Pyrrhosoma in the field (see chapter 8), this result for field gut clearance times was consistent with the laboratory measurements using Chironomids as prey, in which gut clearance times were also approximately twice as long as were found with Daphnia as prey.

In calculating field gut clearance times for larvae of different sizes at different temperature, clearance times with Daphnia were first obtained and then doubled, since this appeared to be the procedure most consistent with the data obtained.

No attempt was made to analyse in detail a number of other variables that might have influenced gut clearance times, though it was shown that starvation had an effect (see fig 30). Here the mean regression with 95 percent confidence limits for the data presented in fig 29a was redrawn for comparison with individual measurements of gut clearance time in 13 larvae starved for a week at 15°C, rather

than the usual time of up to 48 hours. It is obvious that gut clearance times in the group starved for one week were longer than in the larvae starved for up to 48 hours. It was assumed, however, that larvae in the field only rarely had to go without food for more than 24 - 48 hours and the effects of longer starvation were discounted.

12.3b The Quantity of Material in the Gut

In order to avoid killing the larvae, this was estimated indirectly. Larvae were brought back to the laboratory in individual tubes without food and allowed to clear their gut contents completely. All faeces were collected as soon as possible after production, placed on pre-weighed foil trays and dried in a vacuum oven at 60°C. In this way the total dry weight of gut contents per larva, after complete assimilation had taken place, was obtained. From the calorific value of field faeces (chapter 3, table 5, sample 30), this was converted to the total calories in the gut after complete assimilation and, from the percentage assimilation data for larvae of this size, the total calories in each gut before assimilation could be found.

The total calories in each gut before assimilation, multiplied by the number of times in a day this was replaced, gave the field feeding rate in calories per larva per day. Weights of gut contents were obtained in ponds B and F in eleven months, June 1967 - April 1968 inclusive, for senior age class larvae only, since it was impossible to collect the faeces of the junior age class sufficiently accurately. No estimate was made in May for the senior age

class so as not to disrupt emergence. It was found necessary to group faeces from several of the smaller larvae together to obtain satisfactory weights, even with the Cahn Electrobalance, so that mean weights per larva were calculated without standard errors.

Larvae taken in the monthly population samples in E and F were used to obtain the necessary data, together with any extra larvae taken for growth rate estimates. Head widths, from which gut clearance times were calculated, were measured, as were total lengths.

A number of larvae were always taken that had no food in the gut: either they had just defaecated prior to capture or had not fed for some hours through moulting or food shortage. Calculation of the mean caloric content of each larval gut naturally included these zero samples.

The results obtained are presented in table 54.

12.3c Calculation of Field Feeding Rates

Data presented in 12.3a and 12.3b were combined and field feeding rates calculated for the 1966 year class in ponds E and F between June 1967 and April 1968. Field feeding rates as calories ingested per larva per day were given by the equation:

$$\frac{\text{(Mean calories of faeces produced per larva)} \times 24}{(100 - \text{\% Assimilation in terms of calories}) \times \text{(Gut clearance time in h.)}} \times 100$$

Pond temperatures were taken from the temperature curves shown in fig 7 (chapter 2) at the time of collection. Larval lengths (for

percentage assimilation) and head widths (for calculation of clearance time) were taken from table 54.

Results are presented in table 55, which shows the calculated consumption rates (calories per larva per day) on specified dates. These were plotted on mm graph paper and from the areas under the curves, total consumption in the two ponds from June 1967 to April 1968 was found.

POND B. TOTAL CONSUMPTION BY SENIOR AGE CLASS, JUNE 1967 - APRIL 1968 INCLUSIVE =

137.3 calories per larva.

POND F. TOTAL CONSUMPTION OVER SAME PERIOD =

154.3 calories per larva.

It is clear that the results from the two ponds showed close agreement.

12.4 FIELD FEEDING RATES CALCULATED FROM GROWTH RESPIRATION AND FAECES

Larval consumption could also be estimated by summing the calories incorporated into growth (and exuvia) plus the required calories and the unassimilated calories (faeces) i.e. P + R + Ev + F.

Agreement between estimates made in this way and the independent estimates based on gut clearance times provided a check on the accuracy of all the measurements and assumptions made during the study.

All estimates were made on a monthly basis or for shorter time intervals at the hatch and during metamorphosis, as far as usual for

Sample date	Pond	n Number of larvae in sample	Mean dry wt. of faeces produced/larva (mg)	Mean cals of faeces produced/ larva	% not producing any faeces	Mean head width of sample larvae (mm)	Mean length of sample larvae (mm)
12/ 6/67	B	40	0.0038	0.011	32.5	1.49	4.80
13/ 6/67	F	40	0.0051	0.014	10.0	1.50	4.81
10/ 7/67	B	39	0.0093	0.026	15.4	1.96	6.54
10/ 7/67	F	33	0.0084	0.023	21.2	2.04	7.05
1/ 8/67	B	35	0.0113	0.032	25.7	2.39	8.05
2/ 8/67	F	29	0.0226	0.063	13.8	2.74	9.31
4/ 9/67	B	39	0.0296	0.083	23.1	2.96	10.15
5/ 9/67	F	35	0.0377	0.105	8.6	3.00	10.59
2/10/67	B	41	0.0379	0.106	29.3	3.64	11.93
3/10/67	F	35	0.0335	0.094	20.0	3.66	12.13
25/10/67	F	16	0.0707	0.198	6.3	3.81	12.50
13/11/67	B	35	0.0387	0.108	22.9	3.84	12.80
11/11/67	F	33	0.0756	0.211	24.2	3.83	12.83
12/12/67	B	20	0.0337	0.094	25.7	3.81	12.86
13/12/67	F	22	0.0469	0.131	13.6	3.88	13.60
15/ 1/68	B	28	0.0333	0.093	21.4	3.84	13.02
16/ 1/68	F	31	0.0219	0.061	35.5	3.85	13.27
19/ 2/68	B	37	0.0484	0.135	18.9	3.86	12.95
18/ 2/68	F	30	0.0422	0.118	30.0	3.84	13.33
25/ 3/68	B	28	0.0749	0.209	32.1	3.85	13.61
26/ 3/68	F	34	0.0812	0.227	29.4	3.86	13.48
24/ 4/68	B	33	0.0706	0.197	15.2	3.84	14.11
24/ 4/68	F	29	0.0927	0.259	6.9	3.84	13.93

Table 54 Sample data obtained in ponds B and F for 1966 year class on the dry weight of faeces material produced per larva after collection.

Sample date	Pond	Mean temperature at time of collection (°C)	Estimated gut clearance time in field (hours)	Consumption cals per larva per day
12/ 6/67	B	13.4	17.6	0.195
13/ 6/67	F	12.8	18.6	0.243
10/ 7/67	B	15.3	17.9	0.400
10/ 7/67	F	13.9	20.8	0.301
1/ 8/67	B	15.4	20.6	0.379
2/ 8/67	F	14.7	23.9	0.603
4/9/ 67	B	13.0	29.0	0.616
5/ 9/67	F	12.0	32.8	0.677
2/10/67	B	10.8	41.9	0.492
3/10/67	F	9.9	44.9	0.403
25/10/67	F	6.5	57.3	0.652
13/11/67	B	5.0	62.4	0.322
11/11/67	F	4.5	63.9	0.615
12/12/67	B	2.9	68.7	0.255
13/12/67	F	2.6	70.7	0.322
15/ 1/68	B	2.8	69.5	0.247
16/ 1/68	F	3.0	68.9	0.161
19/ 2/68	B	3.1	68.7	0.363
18/ 2/68	F	2.7	69.9	0.307
25/ 3/68	B	6.5	57.7	0.650
26/ 3/68	F	5.3	61.8	0.663
24/ 4/68	B	7.3	55.0	0.624
24/ 4/68	F	5.8	59.8	0.764

Table 55 Calculated consumption (calories per larva per day) on specified dates between June 1967 and April 1968 in ponds B and F.

calculations during these periods: month has again been utilised for convenience to identify these shorter time intervals. Growth was taken from tables 20 - 23 (chapter 7), respiration from tables 43 - 46 (chapter 10) and exuvium production from table 47 (chapter 11), all as calories per larva per month. The total of the 3 components gave calories assimilated per larva per month. From the larval lengths on the first of the month (tables 20 - 23 chapter 7) percentage assimilation could be estimated (fig 19a, chapter 9) and hence the mean percentage assimilation during the month from:

$$\frac{(\% \text{ assimilation on 1st of month}) + (\% \text{ assimilation on 1st of next month})}{2}$$

Therefore total calories consumed per month could be found.

The results are presented in tables 56 - 59. The data for the 1966 year class in ponds B and F between June 1967 and April 1968 (tables 57 and 60) may be compared with the estimates of consumption, using gut clearance time, over the same period viz:-

TOTAL CONSUMPTION PER LARVA, JUNE 1967 - APRIL 1968.

	BY GUT CLEARANCE TIME METHOD	FROM P + R + Ev + F
POND B	137.3 cals	151.2 cals
POND F	154.3 cals	147.7 cals

The estimate from (P + R + Ev + F) was 10.1 percent higher than the estimate based on gut clearance time in pond B and 4.3 percent lower in pond F. The agreement between the two virtually independent estimates is probably as good as can be expected in any

study of this type. It is clear, in fact, that the two methods were not completely independent since both utilised the percentage assimilation data, but since they were otherwise totally different in approach, this does not greatly detract from the value of the observed agreements.

All subsequent calculation of individual consumption were based on the sum of growth, respiration etc., since this appeared to be a reliable estimate and provided data on very small larvae which could not be obtained in any other way.

The pattern of individual consumption in the different year classes and in the two ponds were very similar. Consumption per larva in the second year (as the senior age class) was obviously much higher than in the first year (as the junior age class) but both showed maxima in September, two months after maximum pond temperatures were reached. The absolute maximum monthly ingestion rates per larva occurred in April and May when metabolic rate increased markedly with metamorphosis.

From the data, it appears that a consumption of approximately 185 - 190 calories is required to "produce" one imago from a newly hatched larva in the field.

12.5 THE DIFFERENCE BETWEEN MAXIMUM FEEDING RATES AND FIELD FEEDING RATES

Comparison was made between the actual monthly caloric consumption per larva described in the preceding section and the potential maximum feeding rates in larvae of this size calculated from the data presented in section 12.2. Maximum feeding rates were estimated initially as dry weights consumed per larva per day. As an indication of the

Month	Total assimilated energy (P+R+Ev) cals/larva/month	Mean % assimilation	Total consumption cals/larva/month	
July 1966	0.183	94.70	0.194	
Aug	0.444	94.25	0.472	
Sept	0.693	93.80	0.739	
Oct	0.457	93.50	0.488	
Nov	0.215	93.40	0.231	
Dec	0.175	93.40	0.188	
Jan 1967	0.164	93.40	0.176	
Feb	0.174	93.40	0.187	
Mar	0.275	93.40	0.294	
April	0.826	93.20	0.883	
May	1.461	92.80	1.573	
June	3.842	92.15	4.169	
July	8.762	91.05	9.623	
Aug	14.601	89.75	16.268	
Sept	19.329	88.45	21.854	
Oct	15.889	87.50	18.158	
Nov	7.492	87.15	8.598	Total
Dec	5.404	87.05	6.207	151.189 cals
Jan 1968	6.190	87.00	7.115	
Feb	7.437	86.95	8.554	
Mar	18.028	86.70	20.794	
April	25.849	86.60	29.849	
May 1st-22nd	28.178	86.60	32.537	
May 23rd-30th	0.000	0.00	0.000	

Table 56 Total consumption (calories per larva per month) in pond B; 1966 year class

Month	Total assimilated energy (P+R+Ev) cals/larva/month	Mean % assimilation	Total consumption cals/larva/month
July 1966	8.799	91.20	9.648
Aug	14.330	89.80	15.958
Sept	16.094	88.50	18.185
Oct	15.012	87.65	17.129
Nov	9.730	87.30	11.145
Dec	8.706	87.10	9.994
Jan 1967	8.507	86.95	9.784
Feb	13.565	86.70	15.645
Mar	12.823	86.45	14.833
April	25.243	86.40	29.216
May 1st-24th	27.126	86.40	31.395
May 25th-31st	0.000	0.00	0.000

Table 57 Total consumption (calories per larva per month) in pond B; 1965 year class

Month	Total assimilated energy (P+R+Ev) cals/larva/month	Mean % assimilation	Total consumption cals/larva/month
July 1967	0.116	94.75	0.122
Aug	0.451	94.35	0.479
Sept	0.724	93.80	0.771
Oct	0.443	93.50	0.473
Nov	0.187	93.40	0.201
Dec	0.166	93.40	0.178
Jan 1968	0.166	93.40	0.177
Feb	0.159	93.40	0.170
Mar	0.274	93.40	0.294
April	0.628	93.25	0.673
May	1.698	92.85	1.828
June	6.615	91.85	7.201

Table 58 Total consumption (calories per larva per month) in pond B; 1967 year class.

Month	Total assimilated energy (P+R+Ev) cals/larva/month	Mean % assimilation	Total consumption cals/larva/month	
July 1967	0.111	94.75	0.118	
Aug	0.411	94.35	0.436	
Sept	0.563	93.90	0.605	
Oct	0.519	93.55	0.555	
Nov	0.171	93.40	0.183	
Dec	0.159	93.40	0.170	
Jan 1968	0.162	93.40	0.174	
Feb	0.150	93.40	0.161	
Mar	0.182	93.40	0.195	
(1966 and 1967 year classes joined at this point)				
April 1967	0.484	93.35	0.518	
May	1.138	93.10	1.223	
June	5.033	92.20	5.460	
July	13.055	90.55	14.418	
Aug	14.254	89.10	15.998	
Sept	18.602	88.15	21.102	
Oct	12.901	87.45	14.753	
Nov	10.442	87.10	11.989	Total
Dec	7.117	86.90	8.189	147.666 cals
Jan 1968	5.430	86.80	6.256	
Feb	5.857	86.75	6.752	
Mar	11.246	86.65	12.978	
April	25.722	86.40	29.771	
May 1st-24th	28.851	86.40	33.392	
May 25th-31st	0.000	0.00	0.000	

Table 59 Total consumption (calories per larva per month) in pond F: composite life cycle from 1966 and 1967 year classes.

likely maximum caloric consumption, a calorific value of 5,000cal per g dry weight was assumed for typical prey.

The potential maximum caloric ingestion per larva per month was calculated for the time intervals shown in tables 56-59. The calculation was carried out using mean larval lengths during each month (from tables 20-23, chapter 7) and the regression equation for maximum feeding rate versus larval length at 15°C (section 12.2c) corrected for the mean monthly temperature prevailing in the pond. The latter procedure made use of the percentage change in maximum feeding rate with temperature (section 12.2d). The actual calories consumed per larva per month shown in table 56-59 were calculated as percentages of the estimated maximum potential rates. The results are given in fig 31, where all year classes in the two ponds are plotted together from the hatch in July to March prior to entering metamorphosis. The data show some scatter, but the overall patterns are very similar.

Actual feeding rates were always much less than the potential maximum feeding rates and, at the very most, were never more than 70 percent of the latter and were usually less than 50 percent. Actual feeding rates were closer to the potential maximum in summer (both after the hatch and in the second summer) than in the two winters. Larvae in their first winter showed the lowest values of all, with actual rates only 20 percent of the maximum rates.

12.6 DISCUSSION

Gut contents have been used by many workers to estimate field feeding rates. However, only the present work and that of Phillipson

(1960b) appear to have estimated the amount of material in the gut before digestion from faeces production and percentage assimilation data. Phillipson did not incorporate measurements of gut clearance time however in his study of Mitopus morio, but assumed that the faeces produced in the 24 hours after sampling could be used to calculate food intake per 24 hours. This was only justified if total gut clearance times were longer than 24 hours and, since they were probably shorter than this (19 hours in males, 15 hours in females Phillipson 1960 a), field feeding rates may have been underestimated. This appears to be an additional reason why in many cases food intake estimaes of energy expenditure were less than respiratory estimates (Phillipson 1960 b, table 3). However, providing the estimated weight or calorific value of gut contents is combined with gut clearance time data, as for Pyrrhosoma, the method appears to give very satisfactory results.

Holling (1966) discussed errors in estimating field feeding rates from the weight of gut contents and gut clearance times. The method gives the most reliable results when the capture of a single prey item does not account for most of the material in the gut, when there is no periodicity in feeding and when gut clearance times are relatively long. All these conditions appear to be met by Pyrrhosoma. Methods of measuring gut clearance times have received attention from fisheries biologists. Errors due to variable rates of passage with different prey types (e.g. Hess and Rainwater 1939, Gerking 1962) appear to have been satisfactorily dealt with in the present study

(see chapter 8). It also appears that many of the other possible sources of error known to be operating in fish (see Harrington 1957, Blaxter 1962-3, Davis and Warren in Ricker 1968, Dadikian in Winberg 1956 etc.), were not present in Pyrrhosoma.

Field consumption estimates, by combining growth, respiration and faeces production, have been used by several workers e.g. Golley and Gentry (1964), McNab (1963), Nielson (1961). Winberg (1956) argues that this is probably the best method available for estimating field feeding rates in fish. In the present study, this was probably also true, particularly for small larvae where it is difficult to see how field feeding rates could have been estimated in any other way. However, the method should obviously be checked wherever possible by an alternative procedure, as was done for larger Pyrrhosoma larvae using the gut clearance time approach.

The dependence of feeding rate on prey density has been demonstrated for many species of invertebrate and vertebrate carnivores by Holling (1965, 1966) and also, using a completely different approach, by Brocksen et al. (1968). The exact form of the functional response in Pyrrhosoma, however, was atypical of most invertebrates in which feeding rate is usually a curvilinear response to increasing prey density, i.e. feeding rate increases at a progressively decreasing rate to a sustained maximum. Holling (1959 b, 1961, 1966) has termed this a type 2 response and suggests that it is due to increased prey handling time as more are captured. The linear response shown by Pyrrhosoma (Holling type 1) is much less frequently observed, It may have

been due to the very short time required to capture and consume Daphnia so that handling time was never limiting. Alternatively, it could have been due to the fact that hunger did not affect the reaction distance of Pyrrhosoma to prey (Holling 1968 in Southwood 1968). Further work is required on the functional response of Odonata larvae.

The methods employed to measure field feeding rates were simplified because Pyrrhosoma appeared to show no periodicity in food intake or faeces production. Diurnal periodicity in Aeshna larvae has been demonstrated by Paulian and Serfaty (1944) for locomotory activity; by Berezina (1959) for respiration and feeding and by Pritchard (1964) for faeces production. Further work is required before it is possible to say whether Pyrrhosoma was similar to other Zygoptera in the lack of any obvious circadian rhythms. Clearly it was very different to Aeshna (Anisoptera) in this respect.

The effects of metamorphosis on feeding in Odonata larvae have been examined by several workers. Hormondy (1959) found that feeding stopped for a few days to a week before emergence in Tetragoneuria and Corbet (1962) gives other similar examples. Pyrrhosoma was typical in that feeding stopped with histolysis of the labial muscles on entering stage 3 metamorphosis. However, no previous quantitative measurements appear to have been made showing a steady decline in maximum feeding rate similar to that noted during stage 2 metamorphosis in Pyrrhosoma.

The slopes of the regression lines (b) for maximum feeding rate versus larval wet weight and respiration rate versus larval wet weight were not significantly different. There do not appear to be many studies where these two components have been compared in this way within a single species (Warren and Davies in Gerking 1967).

The effect of temperature on maximum feeding rate was more complex. Below 10°C, maximum feeding rate was depressed more than total metabolic rate, or than was predicted from the effects of temperature on gut clearance time. The latter suggests that maximum feeding rates were not simply a function of gut clearance time at 4-5°C, but were less than gut clearance times would have permitted. The larvae of Anax junius required more intense illumination at lower temperatures before they could perceive moving prey (Crozier et al. in Corbet 1962). Although Pyrrhosoma used the antennae for prey detection, a similar response requiring greater stimulus for prey detection and capture at low temperatures may have been present, as has been shown in A. junius. Because prey capture required greater stimulus at low temperatures, feeding rates were depressed more than was predicted from gut clearance times alone. A similar phenomenon may be present in a more extreme form in larvae of Erithroma najas (Hans) and Coenagrion hastulatum (Charp) which stopped feeding completely at 4°C (Fischer 1965). Dytiscus marginalis larvae appeared to starve to death during winter because respiration rate declined less than feeding rate at low temperatures (Blunck 1924). Laboratory observations showed that feeding in Pyrrhosoma continued even at 2-3°C; this, and the presence of food in

the gut in larvae taken throughout the winter (see table 53) suggests that Pyrrhosoma never experienced temperatures low enough to stop feeding during the present study.

A number of workers have studied maximum feeding rates in Odonata larvae e.g. Fischer (1964), Pacaud (1948), Berezina (1946), Hinman (1934), Gajevskaja (1959). Usually this has been carried out to obtain some idea of the feeding rates in the field and such information has been used to demonstrate the predation pressure that Odonata are likely to excert on prey species. Gajevskaja (1961) expressed surprise at the high maximum levels of consumption, greatly in excess of maintainance requirements, found in Libellula and other Odonata. It is clear from the present study that these maximum potential feeding rates are of little use in providing information on actual field feeding rates. If Pyrrhosoma is typical of other species, arguments on the predation pressure excerted by Odonata larvae in aquatic ecosystems (e.g. Hinman 1934, Berezina 1946, Gajevskaja 1961) that are based on maximum laboratory feeding rates are likely to be erroneous.

Pyrrhosoma appears to be the first invertebrate carnivore in which actual food intake in the field has been compared with the maximum potential energy intake for the same size of larvae at the same temperature. Less detailed studies on similar lines were made for non-carnivore invertebrates by Berner (1962) on the copepod Temora and Burns (1966) (F.H. Rigler pers. comm. 1967) for Daphnia. Burns concluded that Daphnia were feeding at or near to their maximum rates in the field: a similar situation probably existed in Temora so that

Pyrrhosoma feeding well below its maximum feeding rate was clearly quite different in this respect.

In Pyrrhosoma, feeding rate was a function of prey density and it is probable that the changes that occurred in the actual field feeding rates as percentages of the maximum feeding rates were due to natural changes in the density of available prey. Where field feeding rates were a small percentage of the potential maximum rates, as in the winter, prey densities were low and vice-versa. This difference between maximum potential feeding rate and actual feeding rate raises a number of interesting points relevant to current controversy on the balance between animal populations and their food supply (e.g. Wynne-Edwards 1962, Lack 1954). As Odum et al (1962) pointed out "one of the reasons why this question is often debated but seldom answered is that while a great effort is often made to study population dynamics, little effort has been expended on measuring the actual amount of food needed by a population in terms of what is actually available in nature". Although the present study did not attempt to elucidate the problem of population regulation and food supply in Pyrrhosoma, it confirms that ecological energetics may provide a valuable new approach to these problems. For example, were the populations of Pyrrhosoma larvae in ponds B and F "short of food"? Since development times were normal i.e. took two years, it is possible that they were not, in one sense, "short of food". On the other hand, an average individual in these populations rarely fed at more than 40-50 percent of its maximum rate. It is clear that

the Pyrrhosoma larvae with an atypical three year development cycle studied by Macan (1964) must have had actual feeding rates that were an even smaller percentage of the maximum feeding rate - probably less than 10 percent. Food shortage is therefore a continuum, varying between just below the maximum feeding rate to complete starvation. At various levels of food shortage, thresholds are crossed and the behaviour and development of individuals, and of the population, may be expected to change in a characteristic manner. It is suggested that a more precise definition of the amount of food shortage and careful elucidation of energy utilisation at critical "threshold" levels of feeding will provide valuable insight into the problems of population regulation and food supply.

Two independent estimates of field feeding rates were made in the present study, one based on summing growth, respiration and faeces, and the other from gut contents and the rate of gut clearance. These two estimates of field feeding rate agreed within 10.1 percent in one pond and 4.3 percent in the other. The errors were therefore similar to those reported by Engelmann (1961) who found a discrepancy of 5 percent in independent estimates of the components of the energy budget of oribatid mites. Greater precision than this is probably impossible at the present time. It is unfortunate that many workers have been content to balance energy budgets "by difference" e.g. Saito (1965, 1967), Riegert (1965), Mann (1965). Agreement of the type observed in the present study provided a valuable check on the methods and assumptions made for all the energy budget measurements.

Fig. 26. The effect of prey density (Daphnia) on the feeding rate of final instar Pyrrhosoma larvae at 15°C. Larvae had been starved for 48h prior to feeding. The figure shows the mean number of Daphnia consumed in one hour (± 2 standard errors) plotted against the initial prey density. Regression drawn by eye.

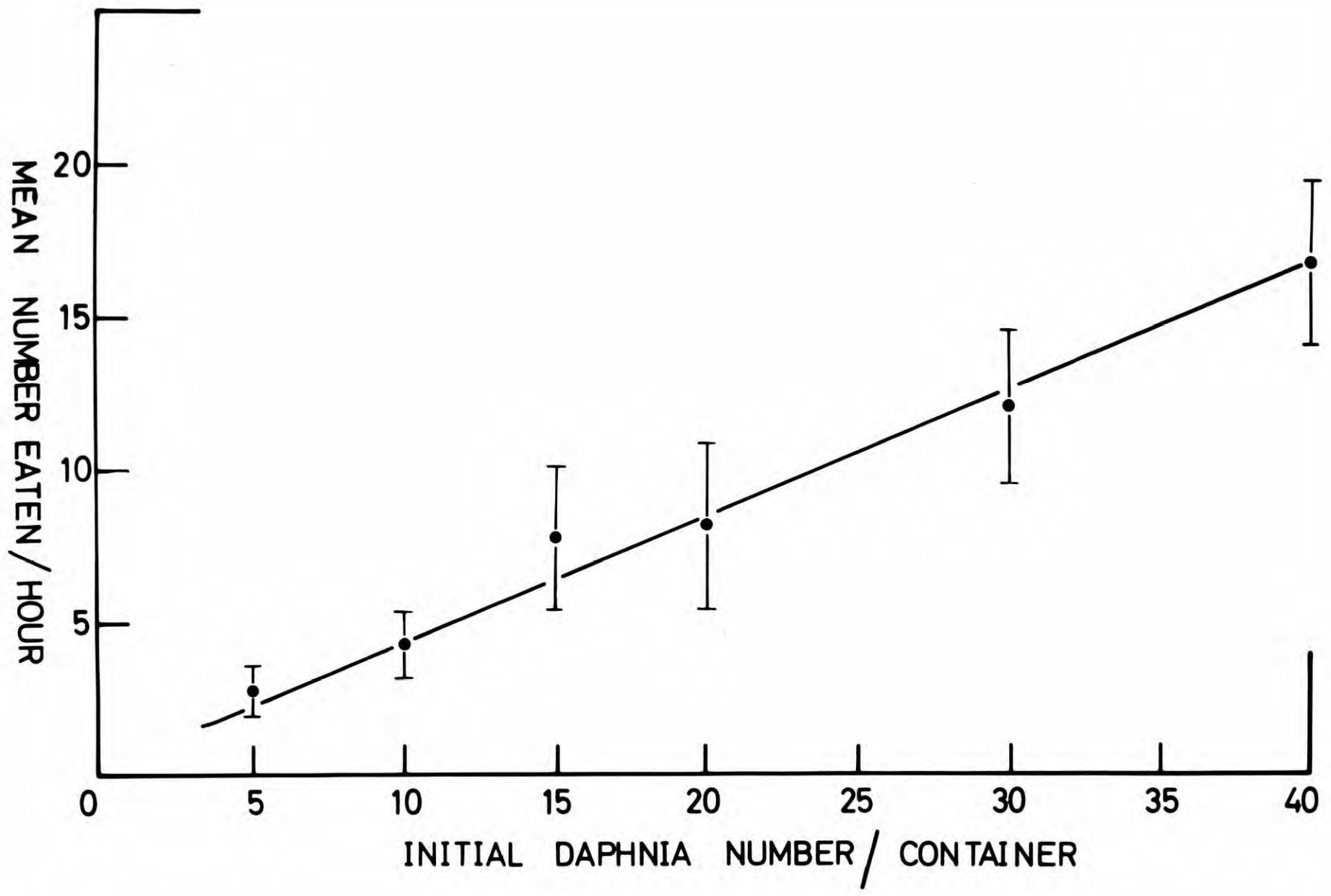
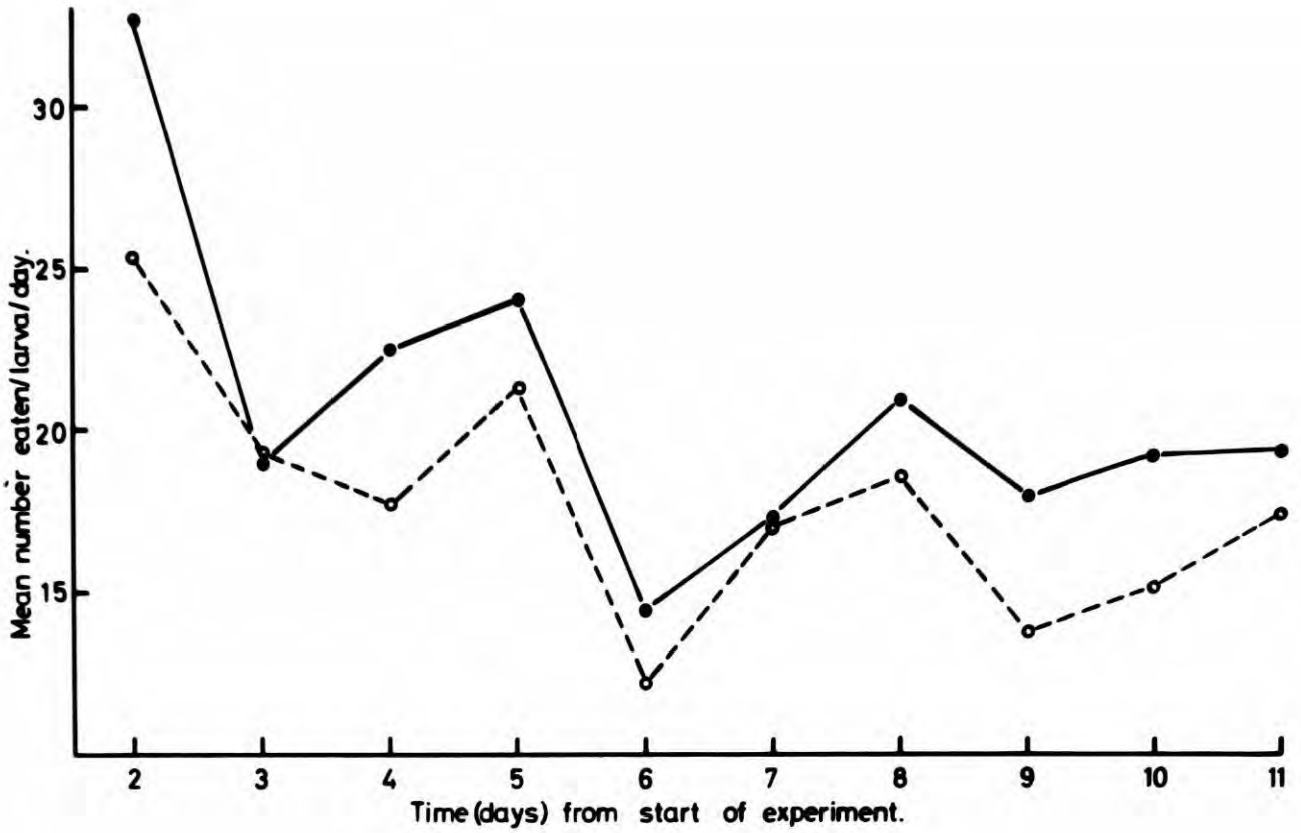

MEAN NUMBER EATEN / HOUR
20
15
10
5
0
5
10
15
20
25
30
35
40
INITIAL DAPHNIA NUMBER / CONTAINER

Fig. 27a. Typical experiments on maximum feeding rate in Pyrrhosoma, showing the mean number of Daphnia consumed per larva per day over 11 days. (Final instar larvae at 15°C). Data from two different groups of larvae (solid and dotted lines) are shown.

Fig. 27b. The experiments shown in 27a (above), but with consumption expressed as mean dry weight eaten per larva per day. It is clear that the dry weight of prey consumed was constant, despite fluctuations in the number of prey consumed.


Mean number eaten/larva/day.
30
25
20
15
2
3
4
5
6
7
8
9
10
11
Time (days) from start of experiment.

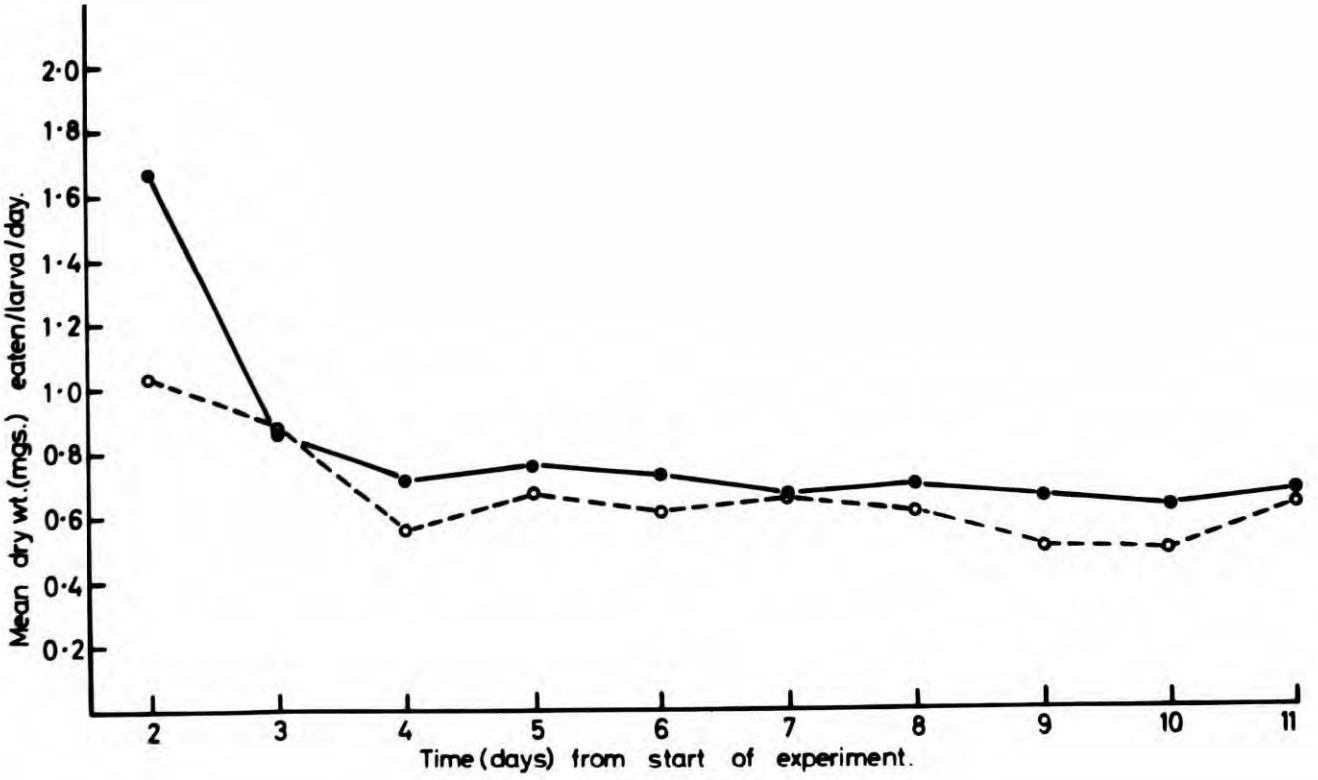
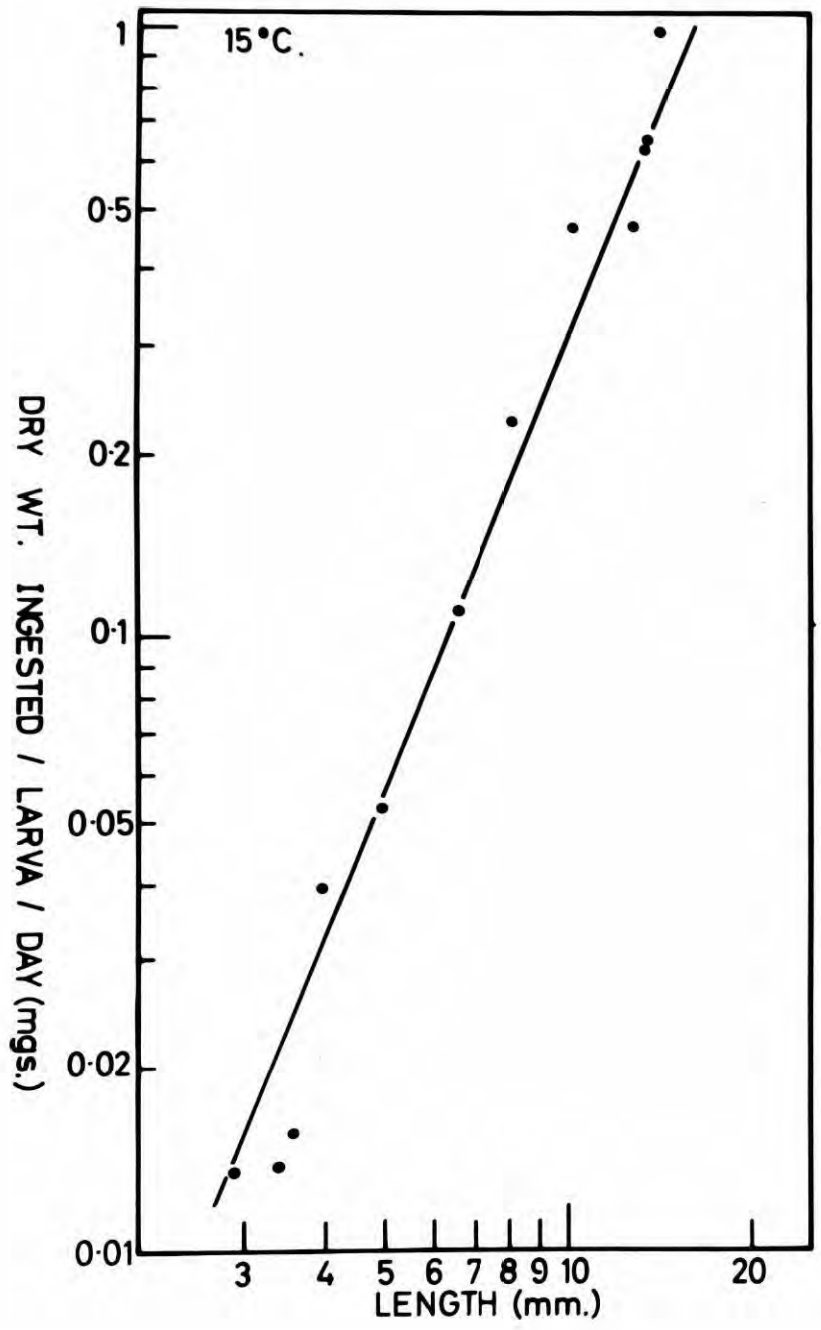

Mean dry wt.(mgs.) eaten/larva/day.
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
2
3
4
5
6
7
8
9
10
11
Time (days) from start of experiment.

Fig. 28a. The effect of temperature on maximum feeding rate in Pyrrhosoma larvae, with Daphnia as prey. Feeding rates expressed as percentages of the estimated rates at 15°C. Regression drawn by eye. Note how temperatures below 10°C depressed maximum feeding rate more than was predicted from the change in gut clearance time.

Fig. 28b. The effect of larval size on maximum feeding rate in Pyrrhosoma at 15°C, with Daphnia as prey. The calculated regression is presented in section 12.2c.


15°C.
1
0·5
0·2
0·1
0·05
0·02
0·01
DRY WT. INGESTED / LARVA / DAY (mgs.)
3
4
5
6
7
8
9
10
20
LENGTH (mm.)

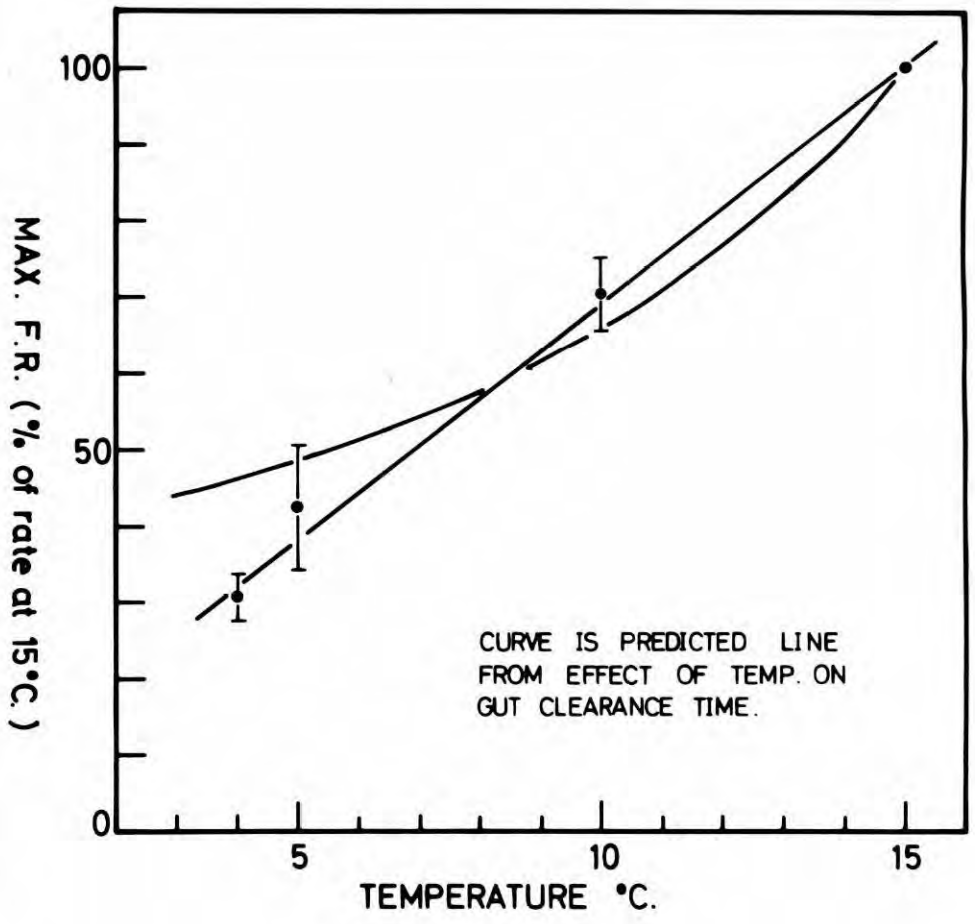
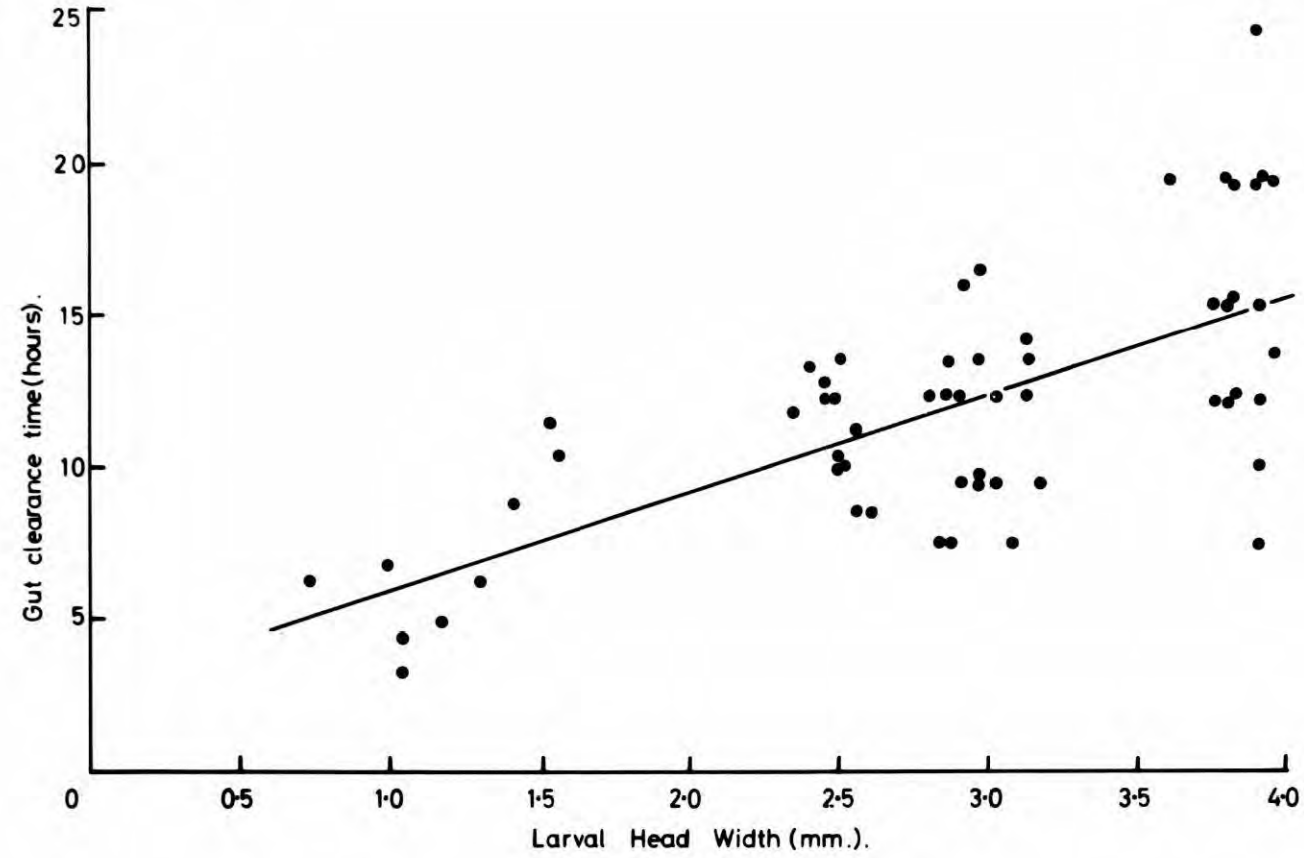

100
50
0
MAX. F.R. (% of rate at 15°C.)
CURVE IS PREDICTED LINE
FROM EFFECT OF TEMP. ON
GUT CLEARANCE TIME.
5
10
15
TEMPERATURE °C.

Fig. 29a. The effect of larval size on gut clearance time in *Pyrrhosoma*, with *Daphnia* as prey at 15°C. The calculated regression is presented in section 12.3a.

Fig. 29b. The effect of temperature on gut clearance time in *Pyrrhosoma*, with *Daphnia* as prey. Clearance times expressed as percentages of the estimated times at 15°C. Regression drawn by eye.


Gut clearance time (hours).
25
20
15
10
5
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
4·0
Larval Head Width (mm.).

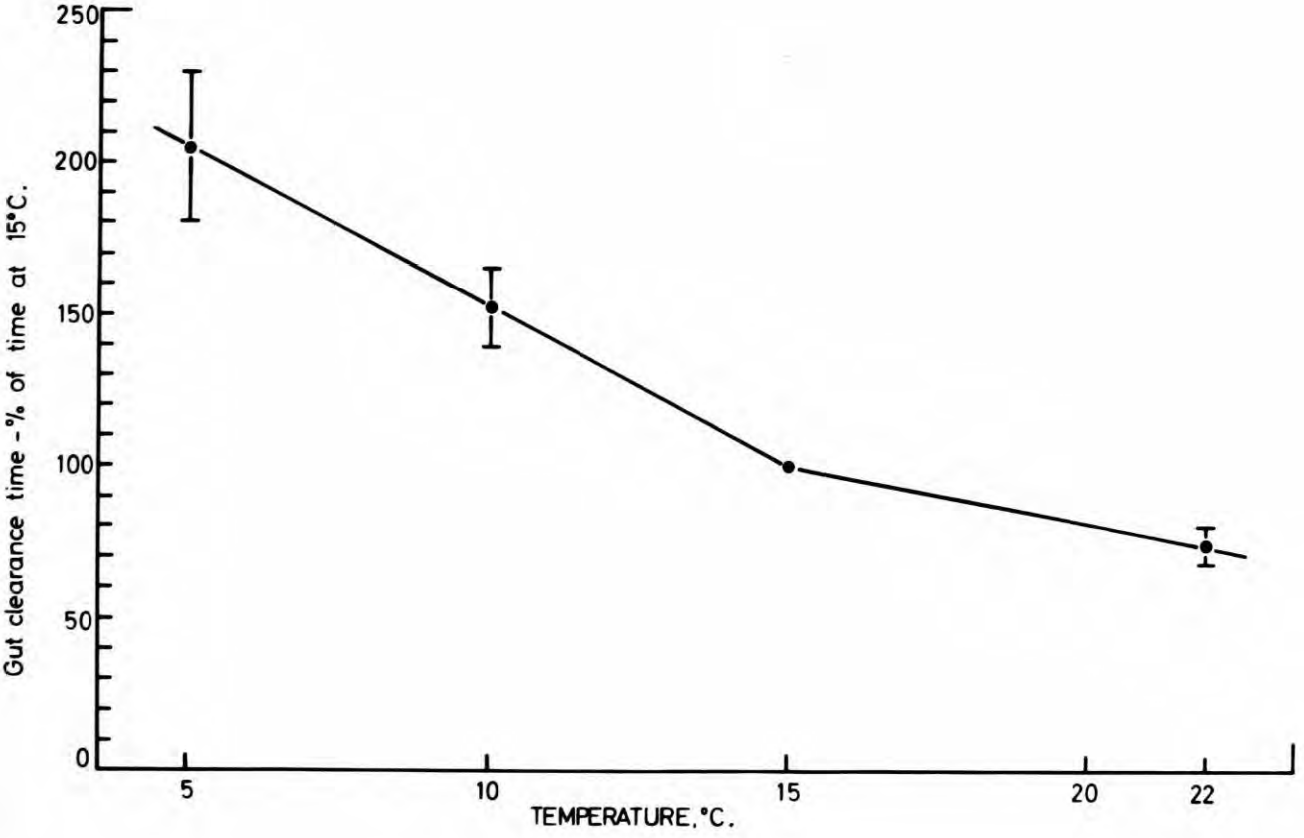
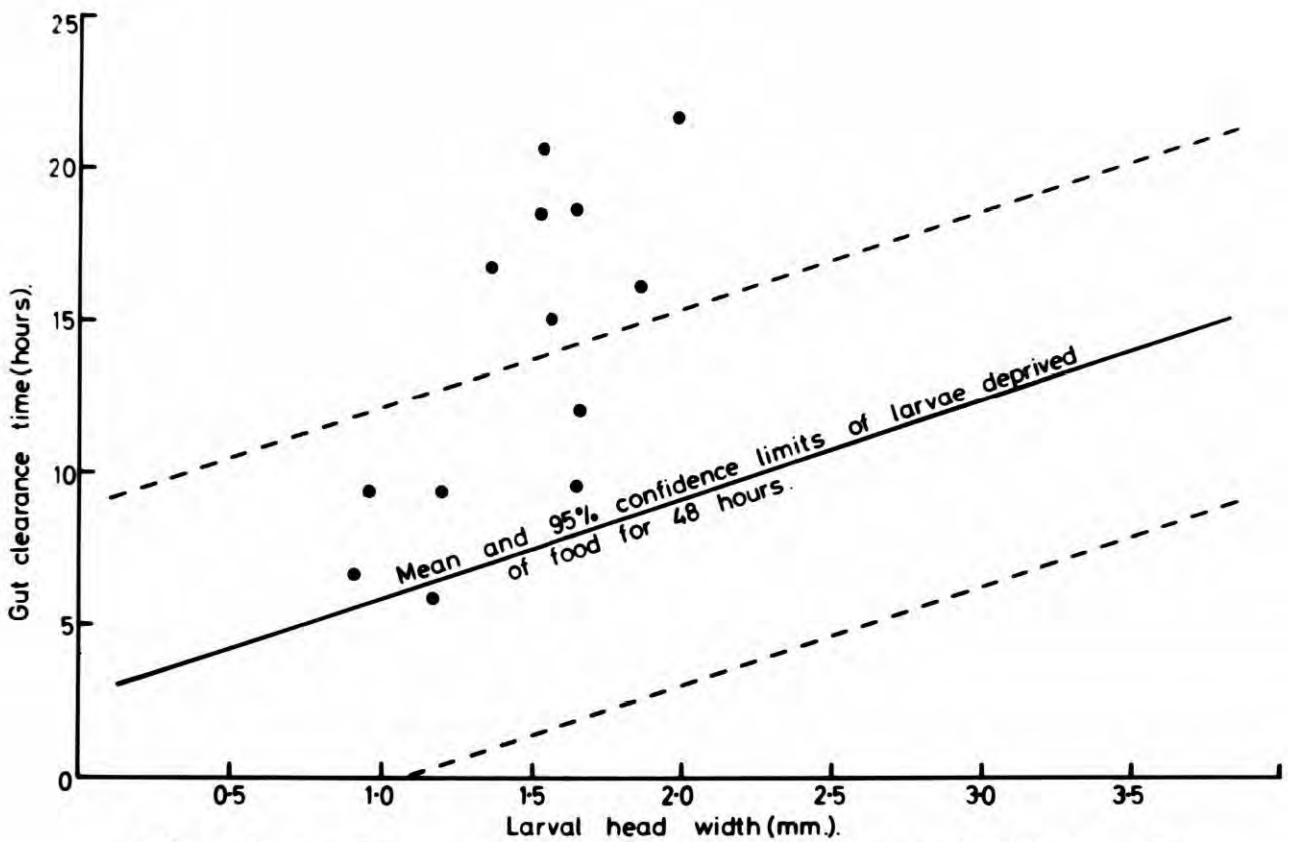
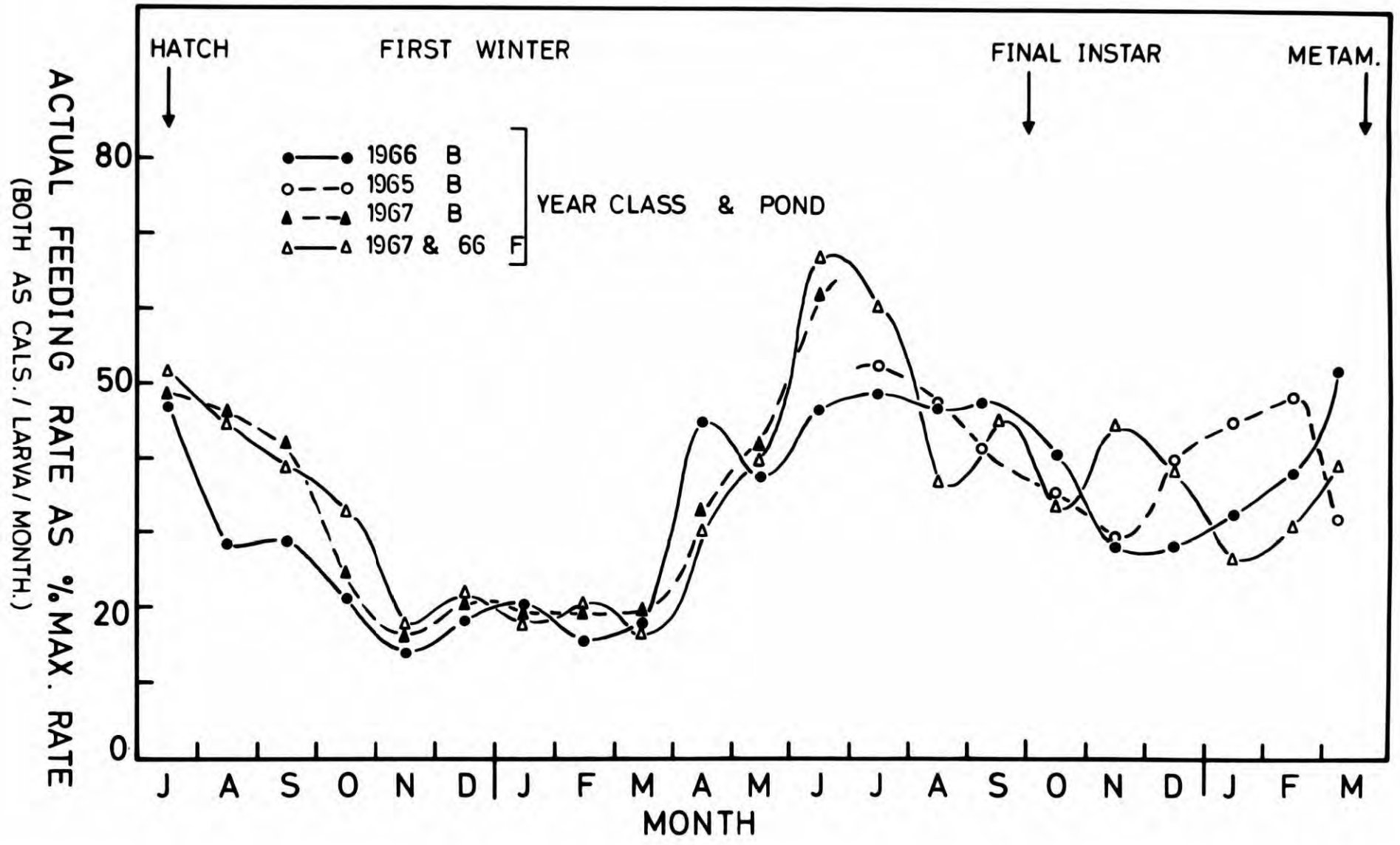

Gut clearance time - % of time at 15°C.
250
200
150
100
50
0
5
10
15
20
22
TEMPERATURE, °C.

Fig. 30. The effect of starvation on the gut clearance time of Pyrrhosoma. See text for details - section 12.3a.



Effect of starvation on gut clearance time in Pyrrhosoma. Individual results for larvae starved for one week at 15°C, compared with the mean for larvae deprived of food for 48hours.

Fig. 31. Actual field feeding rate, (calculated from Σ P, R, Ev. and percentage assimilation) as a percentage of the maximum feeding rate for that size of larva at that temperature. Percentages calculated monthly throughout development for an individual larva.


HATCH
FIRST WINTER
FINAL INSTAR
METAM.
1966 B
1965 B
1967 B
1967 & 66 F
YEAR CLASS & POND
ACTUAL FEEDING RATE AS % MAX. RATE
(BOTH AS CALS./ LARVA/ MONTH.)
80
50
20
0
J A S O N D J F M A M J J A S O N D J F M
MONTH

Chapter 13

FINAL INSTAR DIAPAUSE

13.1 INTRODUCTION

Corbet (1956, 1957b, 1962) considered Pyrrhosoma to be a typical spring emergence dragonfly, and as such it might be expected to possess a diapause in the final instar.

In the "classical" spring emergence species Anax imperator, and also in Pyrrhosoma, Corbet (1956a,b) showed that larvae entering the final instar in spring metamorphosed and emerged without delay. However, larvae entering the final instar in summer did not enter metamorphosis until the following spring. Corbet therefore suggested that this delayed development at a time when conditions were apparently suitable for metamorphosis and emergence was a diapause stage.

Corbet (1957a, 1962) and Corbet et. al. (1960) suggested that diapause served to synchronise emergence in spring emergence species by delaying the development of rapidly growing larvae and thereby allowing more slowly growing members of the population to "catch up". Diapause was probably completed by November or December and the whole population of final instars metamorphosed and emerged together as temperatures rose in the spring.

Corbet (1956) showed that diapause in Anax was facultative, and controlled by photoperiod. However, until the present study, nothing was known about the possible effects of diapause on final instar metabolism in spring emergence Odonata. In most insects diapause results in a considerable reduction in metabolic rate on a unit weight

basis (Clarke 1967, Keister and Buck 1964), and it was clearly important to elucidate the effects of diapause on all possible aspects of the metabolism of Pyrrhosoma. Time prevented a detailed analysis of the factors inducing diapause in Pyrrhosoma, or those controlling its rate of development. However, experiments were conducted to determine whether final instar Pyrrhosoma showed delayed development at relatively high laboratory temperatures (i.e. diapause) and the month by which diapause was normally completed in the field.

13.2 EXPERIMENTS ON PYRRHOSOMA DIAPAUSE

13.2a. Development times in the laboratory

Final instar Pyrrhosoma larvae were collected regularly from the study area. In the winter of 1965-66, the 1964 year class was sampled three times (October, December and March.) In the winter of 1966-67 the 1965 year class was also sampled three times, in January (twice) and February (once). The 1966 year class was sampled throughout the winter of 1967-68, from September on entering the final instar and subsequentally in every month until March. Between 10 and 20 Pyrrhosoma were taken on every sampling occasion.

The larvae were brought back to the laboratory, and placed either singly or in pairs in 500 ml containers; each was provided with Elodea canadensis (Michaux) Potamogeton berchtoldii (Fieber), a few dead leaves, twigs and mud from the pond bottom. The containers were placed on a laboratory window ledge at a mean temperature of 18°C. Larvae were supplied with excess food. Daphnia obtusa

obtained from laboratory cultures were provided as the staple diet, supplemented by small aquatic invertebrates collected from the study area (mainly chironomids, Asellus and Cloeon). Larvae were maintained like this until they emerged.

Fig 32a shows the mean number of days taken to emerge in the laboratory after collection (±2 standard errors), plotted against the date of collecting for the three year classes. The number of days between collection and emergence in the laboratory was defined as the laboratory development time. It is clear that laboratory development times of larvae collected in September or early October were long, usually between 200 and 230 days, but declined rapidly by approximately 55 days per month until early December. From early December onwards, the decrease in laboratory development times with later collection dates was much less (about 10 days per month), so that total laboratory development time only declined from about 60 days in larvae collected in early December, to about 20 days in larvae collected in early April.

The insert to fig 32a shows an interpretation of these laboratory results in which final instars between September and mid December are regarded as undergoing diapause development, and larvae from mid December onwards as undergoing post-diapause (i.e. normal) development. In many insects, diapause development proceeds more rapidly at low temperatures than at high temperatures (Lees 1955). In Pyrrhosoma diapause and post diapause development are envisaged as two distinct processes, in which the former must be completed before the latter,

and therefore before the larvae can metamorphose and emerge. Pyrrhosoma larvae collected in September had to undergo all diapause development in the laboratory at high temperatures (18°C); diapause therefore proceeded very slowly and total laboratory development times were long. However, between September collected larvae and December collected larvae diapause development proceeded rapidly under low temperature field conditions, and each consecutive collection of larvae showed a large decline in the amount of diapause still to be completed. From mid-December onwards, larvae collected from the field had completed all diapause development, and laboratory development times became comparatively short. However, post diapause development proceeded slowly under low temperature field conditions, and each consecutive collection after December showed only a small decline in laboratory development time.

Fig 32b shows an alternative presentation of these data, supporting the above interpretation, in which the mean date of emergence in the laboratory is plotted against the date of collection. In the laboratory the earliest larvae to emerge did so in late January and early February. These larvae were collected in mid December, and had therefore completed diapause development under favourable low field temperatures. Post diapause development was also completed under the most favourable conditions (high temperatures and abundant food in the laboratory) and emergence was therefore very early. Larvae collected before or after mid December had to complete part of either diapause or post diapause development under less favourable conditions,

and emerged much later.

It should be noted that larvae collected before December i.e. those completing most or all diapause development in the laboratory, frequently showed signs of disturbed patterns of metamorphosis. Strong red colouration often developed on the abdomen in early stage 2 metamorphosis, whilst in normal metamorphosis (see chapter 2) this was not observed until late stage 3. Metamorphosis was also slower than usual in these larvae.

12.3b Metabolic effects of diapause

Final instar larvae were collected throughout the winter of 1967-68. Experiments on aspects of their metabolism, measured monthly immediately after collection are reported in chapter 9, section 9.2a (assimilation), chapter 10, section 10.3b (respiration) and chapter 12, section 12.2e (maximum feeding rate).

Percentage assimilation showed no change throughout the final instar: nor was there any sign of any marked depression of metabolic rate of the type normally associated with insect diapause. Only maximum feeding rate showed a change that might be associated with completion of diapause, increasing from approximately 0.65 mg dry weight consumed per larva per day in October, November and December, to 1.0 mg dry weight consumed per larva per day from January onwards. (all at 15°C). However, as pointed out in chapter 12, this increase in maximum feeding rate is only slight, and both diapause and post diapause data fits equally well onto the regression relating larval length (mm) to maximum feeding rate (mg). Nor is the increase in

maximum feeding rate sufficient to account for the difference in laboratory development times of diapause and post diapause larvae. The increase in maximum feeding rate is therefore considered to be of minor or doubtful significance in the termination of diapause. However of undoubted importance is the total absence of any depression in the respiratory rate. This suggests that the diapause in Pyrrhosoma was quite different to normal insect diapause.

13.3 DISCUSSION

The data showed that energy utilisation per day in final instar larvae, measured in the laboratory shortly after collection was similar throughout the winter whether or not they were in diapause. Diapause was therefore ignored in subsequent energy budget calculations. However, larvae maintained in the laboratory at high temperatures were clearly divisible into diapause larvae (those showing delayed development, collected between September and early December) and post diapause larvae (those showing rapid development, collected after early December). Since the diapause larvae maintained in the laboratory at high temperatures did not become abnormally large during their prolonged final instar stage, it is clear that at some point their energy intake must have decreased markedly compared with that of post diapause larvae. Unfortunately, no energy balance measurements were made on diapause larvae that had been maintained in the laboratory at high temperatures for long periods.

The following model is suggested for the way in which diapause may operate in spring emergence Odonata; it is consistent with the observa-

tions on Anax and Pyrrhosoma diapause made by Corbet (1956, 1957 a,b) and in the present study, but is largely unproved.

Larvae moulting to the final instar may possess a "diapause factor", the presence or absence of which is a facultative response to photoperiod. The nature of the "diapause factor" is unknown. It is presumably absent from those larvae moulting to the final instar whilst photoperiod is increasing, but is present when photoperiod is constant or decreasing.

Providing that larvae do not experience high temperatures (above 10°C) for periods of longer than one week, the "diapause factor" does not influence energy utilisation. This would explain the lack of any marked difference in metabolic rates in final instars collected throughout the winter, and measured within one week of collection. However longer exposure to high temperatures (as in the laboratory at 18°C in the present study) activates the "diapause factor", causing a postulated reduction in metabolic rate and an observed delay in development. Presumably field larvae, moulting to the final instar early in July or August (early moult was not noted in the present study, but was observed by Corbet 1957a) experience a similar activation of the "diapause factor" due to high pond temperatures, and in consequence their metabolic rate is depressed, and their development delayed. This allows more slowly growing individuals to "catch-up" and synchronisation is maintained.

The "diapause factor" is gradually lost by the larvae, the rate of loss being most rapid at lower temperatures. Under normal field

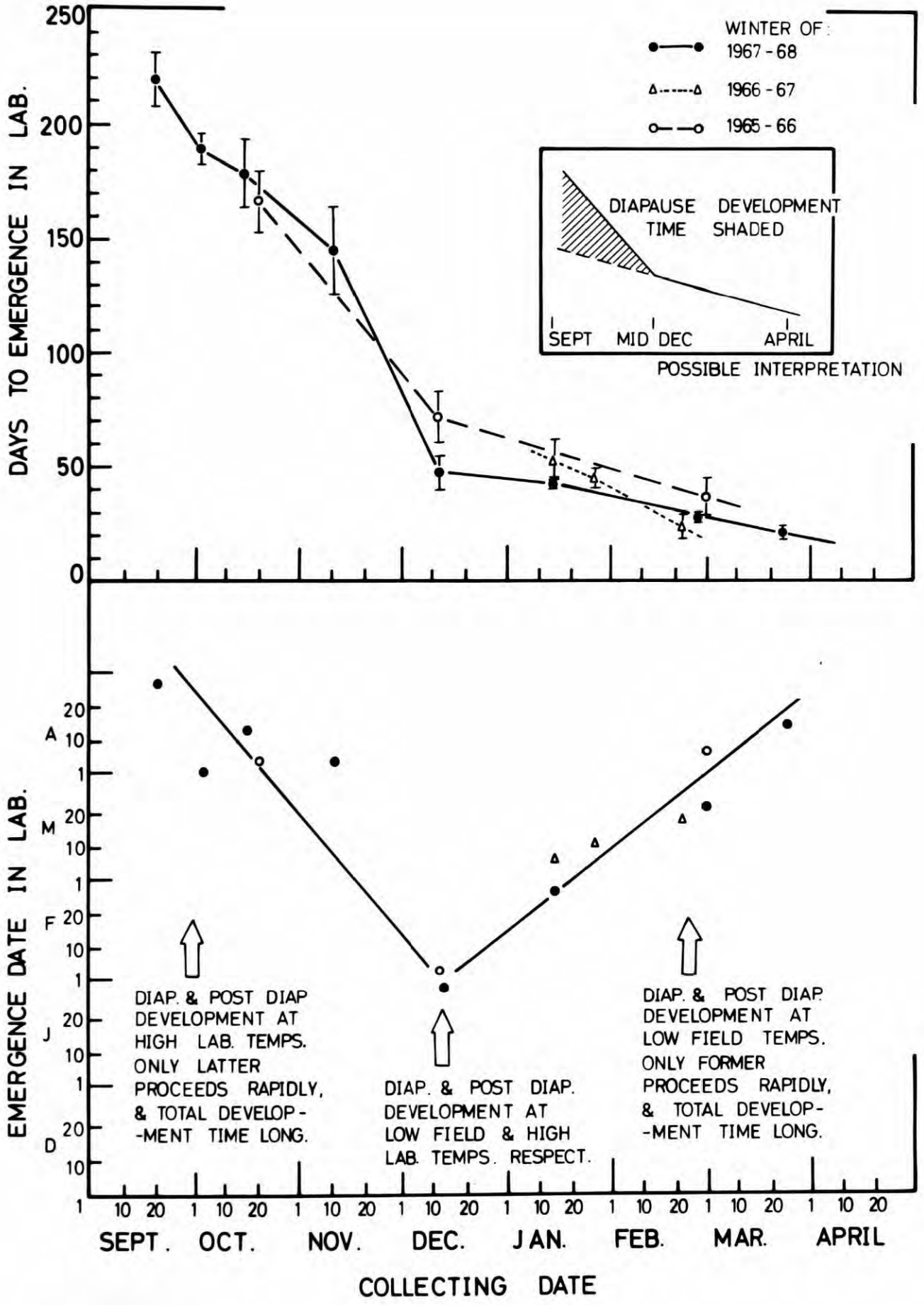
conditions, all "diapause factor" has disappeared by early December, and larvae became post diapause and able to develop normally at high temperatures. However, there are important differences in the effects of temperature in Anax and Pyrrhosoma. In Anax 10°C is optimal for diapause development (i.e. loss of "diapause factor"), which proceeds very slowly at 6°C or 20°C. (Corbet 1956). As pointed out in chapter 7, Anax moults to the final instar one or two months earlier than Pyrrhosoma. Most Pyrrhosoma did not moult to the final instar until October, by which time the mean pond temperature (table 7, chapter 4) was already below 10°C. It is therefore probable that the optimum temperature for diapause development (i.e. loss of "diapause factor") is much lower in Pyrrhosoma than in Anax, and is probably about 5 or 6°C.

There may be other differences between these two species. Emergence in Pyrrhosoma is less "explosive"; for example the $E.M._{50}$ points are later than in Anax (chapter 6). This suggests that the synchronising effects of diapause may be different in the two species. Since Anax is an anisopteran, and Pyrrhosoma a zygopteran, spring emergence and diapause must have been independently evolved in both species. Differences between them must therefore be expected. However, there are also obvious similarities. Anax larvae continued to feed and to move about normally during diapause (Corbet 1956) just as in Pyrrhosoma. This, and the absence of any difference in the metabolic rates of diapause and post diapause Pyrrhosoma measured shortly after collection, suggest that diapause in Odonata is an extremely interesting phenomenon,

very different from normal arthropod diapause, and that it would repay further detailed study.

Fig. 32a. Diapause in final instar Pyrrhosoma larvae. Total days to emergence in the laboratory at 18°C, plotted against the date of collection. (Vertical lines are ± 2 standard errors of the total mean days to emergence).

Fig. 32b. Diapause in final instar Pyrrhosoma larvae. Actual date of emergence in the laboratory, plotted against the date of collection. (Each point is the mean for several larvae collected on the same date). Larvae maintained in the laboratory at 18°C with excess food.


DAYS TO EMERGENCE IN LAB.
250
200
150
100
50
0
WINTER OF:
1967 - 68
1966 - 67
1965 - 66
DIAPAUSE DEVELOPMENT TIME SHADED
SEPT
MID DEC
APRIL
POSSIBLE INTERPRETATION
EMERGENCE DATE IN LAB.
A
M
F
J
D
20
10
1
DIAP. & POST DIAP DEVELOPMENT AT HIGH LAB. TEMPS. ONLY LATTER PROCEEDS RAPIDLY, & TOTAL DEVELOP--MENT TIME LONG.
DIAP. & POST DIAP. DEVELOPMENT AT LOW FIELD & HIGH LAB. TEMPS. RESPECT.
DIAP. & POST DIAP. DEVELOPMENT AT LOW FIELD TEMPS. ONLY FORMER PROCEEDS RAPIDLY, & TOTAL DEVELOP--MENT TIME LONG.
SEPT. OCT. NOV. DEC. JAN. FEB. MAR. APRIL
COLLECTING DATE

Chapter 14

INDIVIDUAL AND POPULATION ENERGY BUDGETS

14.1 INDIVIDUAL ENERGY BUDGETS (Ponds B and F)

14.1a Total energy utilisation per individual during development

Total energy utilisation per larva during development was calculated for the 1966 year class in pond B, and for the 'composite' development cycle followed in pond F, made up partly from the 1966 year class and partly from the 1967 year class. Estimates of energy utilisation (calories per larva per month or specified shorter time intervals) were summed to give total energy utilisation throughout development. Monthly estimates were taken from:

Chapter 12, tables 56 and 59 (C and A)

Chapter 10, tables 43 and 46 (R)

Chapter 11, table 47 (Ev)

Chapter 7, tables 20 and 23 (P).

Pond B. 1966 year class

Total energy utilisation per larva from hatching until the end of stage 2 metamorphosis

C	Consumption	189.151	calories
A	Assimilation	166.067	calories
F	Faeces	23.084	calories
P	Growth	80.164	calories
R	Respiration	81.387	calories
Ev	Exuvia	4.516	calories.

Pond F 'composite' year class

Total energy utilisation per larva from hatching until the end of stage 2 metamorphosis

C	Consumption	185.396 calories
A	Assimilation	162.560 calories
F	Faeces	22.836 calories
P	Growth	80.161 calories
R	Respiration	77.883 calories
Ex	Exuvia	4.516 calories

Data from both ponds omit stage 3 metamorphosis, in which larvae stop feeding and lose weight. (chapter 7). Stage 3 metamorphosis can be accounted for in the above calculations by adding 8.140 calories respired per larva, and subtracting this same amount from total growth.

Energy utilisation by these different components, as a percentage of consumption, is shown in table 60. The percentage of consumption incorporated into growth is the gross growth efficiency K_1 of Ivlev (1945). Ivlev's net growth efficiency K_2 or $\frac{P}{A} \times 100$ was calculated as follows

Pond E K_2 = 48.27 percent

Pond F K_2 = 49.31 percent

It is clear that the two ponds were very similar both in the total energy consumption per larva from hatching to emergence, and also in the fate of ingested energy.

14.1b Monthly changes in energy utilisation by individual larvae.

The previous section is concerned only with overall energy utilisation.

	Energy utilisation as a percentage of consumption (C)	
	Pond B	Pond F
Growth P	44.38 K_1	43.24 K_1
Respiration R	43.03	43.01
Exuvia Ev	2.39	2.44
Faeces F	12.20	12.32
Assimilation A	87.80	87.68

Table 60 Energy utilisation by individual larvae as a percentage of individual larval consumption between hatching and the end of stage 2 metamorphosis.

It is also of interest to compare the energy utilised for growth, respiration etc. as a percentage of individual consumption on a monthly basis.

Growth, respiration, exuvium production and faeces (all as cals. per larva per month) were calculated as percentages of consumption (also cals. per larva per month) from the data presented in chapters 7, 10, 11 and 12. Since the analysis was carried out on a monthly basis (rather than for total development as in section 14.1a), data from the 1965 and 1967 year classes in pond B were included. Finally, data from all year classes in both ponds were pooled, and mean monthly percentages calculated. The results therefore show monthly percentage utilisation of consumed energy in an "average" or "typical" two year Pyrrhosoma development cycle.

Fig 33 shows that the pattern of energy utilisation changed continuously throughout development. The percentage of ingested energy lost in the faeces increased from 5.3 percent at the hatch, to 13.5 percent in stage 2 metamorphosis, as percentage assimilation declined with increasing larval size (chapter 9, and fig 19). Larvae did not grow in their first winter (November-February), so that exuvium production was restricted to two periods, between the hatch and October, and in the second summer between March and entering the final instar in September. Within these restricted periods, exuvium production accounted for between 5 and 16 percent of ingested energy, so that in some months, more energy was lost as exuvia than was lost as faeces.

Most of the ingested energy was utilised in growth and respiration, although the ratio of one to the other varied greatly. During the first winter, (November to February), 93.5 percent of the ingested energy was utilised in respiration : the remainder was lost in the faeces. Alternatively, after the hatch (July, August and September) and during the second summer, more than 55 percent of the ingested energy was utilised for growth. In July of the second year, growth accounted for a maximum of 59.6 percent of ingestion. Clearly gross growth efficiency (K_1) was very high at certain stages of development.

14.2 POPULATION ENERGY FLOW (pond B only)

14.2a Calculation procedure

Total population energy flow was calculated for pond B only. Data

for two years, spanning three year classes were used, viz:

	Senior age class	Junior age class
YEAR 1		
July '66 - June '67	1965 year class	1966 year class
		Becomes senior age class
YEAR 2		
July '67 - June '68	1966 year class	1967 year class

Data from each year class were calculated separately as follows:

i) The mean number of Pyrrhosoma larvae per m^2 each month in each year class was calculated from

$$\bar{N} = \frac{n_2 + n_1}{2}$$

$\bar{N}$ = Monthly mean number per m^2.

n_2 = Number per m^2 of year class on 1st of month 2.

n_1 = Ditto on 1st of month 1.

The numbers in each year class on the first of each month were taken from chapter 5, table 15.

ii) Respiration per m^2 each month by each year class was given by:

$\bar{N}$ x (calories respired per individual per month).

The calories respired per larva per month in each year class were taken from chapter 10, table 43 - 45.

iii) Production per m^2 each month by each year class was given by:

$\bar{N}$ x (calories growth per individual per month).

Growth calories per larva per month were taken from chapter 7, tables 20 - 22.

iv) Exuvium production was similarly calculated from:

$\bar{N}$ x (exuvium production per larva per month)

Exuvium production per larva per month is given in chapter 11, table 47.

v) TOTAL ASSIMILATED CALORIES per m^2 per month by each year class was given by

(i i + iii + iv) above i.e. R + P + Ex.

vi) Mean percentage assimilation each month was taken from chapter 12, tables 56 - 58. Hence TOTAL CALORIES CONSUMED per m^2 per month by each year class was calculated.

vii) Mean monthly biomass (calories per m^2) for each year class was given by:

$$\frac{n_1 \times \begin{bmatrix}\text{caloric content/larva} \\ \text{on 1st of month}\end{bmatrix} + n_2 \times \begin{bmatrix}\text{caloric content/larva} \\ \text{on 1st of next month}\end{bmatrix}}{2}$$

where: n_1 = number of larvae per m^2 in year class on 1st of month.

n_2 = ditto on 1st of next month.

The mean caloric content of one larva on the first of each month is given in chapter 7, tables 20 - 23. The numbers in each year

class on the first of each month were taken from chapter 5, table 15.

(In the above definitions, "month" is also used to indicate specified shorter time intervals during hatching, metamorphosis and emergence).

The final step in the calculation was to combine senior and junior age class data each month to give total population energy utilisation per m^2 throughout the two years of study.

14.2b Population energy flow during two years of study.

Tables 61 - 63 show the results of the calculations described above, for the 1965, 1966 and 1967 year classes in pond 3, between July 1966 and June 1968.

Total annual energy utilisation by the Tyrrhosoma population in the two years of study was as follows.

YEAR 1 1st July 1966 - 30th June 1967

Data from the senior age class (1965 year class) presented in table 62 were combined with the data from the junior age class (1966 year class) presented in the top half of table 61.

B	MEAN ANNUAL BIOMASS	934.1	calories per m^2
R	RESPIRATION	3169.3	calories per m^2 per annum.
P	GROWTH (Production)	3938.8	-"-
Ev	EXUVIA	497.4	-"-
F	FAECES	859.2	-"-
C	CONSUMPTION	8464.7	-"-

YEAR 2 1st July 1967 - 30th June 1968

Data from the senior age class (1966 year class) presented in the

bottom half of table 61 were combined with data from the junior age class (1967 year class) presented in table 63.

$\bar{B}$ MEAN ANNUAL BIOMASS 1420.6 calories per m^2

R	RESPIRATION	3668.1	calories per m^2 per annum
P	GROWTH (Production)	3586.8	- " -
Ev	EXUVIA	302.9	- " -
F	FAECES	987.3	- " -
C	CONSUMPTION	8545.1	- " -

These data are summarised in energy flow diagrams (fig 34).

Estimates of numbers per m^2 and mortality rates suggested that the two years differed markedly as far as Pyrrhosoma population dynamics were concerned (chapter 5). In contrast, the similarity between the two years in terms of annual energy flow is remarkable.

Population consumption was virtually identical in both years and amounted to 8.47 K_{cals} per m^2 per annum in the first year, and 8.55 K_{cals} per m^2 per annum in the second.

At the end of each "population" year in July, mortality had accounted for a large proportion of the total annual population production of 3.94 K_{cals} per m^2 per annum in the first year and 3.59 K_{cals} per m^2 per year in the second. Only those junior age class larvae surviving on 1st July and the final instars which emerged from the pond shortly before the end of the population year remained as 'visible' production.

Exact calculation of the number of final instar larvae surviving to emerge is difficult, but a reasonable estimate was made from the

MONTH	MEAN NUMBER of LARVAE PER m^2 $\overline{N}$	MEAN BIOMASS cals per m^2 B	ALL AS GRAM CALORIES PER M^2 PER MONTH				
			Respiration R	Production (Growth) P	Lost as exuvia Ev	Lost as faeces F	TOTAL CONSUMPTION C
July 1966	362.9	64.9	22.9	39.9	3.8	3.7	70.3
Aug	323.7	107.8	54.8	82.6	6.6	8.8	152.8
Sept	285.5	176.6	67.8	120.1	10.0	13.1	211.0
Oct	251.8	227.7	65.6	33.6	15.8	8.0	123.0
Nov	222.1	216.6	47.8	0	0	3.4	51.2
Dec. 1966	195.9	191.0	34.3	0	0	2.4	36.7
Jan 1967	172.4	168.1	28.3	0	0	2.0	30.3
Feb	152.6	148.8	26.6	0	0	1.9	28.5
Mar	135.2	135.4	29.6	7.5	0	2.6	39.7
April	119.2	148.3	31.7	53.8	12.7	7.2	105.4
May	105.2	193.5	54.2	79.6	19.8	11.9	165.5
June	92.8	306.2	118.9	209.6	28.0	30.4	386.9
Σ	-	-	582.5	626.7	96.7	95.4	1401.3
End of first year of study							
July 1967	81.8	561.3	257.6	412.4	46.7	70.5	787.2
Aug	72.0	961.5	386.2	586.3	78.8	120.1	1171.4
Sept	63.5	1426.1	446.5	645.9	135.1	160.3	1387.8
Oct	56.1	1803.7	373.4	517.9	0	127.3	1018.6
Nov	49.5	1887.3	257.3	113.6	0	54.7	425.6
Dec 1967	43.6	1732.8	202.2	33.4	0	35.1	270.7
Jan 1968	38.4	1567.3	178.9	58.8	0	35.5	273.2
Feb	33.9	1451.8	174.3	77.8	0	37.8	289.9
Mar	30.1	1453.2	266.2	276.4	0	83.2	625.8
April	26.6	1579.9	327.7	359.9	0	106.4	794.0
May 1-22	23.8	1723.9	348.6	322.0	0	103.8	774.4
May 23-30	22.4		182.3	-182.3	0	0	0
Σ	-	-	3401.2	3222.1	260.6	934.7	7818.6

Table 61 Energy utilisation by 1966 year class in pond B over two years of study (calories per m^2 per month)

MONTH	MEAN NUMBER of LARVAE per m^2 $\overline{N}$	MEAN BIOMASS cals per m^2 B	ALL AS GRAM CALORIES PER M^2 PER MONTH				
			Respiration R	Production (Growth) P	Lost as exuvia Ev	Lost as faeces F	TOTAL CONSUMPTION C
July 1966	185.9	1130.3	542.2	987.4	106.2	157.8	1793.6
Aug	119.3	1490.7	609.4	969.7	130.5	194.2	1903.8
Sept	77.1	1564.5	518.0	558.8	164.0	161.2	1402.0
Oct	49.9	1384.4	359.7	389.5	0	105.6	854.8
Nov	32.2	1095.0	190.1	113.2	0	45.6	358.9
Dec 1966	20.9	788.6	102.0	79.9	0	26.9	208.8
Jan 1967	13.4	558.1	62.7	51.3	0	17.1	131.1
Feb	8.8	414.3	45.3	74.1	0	18.3	137.7
Mar	5.8	308.2	56.6	17.8	0	11.7	86.1
April	3.7	223.2	47.6	45.8	0	14.7	108.1
May 1-24	2.5	167.7	36.9	30.9	0	10.7	78.5
May 25-31	2.0		16.3	-16.3	0	0	0
Σ	-	-	2586.8	3312.1	400.7	763.8	7063.4

Table 62 Energy utilisation by 1965 year class in pond during first year of study. (Calories per m^2 per month).

MONTH	MEAN NUMBER of LARVAE per m^2 N	MEAN BIOMASS cals per m^2 B	ALL AS GRAM CALORIES PER M^2 PER MONTH				
			Respiration R	Production P	Lost as Exuvia Ev	Lost as Faeces F	TOTAL CONSUMPTION C
July 1967	116.8	10.4	4.3	8.0	1.2	0.8	14.3
Aug	109.3	27.9	17.4	29.8	2.2	3.0	52.4
Sept	100.3	61.2	24.4	44.6	3.5	4.8	77.3
Oct	92.1	83.8	22.0	13.0	5.8	2.8	43.6
Nov	84.6	83.2	15.9	0	0	1.1	17.0
Dec 1967	77.6	76.3	12.9	0	0	0.9	13.8
Jan 1968	71.2	69.9	11.9	0	0	0.8	12.7
Feb	65.5	64.4	10.4	0	0	0.7	11.1
Mar	60.3	61.1	12.8	3.8	0	1.2	17.8
April	55.4	65.7	12.7	16.2	5.9	2.5	37.3
May	50.8	91.5	27.4	49.3	9.6	6.6	92.9
June 1968	46.7	203.4	94.8	200.0	14.1	27.4	336.3
Σ	-	-	266.9	364.7	42.3	52.6	726.5

Table 63 Energy utilisation by 1967 year class in pond 3 during second year of study (calories per m^2 per annum)

calculated number of final instars per m^2 t the start of the annual emergence, (chapter 6, section 6.1c.) The mean number per m^2, multiplied by the dry weight and calorific value of a stage 3 metamorphosis larva gave the total calories per m^2 surviving to emerge. The number of junior age class larvae present on 1st July is given in chapter 5, table 15. The number on 1st July, multiplied by the caloric content per larva (chapter 7, tables 30 and 32) gave the mean calories per m^2 surviving on 1st July. The results were as follows:

YEAR 1. 1st July 1966 - 30th June 1967

Biomass per m^2 of junior age class surviving on 1st July 1967

= 391.59 calories per m^2

Biomass per m^2 of final instars emerging, May and June 1967

= 151.36 calories per m^2

Total "visible" production at end of year

= 542.95 calories per m^2.

Total mortality (3938.8 - 543.0)

= 3395.8 calories per m^2 per annum

TOTAL MORTALITY 3.40 K_{cals} per m^2 per annum.

YEAR 2. 1st July 1967 - 30th June 1968

Biomass per m^2 of junior age class surviving on 1st July 1968

= 294.66 calories per m^2.

Biomass per m^2 of final instars emerging, May and June 1968

= 1636.15 calories per m^2.

Total "visible" production at end of year

= 1930.81 calories per m^2.

Total mortality (3586.8 - 1930.8)

= 1656.0 calories per m^2 per annum.

TOTAL MORTALITY 1.66 K_{cals} per m^2 per annum.

Clearly, mortality losses (calories per m^2) were approximately twice as high in the first year 1966-67) as in the second year (1967-68) of study, and accounted for a large proportion of annual production, particularly in 1966-67.

14.2c. Relative contribution of the junior and senior age classes to, and monthly changes in, total population consumption in the two years.

Total monthly population consumption (K_{cals} per m^2 per month) was a useful measure of the change in total energy flow with season. Fig 35 shows total monthly population consumption in the two years, with the contribution of the junior and senior age classes distinguished. Data were taken from the last column of tables 61-63.

The contribution of the junior age class to population consumption was usually considerably less than the contribution of the senior age class during the same period. In 1966-67, consumption by the senior age class amounted to 7.06 K_{cals} per m^2 per annum, but to only 1.40 K_{cals} per m^2 per annum in the junior age class. In 1967-68 the corresponding figures were 7.82 K_{cals} per m^2 per annum consumption by the senior age class, and 0.73 K_{cals} per m^2 per annum by the junior age class. Exceptions to the generally small contribution of the junior age class occurred at certain times. In June of both years, after the senior age class had emerged, population energy flow was entirely due to the

junior age class. Also, towards the end of the first year (March-May 1967), senior age class larvae (1965 year class) were present in very small numbers per m^2, and the contribution of the junior age class to total population consumption was proportionally quite large.

The broad pattern of energy flow in the two years was similar. Fig 35 shows that peak population ingestion took place between July and October, declined to a low level between December and February, and increased again in the spring. In detail however, the two years were rather different, primarily due to the very different mortality rates and initial numbers per m^2 of the senior age class in each year. In 1966-67, the senior age class (1965 year class) was initially present in very large numbers, experienced heavy mortality, and was present in very low numbers at emergence. In 1967-68, the senior age class (1966 year class) was initially present in smaller numbers, but experienced a much lower mortality, and in consequence the numbers surviving at emergence were much higher than in 1966-67. (See chapter 5, section 5.2b). Population consumption was therefore much higher in 1966-67 between July and September than in 1967-68. By March, however, the situation in the two study years was reversed, and population consumption in spring was much higher in 1967-68 than in the first year.

Total population consumption in Pyrrhosoma was found to be influenced by three factors viz; pond temperature, population biomass and the density of available prey. The observed monthly changes in population consumption were primarily due to the interaction of these three varia-

bles, and it is interesting to consider in general terms their relative importance.

In chapter 12, an attempt was made (section 12.5, and fig 31) to compare actual food intake per larva in the field, with potential maximum food intake per larva in the laboratory. Since feeding rate was proportional to prey density it may be argued that the nearer the field feeding rate approaches the maximum laboratory feeding rate, the higher the available prey density in the field. Field feeding rates were a greater percentage of the maximum feeding rate in June and July than at any other time (fig 34) so that maximum population consumption in August and September did not appear to be closely synchronised with maximum prey density. However, in very general terms, total population consumption was high when prey density was high and vice versa.

The effects of changes in population biomass and temperature on population consumption were analysed in more detail. Fig. 35 shows mean monthly pond temperatures (see chapter 4, section 4.2) superimposed on the changes in monthly population consumption. Although monthly changes in population consumption tended to follow the temperature curves fairly closely, maximum pond temperatures and maximum population consumption did not coincide, the former being in July and the latter in August or September. It is also clear from the biomass data in table 64 and the data on monthly population consumption in fig 35, that peak population biomass and peak population consumption did not coincide. Clearly the timing of peak population consumption was influenced by both temperature and biomass, and in consequence did not coincide

with the maximum values of either.

Month	Mean monthly biomass (Total of both senior and junior age classes). cals per m^2	
	YEAR 1 1966-67 1965 and 1966 year classes	YEAR 2 1967-68 1966 and 1967 year classes
July	1195.3	571.7
Aug	1598.5	989.3
Sept	1741.1	1487.4
Oct	1612.0	1887.5
Nov	1311.6	1970.5
Dec	979.6	1809.1
Jan	726.2	1637.2
Feb	563.1	1516.2
Mar	443.6	1514.3
April	371.5	1645.5
May	361.1	1815.4
June	306.2	203.4
MEAN ANNUAL BIOMASS	934.1	1420.6

Table 64 Changes in Pyrrhosoma population biomass (calories per m^2) each month in pond 3 during two years of study. (Data from senior and junior age classes presented in tables 61-63).

Fig 36a shows monthly population consumption (K_{cals} per m^2 per month) in the two years of study, plotted against mean monthly pond temperatures. Fig 36b shows monthly population consumption plotted against mean monthly population biomass (K_{cals} per m^2). Total pop-

ulation consumption figures were obtained from the last columns of tables 61-63; mean monthly pond temperatures were taken from chapter 4, section 4.2, and mean monthly Pyrrhosoma biomass from table 64. For mean monthly temperature plotted against monthly population consumption r = 0.65 ($p > 0.001$). For mean biomass plotted against monthly population consumption r = 0.41 (p .1 - .05). The latter is barely significant, and clearly temperature had a much greater effect on the monthly changes in population energy flow than changes in biomass. The small influence of changes in biomass was probably due to the relatively narrow range of biomass observed. Obviously very large changes in biomass outside the limits observed in the present study would have had a marked effect on population energy flow. This is discussed further in chapter 15.

In summary, peak population consumption did not appear to be correlated with either maximum prey density, with maximum biomass or maximum pond temperature. During the whole year, the most important single variable affecting changes in population consumption, and therefore energy flow was pond temperature, at least within the range of Pyrrhosoma larval biomass observed in the present study.

14.2d P/B ratio. Population "turnover"

The P/B ratio, defined as the mean annual production (K_{cals} per m^2 per annum) divided by the mean annual biomass (K_{cals} per m^2) is a measure of the number of times in the year that the population "turns over".

In the two years, the appropriate ratios were:

1966 - 67 $\frac{3.94}{0.93} = 4.24$

1967 - 68 $\frac{3.59}{1.42} = 2.53$

The difference between the two years was slight due to the very different mortality rates and numbers per m^2 of the senior age classes.

14.2e Ecological efficiency, population growth efficiency and P/A ratio

These were calculated for comparison with other single species population energetics studies.

Slobodkin (1960) defined ecological efficiency for a steady state system as

$$\frac{\text{Yield calories to predator}}{\text{Food calories to prey}} \times 100$$

In the present study, following Ricker (1964) a maximum ecological efficiency was calculated by including total mortality as yield to predators. Maximum ecological efficiency was therefore given by

$$\frac{\text{Total population mortality}}{\text{Population consumption}} \times 100$$

(both numerator and denominator as K_{cals} per m^2 per annum)

Pyrrhosoma population biomass at the end of each year was not constant : rather it declined throughout the study.

Population biomass (K_{cals} per m^2) on.

1st July	1966	0.207
"	1967	0.392
"	1968	0.295

This was a decrease of 0.415 K_{cals} per m^2 between July 1966 and July 1967, and of 0.097 K_{cals} per m^2 between July 1967 and July 1968.

The decrease in standing crop was therefore subtracted from the total annual mortality before calculating ecological efficiency (since, in effect, it represented material "imported" from the previous year, and not material produced during the particular year being studied). Ecological efficiency in the two years was then given by

1966 - 67 $\frac{3.280}{8.405} \times 100 = 35.2$ percent

1967-68 $\frac{1.552}{8.545} \times 100 = 18.3$ percent

Two population growth efficiences were calculated

Gross population growth efficiency $\frac{P}{\bar{C}} \times 100$

Net population growth efficiency $\frac{P}{\bar{A}} \times 100$

Numerator and denominator as K_{cals} per m^2 per annum.

For the two years of study these were

Gross population growth efficiency

1966-67 = $\frac{3.94}{8.47} \times 100 = 46.5$ percent

1967-68 = $\frac{3.59}{8.55} \times 100 = 42.0$ percent

Net population growth efficiency

1966-67 $\frac{3.94}{7.61}$ = 51.8 percent

1967-68 $\frac{3.59}{7.56}$ = 47.5 percent

Instead of comparing net population growth efficiences, Engelmann (1966, 1968) used the ratio of P to R to compare the fate of assimilated energy at the population level. By plotting a graph of Log P against Log R (both as K_{cals} per m^2 per annum) he was able to obtain a linear relationship (the "Engelmann line") for poikilotherms of:

$$\text{Log } R = 0.62 + 0.86 \text{ Log } P.$$

Engelmann utilised data from terrestrial and salt marsh populations only, and included no aquatic species. Fig 37 shows the line calculated by Engelmann, for terrestrial poikilotherms on which data for aquatic poikilotherms have been superimposed. (The dotted lines show the limits of scatter of Engelmann's data and not the 95 percent confidence limits). Aquatic population energy flow studies carried out by other workers are shown in fig 37 as open circles, and data obtained for Pyrrhosoma in two years as solid circles. The aquatic studies utilised are shown in table 65. Some of the studies shown in table 65 were not of single species populations. It was considered justified to include these for completeness since Engelmann himself included two "species groups" in his analysis (Engelmann 1961 for Cribatei, and Odum et. al. 1962 for 3 species of Orthoptera).

Also included in table 65 is work by Woodland (1967) on the Australian crayfish Cherax albidus. This was not available when fig 37 was

NUMBER AS IN fig 37	Species	Author	K cals per m² per annum		Log P	Log R
			P	R		
1	Asellus aquaticus	Fitzpatrick (1968)	13.90	51.06	1.144	1.708
2	Several fish species	Mann (1965)	42.6	516.5	1.629	2.713
3	Carnivores	Odum (1957)	67	316	1.826	2.500
4	Top Carnivores		8	13	0.903	1.114
5	Limnodrilus	Teal (1957)	173.8	483.6	2.240	2.684
6	Asellus		104.5	486.1	2.019	2.687
7	Phagocata		113.4	18.7	2.055	1.272
8	Trichoptera		39.2	67.5	1.593	1.774
9	Pisidium		81.8	90.9	1.913	1.959
10	Modiolus	Kuenzler (1961)	16.7	39.0	1.223	1.591
NOT SHOWN IN FIG 37	Cherax (Crayfish)	Goodland (1967)	158	132	2.199	2.121

Table 65 Summary of data shown in fig 37, relating log P to log R (both as K cals per m² per year) in aquatic energetics studies.

completed. Woodland's data may be fitted by eye to fig 37.

The data obtained for Pyrrhosoma in the two years did not fit very closely to the Engelmann line. However, it is clear from fig 37 that data from most of the aquatic studies listed in table 65 fitted reasonably closely. Only the planarian Phagocata studied by Teal (1957) (point 7, fig 37) fitted the line badly. It may therefore be concluded that the relationship between respiration and production (both as K_{cals} per m^2 per annum) for terrestrial and aquatic poikilotherms is similar, and that the relatively poor fit to the line calculated by Engelmann shown by Pyrrhosoma was not typical of most aquatic species. This is discussed further in section 14.3.

14.2f Energy utilisation by Pyrrhosoma as a percentage of the energy entering pond 3.

This calculation necessarily involved a series of approximations. Nevertheless, it was considered sufficiently interesting to be worth attempting. Where approximations had to be made, values giving maximum energy utilisation by the Pyrrhosoma population rather than minimum were chosen in order to give some idea of the maximum likely impact or importance of Pyrrhosoma in the habitat.

In both years of study, the larval Pyrrhosoma population in pond 3 consumed 8.5 K_{cals} per m^2 per annum. Of this, approximately 85 percent (7.22 K_{cals} per m^2 per annum) was derived from browsers, and 15 percent (1.28 K_{cals} per m^2 per annum) from carnivores (chapter 8, section 8.3).

This input to the Pyrrhosoma population represented part of the

production by the prey species. The following average values for annual population production as a percentage of annual population assimilation (or net population growth efficiency) have been given for poikilotherms:

$$\frac{P}{A} \times 100 =$$

21 percent Golley (1968)
23 percent Odum (1957)
25 percent Teal (1962)

In some cases (as in Pyrrhosoma itself section 14.2e), net population growth efficiencies will be higher, but the figure of 21 percent, given by Golley (1968) was utilised in the present calculation as a reasonable average for populations in the field.

Therefore, for the carnivore prey of Pyrrhosoma, total assimilation (K_{cals} per m^2 per annum) was given by

$$\frac{1.28 \times 100}{21}$$

It may be assumed that assimilation is 80 percent of consumption for most carnivores (chapter 9, tables 40 and 41). Therefore, total consumption by carnivore prey of Pyrrhosoma was given by

$$\frac{1.28 \times 100 \times 100}{21 \times 80} = \frac{7.60 \ K_{cals} \text{ per } m^2}{\text{per annum}}$$

Consumption by the carnivore prey of Pyrrhosoma was presumably derived largly from browsers. Therefore, total browser production "supporting" the Pyrrhosoma population was:

$$7.60 + 7.22 = 14.82 \ K_{cals} \text{ per } m^2 \text{ per annum.}$$

Similarly, assuming that this represented 21 percent of the energy assimilated by these browsers, and that assimilation was 30 percent of consumption, total browser consumption was given by:

$$\frac{14.82 \times 100 \times 100}{21 \times 30} = 235.3 \text{ K}_{\text{cals}} \text{ per m}^2 \text{ per annum}$$

Therefore, approximately 235 $K_{calories}$ per m^2 per annum were consumed by that part of the pond's browser populations utilised as prey by the Pyrrhosoma population, either directly or via carnivorous prey. This consumption of 235 $K_{calories}$ per m^2 per annum may be thought of as energy input at the base of the food chain "supporting" the Pyrrhosoma population (Clearly total browser consumption in pond 3 was greater than 235 K_{cals} per m^2 per annum, since only part of the browser populations were "incorporated" into the Pyrrhosoma food chain).

Energy input to pond, and primary production

Total incident shortwave solar radiation at Aycliffe (map ref. NZ420:280) twelve miles (19.3 k_m) south west of Durham city, between May 1967 and April 1968 was 921,720 K_{cals} per m^2 per annum. (R.L. Hughes pers comm. 1968).

Dense Potamogeton covered most of the pond, with Juncus, and Eleocharis round the edges. Most of the primary production in pond 3 was, therefore, probably due to these macrophytes, which are usually more productive than phytoplankton in a similar situation (Westlake 1965). Under these circumstances, net primary production (K_{cals} per m^2 per annum) was probably approximately 0.5 percent of the incident annual solar radiation. An estimate of net primary production in pond 3 was therefore:

$$\frac{921,720}{100} \times 0.5 = 4609 \text{ K}_{\text{cals}} \text{ per m}^2 \text{ per annum.}$$

It was therefore possible to calculate the following percentages for the energy utilised by the Pyrrhosoma population (all figures as K_{cals} per m^2 per annum).

Pyrrhosoma annual production as a percentage of incident solar radiation to pond B.	$\frac{3.6}{921,720} \times 100 = 0.0004$ percent
Consumption by the browsers at base of Pyrrhosoma food chain, as a percentage of incident solar radiation to pond B.	$\frac{235}{921,720} \times 100 = 0.026$ percent
Ditto, as a percentage of net primary production in pond B.	$\frac{235}{4,609} \times 100 = 5.1$ percent
Pyrrhosoma annual production, as a percentage of net primary production in pond B.	$\frac{3.6}{4,609} \times 100 = 0.079$ percent
Pyrrhosoma annual consumption as a percentage of net primary production in pond B	$\frac{8.15}{4,609} \times 100 = 0.18$ percent.

Clearly the Pyrrhosoma population was utilising only a minute fraction of the total incident solar radiation to pond B. More significantly consumption by the browsers "supporting" the Pyrrhosoma food chain (235 K_{cals} per m^2 per annum) accounted for only 5 percent (approximately) of net primary production in pond B. Although this figure was obtained by a series of assumptions, it at least suggests that the total energy

input at the base of the food chain "supporting" Pyrrhosoma was an extremely small percentage of net primary production in pond B.

14.3 DISCUSSION

Teal (1957) and Tilly (1968) have provided approximate data on energy flow through populations of aquatic invertebrate carnivores. Since their data were obtained in complete community studies they are neither as detailed nor as precise as the data obtained for Pyrrhosoma; nevertheless, it is useful to compare the magnitude of carnivore energy flow in these freshwater communities with the figures for Pyrrhosoma in pond B. Their results are presented in table 66. Clearly in most of these invertebrate carnivores, total annual population energy flow (defined as the sum of P + R, or population assimilation) was considerably higher than for Pyrrhosoma. Total energy input (net primary production plus imported organic matter) amounted to approximately 3,000 K_{cals} per m^2 per year in Root Spring (Teal 1957), and to approximately 9,500 K_{cals} per m^2 per year in Cone Spring. (Tilly 1968). In Root Spring, the planarian Phagocata was the only exclusively predatory animal, so that it is not surprising that annual population energy flow in Phagocata was greater than for Pyrrhosoma in pond B, in which Pyrrhosoma was only one of a number of carnivore species (see Appendix 2). In Cone Spring, the number of carnivore species was greater than in Root Spring, but this number was still considerably less than in pond B. Further, energy input to the spring was approximately twice that in pond B. Under these circumstances, it is not surprising that energy flow through most of the carnivore populations in Cone Spring was higher

than through the Pyrrhosoma population in pond B. However, it does suggest that the importance of Pyrrhosoma in pond B, measured in terms of its contribution to total community energy flow was considerably less than that achieved by a number of aquatic invertebrate predators in approximately comparable situations.

The work of Vannote (1963) on the small-mouth bass is the only other comparable study on a single species of aquatic carnivore. Production by the bass, the main predators in a eutrophic stream, amounted to 1.48 K_{cals} per m^2 per annum, rather less than the figure found for Pyrrhosoma. Further work is required on the magnitude of carnivore energy flow in different aquatic habitats.

Population data, based on changes in the numbers of Pyrrhosoma larvae per m^2 suggested that the first and second years of study were quite different. Monthly changes in population energy flow, annual mortality losses, ecological efficiencies and P/B ratios (see sections 14.2b- e) were also different in the two years. In view of these differences, one of the most surprising features of the study was the similarity between the two years in total annual population energy flow. Total population consumption ($K_{calories}$ per m^2 per year) was virtually identical in 1966-67 and 1967-68, whilst annual population production and respiration were very similar (section 4.2b and fig 34) Annual population consumption is a very useful measure of the impact of a predator in an ecosystem, and it appears that the effect, or impact, of Pyrrhosoma in pond B in the two years was virtually identical, despite differences in population dynamics. This could have important

Species	Group	B Mean pop biomass Kcals/m^2	Kcals per m^2 per annum			Author
			Total pop. energy flow A	P	R	
Phagocata	Platyhelminthes	-	131.2	113.4*[1]	18.7	Teal 1957
Pentaneura	Chironomidae	5.0	202.9	86.4	116.5	Tilly 1968
Phagocata	Platyhelminthes	7.6	126.1	32.5 or 114.5 *[2]	13.8	
Heleid A	Diptera Heleidae	0.15	52.8	9.2	43.6	
Heleid B		0.02	1.9	0.5	1.2	
Chauliodes	Megaloptera	3.6	20.9	2.8	18.1	
Rhantus	Coleoptera	0.26	11.0	3.6	7.4	
"Tendipedid R.B"	Chironomidae	0.07	3.5	1.5	2.0	
Percentage of populations in which the above figures exceed those found for Pyrrhosoma.		43.	75.	50.	75.	

Table 66 Energy utilisation by populations of aquatic invertebrate carnivores, for comparison with the data obtained for Pyrrhosoma.

*[1] *[2] Production estimates include mucus.

consequences for studies attempting to elucidate the role of carnivore species based only on population numbers.

Ecological energetics studies extending for periods of longer than one year are not yet sufficiently common to say whether the data for Pyrrhosoma are typical of other species. Wiegert (1965) found that consumption by grasshoppers (largely Melanoplus) in 1959 and 1960 in an old field amounted to 4.78 and 2.64 $K_{calories}$ per m^2 per year. Consumption by spittlebugs (Philaenus) in the same two years amounted to 1.0 and 2.0 $K_{calories}$ per m^2 per year. (Wiegert 1964). Basrawi (1966) (1966) found that total population assimilation in another grasshopper (Chorthippus) also differed, amounting to 0.68 and 0.40 $K_{calories}$ per m^2 per year in 1964 and 1965 respectively. Clearly, for these three herbivore populations total population energy flow was not constant in two consecutive years. However, Saito (1967), studying a diplopod (Japonaria) found that although total population energy flow in 1962-63 and 1966-67 was not identical, it was more similar than the variation in population numbers, suggesting that the population may have been more stable functionally than numerically. Unlike the present study, Saito also found that ecological efficiency in the two consecutive years was virtually identical. Finally Hunt (1966) found that annual production by the brook trout Salvelinus foutinalis varied by only 15 percent over sixty consecutive months, suggesting remarkably stable energy utilisation by the population, similar to the situation in Pyrrhosoma. It is therefore possible that carnivore populations and herbivore or decomposer populations may differ in the degree of stability shown by them in total annual energy flow.

Very few ecological energetics studies have analysed the relative importance of temperature and population biomass changes in controlling seasonal changes in energy flow within one year. Small (1967) found that the size structure of the population in Euphausia had more influence on annual energy flow than temperature, the exact opposite of the situation in Pyrrhosoma. Odum and Smalley (1959) analysed the effects of population biomass change on population energy flow in the salt-marsh grasshopper Orchelimum. Peak population energy flow in the grasshopper did not coincide with maximum biomass, but occurred when the population was composed of a medium number of medium sized nymphs all growing rapidly. This was very similar to the situation in Pyrrhosoma. The timing of peak and minimum energy flow in invertebrate populations (see also Wiegert 1964, 1965) and seasonal changes in population energy utilisation due to changes in population biomass and habitat temperature would repay further detailed study. For example, there is likely to be a major difference in the effects of temperature between those poikilotherms that show complete metabolic acclimatisation and those, like Pyrrhosoma, that show only partial or no acclimatisation to temperature.

Low temperatures markedly depressed metabolic rate in Pyrrhosoma, so that total population consumption and energy flow during the winter was extremely low (fig 35). There is evidence to suggest that prey capture during the winter was more difficult than at other times both from the low winter field feeding rate/maximum feeding rate ratio, implying a lower prey density (chapter 12, section 12.5 and fig 31), and from the large number of extremely small prey items (chiefly Ostracoda)

in final instar faeces during the winter (chapter 8, section 8.2d and table 27). It may therefore be argued that the lack of metabolic acclimatisation to temperature in Pyrrhosoma was an advantage in that the energy demands of the population were lowest when food was most difficult to obtain. Evolution of marked temperature acclimatisation in poikilotherms may be associated, at least partially, with an adequate winter food supply.

The ratio of production to biomass (P/B ratio) or population "turnover" in Pyrrhosoma was typical of the values found for most organisms with a long generation time. K.H. Mann (pers. comm 1967) reported P/B ratios of up to 3.5 for organisms completing development in two or more years; ratios between 3.2 and 6.5 for those developing in one year, and ratios between 5.1 and 11.5 for organisms with more than one generation per year. P/B ratios between 2 and 4 are typical of many aquatic invertebrates (Gerking 1962, Hayne and Ball 1956). Woodland (1967) obtained a value of 2.2 in the crayfish Cherax. The precise relationship between population production and mean generation time requires further investigation.

Considerable attention has been paid in ecological energetics studies to Ecological Efficiency.*1 Slobodkin (1959, 1960, 1964) has argued that in general, ecological efficiency will be found to lie between 5 and 15 percent. A number of ecological energetics studies on one, or a

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*1 Defined by Slobodkin (1960) as the steady state ratio of yield to predators over food ingested by prey.

group of species, have tended to confirm this prediction e.g. Engelmann (1961), Golley (1960), Mann (1965), Saito (1967), Siegert (1965). Similar results have been obtained by considering the ecological efficiency of whole trophic levels e.g. Kozlovsky (1968), Odum (1957), Patten (1959).

Utilisation of the term ecological efficiency for both single species populations and whole trophic levels may give rise to some confusion. If, as Slobodkin suggests, ecological efficiency can be equated with Lindeman's "Progressive Efficiency" (Lindeman 1942), then strictly, ecological efficiency should be applied only to an entire trophic level. However, the experimental work on which Slobodkin based his ideas of ecological efficiency (Slobodkin 1959, 1964) was carried out using single species populations, though in a way that simulated complete ecosystems and whole trophic levels. It may indeed be true that the ecological efficiency of an entire trophic level will not usually exceed 15 percent. However, the ecological efficiency of a trophic level is the mean of the efficiencies of its component species populations. A priori, since, individual net growth efficiencies (Ivlev's K_2, or the ratio of growth to assimation see section 14.1a) can be as high as 60 - 70 percent (Brody 1945, Kinberg 1956), there appears to be no logical reason why the ecological efficiency of a single species population should not be much higher than 15 percent. This is particularly true in a population of individuals all with a high net growth efficiency, and a high percentage assimilation.

Steele (1966) reported an ecological efficiency of 30 percent in

a provisional estimate for whole trophic levels in the North Sea. It is surprising that ecological efficiencies for single species populations in excess of 30 percent have not yet been reported (excluding those cases confused by immigration e.g. Siegert 1964). The two figures obtained for Pyrrhosoma of 35.2 and 18.3 percent, therefore appear to be the highest yet recorded for single species populations. Future work will probably provide further similar examples.

Despite the attention it has received, ecological efficiency is in many ways an unsatisfactory concept, incorporating two quite distinct components both interesting in themselves, but not mutually dependent i.e. population growth efficiency, and the proportion of population production "lost" in mortality. Population growth efficiencies alone would appear to be a more satisfactory basis on which to compare energy transformation by populations.

Gross population growth efficiency (the ratio of population production to population consumption) depends on two factors - the efficiency of assimilation, and the ratio of population production to population assimilation, (or net population growth efficiency).

Gross population growth efficiency in Pyrrhosoma amounted to 46.5 and 42.0 percent in the two years of study. This is considerably in excess of efficiencies previously reported, which have not normally exceeded 15 percent (e.g. Mann 1965, Saito 1967, Qasrawi 1966 Siegert 1965). This exceptionally high gross population growth efficiency shown by Pyrrhosoma was largely due to a high percentage assimilation, since net population growth efficiency, although high, was not exceptional,

being matched by thirteen other species populations (see table 67). However, for many invertebrate species, a net population growth efficiency of less than 30 percent is more usual (see for example the tables summarising the available data on population consumption, production and respiration given by Engelmann 1966, 1968, Golley 1968, and Riegert and Evans 1967). It is not immediately obvious which factors separate those species with a high net population growth efficiency (table 67) from those with a much lower efficiency; the possibility of there being an inverse relationship between population growth efficiency and assimilation efficiency was suggested by Odum and Smalley (1959), but this has not yet been examined in detail. (See also the work of Welch 1968 on individual growth and assimilation efficiencies discussed below).

Population growth efficiencies (Gross and Net) are the means of the individual growth efficiencies of the members of the population; it is therefore convenient at this point to consider individual growth efficiency in Pyrrhosoma. Results were presented in section 14.1a and b. Gross individual growth efficiency (K_1) during complete development was approximately 43 percent; net individual growth efficiency (K_2) was higher, approximately 49 percent. The maximum value obtained for gross individual growth efficiency (K_1) was 59.6 percent in July of the second year of larval life (fig. 33). This is close to the maximum value likely to be achieved by most organisms (Brody 1945). A very high individual net growth efficiency (approximately 70 percent) was noted by Fischer (1967a) in the larvae of Lestes sponsa.

The high individual growth efficiencies of Pyrrhosoma and Lestes

Author	Species	Kcals per m^2 per yr. Population Production P	Population Assimilation A	NET Population Growth Efficiency P/A x 100
Healey (1967)	Onychiurus (Collembola)	2.61	5.65	46%
Qasrawi (1966)	Chorthippus (Grasshopper)	0.35 0.21	0.68 0.40	50.5% 52.1%
Saito (1967)	Japonaria (Diplopoda)	26.9 3.0	57.8 1.5	46.5% 49.8%
Teal (1957)	Pisidium (Mollusca)	81.8	172.7	47.4%
Tilly (1968)	Physa (Mollusca)	169.4	205.4	82.5%
	Pentaneura (Tendipedidae)	86.4	202.9	42.6%
	Tubifex (Annelida)	42.9	71.5	60.0%
	Calopsectra (Heleidae)	6.4	13.7	46.7%
	Naidium (Annelida)	1.2	2.2	54.5%
	Corynoneura (Tendipedidae)	0.9	2.1	42.9%
	Pericoma (Psychodidae)	0.7	1.6	43.8%
	Sphaerium (Mollusca)	0.6	1.0	60.0%
Woodland (1967)	Cherax (Crayfish)	158	290	54%
Present study	Pyrrhosoma (Odonata)	3.94 3.59	7.61 7.56	51.8% 47.5%

Table 67 Studies in which Net Population growth efficiency has exceeded 40 percent.

may be attributed, at least partially, to their habit of remaining motionless (as do most Odonata larvae) for long periods: the energy expended in movement is therefore minimal, and total metabolic rate low. Odonata larvae do not appear to possess a fat body (Corbet 1962). Odum (1968) has compared fat reserves to a "work loop" in carnivores providing energy required for activity in capturing the next meal. Odonata larvae do not need to expend a great deal of energy to capture prey, but remain motionless and wait for prey to swim past. Nor did Pyrrhosoma normally appear to spend long periods without food (chapter 12 and table 54). Therefore, absence of a fat body, low metabolic rate and high growth efficiency may be intimately related to the method of hunting evolved by Odonata larvae; a method which seems to be very economic in terms of energy utilisation.

Welch (1968) analysed the relationship between the individual growth efficiencies of aquatic animals measured in the laboratory (K_1 and K_2) and percentage assimilation. Both gross and net growth efficiencies in Pyrrhosoma were considerably higher than the values predicted from Welch using the assimilation efficiency of 87 - 88 percent (see table 60) observed in Pyrrhosoma. The ecological importance of the relationships noted by Welch requires further investigation; however, if the relationships are found to be valid for a large number of species, then the apparent exceptions (of which Pyrrhosoma may be one) may be of great interest.

The alternative method of comparing the fate of assimilated energy at the population level, the relationship between the log of population production and the log of population respiration or "Engelmann line",

was also examined in the present study (section 14.2e). Data from many aquatic species seem to fit reasonably well to the line calculated by Engelmann (1966) for terrestrial poikilotherms (fig 37), though data from Pyrrhosoma was a relatively poor fit. However, Engelmann had comparatively few points at lower production levels. Addition of a number of studies not available in 1966 (Healey 1967; Learned 1966; Saito 1967; Siegert 1965), suggests that the slope of the line for poikilotherms may be greater than the value of 0.86 which Engelmann found. This steeper slope would bring the data for Pyrrhosoma much closer to that of other poikilotherm studies. However, it is clear that the scatter about the line relating log population production to log population respiration in poikilotherms is large, whatever its precise position. Nevertheless, that fact that the relationship exists, and appears to be similar for both terrestrial and aquatic poikilotherms is of great theoretical interest.

The final calculation attempted for Pyrrhosoma in pond 3 was to estimate Pyrrhosoma population energy flow as a percentage of incoming solar radiation and net primary production. (Section 14.2f). Annual production by Pyrrhosoma amounted to only 0.0004 percent of the total incident short wave radiation to pond 3. This was very similar to the figure of 0.00024 percent found by Vannote (1962) for the relationship between total annual production of small-mouth bass and incident radiation to a small eutrophic stream. Both Pyrrhosoma and the bass appeared to occupy a similar position in the food webs of the two ecosystems.

Other ratios presented in section 14.2f also suggest that the energy

utilised by Pyrrhosoma was an extremely small percentage of the energy entering pond 3. Most significant was the fact that the estimated consumption by the browsers "supporting" the Pyrrhosoma food chain only accounted for approximately 5 percent of net primary production. This raises a number of interesting problems about the factors limiting energy input to the Pyrrhosoma population.

Other energy utilising pathways clearly accounted for some of the remaining 95 percent of net primary production in pond 3. The only exact data on this point is that of Fitzpatrick (1968) for Asellus, which formed the basis of an entirely independent energy flow pathway within the pond (see chapter 8). Fitzpatrick found that the Asellus population in pond 3 assimilated 67.4 K_{cals} per m^2 per year. Since Asellus was equally abundant in ponds 3 and 6, it was reasonable to assume that total annual Asellus energy flow in these two adjacent ponds was approximately similar. Taking an assimilation efficiency of 30 percent, total annual Asellus consumption amounted to at least 200 K_{cals} per m^2 per annum. This figure, in combination with the consumption at the base of the Pyrrhosoma food chain, accounted for approximately 10 percent of net primary production in pond 3.

Some of the remaining net primary production was probably unused, and contributed to the successional accumulation of organic debris in the pond bottom. By far the bulk of net primary production, however, was probably utilised by micro-organisms, particularly aquatic fungi and bacteria. In some aquatic ecosystems, bacterial respiration may be extremely high (Odum 1957, Teal 1962, Pilly 1968). To understand

the factors controlling the division of the pond's energy resources between all the energy utilising processes within the pond ecosystem is a problem extending beyond the limits of the present study and of ecological energetics, and embraces the whole of ecology.

Fig. 33. Pattern of monthly energy utilisation for growth, respiration, exuvium production and faeces as a percentage of monthly consumption in an "average" individual Pyrrhosoma larva throughout development in the field. (Pooled data from all year classes in ponds B and F).

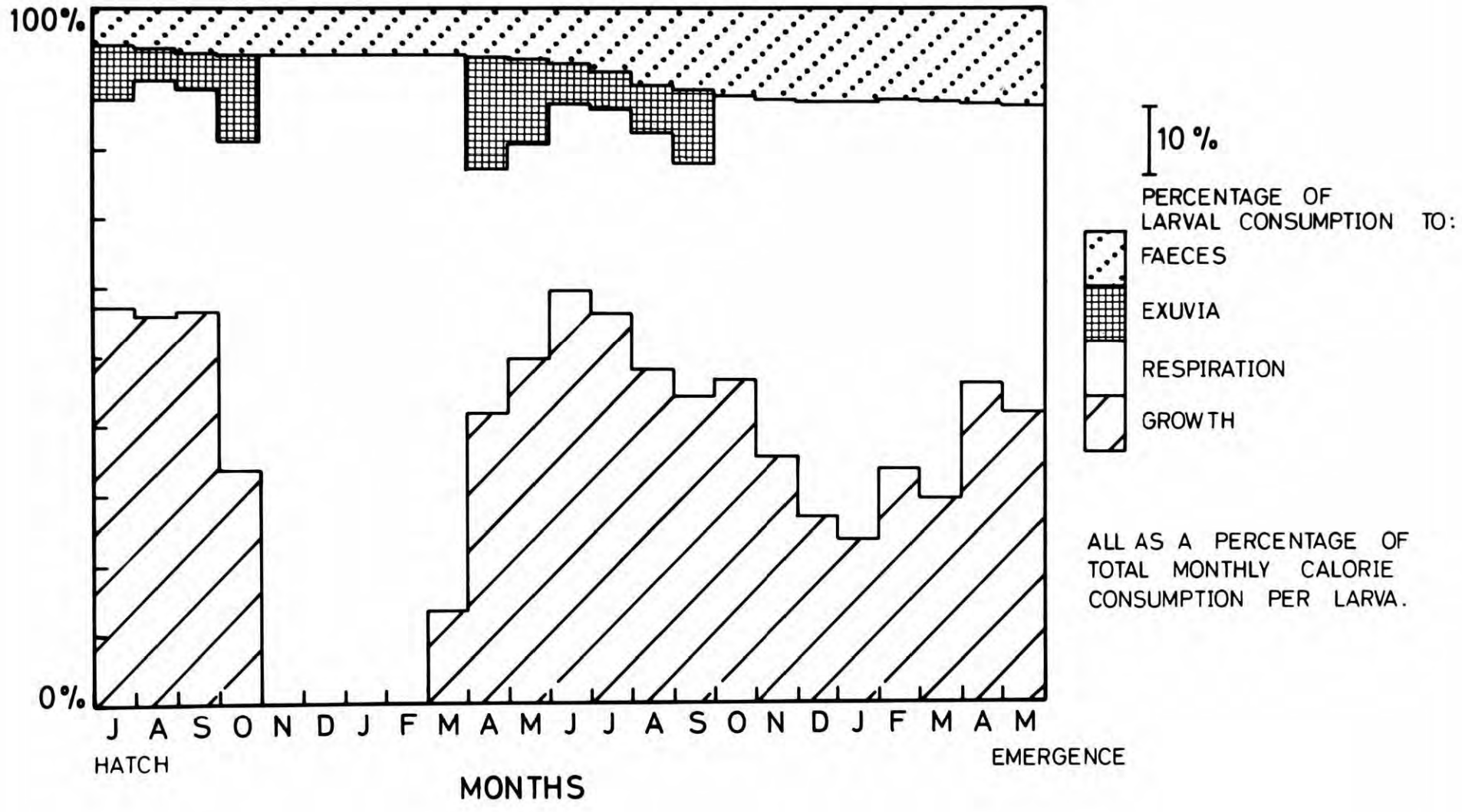
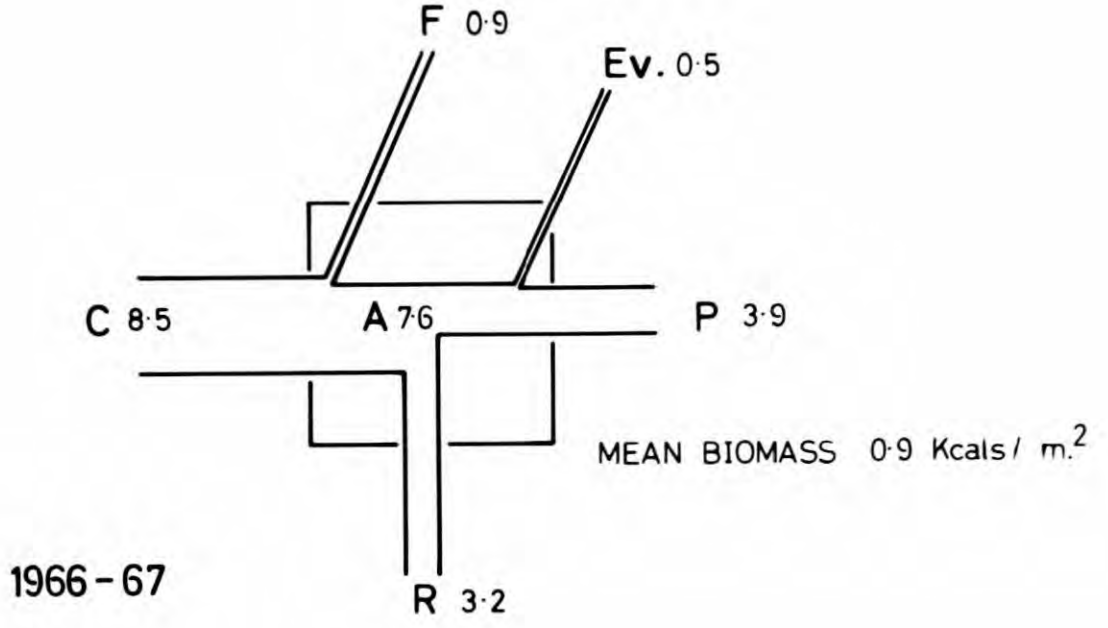
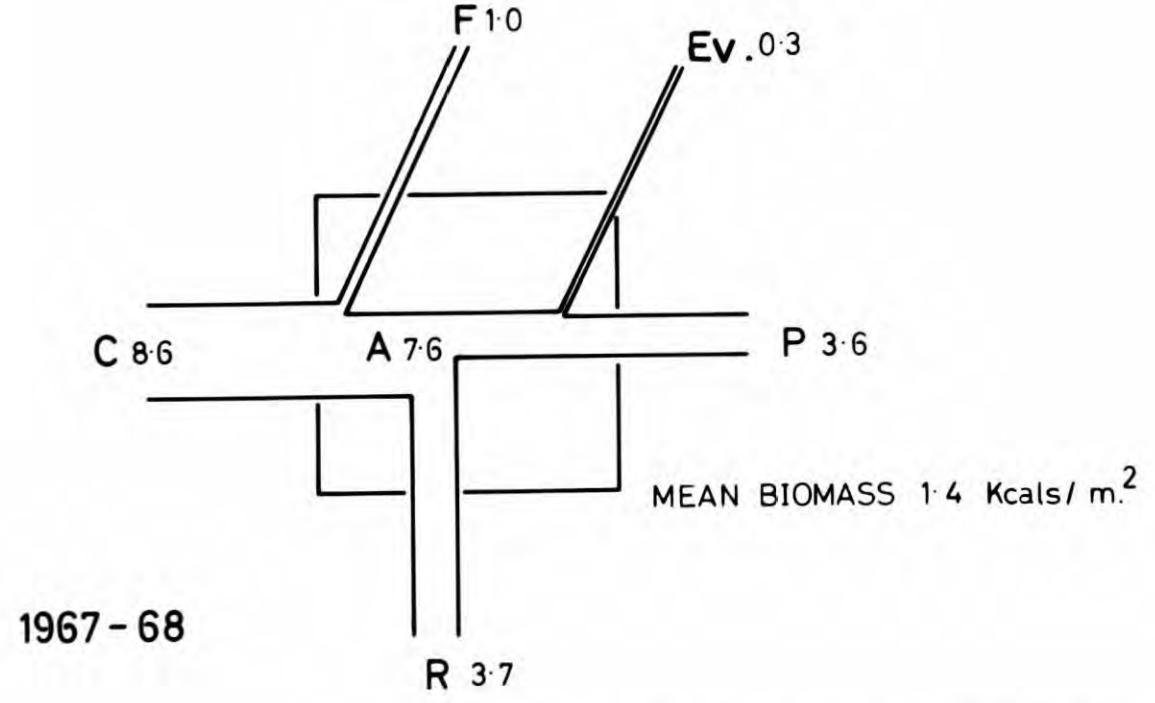

100%
0%
J A S O N D J F M A M J J A S O N D J F M A M
HATCH
EMERGENCE
MONTHS
10 %
PERCENTAGE OF LARVAL CONSUMPTION TO:
FAECES
EXUVIA
RESPIRATION
GROWTH
ALL AS A PERCENTAGE OF TOTAL MONTHLY CALORIE CONSUMPTION PER LARVA.

Fig. 34. Annual population energy flow diagrams for *Pyrrhosoma* larvae in pond B in two consecutive years of study (July 1966 - June 1967 and July 1967 - June 1968).

C = Consumption
A = Assimilation
R = Respiration
P = Production (Growth)
Ev = Exuvium production
F = Faeces
All as Kcals per m^2 per year.





ENERGY FLOW IN Kcals / m.^{2} / annum.

Fig. 35. Changes in total monthly Pyrrhosoma population consumption (K cals per m^2 per month) in pond B in two consecutive years of study, with the contributions of the junior and senior age classes distinguished. Mean monthly pond temperatures are also shown.

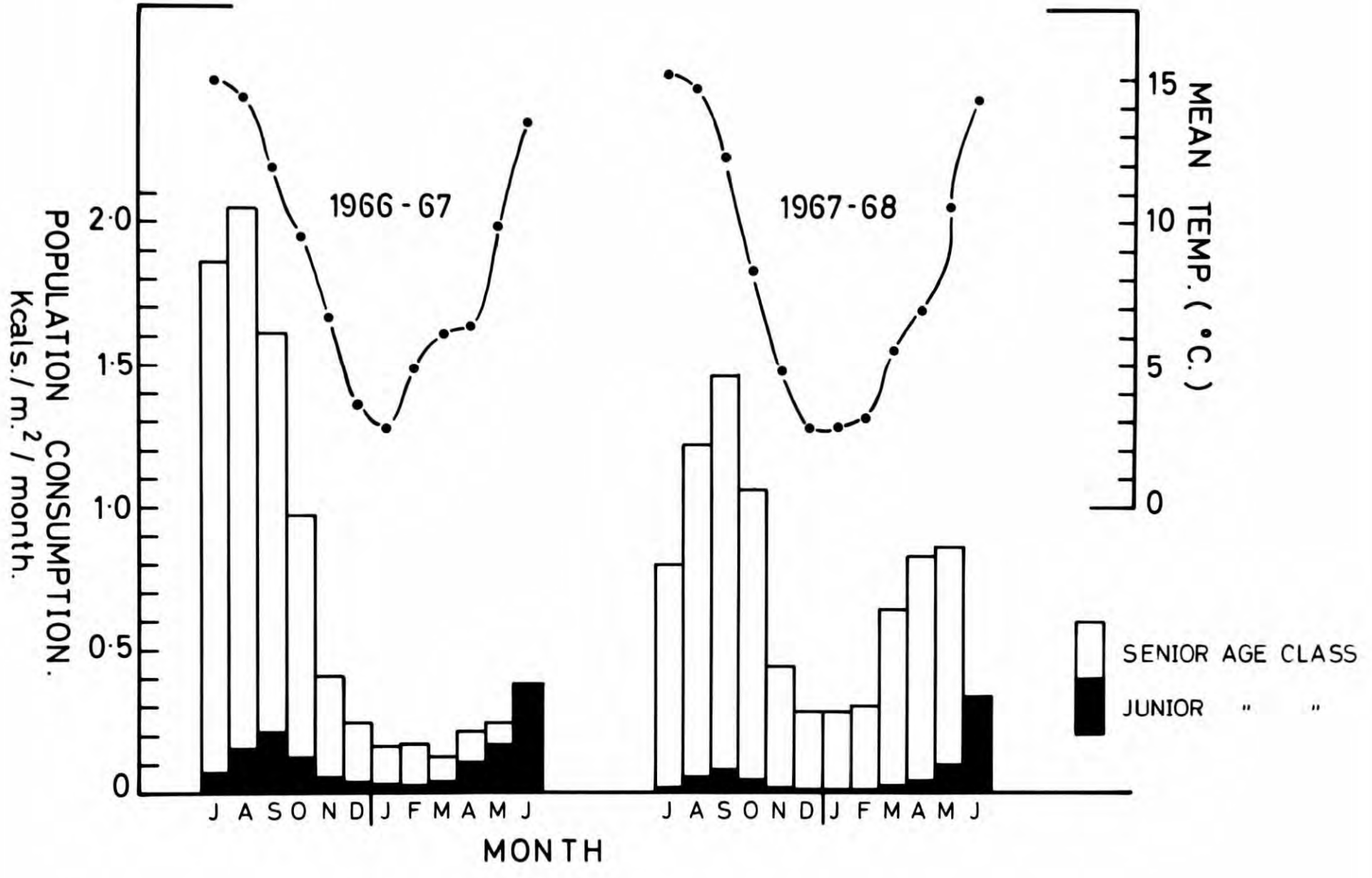

1966 - 67
1967 - 68
POPULATION CONSUMPTION.
Kcals./ m.² / month.
2·0
1·5
1·0
0·5
0
MEAN TEMP. (°C.)
15
10
5
0
J A S O N D J F M A M J
J A S O N D J F M A M J
MONTH
SENIOR AGE CLASS
JUNIOR " "

Fig. 36a. Monthly Pyrrhosoma population consumption, plotted against mean monthly temperature in pond B. The calculated regression is presented in section 14.2c.

Fig. 36b. Monthly Pyrrhosoma population consumption, plotted against mean monthly Pyrrhosoma population biomass in pond B. The calculated regression is presented in section 14.2c.

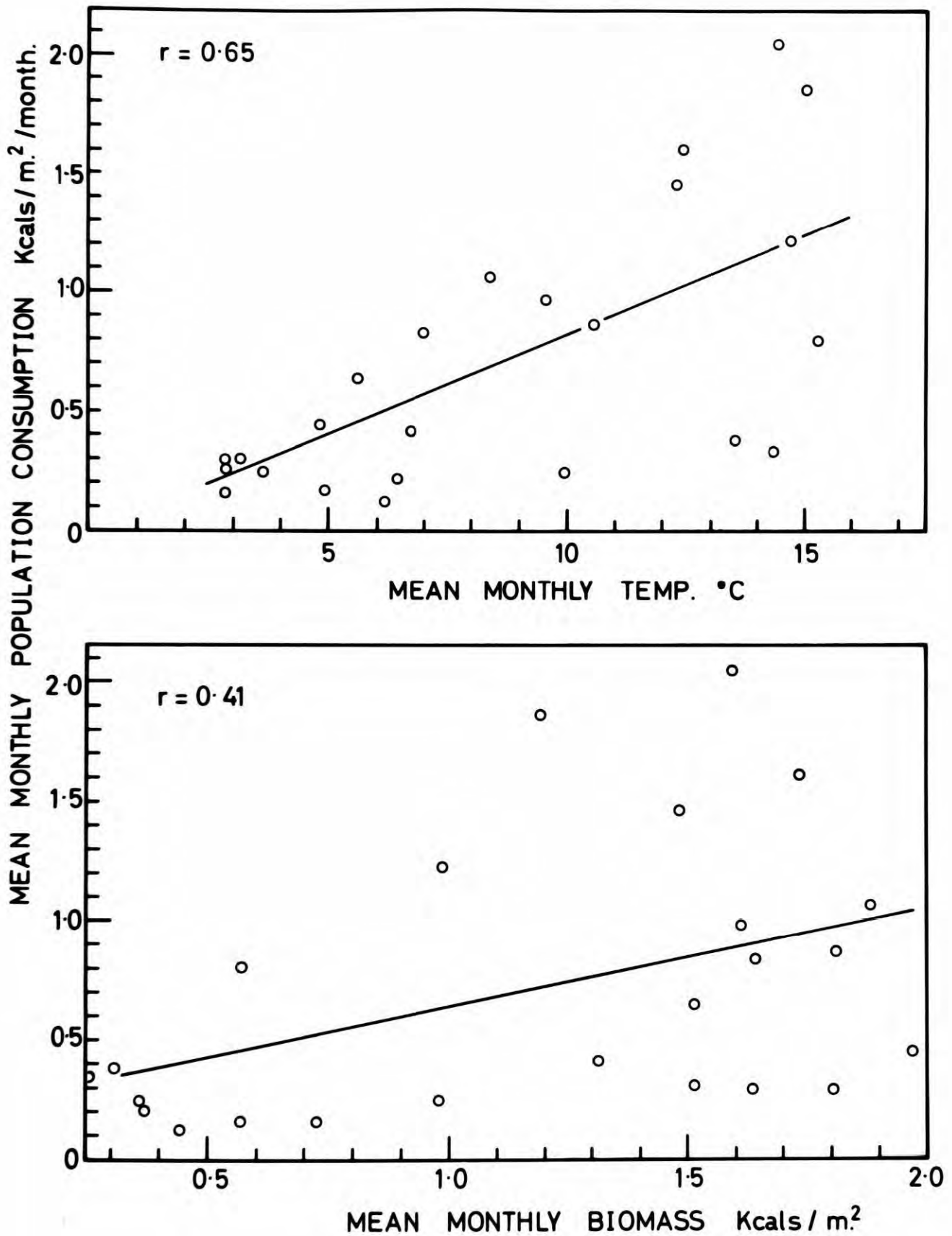
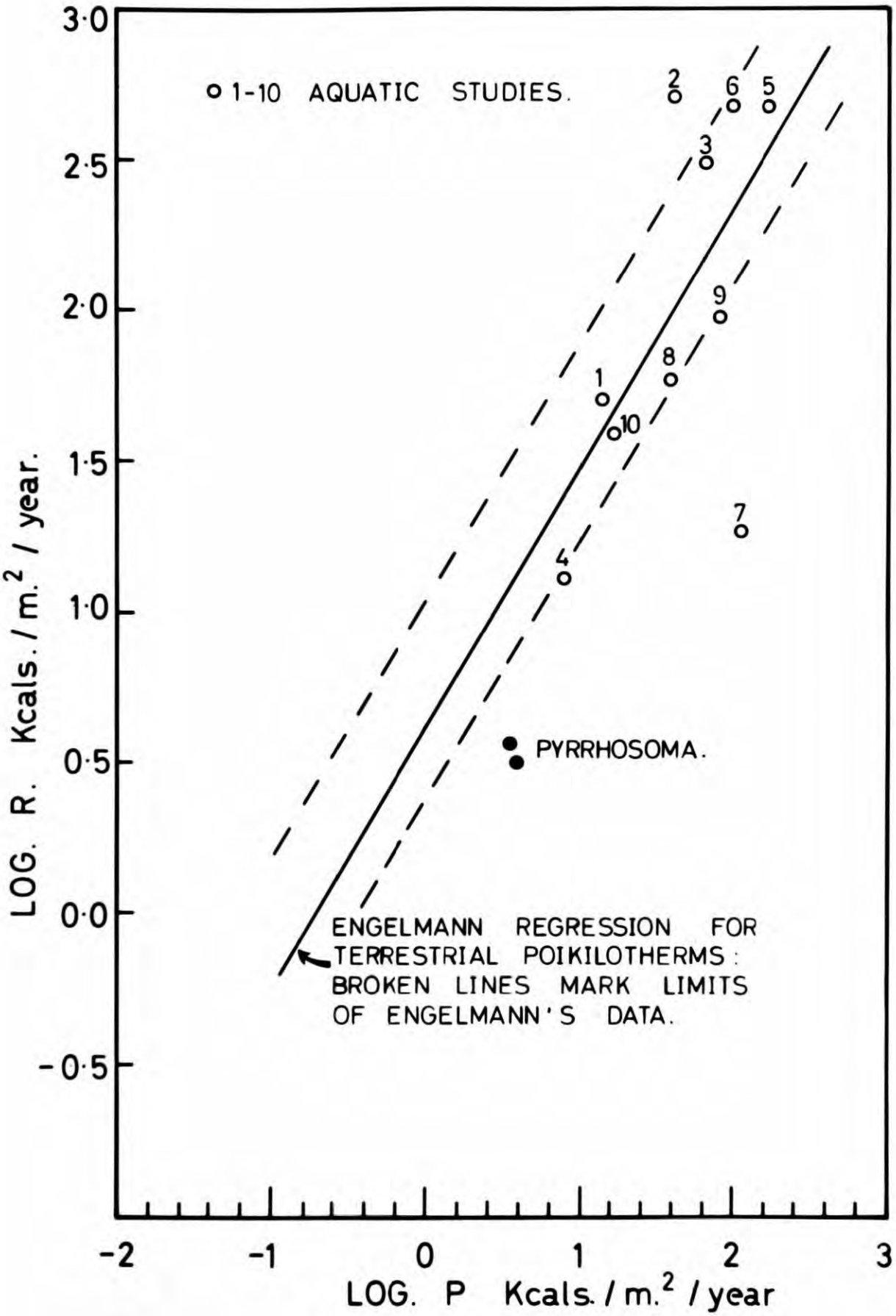

r = 0·65
MEAN MONTHLY POPULATION CONSUMPTION Kcals / m.² /month.
2·0
1·5
1·0
0·5
0
5
10
15
MEAN MONTHLY TEMP. °C
r = 0·41
MEAN MONTHLY POPULATION CONSUMPTION Kcals / m.² /month.
2·0
1·5
1·0
0·5
0
0·5
1·0
1·5
2·0
MEAN MONTHLY BIOMASS Kcals / m²

Fig. 37. The "Engelmann regression" for terrestrial and salt marsh poikilotherms, on which data for aquatic poikilotherms (including Pyrrhosoma) have been superimposed. See text for details. Numbers on the figure refer to the studies listed in table 65. The dotted lines enclose the variation about the line in the individual points observed by Engelmann, and are not the 95 percent confidence limits.


3·0
2·5
2·0
1·5
1·0
0·5
0·0
-0·5
LOG. R. Kcals. / m.² / year.
-2
-1
0
1
2
3
LOG. P Kcals. / m.² / year
o 1-10 AQUATIC STUDIES.
1
2
3
4
5
6
7
8
9
10
PYRRHOSOMA.
ENGELMANN REGRESSION FOR TERRESTRIAL POIKILOTHERMS: BROKEN LINES MARK LIMITS OF ENGELMANN'S DATA.

Chapter 15

CONCLUDING REMARKS

This final chapter deals with some general problems raised during the course of this work. A section of discussion was presented at the end of each chapter: chapters 7 to 10, 12 and 14 deal specifically with a number of important ecological energetics problems.

In two quite different ways, the energy flow through the population of Pyrrhosoma larvae in pond B showed remarkable stability. In chapter 8, it was shown that throughout larval development, Pyrrhosoma derived approximately 85 percent of its energy from browsers and 15 percent from carnivores. In chapter 14, it was shown that total population consumption was identical in two consecutive years of study (approximately 8.5 K_{cals} per m^2 per annum). Neither of these aspects of functional stability within the pond ecosystem were apparent from a more superficial analysis of the number of prey items eaten, nor from the numerical changes in abundance of Pyrrhosoma in the pond.

It is pertinent to ask what factors were responsible for this functional stability, and whether its two aspects were in any way related. The effects of a large number of alternative energy flow pathways within an ecological system (MacArthur 1955) are discussed in chapter 8: undoubtedly this had an important effect in stabilising the pattern of energy flow throughout larval development. The large number of alternative pathways through which the Pyrrhosoma population received its energy supply was probably also of great importance in ensuring stability of energy flow through the larval population in two consecutive years, since this would tend to make the population indepen-

dent of changes in the availability of any one prey species. To this, extent, therefore, the two aspects of functional stability were related.

Hairston et. al. (1960) and Slobodkin et. al. (1967) suggested that carnivore populations are usually energy limited. The data of Menhinick (1967) Tilly (1968) and Pulliam et. al. (1968) tend to support these conclusions: under these circumstances, strict limits on the energy available to each carnivore species within the community, imposed by strong competitive interactions between carnivores may be inferred. The data obtained in the present study are consistent with the hypothesis that the energy available to the Pyrrhosoma population was limited, constant in the two years of study, and that the Pyrrhosoma population made maximum use of the limited energy available to it.

This simple hypothesis raises a number of problems. Seasonal changes in population energy flow in Pyrrhosoma were particularly influenced by the density of available prey, pond temperature and Pyrrhosoma population biomass (chapter 14, section 14.2c). The precise role of each of these factors in the regulation of annual population energy flow was not investigated. However, the regulation of Pyrrhosoma larval biomass is the factor most likely to be involved in the limitation of Pyrrhosoma population energy flow by competitive interactions with other carnivore populations. Control of larval biomass is itself closely linked with the mechanisms of population regulation in Pyrrhosoma.

The function of adult territory in Odonata has been discussed by Corbet (1962) Corbet et. al (1960) Jacobs (1955), Johnson (1964) Moore (1952, 1953, 1957, 1964) and Wynne-Edwards (1962). One important effect

of adult territory in Odonata might be to limit egg input into the habitat, thereby placing a ceiling on larval numbers. Moore (1964) showed that there was an upper limit to the density of adult male Odonata (and hence to ovipositing females) that could exist in any one area. For Pyrrhosoma this was approximately 44 males per 100 m of pond edge. An upper limit on egg input to the habitat, however, is only one possible population regulation mechanism. Macan (1964, 1965 b,c, 1966a) suggested that larval population regulation in Pyrrhosoma may be achieved by the number of suitable "fishing points" available to the larvae.

The work of Holling (1961, 1965, 1966) and of Brocksen et. al (1968) showed the importance of prey density on rates of consumption and total energy flow in carnivores. Larvae that for some reason are forced to occupy "fishing points" where the effective prey density is too low to provide enough food for maintainance presumably die of starvation. Alternatively, larvae occupying "fishing points" within the pond where effective prey density is very high would show correspondingly high consumption and growth rates. Interspecific competition could play an important part in totally excluding Pyrrhosoma larvae from "fishing points" in parts of the pond. This is consistent with the observations on larval distribution in pond 3 (chapter 5), and with the reported niche differences between associations of several species of Odonata larvae in the same habitat (Hornondy 1964; Needham 1949). Intraspecific competition might be expected for suitable "fishing points" within those parts of the pond occupied by Pyrrhosoma (Macan 1965 b,c.).

Most of the above ideas are speculative: they do, nevertheless, suggest ways in which numbers and hence Pyrrhosoma biomass may be limited in response to a limited available energy supply. However, the scheme implies that starvation may be an important cause of larval mortality in Pyrrhosoma, for which there is little evidence. The majority of larvae usually had food in the gut when captured (chapter 12, table 54), whilst predation by Aeshna cyanea larvae rather than starvation was suggested as a possible cause of heavy Pyrrhosoma mortality in the first year of study (chapter 5). It is possible, of course, that starvation only becomes significant in the absence of predation, for which there is some evidence in Pyrrhosoma (Macan 1966a). Clearly, without a great deal more information than is at present available, further discussion of these problems is impracticable.

No ecological energetics study has yet attempted to elucidate the factors responsible for the stability (or otherwise) and regulation of population energy flow from year to year. It is clear from the present study that total annual energy flow may be more stable than changes in population numbers, and it is suggested that ecological studies on the stability and regulation of energy flow in addition to studies on the stability and regulation of population numbers should be attempted.

Whatever the factors were that controlled or limited numbers and energy flow in Pyrrhosoma, it is clear that total energy flow through the Pyrrhosoma population was extremely small compared with estimated total net primary production in pond B, and therefore with total community energy flow. As Odum (1962) has pointed out, the contribution of most

predators to total community energy flow is probably extremely small: table 68 summarises data on this point from a number of terrestrial and aquatic ecosystems. However, the importance of predators in promoting energy flow may lie with their controlling effects on lower trophic levels, rather than their own contribution to total community production or respiration.

The impact of predatory fish populations in aquatic habitats is now well known (see Ball and Hayne 1952; Brooks and Dodson 1965; Hrbáček 1959; Hrbáček et. al 1961; Lellák 1965: Macan 1965 c, 1966 a,b; Macan et. al., 1967; and Straškraba 1965). Apart from the activity of the fish bringing about changes in substrate and vegetation, important changes may take place within the community as a direct result of fish predation. Species composition and relative numerical abundance of many of the invertebrate prey species may alter considerably. Also, fish predation tends to reduce the overall size of many of the prey species in the habitat, with important consequences for community metabolism, since metabolic rates per mg. increase in smaller animals.

Almost nothing is known about possible similar effects being brought about by invertebrate predators. Since the magnitude of the effects of fish predation are due to the quantity of food which they consume, one approach would obviously be to compare total consumption (as K_{cals} per m^2 per annum) of invertebrate carnivores with consumption by predatory fish in the same or a similar habitat. Brocksen et al. (1968) showed that consumption of midge larvae by predatory stonefly larvae (Acroneuria) in artificial laboratory stream communities was at

least equal to, and may have exceeded consumption of the same prey by Sculpins (Cottus) even though the biomass of the stoneflies was less than that of the fish. In this situation, therefore, the effects of the invertebrate predator on lower trophic levels was probably at least as great as the effects of fish predation. Similar data have not been obtained in the field, although Gerking (1962) showed that approximately 50 percent of the total summer benthos production in Tyland Lake was consumed by Lepomis, the blue-gill sunfish. This suggests that total consumption by all the invertebrate carnivores combined was less important than for one fish species. More data comparing predatory fish consumption and invertebrate carnivore consumption in aquatic habitats are required.

In considering the importance of invertebrate carnivores in aquatic habitats, a distinction must be made between those species capable of showing both a numerical and functional response to changes in prey density, and those showing only a functional response. (A numerical response is an increase in the numbers of the predator, usually due to increased predator reproduction, in response to increased prey density. A functional response is an increase in the feeding rate of each individual predator as prey density increases); see Solomon (1949), Holling (1959,b, 1961, 1965, 1966). Hassel (1966) has elaborated these terms, but without more detailed information than is at present available for aquatic systems, use of his more complex terminology is not considered justified in the present context.

Holling (1965) has shown that an invertebrate functional response

Author	Habitat	Carnivores Studied	CARNIVORE RESPIRATION AS A PERCENTAGE OF TOTAL CONSUMER RESPIRATION	CARNIVORE PRODUCTION AS A PERCENTAGE OF TOTAL CONSUMER PRODUCTION	CARNIVORE ASSIMILATION AS A PERCENTAGE OF TOTAL CONSUMER ASSIMILATION
Macfadyen (1963)	Limestone Grassland	All carnivores in community	1.38	-	-
Max. and min. figs.	Spruce forest floor	Ditto	37.43	-	-
Menhinick 1967	Lespedeza field	Arthropod carnivores above the soil surface	11.94	7.69	11.11
Nelson and Scott 1962	Middle Oconee River	Mainly carnivorous insect larvae	-	8.83	-
Odum 1957	Silver Springs	Carnivores & Top carnivores	4.8	3.72	-
Sitaromaiah 1967	Tatayya gunta pond	All carnivores	1.32	-	1.31
Teal 1957	Root Spring	All carnivores	4.85	21.41	-
Teal 1962	Georgia Salt Marsh	All carnivores	7.4	-	-
Tilly 1968	Cone Spring	All carnivores	10.1	17.5 or 25.4	15.2

Table 68 Summary of carnivore energy flow as a percentage of equivalent figure for total consumers, including carnivores; (bacteria have been excluded). It is clear that carnivores are usually unimportant in their contribution to total community energy flow.

alone is unable to regulate or control prey populations. Either the prey declines to extinction (which is an established predator : prey system must be exceptional) or else the prey increases beyond the control of the predator. Predators showing a numerical response, however, are clearly potentially capable of regulating their prey though whether any aquatic invertebrate predator exerts a density dependent regulating effect on its prey does not appear to have been clearly demonstrated. Nevertheless, the potential of these two types of predator for the regulation of energy flow through lower trophic levels is very different.

Regulation of prey numbers by strong predation pressure arising from a numerical response, logically implies a reduction in prey number and biomass below that which might be expected in the absence of predation. In consequence, the consumption rate of the total prey population may be considerably reduced e.g. Flanders and Badgley (1963), Wright et. al (1960), with important effects on the pattern of community energy flow. However, because the prey species is reduced in numbers, the food supply and hence consumption rate per individual prey may be increased. This may have further important consequences (Globodkin and Richman 1956, Ricker 1946), including a change in age structure of the prey population (increasing the proportion of young individuals) and an increase in their growth and reproductive rates, again with important effects on community energy flow. Warren et. al (1964) have also demonstrated the effect of increasing the food supply per individual on production in aquatic habitats. Reduction of prey biomass by a predator may also lead to an increase in turnover rate i.e. the P/B ratio

increases (Hayne and Ball 1956).

It is unlikely that invertebrate predators showing only a functional, non-regulating, response can have such a marked effect on their prey species as those listed above.

To be potentially capable of prey regulation, the predator numerical response must be relatively rapid compared with the generation time of the prey. Excluding Protozoa and Rotifera, aquatic invertebrate carnivores potentially capable of showing a strong numerical response include the Turbellaria (although Reynoldson and Young 1965 suggest that Polycelis is an ineffective predator "and does not influence the numbers of its prey decisively"), Leptodora, several species of Copepod, and Leeches, (for example an increase in the numbers of Glossiphonia apparently caused a big decline in prey abundance (Dineen 1953)). Aquatic invertebrate predators showing only a functional response might reasonably be expected to include forms with a restricted breeding season and long larval development time, long that is compared with the generation time of the prey . In this case the predator could not be expected to show a numerical response to increasing prey density. Clearly included in this category are such predatory insect larvae as Chaoborus, Plecoptera and of course Odonata.

Odonata larvae may be regarded as the "type example" of those aquatic invertebrate carnivores that show only a functional, non-regulating response to increases in prey density. In view of what has been said above the effect which they have on their prey species, and hence on community energy flow might be expected to be very small. Aggregations of larvae - see chapter 5 - caused by movements into regions of high prey density,

and therefore a form of aggregative response, (see Hassel 1966), may partially compensate for the lack of ability to increase the total numbers in the habitat through reproduction, but the effect is unlikely to be very great. On rare occasions, Odonata larvae have been considered responsible for causing very heavy mortality in a prey species e.g. Davies and Reynoldson (1967), Kingsbury (1937), Young and Reynoldson (1965), and Aeshna cyanea in the present study - see chapter 5. Usually, however, they appear to have a negligible effect on their prey (Corbet 1962; Corbet et. al. 1960), and hence, it might be inferred, on the regulation and control of total community energy flow.

The data obtained for Pyrrhosoma may be observed against this general background. Energy flow through the Pyrrhosoma population was an extremely small percentage of the estimated total net primary production in pond B, and in terms of its contribution to total community energy flow, Pyrrhosoma was clearly unimportant. However, unlike those predators capable of showing a numerical response, its controlling and regulating effects on energy flow through lower trophic levels were probably also negligible. The range of prey species taken was wide (chapter 8) and it is doubtful if any one prey species was significantly affected by Pyrrhosoma predation, whilst the total amount of energy entering the base of the Pyrrhosoma food chain amounted to approximately 5 percent of net primary production in pond B. This is unlikely to have exerted a significant influence on the total pattern of energy flow within the pond. The fact that the pond supported other key energy utilising pathways e.g. the Asellus food chain (see chapter 8), that were indepen-

dent of the Pyrrhosoma food chain would also tend to reduce the impact of Pyrrhosoma within the total pond ecosystem.

It must therefore be concluded that Pyrrhosoma was not exerting an important effect on the energy flow through the study ponds. Rather an impression of "minimum impact" is created which logically would appear to be of great advantage to a predator (Slobodkin 1968). The mechanisms of population regulation in Pyrrhosoma are not fully understood. Clearly, however, some factor or group of factors prevented the Pyrrhosoma population from increasing to a level where it might seriously have begun to affect its prey. Yet annual Pyrrhosoma emergence from a substantial larval population was certainly in excess of that required to ensure the continued survival of the population at approximately the present level, at least for the foreseable future. This unobtrusive balance between Pyrrhosoma, its prey and the habitat which it occupies may account in no small way for its particular success as a species in a group that are themselves remarkable for their long evolutionary success.

The following papers were prepared during the course of this work.

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Lawton, J.H. (1969). Studies on the ecological energetics of Damselfly larvae. Read at the British Ecological Society, London, January 1969.

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Appendix 1

DEFINITION OF SYMBOLS

The equations normally used to describe ecological energy transformations are presented in chapter 1. The symbols used throughout this thesis are those recommended for use during the International Biological Programme, and are taken from Ricker (1968).

B - Population biomass, standing crop, or biocontent, expressed in energy units (calories per m^2).

C - Consumption : the total intake of food energy during a specified time interval.

F - Faeces or egesta : that part of the food energy that is not absorbed and leaves the alimentary canal.

U - Excreta : that part of the material absorbed which is passed from the body as urine.

A - Assimilation : that part of the food energy that is absorbed into the body through the alimentary canal (C - F). This definition differes slightly from that given in Ricker (1968) - see below.

R - Respiration : that part of assimilation which is converted to heat or mechanical energy, and is used

up in maintainance of life processes.

P - Growth or production : the increase in biomass. That part of the assimilated energy incorporated into new biomass. (It does not include Ev.)

Ev - Exuvium production : that part of the assimilated energy lost in the moulted exuvia. This definition is not included in Ricker (1968) and has been added for the purpose of this work.

The following equations clarify the interrelationships of these functions.

$$C = P + R + F + U + Ev.$$

$$A = P + R + U + Ev.$$

$$A = C - F$$

Strictly Assimilation can be distinguished from Absorption. Following Ricker (1968), we may write:

$$\text{Absorption} = C - F$$

and $$\text{Assimilation} = C - F - U.$$

In the present study, U, the energy lost as urine was not measured, since its contribution to the total energy budget was probably negligible (see chapter II). In this case, the two terms Assimilation and Absorption become virtually synonimous, and throughout the study, Assimilation has been used in the context

$$\text{Assimilation } (A) = C - F$$

With the exception of biomass, which has no time dimention, all symbols were used in two ways

i) To describe energy transformations by individual larvae:

calories per larva per unit time

ii) To describe energy transformations by larval populations:

calories per m^2 per unit time.

Distinction between these two uses is obvious from the context in which they occur.

Appendix 2

LIST OF ANIMALS RECORDED FROM POND B

This list includes all animals taken in pond B during the study. Genera or even families have been listed for completeness when no specific identification was made.

Voucher specimens (preserved in 70 percent alcohol) are kept by the author and may be examined on request.

The list is necessarily incomplete and includes no Protozoa or Rotifera. It does, however, include all the larger metazoa taken during the three years of field work, however rare. To distinguish these rare species from the commoner forms, two symbols were used:

* A dominant form (or key species), usually present in any net sweep (if seasonal, then present thus 'in season').

\+ Very rare. Less than ten occurrences in three years.

(Carn) signifies that the species was predominantly carnivorous.

Mollusca

Limnaea pereger.

Pisidium sp.

\+ Planorbis planorbis.

Annelida

(Hirudinea)

\+ Glossiphonia complanata. (Carn)

Annelida

(Oligochaeta)

Chaetogaster sp.

\+ Eiseniella tetraedra.

Lumbriculidae.

Tubificidae.

Arthropoda

(Arachnida)

\+ Argyroneta aquatica. (Carn)

* Hydracarina of several unidentified species (Carns.)

Arthropoda

(Crustacea)

* Asellus aquaticus.

* Acanthocyclops viridis (Carn.)

* Copepoda of several other species (some Carns.)

Chydorus sphaericus

Other Chydorus spp.

* Ostracoda.

* Simocephalus vetulus.

Arthropoda

(Insecta)

Coleoptera: adults and larvae.

Agabus sp.

Curculionidae.

Dytiscus marginalis. (Carn)

Dytiscidae of several other species. (Carns.)

Gyrinus sp.

* Haliplus sp.

Diptera : larvae.

Anopheles sp.

Ceratopogonidae. (some Carns.)

* Chaoborus sp. (Carn)

* Chironomidae of several species.

Chironomus sp. (sensu stricto).

Dixa sp. (Carn)

Tanypodinae. (Carn)

Tipulidae.

Ephemeroptera : larvae.

* Cloeon dipterum.

Caenis sp.

Hemiptera : adults and nymphs.

* Corixa punctata.

Gerris spp.

Nepa cinerea. (Carn)

* Notonecta glauca. (Carn)

Notonecta obliqua. (Carn)

* Notonecta obliqua var. delcourti. (Carn)

* Sigara spp.

Lepidoptera : larvae.

Nymphula nymphaeta

Megaloptera : larvae.

Sialis sp. (Carn)

Odonata : larvae.

Aeshna cyanea. (Carn)

* Coenagrion puella. (Carn)

Enallagma cyathigerum. (Carn)

Ishnura elegans. (Carn)

* Lestes sponsa. (Carn)

* Pyrrhosoma nymphula (Carn)

Plecoptera : larvae.

Nemurella sp.

Trichoptera : larvae.

* Limnephilus spp.

Triaenodes sp.

Vertebrata

(Amphibia)

Bufo bufo. (Carn)

Rana temporaria. (Carn)

Triturus palustris. (Carn)

Triturus vulgaris. (Carn)

Appendix 3

INFORMATION ON THE FOOD OF THE MAIN PREY SPECIES TAKEN BY PYRRHOSOMA

The food of the main prey species taken by Pyrrhosoma was determined by personal observation, and from the following references.

Asellus

Gerking (1962), Fitzpatrick (1968)

Ceratopogonidae

Lindeman (1941), Dineen (1953)

Chaoborus

Lindeman (1941)

Chironomids, (except Tanypodinae)

Badcock (1949) Berg (1950) Bryce (1960) Gerking (1962) Lindeman (1941)

Cloeon dipterum

Chapman and Demory (1963) Clennel (1967)

Copepoda

Gerking (1962), Fryer (1957) Lindeman (1941)

Dytiscidae

Jones (1950)

Hydracarinae

Dineen (1953) Gerking (1962) Lindeman (1941)

Oligochaeta

Lindeman (1941)

Simocephalus vetulus

Gerking (1962) Jørgensen (1966) Macan (1961 1963)

Tanypodinae

Badcock (1949), Bryce (1960) Rutner (1963.