SEASONAL REGULATION IN *PYRRHOSOMA NYMPHULA* (SULZER) (ZYGOPTERA: COENAGRIONIDAE)
1. SEASONAL DEVELOPMENT IN NATURE

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Larval development in a northern population of the Western Palaearctic *P. nymphula* has been studied in the field and laboratory to identify responses to physical factors that regulate the time of its annual emergence. In the field, as in more southerly British populations, development is normally semivoltine. Typically, larvae overwinter first in a range of early instars and enter the penultimate (F-1) instar in their second summer, remaining in that instar until late August, after which they enter the final (F-0) instar. rapidly during the next month and overwinter in that instar. Arrest of the senior age-cohort in F-1 during summer and then in F-0 during the winter reduces temporal variation among larvae and contributes greatly to synchronisation of metamorphosis and then emergence in early summer (May to early July). A variable, usually small, proportion of the senior cohort spends the second winter in F-1. In spring such larvae enter F-0 rapidly in May and proceed directly to metamorphosis and emergence. Such individuals are smaller, as F-0 and as adults, than those that overwintered as F-0 and they constitute a second, later component of the emerging population.

INTRODUCTION

Our aim here has been to identify the main responses to physical environmental factors that enable the dragonfly *Pyrrhosoma nymphula* (Sulzer) to regulate the time of its seasonal emergence. A prerequisite was to characterize the pattern of seasonal development in the population in which responses were to be studied. In this paper we provide such information as context for accounts of experimental work which follow.

P. nymphula has been relatively well studied ecologically among Palaearctic Zygoptera. In sites in southern England it is a typical "spring" species (sensu

CORBET, 1954), having an early, synchronised emergence (CORBET, 1952) and spending its second winter (as a larva) in the final instar (CORBET, 1957b). The most detailed work has been by MACAN (1964, 1974) who observed a population for more than 20 years in a small tarn in the English Lake District; there also *P. nymphula* was semivoltine, although some larvae in exceptionally large cohorts took three years to complete development (a finding that led to MACAN's 1977 suggestion, later confirmed by HARVEY & CORBET (1985, 1986), that larvae are territorial). LAWTON (1970, 1971) confirmed that this species is semivoltine in northern England (Durham); and the results obtained by SAVAN (1979) from southern England (Berkshire) are consistent with this. The work we report here was undertaken in Angus, Scotland, by far the most northerly locality in which *P. nymphula* has been studied.

THE STUDY SITE

Dykehead Pond (NO 375606; 56°44'N., 3°1'W) is situated about 260 m above m.s.l. close to the boundary between lowland and highland Scotland, just north of Kirriemuir, Angus. The pond is ca. 100 m long and up to 30 m wide and was formed by damming a small stream. It is bordered on three sides by a plantation of Scots Pine, *Pinus sylvestris* L., and Larch, *Larix* sp., and on the fourth by a small road. Its vegetation is typical of small acid ponds: most of the pond is occupied by *Potamogeton natans* L.; and *Carex rostrata* Stokes and *Juncus effusus* L. grow around the edge. Several large (3-m diameter) floating rafts of *Sphagnum* have been partially colonised by *J. effusus*. Other plants include *Menyanthes trifoliata* L. and *Potentilla palustris* (L.). Foliage of *P. natans* dies back in early spring just before new growth starts; this contributes to the thick (> 1 m) layer of decaying organic matter on the bottom of the pond. *C. rostrata* and *J. effusus* die back in the winter, fresh shoots appearing in early spring.

P. nymphula occupied the pond during 1981 to 1984; other Odonata seen there comprised: *Lestes sponsa* (Hansemann) and *Sympetrum danae* (Sulzer), both common as larvae and adults; *Enallagma cyathigerum* (Charpentier), sometimes common as adults; *Aeshna juncea* (L.) found occasionally as larvae and adults; and *Ischnura elegans* (Vander Lind.) found once as an adult.

MATERIAL AND METHODS

Water temperature

Two alcohol-mercury maximum and minimum thermometers, shielded by polystyrene from direct solar radiation, were suspended beneath a float so that they remained 5 and 45 cm, respectively, below the water surface. They were installed on 27 October 1981 close to the edge of a *Sphagnum* mat projecting towards the centre of the pond, and left there until 1 October 1984. At each visit, maximum, minimum and ambient temperatures at each depth were recorded to the nearest degree C between 1300 and 1400 h G.M.T. (solar noon falling between 1203 and 1220 h), this being near to the warmest time of the day; the thermometers were then reset. Because visits were irregular, water temperature (Fig. 1) has been portrayed as the seasonal march of ambient temperature 5 cm below the water surface, which is probably close to where *P. nymphula* larvae live during the season of active growth.

Water level

A metal rod, diameter 2 cm, was placed vertically in the bottom of the pond on 5 May 1982 such that its top was at the water surface. At each subsequent visit the distance between the water level and the top of the rod was recorded to monitor fluctuations in level.

Sampling larvae

Larvae were collected at intervals between November 1981 and April 1984 amongst emergent plants, especially *Potentilla palustris,* and amongst *Potamogeton natans,* along a short (10-m long) section of the northern edge of the pond, chosen for accessibility. We used a dip net of mesh diameter ca. 0.8 mm; a net of finer mesh (ca. 0.3 mm) was used amongst *P. natans* to collect very small larvae that might not have been retained by the net with coarser mesh. Net contents were emptied into water in shallow, white, plastic trays and any larva found was placed in water in a separate tube (15x75 mm) and returned to the laboratory for examination. The number of larvae collected on each occasion varied according to the availability of larvae and the number needed for experiments. We always tried to obtain at least 30 larvae during a collection. No attempt was made to sample quantitatively (to estimate absolute density) partly because to do so would have entailed unacceptable destruction of the vegetation.

In Dykehead Pond, larvae of *P. nymphula* could be identified unequivocally in all instars by their shape (cf. GARDNER & MacNEILL, 1950).

Head width and body length (which excluded antennae and caudal lamellae) were determined to the nearest 0.1 mm under a binocular microscope at x 10 magnification using an eyepiece graticule. Presence of antepenultimate, penultimate and final instars (designated F-2, F-1 and F-0 respectively) was recorded, the instars being identified on the basis of head width and the proportion of the abdomen covered by wing-sheaths. Within F-0, interecdysial stages were recorded at x 10 or x 20 magnification according to the categories described by CORBET & PROSSER (1986); these categories, which extend and refine those described by LAWTON (1971), indicate recent entry to F-0, developmental stages that precede the onset of metamorphosis, and apolysis before emergence.

Sampling adults

At each visit the presence or absence was recorded of teneral, immature and mature adults. Visits were made more frequently during the maturation and reproductive periods. During 1983 head width of newly emerging adult males (24-32 h post-emergence) was measured with dial calipers to within 0.1 mm.

RESULTS

WATER TEMPERATURE

Figure 1 shows a seasonal peak between mid-May and mid-July (the emergence period of *P. nymphula*). Temperature varies more when the pool is warming than when it is cooling. Maximum and minimum temperatures (° C) recorded at 5 and 45 cm depths over the whole period were as follows: at 5 cm — maxima 4 (October) to 28 (July-August) and minima 1 (December-March) to 14
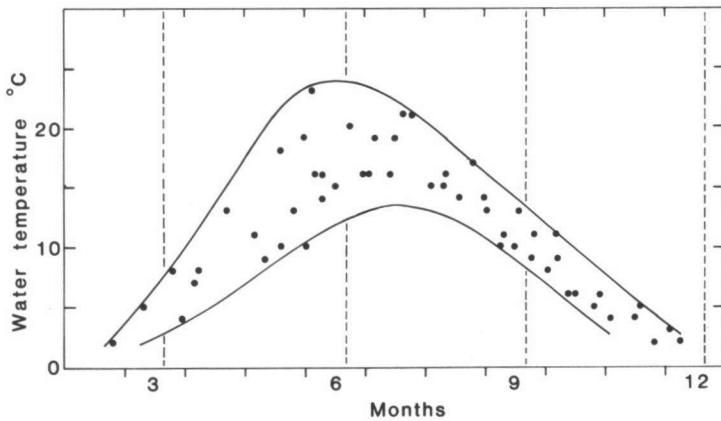
Fig. 1.Dykehead Pond: seasonal march of water temperature 5 cm below the prevailing water surface between 1300 h and 1400 h GMT. Each point represents a record made between October 1981 and October 1984, regardless of year. — Limit lines are drawn by eye. Positions of the equinoxes and solstices are shown.

(July-August); at 45 cm — maxima 4 (October) to 21 (June) and minima 2 (December-March) to 13 (June-August).

A complete ice cover was encountered intermittently between November and March. During winter 1981/82, which was exceptionally cold, ice cover was continuous between 1 December and late February, being at least 20 cm thick during January and early February; the ice had almost melted by 10 March.

WATER LEVEL

Water level fell steadily by ca. 50 cm each year from about May until August or September when it stabilised before rising again before spring.

LARVAL DEVELOPMENT

The two age-cohorts could usually be distinguished easily, a conspicuous bimodality being evident in head width/frequency distribution for most collections, except those made during October to March which consisted almost entirely of F-0. This apparent disappearance of the junior cohort during winter has been noted before (CORBET, 1957b; LAWTON, 1970) and presumably reflects the occupation by small larvae of a microhabitat where they escape collection by net. Dates of collection and sample sizes for each cohort are recorded in Table I. The mean head width of each cohort on each collection date is shown in Figure 2. Development is clearly semivoltine.

Table I

P. nymphula: numbers of larvae collected from Dykehead Pond, 1981-1983

Date	Junior cohort	Senior cohort	Date	Junior cohort	Senior cohort
1981					
May 25	20	*	Sept. 15	45	6
July 27	0	26	Oct. 6	29	9
Aug. 28	0	28	15	0	2
Sept. 30	3	30	Dec. 2	0	3
Oct. 20	3	30	**1983**		
27	0	30	May 10	13	5
Nov. 2	0	30	18	3	26
10	0	30	25	50	26
17	0	30	June 1	51	16
Dec. 1	0	17	8	14	16
1982			15	14	6
Feb. 10	0	5	22	0	7
25	0	5	July 15	0	76
Mar. 10	2	9	26	0	72
25	0	28	Aug. 3	4	71
April 7	0	25	9	3	47
21	0	62	17	0	50
May 5	0	3	24	0	66
12	0	4	Sept. 1	2	49
31	0	5	8	2	60
June 4	0	2	14	1	32
9	0	4	22	0	23
18	0	13	Oct. 5	3	69
July 2	0	37	12	0	31
12	0	30	24	0	36
20	1	30	Nov. 14	0	71
Aug. 3	30	14	25	0	18
14	31	21	Dec. 1	0	15
20	28	2	7	0	15

* — Senior cohort present, but not sampled.

Seasonal occurrence of F-1 (the penultimate instar) is shown in Figure 3. Two senior cohorts are shown in each calendar year: entries before the summer solstice represent the senior cohort destined to emerge the same year, and entries after the summer solstice represent the senior cohort destined to emerge the following year. The seasonal occurrence of F-1 varies somewhat between years. The cohort that emerged in 1981 (the "1981 emergence cohort") was sampled on only two occasions in 1981, during May, and no F-1 were collected. The 1982 emergence cohort showed an increase in F-1 during 1981, reaching a peak of about 80% in F-1 in August; by early October no F-1 were present in samples; a few F-1 were present during March and April 1982, strongly suggesting that some of the senior cohort overwintered as F-1; and by May 1982 no F-1 were present. The 1983

emergence cohort began to
enter F-1 during early July, and
by mid-August about 90%
were in this instar. This cohort
was not well represented in the
pond, and sample sizes during
the latter part of 1982 were
small, resulting in considerable
between-collection variation in
the percentage of F-1, but ap-
parently, compared with the
pattern in other years in this
and other studies (CORBET,
1957b; MACAN, 1964, 1974;
LAWTON, 1970), an unu-
sually large proportion of the
cohort overwintered as F-1
during 1982/83. This conclu-
sion is supported by the first col-
lection made the next spring,
on 10 May, which consisted of
four F-1 and one F-0. The 1984
emergence cohort began to
enter F-1 during early July
1983 and by mid-August more
than 90% were in that instar, a
percentage sustained until mid-
-September. Larval growth
(Fig. 2) levels off at this time.
By late October virtually no
larvae were in F-1.

Seasonal occurrence of F-0
(the final instar) is shown in
Figure 4. Larvae of the 1982
emergence cohort began to
enter F-0 during late August
1981, and by mid-September
almost all had done so. A few
entered F-0 during April 1982
and by May no F-1 remained.
The 1983 emergence cohort
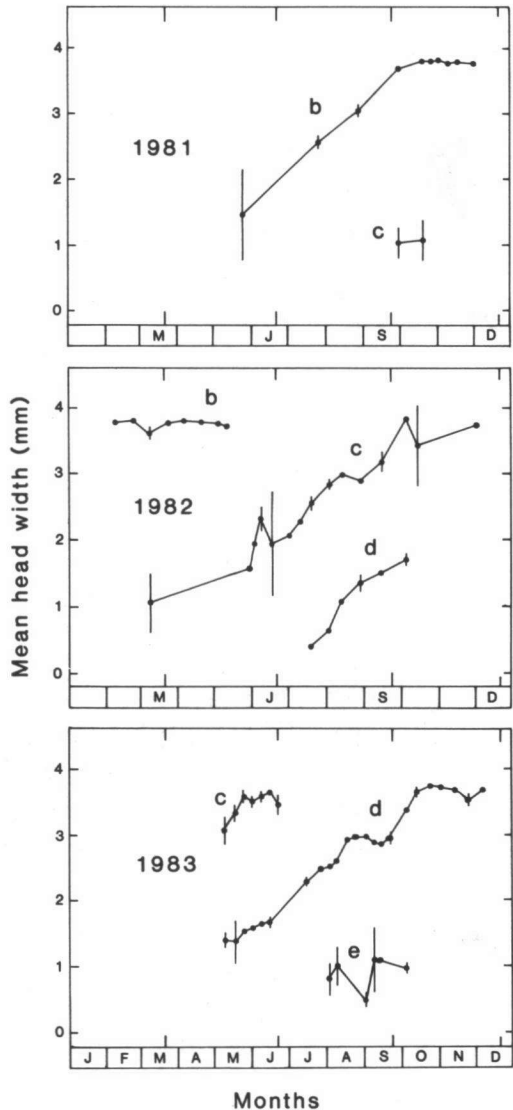began to enter F-0 during Sep-

Fig. 2. *P. nymphula:* seasonal growth of larvae of succes-
sive emergence cohorts, b-e, during 1981-183. — A
vertical bar indicates the standard deviation unless it is
very small.

tember 1982 but there was a second, substantial entry to F-0 during May 1983 by larvae that must have overwintered as F-1 (and perhaps also as F-2). Larvae of the 1984 emergence cohort began to enter F-0 during early September, and by mid-October almost all had done so.

Categories of interecdysial development were first recognized and described during 1981 and so were unavailable for use until 1982. Seasonal occurrence of stages E.2 and E.4, that refer to mesial expansion of the facetted area of the compound eye before the onset of metamorphosis, is shown in Figure 5. In the first collection of 1982, made in February, 60% (of F-0) were in E.2, the pre-expansion stage. The proportion in E.2 decreased steadily during spring, and by April all larvae had attained E.4, expansion having been completed. The 1983 emergence cohort exhibited a different pattern: all larvae that overwintered as F-0 did so in stage E.4, but during the following spring the proportion of larvae in E.4 decreased and there was an increase in the proportion in E.2, corresponding to the period when larvae that had overwintered as F-1 were entering F-0 (see Fig. 3 for 1983). The 1984
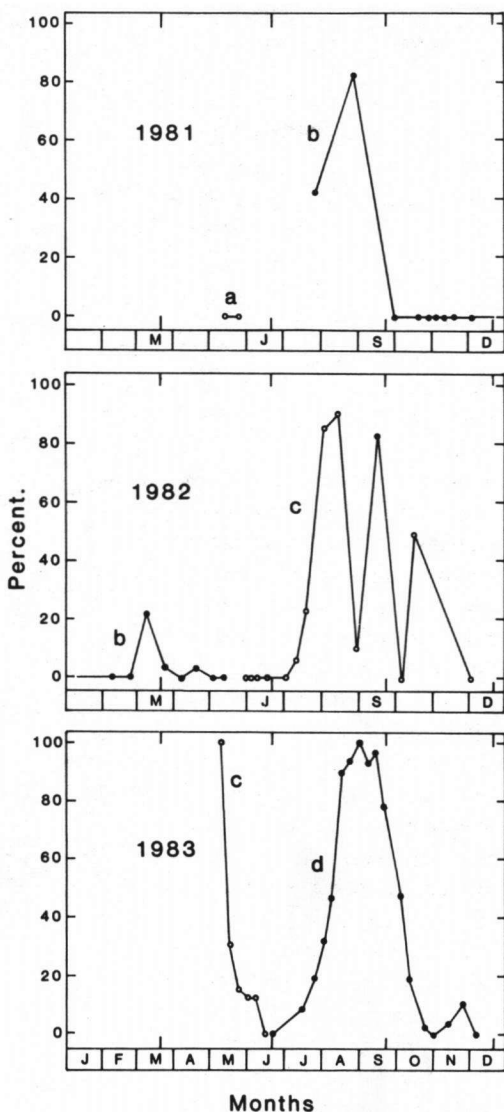

Fig. 3. *P. nymphula:* seasonal occurrence of penultimate-instar (F-1) larvae expressed as a percentage of successive emergence cohorts, a-d, during 1981-1983.

emergence cohort overwinter-
ed partly (about 40%) in E.2
and partly in E.3, the stage
when expansion of the
compound eye has begun but is
incomplete; extremely few
larvae of this cohort had at-
tained E.4 by December 1983.

Seasonal occurrence of me-
tamorphosis, as indicated by
changes in the wing-sheaths
during F-0, is shown in Figure
6. Metamorphosis is always
confined to spring but the
pattern of its onset differed
slightly in 1982 and 1983. In
1982 larvae first showed signs
of metamorphosis between 7
and 21 April, and all were
doing so by 5 May. In 1983
larvae first showed signs of me-
tamorphosis between 10 and 18
May, and by 1 June all larvae
that had overwintered as F-0
(recognised as such by head
width and by having attained
stage E.4 in April) had begun
metamorphosis; but mean-
while the considerable number
of larvae that had overwintered
as F-1 and entered F-0 during
May (see Fig. 3 for 1983) had
not yet begun metamorphosis
and so the percentage of F-0
metamorphosing fell to zero
(on 1 June). By the time the
next collection was made, on 8
June, some of these larvae had
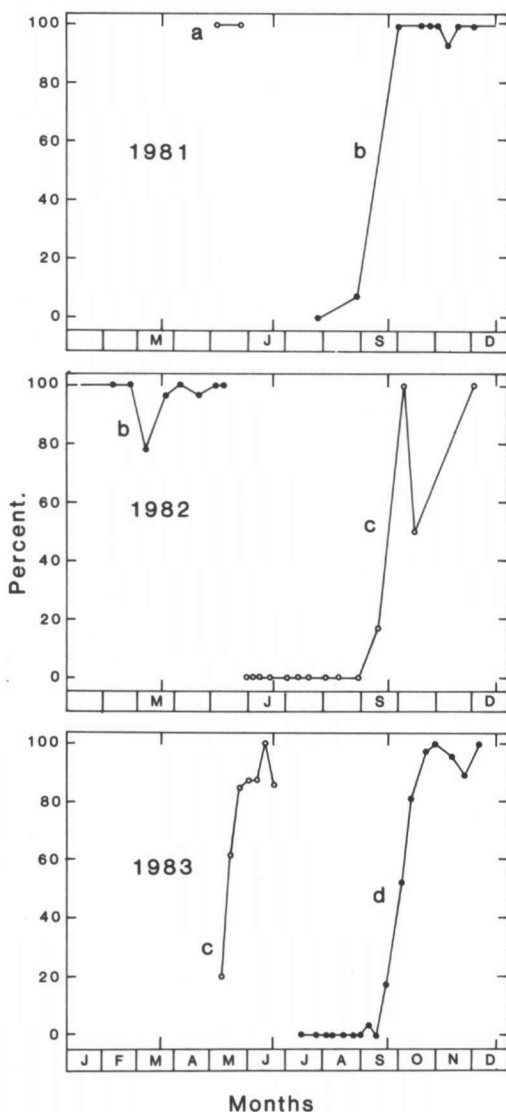begun metamorphosis and by
15 June all had done so.

Fig. 4. *P. nymphula:* seasonal occurrence of final-instar
(F-0) larvae expressed as a percentage of successive
emergence cohorts, a-d, during 1981-1983.

ADULT OCCURRENCE

Emergence usually began during mid-May, the first teneral adults being encountered at the pond on 13 May 1981 and 18 May 1982. In 1983 inclement weather throughout May and June resulted in most visits to the pond being made on days that were unsuitable for dragonfly activity. In 1983 emergence was not detected until 7 June. The first mature adult was seen 12 days and 8 days after emergence began in 1982 and 1983 respectively; the estimate for the duration of the maturation period is likely to be precise in 1983 when visits to the pond were made daily during this period. A second pulse of emergence in 1983 began on 21 June and these individuals which, having been measured, could be distinguished by having a smaller head width (see HARVEY & CORBET, 1985), returned to the pond as mature adults on 27 June, thus taking only 6 days to mature.

Fig. 5. *P. nymphula:* seasonal occurrence during 1981 and 1982 of final-instar (F-0) larvae in two stages of mesial expansion of the compound eye: E.2, no expansion detectable (closed circles); —E.4, expansion complete (open circles). — Successive emergence cohorts, b–d, are indicated.

THE TWO PEAKS OF EMERGENC

Summarised here is evidence (derived entirely from 1983) that there are two peaks of emergence, the earlier consisting of individuals that have overwintered as F-0 and the other consisting of individuals that have overwintered as F-1 or perhaps an earlier instar.

There was a rapid entry from F-1 to F-0 during May (Figs 3, 4).

Collections on 18 and 25 May included F-0 of two kinds: (a) larvae already metamorphosing (as would be expected among larvae that had overwintered as
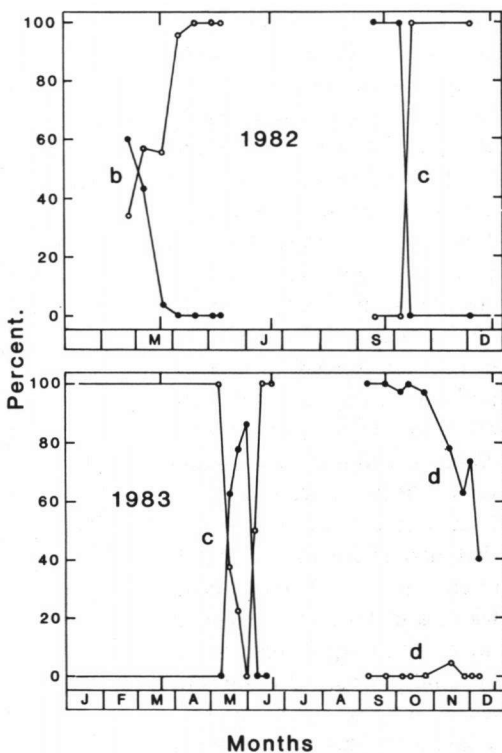
F-0) and with a mean head width of 3.96 mm (LCL = 3.87, UCL = 4.03, N = 11); and (b) larvae still in stage E.1 and that must therefore have entered F-0 very recently — probably within the last 8 days (see CORBET & PROSSER, 1986) and with a mean head width of 3.63 mm (LCL = 3.60, UCL = 3.66, N = 27).

The means of head width are significantly different (t = 10.42, df = 36, P < 0.001): types (a) and (b) remained distinct in collections made between 18 May and 22 June inclusive, that is up to and including the last collection of the 1983 emergence cohort. The two types could be distinguished by head width throughout this period and by interecdysial stage up to 8 June, when the first larvae of type (b) had begun metamorphosis. Thus no F-0 of type (a) were collected on 1 June, but two of type (a) were collected on 8 June by which time some of type (b) were showing the earliest detectable sign of meta-morphosis (stage W.2). All F-0 collected after 8 June (i.e. on 15 and 22 June) were of type (b).

The finding that adults that emerged in the first peak are larger than those that emerged in the second, and that size in F-0 and the adult are closely correlated (HARVEY & CORBET, 1985) is consistent with the conclusions stated above. The mean head width of newly emerged adult males in 1983 fell abruptly between 18 and 21 June, and remained low on 22 and 27 June (Fig. 7); this supports the view that the second pulse of emergence began in the third week of June in 1983.

Fig. 6. *P. nymphula:* seasonal occurrence during 1982 and 1983 of metamorphosis expressed as the percentage of successive emergence cohorts, b–d, at or beyond stage W.2 of wing-sheath development.

Additional observations that can usefully be included are those derived from the Fish Pond, Berkshire (SU 651661; 51°23′N., 1°2′W.) in the course of a population study of *P. nymphula* (CORBET, 1952). There, in 1951 and 1952, the proportion of mature adults bearing the larval stages of the hydracarine mite
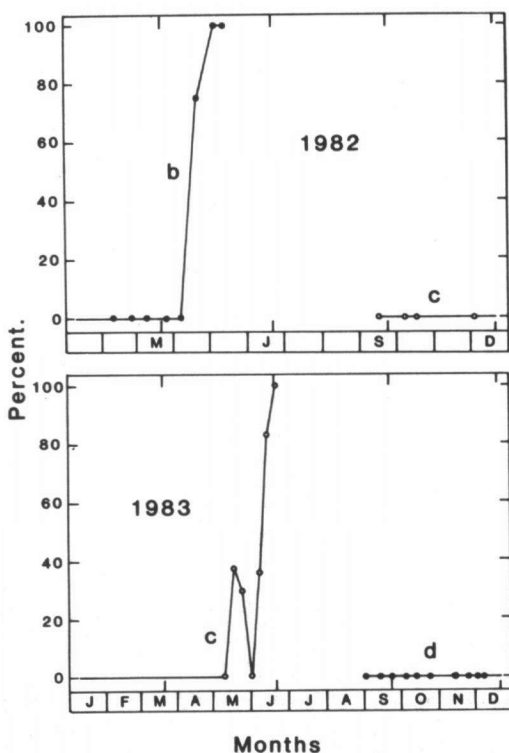
Arrenurus cuspidifer Piers (P. Münchberg, 1954, pers. comm.) were recorded daily during the flying season. These mites drop off the dragonfly host within 2 days of its first arrival at water as a mature adult and so can be used in a heavily infested population of dragonflies to indicate the frequency of newly mature adults at water. The course of this parasitism in 1951 and 1952 is consistent with a second peak of emergence occurring about 5-6 weeks after the first (CORBET, 1953).

DISCUSSION

Seasonal development of *P. nymphula* at Dykehead Pond resembles closely the patterns mentioned earlier from more southerly localities in England. *P. nymphula* is a semivoltine spring species, exhibiting a synchronised moult to F-0 shortly before the autumn equinox. This synchrony is preceded, and made possible, by an accumulation of larvae in F-1 during the summer. The date of first emergence at Dykehead Pond in 1981 and 1982 (13 and 18 May) corresponds well with that reported by CORBET (1957b) (20 May) and MACAN (1964) (6 and 18 May); in 1983, when inclement weather persisted during this period, emergence was first detected on 7 June. An apparent difference between studies relates to the date of first hatching of eggs. CORBET (1957b) found eggs beginning to hatch by mid-June or even earlier whereas LAWTON (1970)

Fig. 7. *P. nymphula:* size of newly emerged adult males during the emergence period in 1983. Mean size decreased abruptly in the third week of June. — A vertical bar indicates the standard deviation and a number the sample size.

did not detect newly hatched larvae sooner than early July and MACAN (1964) not until August. In Dykehead Pond junior-cohort larvae were first detected on 20 July (see Fig. 2 for 1982). This apparent discrepancy may reflect the difficulty of collecting small larvae.

The early hatching date reported by CORBET (1957b) has implications for the existence of occasional univoltine development, which may be a feature of populations in shallow, productive ponds. Given an early reproductive period
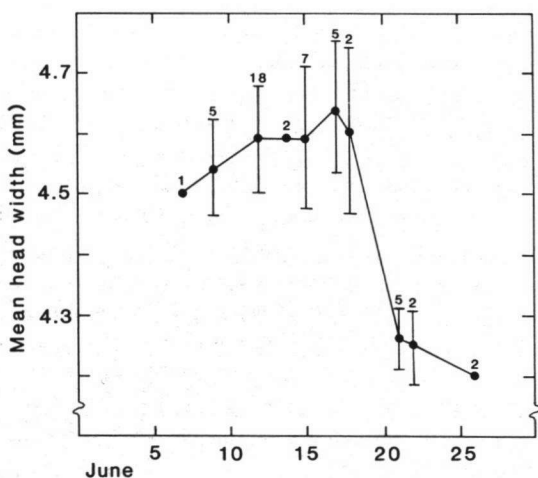
and a warm summer, followed by a mild winter and an early spring, it is conceivable that a larva could reach F-1 by mid-May, 11 months after hatching from the egg and early enough, according to our study at Dykehead Pond, to enable it to emerge within the next two months. However the late dates of hatching reported from sites in northern England (MACAN, 1964; LAWTON, 1970) and Scotland (this study) make it unlikely that univoltinism often occurs in Britain other than in southern England.

Our observations at Dykehead Pond have confirmed the earlier inference (CORBET, 1957b) that the second, smaller peak of emergence (as has been unequivocally demonstrated for *Anax imperator* Leach in southern England (CORBET, 1957a)) comprises individuals that overwintered as F-1 (and some perhaps as F-2) and then entered F-0 in spring. We have found that in *P. nymphula* adults derived from such larvae are smaller than those emerging in the first, main peak (HARVEY & CORBET, 1985).

Although our series of observations at Dykehead is confined to three years, we infer from the uniformity and pattern of seasonal development of *P. nymphula* elsewhere in Britain that it is rare for less than 90% of the senior age-cohort to overwinter as F-0. That close to 100% of this cohort overwintered as F-1 in 1982/83 we regard as possibly due to the exceptionally cold winter of 1981/82 and its likely effect on the temperature regime during the succeeding spring and summer, the season when much of the larval growth has to be completed. For example the onset of metamorphosis (a useful indicator of accumulated water temperature during spring) occurred almost a month later in 1983 than in 1982 (Fig. 6). If this supposition is correct it means that winter weather conditions can influence the relative size of the second emergence peak and thus determine the temporal pattern of oviposition more than a year later. This relationship shows how (because emergence is restricted to early summer) a cold winter followed by a cold summer could readily prolong development by one year — a circumstance attended by an increase in mortality of perhaps 60 to more than 99% (LAWTON, 1970). By such means may local climate dictate the limits of distribution of a semivoltine dragonfly.

Our knowledge of the life history of *P. nymphula* in Britain indicates that three events play a key role in its seasonal regulation: (1) synchronised entry to the final instar in early autumn; (2) absence of emergence in autumn; and (3) temporal restriction of emergence during spring and early summer. The responses that regulate these events have been investigated in experimental studies to be described in succeeding papers.

REFERENCES

CORBET, P.S., 1952. An adult population study of Pyrrhosoma nymphula (Sulzer): (Odonata: Coenagrionidae). *J. Anim. Ecol.* 21: 206-222.

CORBET, P.S., 1953. *The seasonal ecology of dragonflies.* Ph. D. thesis, Univ. Cambridge.

CORBET, P.S., 1954. Seasonal regulation in British dragonflies. *Nature, Lond.* 174: 655 and 777.

CORBET, P.S., 1957a. The life-history of the Emperor Dragonfly Anax imperator Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.

CORBET, P.S., 1957b. The life-histories of two spring species of dragonfly (Odonata: Zygoptera). *Ent. Gaz., Lond.* 8: 79-89.

CORBET, P.S. & R.J.S. PROSSER, 1986. Diagnosis of interecdysial development in final-instar larvae of Pyrrhosoma nymphula (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* 15: 23-28.

GARDNER, A.E. & N. MacNEILL, 1950. The life history of Pyrrhosoma nymphula (Sulzer) (Odonata). *Ent. Gaz., Lond.* 1: 163-182.

HARVEY, I.F. & P.S. CORBET, 1985. Territorial behaviour of larvae enhances mating success of male dragonflies. *Anim. Behav.* 33: 561-565.

HARVEY, I.F. & P.S. CORBET, 1986. Territorial interactions between larvae of the dragonfly Pyrrhosoma nymphula: outcome of encounters. *Anim. Behav.* 34: 1550-1561.

LAWTON, J.H., 1970. A population study on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). *Hydrobiologia* 36: 33-52.

LAWTON, J.H., 1971. Ecological energetics studies on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). *J. Anim. Ecol.* 40: 385-423.

MACAN, T.T., 1964. The Odonata of a moorland fishpond. *Int. Revue ges. Hydrobiol. Hydrograph.* 49: 325-360.

MACAN, T.T., 1974. Twenty generations of Pyrrhosoma nymphula (Sulzer) and Enallagma cyathigerum (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica* 3: 107-119.

MACAN, T.T., 1977. The influence of predation on the composition of freshwater animal communities. *Biol. Rev.* 52: 45-70.

SAVAN, B.I., 1979. *Studies on the foraging behaviour of damselfly larvae (Odonata: Zygoptera).* Ph. D. thesis, Univ. London.