

Spatial distribution, life history and estimates of survivorship in a fourteen-species assemblage of larval dragonflies (Odonata: Anisoptera)

SCOTT A. WISSINGER Department of Biological Sciences, Purdue University, West Lafayette, Indiana, U.S.A.

SUMMARY. 1. Spatial and temporal changes in larval densities were used to infer patterns of habitat use and survivorship in a fourteen-species assemblage of dragonflies (Odonata: Anisoptera) in a small fishless pond. The density of all species combined peaked at $>1000\text{ m}^{-2}$ in late summer. Most species (e.g. *Libellula* spp.) were restricted to shallow, nearshore habitats ($<1.0\text{ m}$ in depth), but a few (e.g. *Epitheca* spp.) also used deeper areas of the pond. Only *Perithemis tenera* was most abundant in deep habitats.

2. Because many species exhibited temporal shifts in their use of habitats, it was necessary to estimate survival from changes in population size, calculated as the product of density and habitat area, summed across habitats. In most species, periods of high mortality in autumn and spring were separated by 3–4 months of negligible mortality in winter. Survivorship was linear only in the two species that completed all of larval development in summer (*Sympetrum vicinum* and *Pantala flavescens*). Average survival rates for these two species (-0.0049 and -0.0079 \log density d^{-1}) were similar to those in previous studies (Lawton, 1970; Benke & Benke, 1975).

3. Survivorship in many species was confounded by other life history phenomena such as (i) mixed voltinism, (ii) overlapping migrant and resident cohorts, and (iii) asynchronous development within species. Asynchrony made it difficult to estimate initial and final population sizes, hence total larval survivorship. However, based on emergence data, only 0.4–3% of larvae survived after peak abundance. None of this mortality can be ascribed to vertebrate predation, and only a little to overwintering stress and starvation. Thus, predation by invertebrates might play a major role in the regulation of these populations.

Introduction

Dragonfly (Odonata: Anisoptera) larvae are among the most conspicuous invertebrate predators in the littoral zone of small lentic

habitats (Benke & Benke, 1975; Crowley & Johnson, 1982). These larvae are thought to play an important role in pond food webs, as predators on both other invertebrates (Benke, 1976, 1978; Thorp & Cothran, 1984) and vertebrates (Caldwell, Thorp & Jervey, 1980; Smith, 1983; Travis, Keen & Julianna, 1985),

Correspondence: Dr Scott A. Wissinger, Biology Department, Allegheny College, Meadville, PA 16335, U.S.A.

and as prey for fish (Benke, 1978; Thorp & Bergey, 1981; Bohanan & Johnson, 1983; Morin, 1984a, b; Pierce *et al.*, 1985). Surprisingly, there are few quantitative data on their population dynamics. A few studies describe patterns of larval abundance and survivorship for a single species (Corbet, 1957; Lawton, 1970; Ubukata, 1981; Johnson, 1986), but only one provides such data for a number of species in the same assemblage (Benke & Benke, 1975). The purpose of this paper is to report spatiotemporal patterns of abundance and survivorship for fourteen species of dragonfly larvae that co-occur in a small pond in Indiana, U.S.A. These data provide an opportunity to compare seasonal patterns of survivorship among species with a variety of other life history characteristics, and illustrate why survivorship should be inferred from changes in total population size, rather than from density *per se*, when densities vary between different habitats within a pond.

The fourteen species considered in this paper were the most abundant of the twenty anisopteran dragonflies that complete their life cycle at the study site (Wissinger, 1988b). Six species, *Libellula lydia* (Drury) (= *Platthemis lydia*), *Libellula luctuosa* Burmeister, *Perithemis tenera* (Say), *Tramea lacerata* Hagen, *Erythemis simplicicollis* (Say) (= *Leptthemis simplicicollis*) and *Epitheca cynosura* (Say) (= *Tetragoneuria cynosura*), account for about 75% of the larval assemblage, and eight others, *Anax junius* (Drury), *Sympetrum vicinum* (Hagen), *Pachydiplax longipennis* (Burmeister), *Libellula pulchella* (Drury), *Epitheca princeps* (Hagen) (= *Epicordulia princeps*), *Leucorrhinia intacta* Hagen, *Celithemis elisa* (Hagen) and *Pantala flavescens* Fabricius, comprise most remaining larvae. Nomenclature follows that of Walker & Corbet (1975). The taxonomic composition of this assemblage is typical of that found in other small fishless ponds in Indiana (Wissinger, 1986).

Previous studies with aquatic insects suggest that life history characteristics such as voltinism (number of life cycles completed per year), phenology (seasonal timing of development) and degree of synchrony (intraspecific variability in the timing of development), can confound the interpretation of patterns of survivorship in aquatic insect populations (Benke, 1984; Butler, 1984). The following life history

summary provides the context for the interpretation of survivorship data in this paper. This summary is based on detailed data from all of the life stages of these species (Wissinger, 1988b).

Most species in this study oviposit in spring and summer. The eggs hatch within a few weeks, and larvae complete development (10–14 moults) and emerge to the adult stage within 1 year (i.e. most are univoltine). In one species (*Epitheca princeps*) some individuals require 2 years to complete larval development (semivoltine), and in two others (*Erythemis simplicicollis* and *Pachydiplax longipennis*) some individuals complete a second generation in one summer (bivoltine). The life histories of individual *Tramea lacerata* and *Anax junius* are more variable because some originate from adults that emerge from the pond, while others are from adults that immigrate in spring. All larvae of *Pantala flavescens* are from immigrating adults. Most larvae in these migratory cohorts emerge at the end of their first summer and emigrate without ovipositing. *Sympetrum vicinum* oviposits in autumn, but the eggs diapause until spring, so that all of larval development occurs in summer. Oviposition in eleven of the fourteen species is extremely asynchronous so that different broods of conspecifics hatch during a 2–3-month period in spring and summer. Larvae synchronize to some extent in a few of these asynchronous breeders, but in most larval development remains asynchronous through emergence the following summer. Development is synchronous throughout the life cycles of *Epitheca cynosura* and *Leucorrhinia intacta*, and within year classes of *Epitheca princeps*.

Study site

Data were collected in a 0.12 ha pond located on the Horticulture Research Farm of Purdue University in Tippecanoe County, Indiana (40° 20' N latitude). The 10-year-old pond has maximum and average depths of 2.5 and 1.0 m, respectively. Spatial habitats in the pond were divided into four categories delimited by depth and basin morphology (Fig. 1). The first is a shallow (<0.5 m) littoral shelf that extends from 0.5 to 3.0 m from the shoreline. It is nearly flat and seasonally vege-

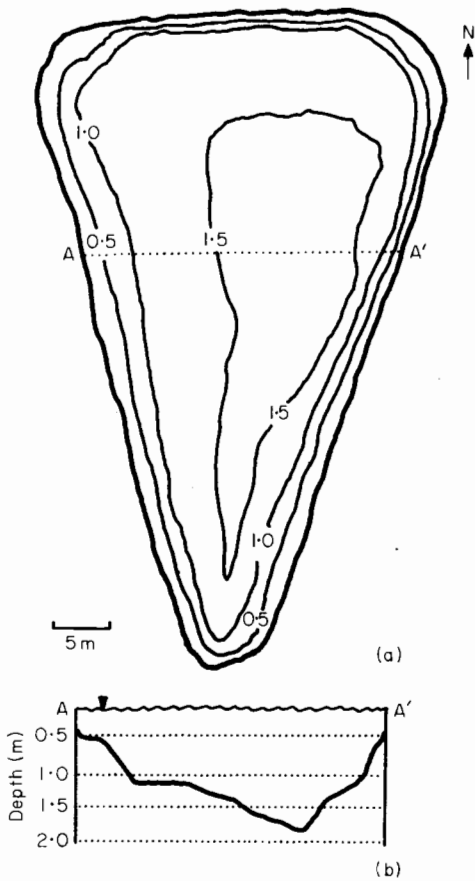


FIG. 1. Aerial view (a) and cross-section (b) of Hort Farm Pond. Depths are given in metres. The vertical axis in the cross-section is exaggerated.

tated by *Potamogeton foliosus* Rafinesque in spring and early summer, followed by *Chara* sp. in late summer and autumn. Emergent vegetation consists of narrow patches of rushes (*Scirpus* sp.) that cover about 10% of the shoreline. The remainder of the perimeter is lined by semiterrestrial willows (*Salix* sp.), sedges (*Carex* sp. and *Juncus* sp.) and grasses that overhang the banks. The substrate is uniform with a 4–8 cm thick surface layer of plant debris and detritus overlying a clay bottom. This nearshore shelf accounts for about 16% of the total pond area.

The second habitat type is a more steeply-sloping area that extends from the outer edge of the nearshore shelf (0.5 m in depth) to the central basin of the pond (1.0 m in depth).

Vegetation is similar in composition and density to that of the shelf but is taller. There is less allochthonous plant debris than on the shelf, but there is a thick accumulation of fine autochthonous detritus at the base of the slope. The slope habitat is more uniform in width (2 m) than the shelf but is nearly identical in size (17% of the total pond area).

The bottom of the slope gives way to a more spacious and gentle-sloping central basin that varies from 1.0 to 2.5 m in depth. This basin was divided into two categories based on depth. The shallower basin category (1.0–1.5 m) is the largest habitat (42% total pond area), is nearly flat, and is sparsely vegetated with *Chara* sp. The deepest habitat category (>1.5 m) is less extensive (27% total pond area) and occurs as an irregular trough in the central region of the basin. Vegetation in the latter is sparse (*Chara* sp.) to absent, and the bottom is covered by black organic detritus.

The uniform depth at which the margins of these areas occur, and the homogeneity of substrate and vegetation within them, suggested they could be treated as distinct habitat categories for assessing the spatial distribution of larvae. In addition, three of the depth categories correspond to those used in a similar study (Benke & Benke, 1975), and are therefore useful for comparing data between study sites.

Zygoptera are abundant in shallow habitats, especially *Ischnura verticalis* (Say), *Enallagma civile* (Hagen), *E. aspersum* (Hagen) and *I. posita* (Hagen). Less abundant species include *E. signatum* (Hagen), *Argia violacea* (Hagen), *Lestes disjunctus* (Selys) and *L. eurinus* Say. The non-odonate benthos in shallower habitats (<1.0 m in depth) is dominated by numerous herbivorous and predatory chironomids, two genera of Ephemeroptera (*Caenis* sp. and *Callibaetis* sp.), chydorid Cladocera, and a variety of Hemiptera and Coleoptera. Of the latter, the larvae of dytiscids, hydrophilids and gyrenids are seasonally abundant predators. Density and diversity of these taxa decrease with depth. Ceratopogonids, and several chironomids dominate the benthos at depths >1.0 m.

During 1982–83 there were no fish in the pond. Although a variety of centrarchids had been introduced, they never survived winter. The herbivorous tadpoles of hylid and ranid

frogs are abundant, but the predatory larvae of salamanders are rare.

Methods

Dragonfly larvae were monitored in nearshore habitats (<0.5 m) of this pond from September 1981 to November 1984. The data presented here are from 1982–83 when all four of the spatial habitats in the pond were sampled. During this period, six samples were taken monthly in each habitat (total of twenty-four) during the nine ice-free months of the year. Samples in the nearshore shelf (>0.5 m) were taken with a 0.25 m² galvanized drop box (after Benke, 1969), and at greater depths with a 0.05 m² Ekman grab. Paired samples taken with the two devices in the nearshore habitat resulted in nearly identical mean densities, although sample variances were larger with the dredge (Wissinger, unpubl. data).

Vegetation and detritus in the drop box

were removed to the clay substrate with a 1 mm mesh D-net and repeatedly washed in 40-litre buckets. Ekman samples were cleaned in a similar manner. The cleaned samples were picked at the pond for live odonate larvae. Larvae were returned to the sample location after identification and instar-sorting. Small larvae that could not be identified in the field were retained for more detailed study. Hatching and larval recruitment were monitored from May to September by taking qualitative samples with a finer net (0.5 mm mesh). Population sizes at emergence are based on daily collections of exuviae (larval skins) from the entire pond perimeter from March to November. More detailed information about phenologic patterns of emergence, adult flight seasons, and oviposition are presented elsewhere (Wissinger, 1988b).

Data were analysed with ANOVA using SPSS (Nie *et al.*, 1975). Only those depth categories used by a species were included to avoid meaningless depth×date interactions.

TABLE 1. Mean densities ($n=6$) of anisopteran larvae for all species combined for each depth/date category. Row means are average densities for each date. Column means are average densities for each depth. Percentage grand totals are in parentheses. Two-way ANOVA is given below.

Date	Depth category				Mean (% G.T.)
	<0.5 m	0.5–1.0 m	1.0–1.5 m	>1.5 m	
June 1982	483	70	7	0	141 (8%)
July	1312	263	80	3	415 (24%)
Aug.	1196	237	117	7	389 (22%)
Sept.	542	144	80	11	187 (11%)
Oct.	328	147	87	7	148 (9%)
Nov.	301	138	87	10	133 (8%)
March 1983	219	117	70	13	105 (6%)
April	390	90	50	10	135 (8%)
May	251	70	37	7	91 (5%)
Mean (% G.T.)	558 (72%)	142 (18%)	68 (9%)	8 (1%)	

ANOVA

Source of variation	Sum of squares	df	Mean square	F	Significance
Main effects					
Date	2.83×10^6	8	3.54×10^5	26.81	$P < 0.001$
Depth	1.04×10^7	3	3.35×10^6	253.52	$P < 0.001$
Interactions					
Date×Depth	5.46×10^6	24	2.42×10^5	17.25	$P < 0.001$
Explained	1.83×10^7	35	3.55×10^6	39.65	$P < 0.001$
Residual	2.37×10^6	180	1.32×10^4		
Total	2.07×10^7	215	9.63×10^4		

Other departures from homoscedasticity were minor and should have little effect on this test's ability to distinguish between treatment means (Scheffé, 1959; Morin, 1983).

Results

Patterns of larval abundance

Densities of all species combined were highest in the shallow shelf habitat during July and August where they exceeded 1000 m^{-2} . In all depth categories, densities decreased rapidly during autumn, remained the same in winter, and decreased again in spring (Table 1). On all

dates, densities were highest in the nearshore shelf ($<0.5\text{ m}$) and slope ($0.5\text{--}1.0\text{ m}$) habitats. ANOVA indicated the effects of date and depth on total larval densities were highly significant, as was the depth \times date interaction (Table 1). This two-way interaction reflected an increase in the proportion of larvae in habitats $>0.5\text{ m}$ from about 20% in July and August to almost 50% by winter. The reverse occurred in spring with fewer than 15% of larvae at depths $>0.5\text{ m}$ by May.

The major patterns of distribution and habitat shifts can be illustrated by the six species shown in Fig. 2. Four species (*Erythemis*

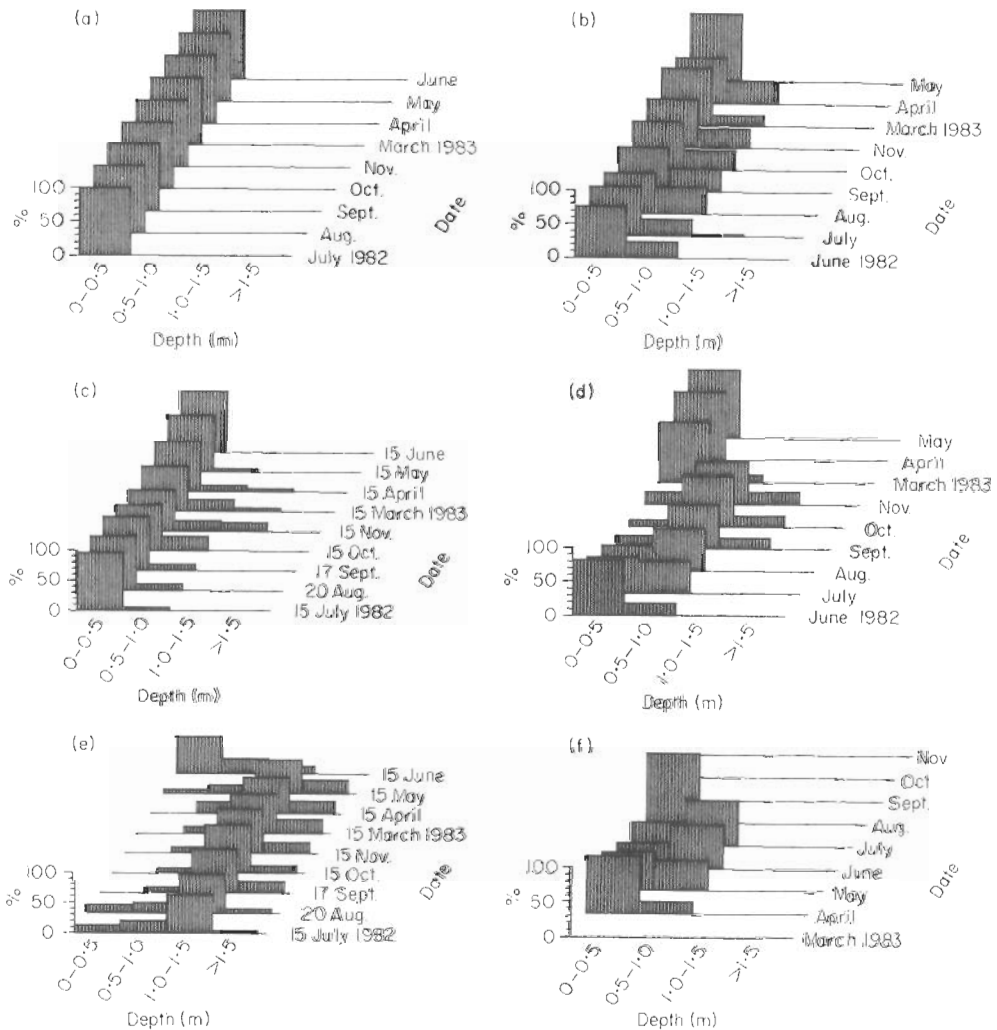


FIG. 2. Major patterns of habitat use for the fourteen species in this study. Histograms represent the percentage of larvae in each depth category on a given date. (a) *Erythemis simplicicollis*; (b) *Tramea lacerata*; (c) *Libellula lydia*; (d) *Epiplatya cynosura*; (e) *Perithemis tenera*; (f) *Sympetrum vicinum*.

simplicicollis, *Pachydiplax longipennis*, *Anax junius* and *Pantala flavescens*) were restricted to the nearshore shelf (<0.5 m) (Fig. 2a). The remaining species used at least two habitat categories and shifted toward deeper habitats in winter. In most species the majority of larvae remained in the two shallow habitat categories, despite this proportional shift in winter (*Tramea lacerata*, *Sympetrum vicinum*, *Leucorrhinia intacta*, and *Celithemis elisa*, *Libellula lydia*, *L. luctuosa* and *L. pulchella*) (Fig. 2b, c). However, movement to deeper habitats was more dramatic in *Epiheca cynosura* and *E. princeps* so that by winter the majority of larvae occurred at depths <0.5 m (Fig. 2d). *Perithemis tenera* was the only species that used all spatial habitats, and was always most abundant at depths >0.5 m (Fig. 2e). *Sympetrum vicinum* larvae used the two most shallow habitats in summer (Fig. 2f). The abundance of each of the fourteen species in each habitat on a given date is given in Wissinger (1986).

Seasonal patterns of survival

Survival within generations or life stages of insects is usually described by temporal changes in density (e.g. Varley, Gradwell & Hassell, 1973; Southwood, 1978). However, in this study, changes in total population size,

rather than density *per se*, are better for estimating survival for two reasons. First, species occur in habitats of different size (area) so that densities correspond to different total numbers of individuals. Second, changes in density in a particular habitat can be due to movements between habitats (see above) as well as to mortality. For these reasons, survival rates in this study are based on temporal changes in total population size, calculated on a given date as the product of mean density in a habitat and area of that habitat, summed over habitats. Thus, the sample variances associated with mean densities do not appear around estimates of total population size (Fig. 3).

Seasonal patterns of survival are most easily inferred for species such as *Epiheca cynosura* and *Leucorrhinia intacta*, which are univoltine and develop synchronously (Benke & Benke, 1975; Benke, 1984). Survival rates for these species were lowest during summer and early autumn with only 30–40% of the initial population remaining by winter (Table 2). Survival was comparatively high during winter (88–90%), but decreased again in spring (Fig. 3a, b). Population sizes at the beginning of emergence were 15% as large as those at peak larval abundance during the previous summer (Table 2).

To varying degrees, the relatively asynchro-

TABLE 2. Survival rates for different intervals during the larval development of fourteen dragonflies. Values are proportions surviving during the interval indicated in column headings. The dates for peak abundance and pre-emergence samples vary among species.

Species	Survivorship					
	Peak to Nov.	Nov. to March	Peak to pre-emerg.	Peak to emerg.	Pre-emerg. to emerg.	Total larval
<i>L. lydia</i>	0.29	0.72	0.12	0.02	—	—
<i>P. tenera</i>	0.58	0.91	0.36	0.03	—	—
<i>L. luctuosa</i>	0.24	0.93	0.13	0.02	0.25	0.08
<i>T. lacerata</i>	0.14*	0.38	0.05	0.01*	—	—
<i>E. cynosura</i>	0.27	0.88	0.14	0.03	0.36	0.09
<i>E. simplicicollis</i>	0.20*	0.85	0.08	0.01*	—	—
<i>S. vicinum</i>	—	—	0.07	0.01	—	—
<i>A. junius</i>	0.39*	0.69	0.23	0.01*	—	—
<i>P. longipennis</i>	0.29*	1.00	0.17	0.01*	—	—
<i>L. pulchella</i>	0.36	0.93	0.18	0.03	0.24	0.11
<i>E. princeps</i>	0.40	0.75	0.32	0.01*	—	—
<i>L. intacta</i>	0.36	0.90	0.15	0.01	0.19	0.08
<i>C. elisa</i>	0.37	0.78	0.08	0.004	—	—
<i>P. flavescens</i>	—	—	0.16	0.01	—	—

*These data are confounded by emergence, hatching, and/or generation overlap.

nous development of most other species at Hort Farm Pond complicated the interpretation of abundance data. In most species the long period of recruitment during summer meant that initial population sizes could not be calculated, and that survival rates could not be estimated until early fall when hatching was complete (Fig. 3c-f). When population sizes were increasing in summer, mortality in early broods was obscured by the recruitment of later broods.

After hatching was complete, seasonal patterns of mortality in most of these asynchronous species was similar to that in the synchronous species above; i.e. survival rates were much lower in autumn and spring, than during winter (Fig. 3c-f). In the asynchronous species that were strictly univoltine (e.g. *Libellula lydia*, *Libellula luctuosa*, *Libellula pulchella*, *Celithemis elisa*), fewer than 20% of the larvae present at peak abundance in autumn, survived to the beginning of emergence in spring (Table 2). Survival rates in late spring and early summer for these species are obscured by the protracted emergence periods.

Estimating survival for the remainder of the species was further complicated by multiple emergence/recruitment periods, and/or generation overlap (Table 2). In *Erythemis simplicicollis* and *Pachydiplax longipennis* populations the emergence and subsequent recruitment of a second generation in autumn biased the survival rates calculated for larvae in cohorts that hatched earlier in the year (Fig. 3g, h). In *Tramea lacerata* and *Anax junius* the influx of migratory adults in spring, and the emigration of their offspring in autumn, made it difficult to estimate survival in cohorts that originated from resident adults (Fig. 3i, j). Finally, the year-round presence of first and second year larvae make it difficult to infer cohort survival in the semivoltine species *E. princeps* (Fig. 3k). While survival rates are certainly less accurate for these species, than for the univoltine species described above, the overall seasonal patterns are similar with the following exceptions. (1) Winter survival rates in the *T. lacerata* population were considerably lower (38%) than for other species (Fig. 3i, Table 2). *T. lacerata* survival in winter was similarly low in three other years at this study site. (2) Seasonal patterns of survival in *P. tenera* differed from all species in that survival rates

were not lowest in autumn, rather, most larvae died before and during emergence in spring (Fig. 3l).

Average survival rates could not be estimated for the twelve species above because of non-linear seasonal patterns of mortality. However, survival rates were approximately constant in the two species that did not overwinter as larvae (Fig. 3m, n). *Sympetrum vicinum* overwinters in the egg stage, and *Pantala flavescens* is a migratory species that completes larval development in one summer. Average survival rates for these species were estimated using the linear regression equation, $\log N(t) = -kt + \log N(0)$, where $N(t)$ is the population size at time t (in days), $N(0)$ is the maximum population size at hatching, and k is survivorship rate. Average survivorship values of -0.0048 and -0.0068 log population size d^{-1} do not include data that overlap with emergence (Fig. 3m, n). Because *P. flavescens* uses only one spatial habitat category, and *S. vicinum* uses only the two that are similar in size, survival rates calculated from densities (-0.0049 for *S. vicinum* log density d^{-1} , and -0.0079 log density d^{-1} for *P. flavescens*) differ only slightly from those based on population sizes.

Total larval survivorship

Total survivorship during the larval stage was difficult to estimate for most species because of asynchronous hatching and emergence. The best estimate available for most of these species was based on comparing the population size at peak abundance to the number of exuviae collected for that species. This comparison indicated that only 0.4-3% of the individuals present at peak abundance survived to emergence, including mortality during metamorphosis (Table 2). A better estimate of survival from peak abundance to the final instar was calculated for the four species that emerged most synchronously (*E. cynosura*, *Leucorrhinia intacta*, *Libellula luctuosa*, *Libellula pulchella*). In these four populations, most (90%) individuals were in the final two instars during the last 2 months before the onset of emergence (Wissinger, 1988b). Survival rates of final instars during the last few weeks before emergence was assumed to be similar to that during the

previous month. This assumption is probably reasonable in a fishless pond with few invertebrate predators as large as late instars of these species. Given this assumption, total larval survivorship for these species was 8–11%, not including early instar mortality (Table 2).

The data for these four species also suggest that only 19–36% of the final instars survived to become teneral adults (Table 2). Observations made while collecting exuviae provided some information on the sources of mortality during emergence. Emerging and transforming

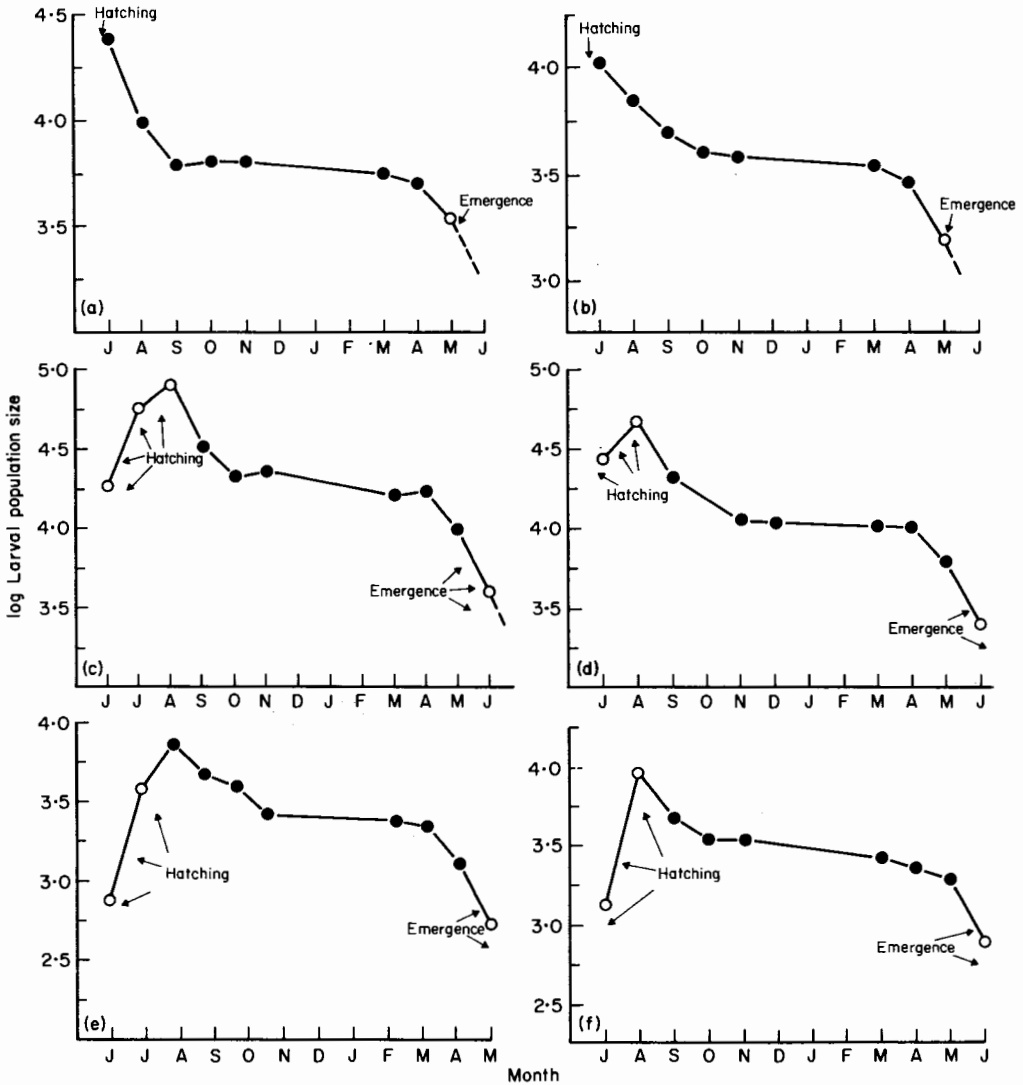


FIG. 3. Larval population size versus time for the fourteen dragonfly species in this study. Changes in population size between closed points are most useful for estimating survival rates because they reflect only larval mortality. Changes in population size between open points are confounded by recruitment (hatching of eggs), emergence (transformation to the adult phase), and/or overlap of different generations (see text). Linear regression was used to estimate average survival rates for the two species (*Sympetrum vicinum* and *Pantala flavescens*) with approximately constant rates of larval mortality. (a) *Epiheca gynosura*; (b) *Leucorrhinia intacta*; (c) *Libellula lydia*; (d) *Libellula luctuosa*; (e) *Libellula pulchella*; (f) *Celithemis elisa*; (g) *Erythemis simplicicollis*; (h) *Pachydiplax longipennis*; (i) *Tramea lacerata*; (j) *Anax junius*; (k) *Pentthemis tenera*; (l) *Epiheca princeps*; (m) *Sympetrum vicinum* ($\log N_T = 0.0048T + 4.34$; $r^2 = 0.96$); (n) *Pantala flavescens* ($\log N_T = -0.0068T + 3.94$; $r^2 = 0.98$).

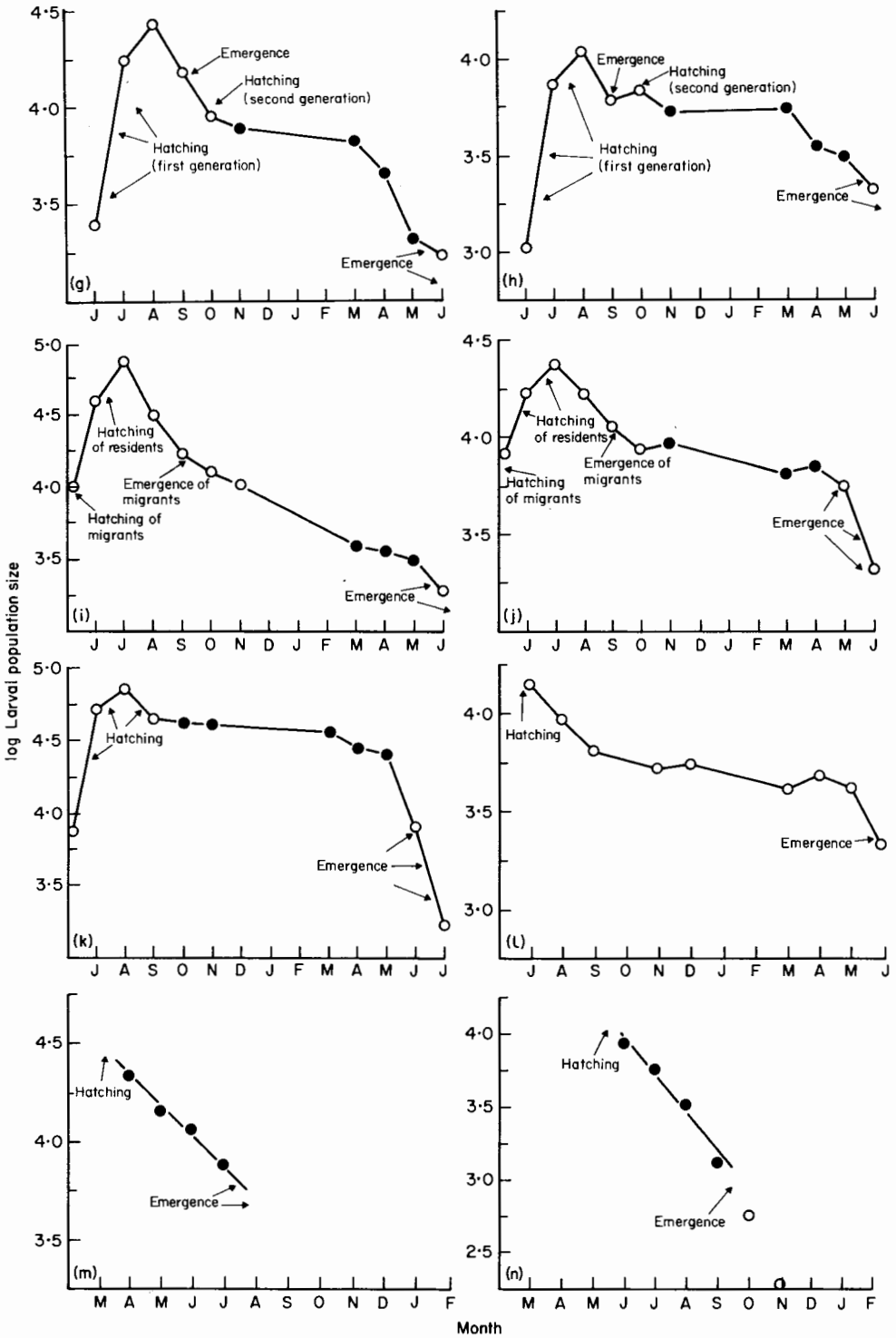


FIG. 3 (continued)

larvae were attacked by ranid frogs, spiders (*Dolomedes* sp.), grackles (*Quiscalus quiscula* (Linnaeus)) and red-wing blackbirds (*Agelaius phoeniceus* (Linnaeus)). Both species of birds were also observed frequently to prey on teneral adults as they left the emergence site. The wings of the larger species were often removed at the pond before the dragonfly was carried away. During peak emergence in July, the dismembered wings of up to 50% of individuals that emerged on a given day were collected from the pond perimeter (Wissinger, unpublished data).

Discussion

Spatiotemporal patterns of larval abundance

The spatial and temporal patterns of abundance for all species combined at my study site are similar to those reported for a small pond in southeastern United States (Benke & Benke, 1975). In both studies, larval abundances were highest in nearshore habitats (0–1.0 m), where they peaked at densities greater than 1000 m⁻² in July and August. Anisopteran larvae in this study were slightly less abundant at intermediate depths (0.5–1.0 m) than in Benke's study, perhaps reflecting the lower relative abundance of the species that frequently use these habitats (*Epiptera* spp.). *Perithemis tenera* was the only species that used the deepest habitats at my study site, and during most of the year was segregated in space from most other species in the assemblage. The period of highest mortality in this species occurred in late spring when these larvae moved into shallower habitats to emerge (Fig. 3e). Morin's (1984a) results suggest that this small species is able to coexist with larger odonate species at his study site because it is least vulnerable to fish predation. The results of this study suggest that in the absence of fish, coexistence of *P. tenera* with larger odonates might be more related to habitat segregation.

A number of the species in this study shift toward deeper habitats in winter. In autumn, some of this inter-habitat movement can be interpreted as initial dispersal from near-shore oviposition sites, and in spring, as movement towards shore to emerge (Corbet, 1957; Lawton, 1970). However, in some species (especially *L. lydia*, *E. cynosura*, *E. princeps*) the

shift towards deeper habitats was more obviously related to the onset of winter, and may reflect dispersal to more favourable overwintering sites (Corbet, 1957; Lawton, 1970). It is also possible that this shift is related to the onset of diapause in later instars. In the species that exhibited the most dramatic shifts, most or all of the larvae at depths >1.0 m were final or F-1 instars (Wissinger, 1986).

Regardless of the function of these habitat shifts, they affect the validity of using density data for calculating survival rates. Temporal changes in density in a particular habitat will be due to both mortality and inter-habitat migration. Although larval densities are often low in deeper habitats, the total number of larvae in these habitats can be a significant proportion of the population because of their expanse compared to nearshore habitats. In this and previous studies (Benke & Benke, 1975; Thorp & Diggens, 1982), the numerical abundance of *Perithemis tenera* at emergence can only be reconciled after recognizing that larvae of this species occur at low densities in the deepest and most spacious habitats in the pond.

Survival during larval development

Linear regression is appropriate for estimating average survival rates in previous studies because mortality is relatively constant throughout development (Lawton, 1970; Benke & Benke, 1975). Survival rates for *Pyrrosoma nymphula* and *Enallagma cyathigerum* ranged from -0.0012 to -0.0062 log density d⁻¹ (Lawton, 1970; Macan, 1964, 1966), compared to -0.0028 to -0.001 log density d⁻¹ over three separate years for *Ladona deplanata*, *Epiptera cynosura* and *Celithemis fasciata*. In this study, mortality was constant for only the two species that do not overwinter as larvae (Fig. 3m, n). Average survival rates of -0.0049 log density d⁻¹ for *S. vicinum* and -0.0079 log density d⁻¹ for *P. flavescens* are of similar or slightly larger magnitude than those in other studies.

Mortality is not constant for most species in this study because periods of high mortality in autumn and spring are separated by a 3–4-month period of negligible mortality in winter (Figs. 3a–l). A similar two-season pattern in mortality is observed in other odonate popula-

tions in high latitude (or altitude) habitats (Ubukata, 1981; Johnson, 1986; but see Lawton, 1970). In contrast, mortality remains high during winter at lower temperate latitudes, even though there is a plateau in development (Benke & Benke, 1975). This difference in over-wintering mortality between studies could be related to latitudinal differences in predator activity. Predation by both invertebrates (including other odonates) and fish (Keast, 1966, and references therein) should be less intense on odonate larvae in winter at higher latitudes than at lower latitudes.

Although freezing and oxygen stress may be important mortality factors during winter in shallow, temporary habitats (Sawchyn & Gillet, 1974; Sawchyn, 1975; review by Norling, 1984), my data suggest abiotic sources of mortality are negligible for most species in this permanent pond. *Tramea lacerata* was the only species that suffered high mortality between November and March. Populations of this species in northern United States and in Canada are thought to be maintained exclusively by long-distance migrants (Walker & Corbet, 1975). This study site may be near the northern limit that *T. lacerata* can survive winter as larvae.

In populations with synchronous development and constant survival rates, initial and final larval abundances can be extrapolated from linear regression to estimate total larval survivorship. Values include 0.5–15% for separate populations of *Pyrrhosoma nymphula*, 50% for *Enallagma cyathigerum* (Lawton, 1970; data from Macan, 1964, 1966), and 3-year ranges of 0.5–32% for *Ladona deplanata*, 7–8.9% for *Epitheca cynosura* and 3.2–14.6% for *Celithemis fasciata* (Benke & Benke, 1975). In comparison, estimates of total larval survivorship in this study ranged from 8% to 11% for the four species for which such a value can be estimated (Table 2).

Total larval survivorship for *E. cynosura* in this fishless pond (9%) was nearly identical to that found in a pond with fish (7–8.9%; Benke & Benke, 1975). The high mortality during larval development for this and most other species (>90%) in this pond is surprising given the absence of vertebrate predators and the low mortality in winter. It is also unlikely that starvation is responsible for a significant proportion of this mortality (Lawton, Thompson &

Thompson, 1980; Wissinger, 1988a). Thus, invertebrate predation and/or parasitism may play an important role in limiting these populations. Odonate larvae are themselves among the largest and most abundant invertebrate predators in this pond, and their known proclivity to attack each other (Merrill & Johnson, 1984; Robinson & Wellborn, 1987; Wissinger, 1988a) makes inter-odonate predation a likely source of some of this mortality.

Survival during emergence

Estimates of survival during emergence in previous studies range from 100% in a fishless pond (Lawton, 1970), to only 5–20% in a pond with fish (Benke & Benke, 1975). Estimates of survival during emergence for four species in this study (19–36%) were more similar to those found by Benke & Benke, but cannot be attributed to fish predation. The frequency with which predation by terrestrial predators was observed during and immediately after emergence at this study site implies that the transition to the adult stage is an extremely vulnerable point in the life cycle of these organisms, and that dragonflies might be an especially strong trophic link between aquatic and terrestrial food webs (see also Jacobs, 1955; Corbet, 1957; Orians & Horn, 1969; Orians, 1980). This observation, coupled with more quantitative survivorship data during the larval stage (Table 2), support Benke & Benke's (1975) assertion that fewer than 1% of the newly-hatched odonate larvae will survive to become reproductive adults.

Acknowledgments

Comments by R. D. Howard, P. M. Waser, W. P. McCafferty, A. C. Benke and P. S. Corbet improved an earlier version of this paper. I am especially grateful to Rick Howard for his support and guidance during this study. I thank the Horticulture Department of Purdue University, and particularly the late E. M. Evans, for allowing me free and patent access to this pond. The study was supported by a Purdue Research Foundation Fellowship, a Sigma Xi Grant-in-Aid, and Research Initiation and Support Grant, SER 77-06731, to Purdue University from the National Science Foundation.

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