

PREY DENSITY AND SURVIVAL IN DAMSELFLY LARVAE: FIELD AND LABORATORY STUDIES

D.J. THOMPSON

Department of Zoology, The University, P.O. Box 147,
Liverpool L69 3BX, United Kindom

Faecal-pellet production by larvae of the damselfly *Ischnura elegans* was examined in the field throughout one year (1975). In only two months, May and November, did production deviate significantly from a mean figure. There was no evidence of diurnal periodicity in faecal-pellet production. In a controlled laboratory experiment in which prey density, temperature and larval instar were variables, prey density and larval instar contributed significantly to differences in faecal-pellet production. A comparison of field and laboratory faecal-pellet production and development rates and survival at known prey densities in the laboratory, suggests that larvae at the study site suffered little or no reduction in development rate and survival due to food shortage. The consequences of these findings for the control of larval damselfly populations are considered.

INTRODUCTION

In their review of arthropod predator-prey systems, HASSELL, LAWTON & BEDDINGTON (1976) and BEDDINGTON, HASSELL & LAWTON (1976) distinguished two components of predation. The first was the prey death rate (due to predation); the second was the predator's rate of increase. They divided the prey death rate into three sub-components: the effects of prey density, predator density and the relative distributions of prey and predator populations. The predator rate of increase was also divided into three sub-components: the development rate of each instar, the survival rate between instars and the fecundity of the adults. Each of the sub-components of the predator rate of increase is influenced by each sub-component of the prey death rate.

THOMPSON (1975, 1978a) has investigated the effects of prey density on the prey death rate in the laboratory for an aquatic, in-

vertebrate predator, larvae of the damselfly, *Ischnura elegans* Lind. feeding on *Daphnia magna* Straus. This work was extended to the field (THOMPSON 1978b,c) when it was shown that *Ischnura* is a strongly polyphagous predator whose diet follows closely the composition of potential prey items in the field. There was no evidence that the larvae were closely 'coupled' to a particular prey species.

LAWTON, THOMPSON & THOMPSON (1980) studied the effects of prey density on survival and development rates of the same *Ischnura-Daphnia* system in the laboratory. The aim of the present paper is to extend the work of LAWTON et al. to the field, to obtain estimates of prey density and field feeding rates, then to investigate the extent to which survival and the development rates are reduced in the field (from laboratory maxima) due to prey availability.

In other words, we know the impact of the predator on its prey (THOMPSON 1978b,c). What is the reciprocal interaction—the effect of the prey on the dynamics of the predator?

There are some data available which are relevant to the problem; BENKE (1978) has stated that odonate larvae rarely die from starvation in the field, on the basis of the examination of over 10,000 larvae over 4 years. LAWTON (1971b) has shown that *Pyrrhosoma nymphula* (Sulz.) larval feeding rates were considerably lower in the field than for the appropriate larval-size/temperature combination in the laboratory. It is not possible from his study to say whether the reduction from maximum possible feeding rates would have been sufficient to cause reductions in survival and/or development rates.

The results presented in this paper are organised into three parts: the first describes the estimation of food consumption by *Ischnura* larvae in the field throughout the year based on measurements of faecal pellets; the second describes an experiment in which faecal-pellet production is measured for larvae which have been maintained at controlled temperatures and prey densities in the laboratory from which estimates of field prey density can be made; the third combines the results of the first two and describes how survival and development would be influenced by the field prey densities. Finally, in the Discussion, the factors which may control larval damselfly populations are considered.

METHOD

The aim of the field work was to discover at what prey density *Ischnura* could be found in its natural state. It has been shown from

faecal-pellet analysis (THOMPSON 1978b) that *Ischnura* larvae feed on a wide variety of prey, some planktonic and some benthic forms. It is consequently difficult to assess the number of prey available to a damselfly larva without having very good knowledge of its microhabitat. Therefore the larvae themselves were used to assess prey density.

Before larvae could be collected on a regular basis for faecal-pellet determination, it was necessary to know whether there was any periodicity of defaecation in the field. LAWTON (1971a) found there was none in larvae of *Pyrrhosoma nymphula* (Sulz.) but PEARLSTONE (1973) maintained that larvae of *Enallagma boreale* Selys defaecated most often around dawn.

In May 1974, samples of twelve penultimate instar larvae were taken from the study site (the Pocklington Canal near York, England) at two-hourly intervals throughout one day. The larvae were isolated into separate tubes and left to defaecate. The faecal pellets were later collected, dried in a vacuum oven at 60°C for one week, then weighed on a Cahn Electrobalance. Figure 1 shows a plot of faecal-pellet weight against time through the day. As one might expect there is a large spread in the data at each time interval since some larvae would have defaecated just prior to capture and some would have full guts. Analysis of variance revealed that there was no statistically significant difference in gut contents (as judged by

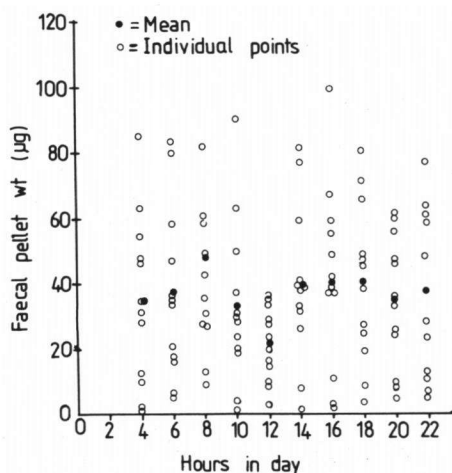


Fig. 1. The relationship between gut contents (as measured by faecal-pellet production) of instar 11 *Ischnura* and time during one day in May 1974.

faecal-pellet weight) during these times ($F_{9, 110} = 0.8345$; $p > 0.05$) which suggests there was no periodicity in defaecation.

Damselfly larvae were collected from the Pocklington Canal one day each month during 1975 as part of a regular sampling programme (THOMPSON 1977). The larvae were hand-sorted in the field and placed immediately in separate tubes. The larvae were maintained in these tubes until they had voided their guts. They were then measured and assigned to an instar class (see THOMPSON 1975, 1978b); the faecal pellets were dried and weighed in the manner described above.

RESULTS

FIELD FAECAL-PELLET PRODUCTION

From the weighings the mean faecal-pellet weight for each instar/month combination could be calculated. Typical plots of faecal-pellet production against larval head width are shown in Figure 2 for four months in 1975. Figure 2 also shows a curve for faecal pellet production against larval head width obtained by feeding starved larvae a large excess of *Daphnia* for twenty-four hours at 16°C in the laboratory, collecting all the faecal pellets produced in this period and in a subsequent twenty-four hour period of food deprivation. This curve gives a very crude estimate of the maximum pellet production one could have expected to find from field faecal pellets.

There was for the most part a logarithmic relationship between faecal-pellet production and larval head width (Fig. 2a, b and d), though occasionally a linear model gave a better fit. However, the linear model requires unrealistically high intercepts on the abscissa, and so is of little predictive use. The data shown in Figure 2 have been replotted in Figure 3 together with the data from other months to show faecal-pellet production by larvae of the last five instars of *Ischnura* month by month. Figure 3 shows that in general faecal-pellet production within any particular instar is fairly constant throughout most of the year. However, there is some evidence for a spring peak (May is particularly high) and some decline in autumn (November is very low). The factors which determine the level of food in the guts of the damselfly larvae collected, are the feeding rate and gut clearance rate. The feeding rate depends mainly on the density of prey in the patch of habitat in which the damselfly finds itself and the temperature, whereas gut clearance rate depends mainly on temperature (note that larvae continue to produce empty faecal pellets even when starved). THOMPSON (1975, 1978b) showed that feeding

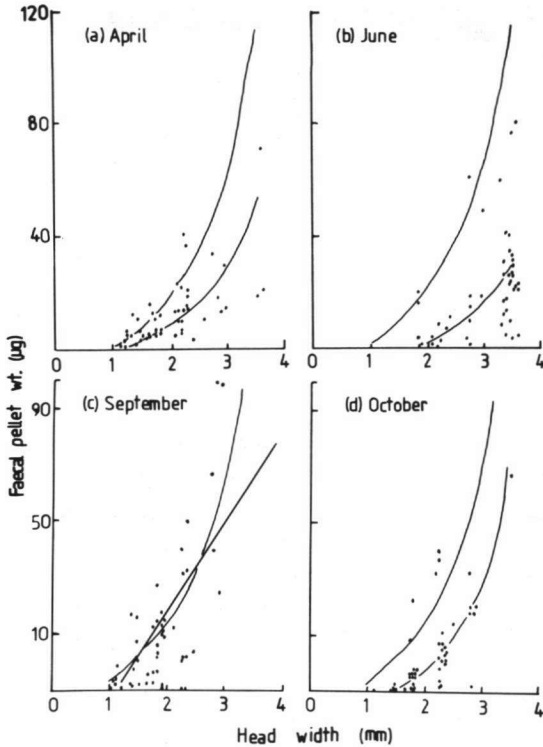


Fig. 2. The effect of instar number as measured by larval head width on faecal-pellet production in four selected months of the year (see text for details).

rate increases with larval size for any particular prey size and with temperature. LAWTON (1971a) has shown that respiration rate and gut clearance rate also increase with larval size and temperature. The assumption made in this section is that the effects of temperature and larval size on feeding rate and gut clearance rate are similar and balance one another, so that differences in faecal-pellet production can be attributed just to changes in prey density and larval size. Analysis of variance of the faecal-pellet weights for each instar revealed that there was no significant difference in instars 8 and 12

($F_{8,40} = 2.14$; $0.10 > p > 0.05$ and $F_{10,74} = 1.55$; $p > 0.05$ respectively). Significant differences were revealed in instars 9, 10 and 11. In November, the pellet production in all instars was consistently lower than in other months and in May, it was consistently higher. These differences can probably be attributed to major changes in

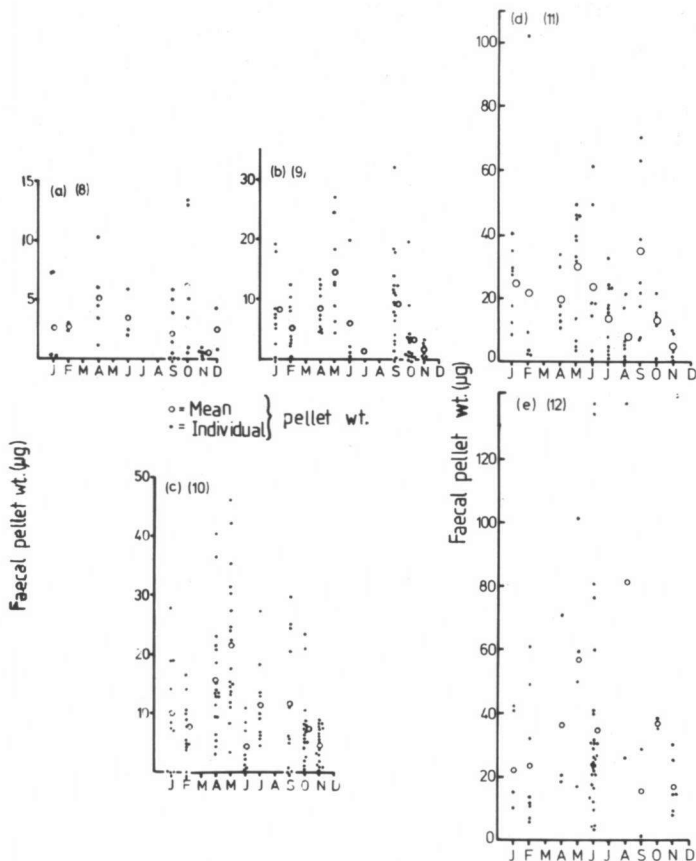


Fig. 3. The relationship between faecal-pellet weight and month of the year for five instars of *Ischnura* (a) 8; (b) 9; (c) 10; (d) 11; (e) 12.

prey availability in these months, though definite evidence is lacking.

Figure 4 shows the mean faecal-pellet weights obtained from the monthly samples for instars 5-12. Data from May and November were excluded from this analysis.

LABORATORY FAECAL-PELLET PRODUCTION

In this section an experiment is described which attempts to relate the field faecal-pellet production described above with faecal-

-pellet production from controlled laboratory experiments in which prey densities and temperatures were known.

A factorial experiment was performed with three predator sizes, instars 10-12, at three temperatures, 8, 12 and 16°C, and six prey densities, 1, 5, 10, 25, 40 and 60 size-class C (determined by sieving; mean length $1.695\text{mm} \pm 0.022$ (1S.E.)) *Daphnia magna* Straus/75 ml. Four replicates were used for each predator size/temperature/prey density combination.

The experimental procedure was as follows: for four days the larvae were fed in 75 ml of dechlorinated tap water in 100 ml beakers in the dark; each morning, the *Daphnia* were all replaced by freshly sieved class-C *Daphnia*. In the afternoon of the fourth day, the larvae were removed from the beakers and placed in separate tubes, where they were kept until they had defaecated, just as if they had been

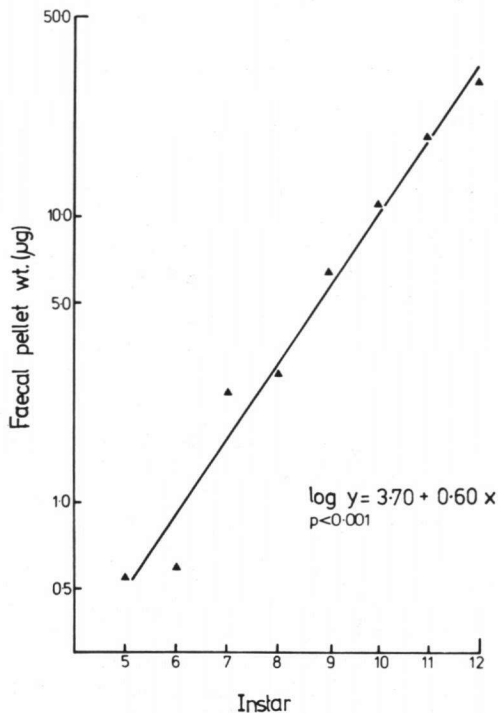


Fig. 4. The relationship between mean faecal-pellet weight and instar number throughout the year (excluding data from May and November – see text).

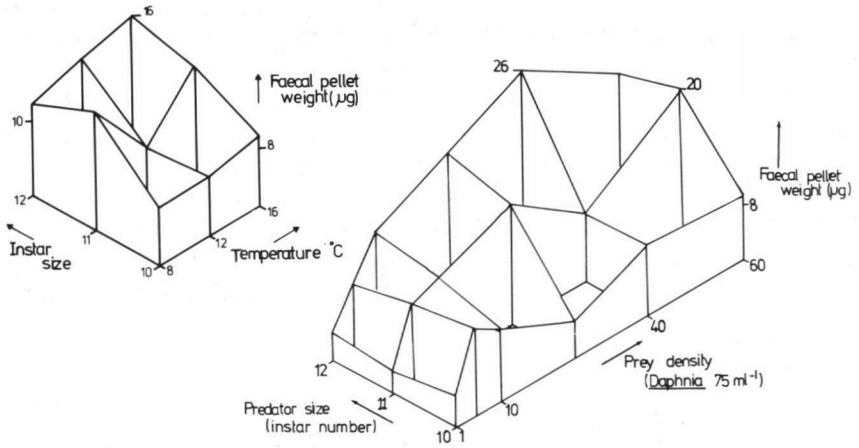
collected from the Pocklington Canal. The faecal pellets were dried and weighed in the manner described above.

Table I

Analysis of variance table for the factorial experiment relating faecal-pellet production to predator size, temperature and prey density

Source	Degrees of freedom	Sums of squares	Mean square	F	P
Predator size (1)	2	1263.227	631.614	7.262	< 0.01
Temperature (2)	2	390.442	195.221	2.245	NS
Prey density (3)	5	3535.120	707.024	8.129	< 0.01
Interactions	44	6642.730	150.971	1.736	< 0.01
1*2	4	918.600	229.650	2.640	< 0.05
1*3	10	3267.325	326.733	3.757	< 0.01
2*3	10	1002.782	100.778	1.153	NS
1*2*3	20	1454.024	72.701	0.836	NS
Error	162	14090.023	86.979		
Total	215	25922.081			

A three-way analysis of variance was performed on the data. The result is shown in Table I. The analysis of variance reveals, as one might have expected from the field data, that both predator size and prey density significantly affect the faecal-pellet weights, and temperature does not. This supports the assumption made above that temperature affects feeding rate and gut clearance rate to an equivalent degree. However, this interpretation is slightly complicated by two significant interactions, between predator size and temperature, and predator size and prey density. The interaction profiles are shown in Figures 5 and 6 respectively. The reason for the significant interaction between instar size and temperature is largely due to the results for penultimate-instar larvae at 12°C; faecal-pellet production rises only very slightly with temperature for instar-10 larvae and a little more for final-instar larvae. There is no obvious explanation for such an anomaly and I have assumed throughout the rest of this section that faecal-pellet weights are independent of temperature in all instars. The second significant interaction between predator size and prey density was to be expected on the basis of functional responses between predators and prey of different sizes (THOMPSON, 1975); it was not surprising that faecal-pellet weights increased with prey density, nor that the increase was more marked at high than low prey densities with increased predator size.



Figs 5-6. Interaction profiles showing the effect on faecal-pellet production of (5) instar size and temperature; — (6) predator size and prey density.

Since temperature did not affect the weight of faecal pellets produced in this experiment, one is justified in pooling the data over temperature; this is effectively what the interaction profile of predator size and prey density (Fig. 6) has done. This finding is supported by FOLSOM (1980).

The curves of faecal-pellet weight against prey density show a negatively accelerating rise towards an asymptote, similar to those of the type-2 functional-response curve. Consequently, smooth curves were fitted to the data using the disc equation (HOLLING 1959), but with faeces production rather than prey consumption as the dependent variable. The data (pooled over temperature) with the fitted curves are shown in Figure 7. Also shown is a fitted curve through the upper 95% confidence intervals which enable some minimum estimate of field prey availability to be made.

COMPARISON OF FIELD AND LABORATORY FAECAL-PELLET PRODUCTION

The mean faecal-pellet weights for instars 10, 11 and 12, derived from Figure 5 are 10.44, 19.10 and 34.95 μg respectively. When these figures are compared with the appropriate graphs in Figure 7, it is apparent that the mean faecal-pellet weights obtained from the field fall above the asymptotic mean values obtained in the laboratory, and in final instars, it is even above the asymptote of the upper 95% confidence interval fitted curve.

It is not possible, therefore, to read off from the graph the prey density at which the larvae are typically found in the field. However it is possible to say with some confidence that these field prey densities do not correspond to prey densities at which the faecal-pellet production was increasing in the laboratory experiment. The question remains then, "Are the prey densities corresponding to the asymptotic levels of faecal-pellet production, greater or less than those at which significant reductions occur in development and growth rates and survival?"

LAWTON et al. (1980) showed, under identical laboratory con-

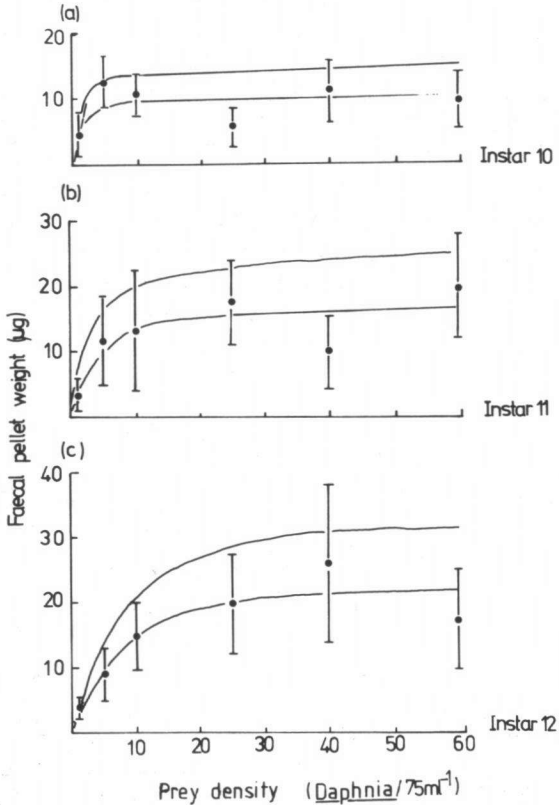


Fig. 7. The relationship between faecal-pellet weight and prey density for three instars of *Ischnura*: (a) 10; (b) 11; (c) 12. Curves are fitted through the mean values and the upper 95% confidence intervals.

ditions that the prey densities over which significant reductions in survival occurred were narrow. In instar 10, for example, the range of prey availability between which all larvae died and all larvae moulted safely to instar 11 was less than 1 *Daphnia* per day. The range in instar 11 was about 8 *Daphnia* per day. Significantly, the upper prey densities of these ranges were below the prey density which marked the beginning of the asymptote in the present experiment. This suggests that *Ischnura* larvae in the field experienced on average, prey densities well in excess of those which lead them to die of starvation.

Although the mean prey density in the Pocklington Canal was greater than that which led to starvation of larvae, there was one month in which conditions were particularly poor. The month of November gave low faecal-pellet returns and the mean pellet weights (\pm 1 S.E.) for instars 10 to 12 were $4.73 \pm 1.65 \mu\text{g}$, $4.74 \pm 0.68 \mu\text{g}$ and $12.60 \pm 3.15 \mu\text{g}$ respectively ($n=20$, 6 and 6). These pellet weights would correspond to prey densities of 1, 1.5 and 7.5 *Daphnia* equivalents per 75 ml and would have caused, had they persisted, much reduced development rates and survival chances. LAWTON et al (1980) have shown for instar-11 larvae fed one standard *Daphnia* per day at 16°C, that the mean length of time the instar lasts before the animal dies is 133 days. Thus greatly reduced prey densities in one month, particularly in winter, when growth is not occurring are probably not very important to *Ischnura* larvae.

DISCUSSION

The estimation of prey availability for damselfly larvae or indeed any other freshwater invertebrate sit-and-wait predator is a difficult problem. Various methods have been used to estimate prey density in areas in which damselfly larvae occur; the most effective method being the use of a large cylinder which can be sunk in to the substrate. However, since within a column of water it is not possible to see exactly where the larvae are resting, it is not clear whether prey density and prey availability to the predator are the same quantity. Indeed one would expect sit-and-wait predators to ensure that they were stationed in those parts of the vegetation in which prey density was locally highest, so that conventional methods of assessing prey density may actually be underestimated.

The aim of the experiment was to use the larvae themselves to estimate prey density. The faecal-pellet production in the laboratory then became a kind of bioassay against which field faecal-pellet production could be measured.

The experiment is not entirely satisfactory; ideally the laboratory damselfly larvae should probably have been fed at random intervals during the day and night rather than be fed with a certain number of prey at one time in the morning. It is also curious that the mean pellet weights for field animals in particularly good months (such as May) are well above the asymptotic levels for both the mean and 95%-confidence-interval fitted curves of the laboratory animals. The concept of "*Daphnia* equivalents" may therefore be misleading and in future work it may be necessary to use other kinds of prey in the laboratory feeding studies, such as chironomids. It is likely that the reason for the discrepancy in the estimates of field prey density in November 1975 between instar 12 and instar 10 and 11 larvae was that the final instar larvae were able to utilise an additional prey type or size which the others could not (THOMPSON 1978c).

Even allowing for the approximations that have been made on the way, these results provide good, though not unequivocal evidence that *Ischnura* survival in the field was not limited by low prey availability throughout most of the year. Indeed in the only month in which prey availability was significantly less than mean availability (November) the water temperature was too low for growth to occur.

The only study directly comparable with the present one is that of LAWTON (1971b). He found that feeding rates in the field were always considerably less than the maximum laboratory feeding rate, and at the most were 70% of the latter. They were closer to the maximum in summer than in winter, when they fell to as low as 20% of the maximum. Assuming that *Pyrrhosoma* is similar to *Ischnura*, a feeding rate that was 20% of the maximum would lead to some decline in development rate and some animals may not survive the next moult. However, it is clear that control in at least two damselfly populations is not mediated through food shortage.

Several authors have noted that damselfly larvae experience high and constant death rates throughout development (BENKE 1976, 1978; BENKE & BENKE 1978; LAWTON 1970; MACAN 1964, 1966). If damselfly larvae are not starving to death in the field, what factors are controlling their numbers?

CORBET, LONGFIELD & MOORE (1960) and CORBET (1962) state that odonate larvae are eaten by a wide range of freshwater (and terrestrial) predators. However, most authors agree that fish are the most important predators (BENKE 1978; CORBET 1961; GERKING 1962; LEONARD 1940; WRIGHT 1946).

In order to compare published findings with the observations made in the present study, it is necessary to look at more controlled

systems in which Zygoptera similar to *Ischnura* were the dominant odonates. Two such studies are those by HALL, COOPER & WERNER (1971) on the production dynamics and structure of freshwater animal communities, and MACAN (1964, 1965a,b, 1974) on the fauna of a moorland pond before and after introduction of fish. HALL et al. found in their artificial ponds containing fish that the standing crops of damselfly larvae were a tenth of those in ponds without fish. Their experiment illustrates the potential role of fish as controllers of damselfly populations (see also MITTELBACH, 1981).

Macan found in his studies of a moorland fish pond before and after the introduction of trout (*Salmo trutta* L.), that the number of the dominant zygopterans (*Pyrhosoma nymphula* and *Enallagma cyathigerum*) that reached the final instar were the same each year, both before and after the introduction of trout, even though examination of trout stomachs revealed that both were preyed upon heavily. Macan's explanation for this phenomenon was that the amount of suitable vegetation in the pond determines the number of damselflies that are able to reach maturity. In the absence of fish and when initial larval numbers are high, it is those individuals occupying the most favourable fishing sites on the vegetation that are able to grow while others obtain less food from less suitable fishing points and consequently require longer to develop (see LAWTON et al. 1980). This explanation is consistent with the present study.

For those studies in which we have detailed information, the abundance of larval damselflies seems not to be limited by low availability of prey. Mortality from starvation is probably a rare event. It seems that we must look to the existing fishing-site/fish-predation hypotheses to account for the abundance of larval damselfly populations.

NOTE— Since the completion of this manuscript, two referees have brought my attention to the work of FOLSOM (1980).

ACKNOWLEDGEMENTS

I thank Drs J.H. LAWTON and M.G. UTTLEY for comments on the first draft of the manuscript.

REFERENCES

- BEDDINGTON, J.R., M.P. HASSELL, & J.H. LAWTON, 1976. The components of arthropod predation. II The predator rate of increase. *J. Anim. Ecol.* 45: 165-186.
BENKE, A.C., 1976. Dragonfly production and prey turnover. *Ecology* 57: 915-927.
BENKE, A.C., 1978. Interactions among coexisting predators - a field experiment with

- dragonfly larvae. *J. Anim. Ecol.* 47: 335-350.
- BENKE, A.C. & S.S. BENKE, 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology* 56: 302-317.
- CORBET, P.S., 1961. The food of non-cichlid fishes in the Lake Victoria basin, with remarks on their evolution and adaptation to lacustrine conditions. *Proc. zool. Soc. Lond.* 136: 1-101.
- CORBET, P.S., 1962. A biology of dragonflies. Witherby, London.
- CORBET, P.S., C. LONGFIELD & N.W. MOORE, 1960. Dragonflies. Collins, London.
- FOLSOM, T.C., 1980. Predation ecology and food limitation of the larval dragonfly *Anax junius* (Aeshnidae). Unpublished Ph.D. thesis, University of Toronto, 138 pp.
- GERKING, S.D., 1962. Production and food utilization in a population of bluegill sunfish. *Ecol. Monog.* 32: 31-78.
- HALL, D.J., W.E. COOPER & E.E. WERNER, 1971. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15: 839-928.
- HASSELL, M.P., J.H. LAWTON & J.R. BEDDINGTON, 1976. The components of arthropod predation. I. The prey death rate. *J. Anim. Ecol.* 45: 135-164.
- HOLLING, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Ent.* 91: 385-398.
- LAWTON, J.H., 1971a. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *J. Anim. Ecol.* 40: 385-423.
- LAWTON, J.H., 1971b. Maximum and actual feeding rates in larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *Freshwat. Biol.* 1:99-111.
- LAWTON, J.H., B.A. THOMPSON & D.J. THOMPSON, 1980. The effect of prey density on survival and growth of damselfly larvae. *Ecol. Ent.* 5: 39-51.
- LEONARD, J.W., 1940. Further observations on the feeding habits of the Montana grayling (*Thymallus montanus*) and the bluegill (*Lepomis macrochirus*) in Ford Lake, Michigan. *Trans. Am. Fish Soc.* 69: 244-256.
- MACAN, T.T., 1964. The Odonata of a moorland fish pond. *Int. Rev. ges. Hydrobiol.* 49: 325-360.
- MACAN, T.T., 1965a. The fauna in the vegetation of a moorland fish pond. *Arch. Hydrobiol.* 61: 273-310.
- MACAN, T.T., 1965b. The effect of the introduction of *Salmo trutta* into a moorland fish pond. *Mitt. int. Verein. theor. angew. Limnol.* 13: 194-197.
- MACAN, T.T., 1966. The influence of predation on the fauna of a moorland fish pond. *Arch. Hydrobiol.* 61: 432-452.
- MACAN, T.T., 1974. Twenty generations of *Pyrrhosoma nymphula* (Sulzer) and *Enallagma cyathigerum* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica* 3: 107-119.
- MITTELBACH, G.G. 1981. Foraging efficiency and body size; a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386.
- PEARLSTONE, P.S.M., 1973. The food of damselfly larvae in Marion Lake, British Columbia. *Syesis* 6: 33-39.
- THOMPSON, D.J., 1975. Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *J. Anim. Ecol.* 44: 907-916.
- THOMPSON, D.J., 1977. Field and laboratory studies on the feeding ecology of damselfly larvae. Unpublished D. Phil. thesis, University of York.
- THOMPSON, D.J., 1978a. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *J. Anim. Ecol.* 47: 757-768.
- THOMPSON, D.J., 1978b. The natural prey of larvae of the damselfly *Ischnura elegans* (Odonata: Zygoptera). *Freshwat. Biol.* 8: 377-384.
- THOMPSON, D.J., 1978c. Prey size selection by larvae of the damselfly *Ischnura elegans* (Odonata). *J. Anim. Ecol.* 47: 769-786.
- WRIGHT, M., 1946. The economic importance of dragonflies (Odonata). *J. Tenn. Acad. Sci.* 21: 60-71.