

## DIETARY NICHE OVERLAP AND MUTUAL PREDATION AMONG COEXISTING LARVAL ANISOPTERA

R.J. MERRILL and D.M. JOHNSON

Department of Biological Sciences, East Tennessee State University,  
Johnson City, Tennessee 37614, United States

Received December 20, 1983 | Accepted February 2, 1984

Larval populations of *Tetragoneuria cynosura*, *Celithemis elisa*, *C. fasciata*, and *Sympetrum vicinum* coexist in allochthonous detritus habitats of Bays Mountain Lake (Sullivan County, Tennessee, U.S.A.). Their diets were described by fecal pellet analysis to determine whether size differences among larval cohorts reduced dietary overlap within seasons. Differences in larval development time within this assemblage resulted in considerable size overlap among co-occurring larvae. Some species-specific differences in diet were found (e.g., *T. cynosura* tended to concentrate on insect prey, while *S. vicinum* took more microcrustaceans); but there was considerable dietary overlap among species within seasons. Most ate a disproportionate number of medium-sized cladocerans, ostracods, oligochaetes, burrowing and climbing midges, trichopterans and odonates. Fewer copepods, large and small cladocerans, and sprawling midges were eaten than might have been expected from estimates of prey abundance. The similarities out-weighed the differences, such that niche-overlap indices (Hurlbert's  $L_j$ ) were always greater than 1.0 (range 2.4 to 8.7). — A comparison of diets among larvae within species found no consistent reduction of dietary overlap among instars. Larger instars were often more specialized due to predation on relatively rare large prey (e.g., odonate and trichopteran larvae), but they did not omit smaller items (e.g., chydorid cladocerans and ostracods) from their diets. Thus smaller instars experienced relatively high niche overlap with their larger conspecifics. — The incidence of mutual predation among odonate larvae was very high during seasons when very small instars coexisted with large ones. The increase in this ultimate form of "interference" competition may be a more important consequence of seasonal segregation of life histories than reduced "exploitation" competition due to reduction of dietary niche overlap.

### INTRODUCTION

One of the interesting features of odonate life histories in the temperate zone is

the seasonal regulation of larval development which results in species-specific seasons of emergence, adult activity, and oviposition (CORBET, 1980). Since this phenomenon was first recognized (CORBET, 1954), there has been considerable interest in its influence on the ecology of larval populations (i.e., LUTZ & JENNER, 1964; KORMONDY & GOWER, 1965; LUTZ, 1968a, 1968b; PAULSON & JENNER, 1971; LUTZ, 1974a, 1974b; KIME, 1974; SAWCHYN & GILLOTT, 1975; BENKE & BENKE, 1975; INGRAM, 1976; INGRAM & JENNER, 1976; JOHANNSSON, 1978; JOHNSON et al., 1980).

G.E. Hutchinson's "Homage to Santa Rosalia" (HUTCHINSON, 1959) focused much of the interest in seasonal segregation of life histories on its importance in reducing "exploitation" competition among coexisting populations. This hypothesis, as applied to larval odonates, rests on a sequence of three important assumptions: (1) Differences between coexisting species with respect to oviposition season imply differences between the average body sizes of individuals within larval cohorts throughout the year; — (2) Larval size influences diet such that these size differences result in reduced dietary overlap within seasons; — and (3) Food is often limiting within larval odonate assemblages, so reduction of overlap should facilitate coexistence.

This attractive hypothesis has often been used to interpret observations of seasonal segregation (i.e., KORMONDY & GOWER, 1965; INGRAM & JENNER, 1976; JOHANNSSON, 1978; JOHNSON et al., 1980); however, research to date has not provided convincing corroboration.

Of these three assumptions, the first has been most frequently corroborated: seasonal segregation of life histories is often reflected in differences in average body size of co-occurring odonate populations (KORMONDY & GOWER, 1965; PAULSON & JENNER, 1971; KIME, 1974; SAWCHYN & GILLOTT, 1975; BENKE & BENKE, 1975; INGRAM & JENNER, 1976; JOHANNSSON, 1978; JOHNSON & CROWLEY, 1980b). But many populations of larval odonates are composed of a very broad range of sizes at any one time (PAULSON & JENNER, 1971; JOHNSON & CROWLEY, 1980b); thus, emphasis on differences among means may tend to obscure the existence of considerable overlap in the ranges for particular pairs of species (BENKE, 1978). It is important to recognize that the simple logic underlying this assumption breaks down if one or more species in the assemblage exhibits a life cycle with different length from the others — a complication that plays an important role in the present study.

The second of these assumptions, that size differences among larvae reduce dietary overlap, has not been studied so intensively as the first. Most information on diets of larval odonates is for particular species which have been studied throughout a year (CHUTTER, 1961; FISCHER, 1967; ROSS, 1967; LAWTON, 1971; PEARLSTONE, 1973; CLOAREC, 1977; THOMPSON, 1978; BAKER & CLIFFORD, 1981; FOLSOM & COLLINS, 1982). In such

studies, inferences about the effect of larval size on diet are often confounded with seasonal changes in the availability of prey. A few studies have compared the diets of species co-occurring within the same habitat and season (PRITCHARD, 1964; BENKE, 1972; KIME, 1974; JOHANSSON, 1976). Most reviews of the available evidence (THOMPSON, 1978; JOHNSON & CROWLEY, 1980a; CORBET, 1980) conclude that, though larger larvae eat a broader range of prey sizes, they do not cease eating smaller items; this results in considerable dietary overlap among larvae despite apparently large size differences (cf. WILSON, 1975).

Evidence supporting the third assumption, that competition for food is often important within larval odonate assemblages, has been largely speculative to date. Some have inferred that competition must be important from the observed diversity of morphological adaptations for habitat specialization among odonates (WRIGHT, 1943; CORBET, 1962; NESTLER, 1980). Others cite documentation of less-than-full guts in field-collected larvae as evidence that particular populations have been food-limited (GRIFFITHS, 1970; LAWTON, 1971; PEARLSTONE, 1973); but recent studies offer counter-examples (FOLSOM & COLLINS, 1982; THOMPSON, 1982). Food limitation has not been found to affect survival or development in any field population; but, should it exist, it is expected to influence population fitness through larval development time rather than directly through mortality (LAWTON et al., 1980). A few field experiments suggest that odonate densities may be regulated below "carrying capacity" by either fish predation (MORIN, 1984) or mutual predation among odonate larvae (BENKE, 1978), thus reducing the potential for "exploitation" competition.

Since 1977 there has been a continuing effort to understand the factors determining odonate community structure in lentic littoral zone habitats within Bays Mountain Park, City of Kingsport (Sullivan County), Tennessee, U.S.A. JOHNSON et al. (1980) list thirty-five species collected there as larvae. Analyses of overlap with respect to habitat and seasonality (JOHNSON & CROWLEY, 1980b; CROWLEY & JOHNSON, 1982) have identified a diverse assemblage of generalists which utilize the abundant submersed macrophyte and allochthonous detritus habitats within Bays Mountain Lake. Seasonal segregation of life histories has been implicated as a potentially important mechanism reducing overlap within this assemblage (JOHNSON & CROWLEY, 1980b; CROWLEY & JOHNSON, 1982).

Life histories of the four species of Anisoptera whose larval diets will be compared in this study provide excellent examples of seasonal segregation of adult activity among co-occurring populations. JOHNSON et al. (1980) describe adult flight seasons at Bays Mountain Park: *Tetragoneuria cynosura*, a typical "spring" species, flies from late April through June; *Celithemis elisa* and *C. fasciata* exhibit long overlapping flight seasons (late May through September) which are characteristic of "summer" species; and *Sympetrum vicinum* flies from

mid-July until very late in the fall. This seems an ideal assemblage with which to test the hypothesis, stated most explicitly for Anisoptera by JOHANNSSON (1978), that temporal separation of oviposition results in cohorts of larvae which can subdivide prey resources in ways that permit coexistence of several populations (cf. also JOHNSON & CROWLEY, 1980a). It is worth noting that two of these species, *T. cynosura* and *C. fasciata*, were important components of the "early" and "late" emerging groups whose population interactions have been studied experimentally in Dick's Pond, South Carolina (BENKE, 1978; BENKE et al., 1982).

In Bays Mountain Lake, *Tetragoneuria cynosura* has a two-year larval period while the other three species are univoltine (JOHNSON & CROWLEY, 1980b). Though *T. cynosura* oviposits earlier, *Celithemis* larvae grow faster during late summer, catch up during the fall, and emerge the following summer (JOHNSON & CROWLEY, 1980, fig. 5). *Sympetrum vicinum* probably overwinters in the egg stage (BOEHMS, 1971), hatches to begin the summer much smaller than *Celithemis*, but grows very rapidly during mid-summer to emerge by late July. These differences in the timing of larval development result in considerably more overlap with respect to size within seasons than might have been expected from adult flight season alone. Thus, the first assumption mentioned above does not apply well to this assemblage.

CROWLEY & JOHNSON (1982) describe overlap with respect to habitat and seasonality axes among larval populations of *Tetragoneuria cynosura*, *Celithemis elisa* and *C. fasciata* in Bays Mountain Park from July 1977 through June 1980. These populations experienced relatively high overlap with respect to habitat which was reduced somewhat by different distributions of biomass among months. Two-dimensional estimates of overlap (CROWLEY & JOHNSON, 1982, tab. 8) were relatively constant from year to year for *T. cynosura* and *C. elisa* ( $L_{ij} = 0.76, 0.61$  and  $0.72$  for three consecutive years); but those involving *C. fasciata* were not: overlap with *T. cynosura* was increasing ( $L_{ij} = 1.04, 1.19$  and  $1.61$ ) while that with *C. elisa* declined ( $L_{ij} = 0.97, 0.46$  and  $0.00$ ). These trends were primarily due to changes in habitat utilization by a declining *C. fasciata* population. The diet analyses to be presented here are based on collections made during this same period.

The goal of the present research was to describe the diets of dominant Anisoptera larvae from the detritus habitats at Bays Mountain Lake. Such data could determine whether body size differences within or among these co-occurring populations tend to reduce dietary overlap. It could also suggest whether mutual predation among odonate larvae is an important phenomenon within this assemblage. Studies such as this should contribute to our understanding of the relative importance of competition and predation as interactions affecting littoral benthic community structure.

## METHODS

This study was conducted in allochthonous detritus habitats of Bays Mountain Lake, a shallow eutrophic lake within the forested watershed of Bays Mountain Park. JOHNSON & CROWLEY (1980b) describe this habitat, the assemblage of odonate larvae found there, and the life histories of the dominant species. Anisopteran larvae were collected with a sweep net at two-week intervals during the following periods: April-October 1978; March-November 1979. Each was placed in a separate container, returned to the laboratory, and held until a fecal pellet was produced. The larvae were then identified to species using available keys (NEEDHAM & WESTFALL, 1955) and reference collections. They were assigned to instar categories after comparing head-width measurements to frequency distributions for specimens collected at Bays Mountain Park (P.H. Crowley, unpublished; cf. JOHNSON & CROWLEY, 1980b). Sixteen small *Celithemis* that could not be identified confidently to species were assigned to *C. fasciata* because that species has been observed to emerge about one month later than *C. elisa* (JOHNSON & CROWLEY, 1980b):

Fecal pellets were studied using standard techniques (PRITCHARD, 1964; LAWTON, 1970; JOHANNSSON, 1976; THOMPSON, 1978). Each pellet was dehydrated, mounted in balsam, and then spread apart on an indexed microscope slide. Slides were examined at 100x magnification, and prey fragments were identified to the lowest taxon possible by comparison with an extensive reference collection (MERRILL, 1981). The number of each prey type in each pellet was estimated as the minimum number required to account for observed fragments. Data were grouped by season (spring = March, April and May; summer = June, July and August; fall = September, October and November), and dragonfly species and instar. The two year-classes of *Tetragoneuria cynosura* (cf. JOHNSON & CROWLEY, 1980b, fig. 5) have been treated as separate populations in this analysis. Instars assigned to the second year-class, Tc2, were: spring, 0 and 1; summer, 1 and 2, fall, 0 and 1. Instars are numbered in reverse order (e.g., 0=final, 1=penultimate, etc.) following the convention suggested by BENKE (1970).

Estimates of prey abundance were obtained from a year-long comprehensive sampling program conducted from August 1979 through August 1980. Complementary sampling procedures were used to insure adequate estimates for all benthic taxa (WHITESIDE & LINDEGAARD, 1980). Densities of microcrustacea and mites were based on two Inverted-funnel Samplers (BRAKKE, 1976) placed over-night in randomly selected detritus locations at weekly intervals. Densities of macrobenthic taxa were based on six samples using a Gerking Sampler (GERKING, 1957) from randomly selected detritus locations at monthly intervals. Gerking samples were washed using 0.5 mm mesh sieves, sorted by sugar flotation (ANDERSON, 1959), and then identified and counted under a dissecting microscope. Rough estimates of sampling efficiency are comparable (about 90%) for both Inverted-funnel Samplers (WHITESIDE & WILLIAMS, 1975) and sugar flotation (ANDERSON, 1959). Mean densities of each taxon were calculated from all samples taken within each season by multiplying the mean number per sample by appropriate factors to convert them to numbers per square meter of bottom: 226.35 for Inverted-funnel samples; 14.88 for the "top" part of Gerking samples; and 44.44 for the "bottom" part of Gerking samples (Ekman grab). A more comprehensive report of this sampling program will be published later.

## RESULTS

A total of 392 middle-to-late instar larvae were collected for diet analysis during this study. Their distribution among species and instars within season (Tab. I) is presented in Figure 1 to illustrate the considerable overlap in size that was observed despite seasonal segregation of adult flight seasons. Head-width

ranges characteristic of each instar are very similar, except that the final instar of *T. cynosura* may reach sizes somewhat larger than the others (JOHNSON & CROWLEY, 1980b). The groups identified as instar 3 also contain some smaller individuals that were not numerous enough to warrant separate analysis. Mean instars were calculated (BENKE, 1970) to establish rank order of the observed size differences among populations within seasons. The apparent overlap between *S. vicinum* and the two *Celithemis* in the summer may be somewhat misleading, because the two genera were actually collected

at distinct times during that season: most *Celithemis* were collected during June, and most *Sympetrum* during July and August (MERRILL, 1981). Failure to collect any *Celithemis* in the fall may be attributed to their being concentrated in submerged macrophyte habitats or to the fact that most were in smaller instars.

The 808 prey items identified in dragonfly fecal pellets were grouped into 14 categories defined in Table II. Seasonal abundance estimates for each category in allochthonous detritus habitats of Bays Mountain Lake are presented in Table III. The number of each prey category in dragonfly fecal pellets is presented by species/instars and season in Table I. These data provide the raw materials for all analyses which follow.

The relative abundance of potential prey in allochthonous detritus habitats for each season is compared with the diets of co-occurring dragonfly populations in Figure 2. Inspection of this figure suggests: (1) diets of all dragonfly populations were similar, composed primarily of cladocerans, ostracods, oligochaetes and midges; (2) none of these populations exploited the abundant cyclopoid copepods; and (3) odonate and trichopteran larvae were important diet items for most dragonflies during the summer and fall. Figure 2 suggests more similarities than differences among diets of these populations when they co-occur — similarities that extend beyond the general categories of prey eaten to include similar

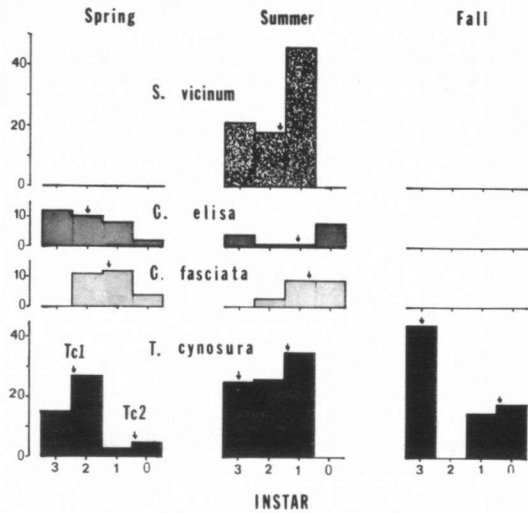


Fig. 1. Anisopteran species/instar frequencies by season in collections from allochthonous detritus habitats at Bays Mountain Lake: April 1978 - November 1979. Instars are numbered in reverse order (0, ultimate; 1, penultimate; etc.). Arrows indicate mean instar value (BENKE, 1970) for each species (or year-class).

Table I

The diet of Anisoptera larvae from allochthonous detritus habitats in Bays Mountain Lake. (Frequency of prey items after data were grouped by season, larval species/instar, and general categories of prey)

SPRING	<i>Tetragoneuria cynosura</i>	<i>Celithemis elisa</i>	<i>Celithemis fasciata</i>	
Instar	0 1 2 3	0 1 2 3	0 1 2 3	
Number of larvae	5 3 27 15	4 12 11 0	2 8 10 12	
Small Cladocera	0 0 0 1	0 0 0 —	1 0 0 2	
Medium Cladocera	10 1 7 14	2 10 13 —	1 25 14 6	
Large Cladocera	0 0 0 0	0 0 0 —	0 0 0 0	
Ostracoda	1 0 1 0	0 1 5 —	1 4 4 3	
Oligochaeta	4 0 4 1	0 0 1 —	0 1 0 1	
Burrowing midges	9 1 15 6	9 8 8 —	0 1 4 1	
Sprawling midges	2 0 4 3	2 3 3 —	0 5 2 2	
Climbing midges	0 1 2 2	1 2 4 —	1 0 0 0	
Trichoptera	0 0 1 0	0 1 0 —	0 0 0 0	
Odonata	2 0 1 0	0 1 0 —	0 1 0 0	
Misc. insects	0 0 0 0	0 0 0 —	0 0 1 0	
Acari	0 0 0 0	0 0 0 —	0 1 0 0	
SUMMER	<i>Tetragoneuria cynosura</i>	<i>Celithemis elisa</i>	<i>Celithemis fasciata</i>	<i>Sympetrum vicinum</i>
Instar	0 1 2 3	0 1 2 3	0 1 2 3	0 1 2 3
Number of larvae	0 35 26 25	9 9 3 0	8 1 1 4	0 46 18 21
Small Cladocera	— 0 0 1	0 1 0 —	0 0 — 0	— 0 0 0
Medium Cladocera	— 16 10 20	6 11 4 —	2 1 — 3	— 52 8 0
Large Cladocera	— 0 0 0	0 0 0 —	0 0 — 0	— 0 1 0
Ostracoda	— 1 4 6	4 4 2 —	2 1 — 1	— 6 4 1
Oligochaeta	— 8 3 6	4 3 2 —	2 0 — 1	— 4 2 0
Burrowing midges	— 33 10 12	2 3 3 —	4 0 — 0	— 3 2 0
Sprawling midges	— 3 2 6	2 2 1 —	3 1 — 0	— 4 4 1
Climbing midges	— 17 4 3	2 1 0 —	5 0 — 0	— 6 1 0
Trichoptera	— 1 0 0	2 1 0 —	2 1 — 1	— 4 2 0
Odonata	— 5 10 3	1 1 0 —	1 0 — 1	— 2 4 1
Misc. insects	— 0 0 0	0 0 0 —	1 0 — 0	— 2 0 0
Acari	— 0 0 1	0 0 0 —	0 0 — 0	— 1 1 1
FALL	<i>Tetragoneuria cynosura</i>			
Instar	0 1 2 3			
Number of larvae	18 15 0 44			
Small Cladocera	0 0 — 1			
Medium Cladocera	9 1 — 18			
Large Cladocera	0 0 — 0			
Ostracoda	7 4 — 2			
Oligochaeta	2 0 — 4			
Burrowing midges	3 3 — 8			
Sprawling midges	0 0 — 1			
Climbing midges	0 0 — 2			
Trichoptera	5 2 — 2			
Odonata	1 2 — 2			
Misc. insects	0 0 — 0			
Acari	0 0 — 2			

tendencies to eat certain prey disproportionately to abundance. The importance of mutual predation among odonate larvae is indicated by the fact that 7.4% of the individuals studied had eaten at least one odonate. Odonate larvae represented 5.4% of the prey items identified, ranging from 1.4% of *Celithemis* diets in spring to 12% for second year-class *T. cynosura* in summer.

The frequencies of prey categories in fecal pellets (Table I) were subjected to a G-test for Independence (SOKAL & ROHLF, 1981, p. 735) after grouping for

Table II

Prey taxa identified in the fecal pellets of Anisoptera larvae (or presumed to have been potential and identifiable prey) from allochthonous detritus habitats in Bays Mountain Lake. (Categories used to group frequency data during subsequent analyses are defined)

---

CATEGORY: Prey taxa, identified (or assumed)

---

(CYCLOPOIDA)<sup>1</sup>

SMALL CLADOCERA<sup>3</sup>: *Alona barbulata*, *A. guttata*, *Chydorus*, (*Bosmina*)<sup>2</sup>

MEDIUM CLADOCERA<sup>3</sup>: *Alona affinis*, *Pleuroxus*, *Kurzia*

LARGE CLADOCERA<sup>3</sup>: *Daphnia*, (*Simocephalus*, *Sida*)<sup>1</sup>, (*Eurycercus*)<sup>2</sup>

OSTRACODA

OLIGOCHAETA

BURROWING MIDGES<sup>4</sup>: *Chironomus*, *Dicrotendipes*, *Glypotendipes*, *Nilothauma*, *Pseudochironomus*, *Stenochironomus*, Tanytarsini, Ceratopogonidae, (*Cryptocladopelma*<sup>5</sup>, *Pagastiella*, *Strictochironomus*, *Xenochironomus*, *Clintotanypus*)<sup>2</sup>

SPRAWLING MIDGES<sup>4</sup>: *Cryptochironomus*, *Parachironomus*, *Psectrocladius*, *Ablabesmyia*, *Labrundia*, *Procladius*, (*Potthastia*, *Corynoneura*, *Larsia*, *Tanypus*)<sup>2</sup>

CLIMBING MIDGES<sup>4</sup>: *Endochironomus*, *Lauterborniella*, *Microtendipes*, *Phaenospectra*, *Poly-pedilum* (*Paralauterborniella*)<sup>2</sup>

TRICHOPTERA

ODONATA: Anisoptera, Zygoptera

MISC. INSECTS: Ephemeroptera, Lepidoptera, (Coleoptera, Megaloptera, Diptera other than midges)<sup>2</sup>

ACARI

(NEMATODA)<sup>1</sup>

---

<sup>1</sup> Taxa assumed to be potential prey because they have been found in Anisopteran fecal pellets from this habitat in a subsequent study (R.E. Bohanan, pers. comm.).

<sup>2</sup> Taxa which were present in the benthos, but have not been identified in Anisopteran fecal pellets. They were assumed to be potential prey based on published literature and intuition.

<sup>3</sup> Cladoceran size categories are based on adult female lengths reported by BROOKS (1959): small < 0.5 mm; 0.5 mm < medium < 1.5mm; large > 1.5 mm.

<sup>4</sup> Behavioral categories for midge larvae are from CUMMINS & COFFMAN (1978).

<sup>5</sup> Behavioral classification not given by CUMMINS & COFFMAN (1978); assigned after consultation with Charles N. Watson.

each pair of species (or year-classes) present during each season. The probabilities associated with the null hypothesis that observed differences in diet were attributable to change are presented in Table IV. Note that during the spring the diet of *C. fasciata* was found to be significantly different from both *C. elisa* and the first year-class of *T. cynosura*. During the summer, the second year-class of *T. cynosura* had a diet significantly different from every other population; and *S. vicinum* differed from both year-classes of *T. cynosura*.

In order to suggest whether these statistically significant differences might also be biologically meaningful in reducing overlap, the proportions presented in Figure 2 were used to calculate indices of dietary overlap ( $L_{ij} = \sum P_{ik} P_{jk} / P_k$ ) where  $P_k$  is the proportion of potential prey in the benthos in category k, and  $P_{ik}$



Table III

Seasonal mean densities (number per square meter) of benthic organisms in allochthonous detritus habitats of Bays Mountain Lake: August 1979 - August 1980. The sampling method used for each category is indicated in the first column: F, inverted funnel sampler, two 5-funnel samples each week; G, Gerking sampler, six replicates per month.

Prey	Sampler	Spring	Summer	Fall
Identified				
Small Cladocera	F	5368	1091	1339
Medium Cladocera	F	1499	3640	5654
Large Cladocera	F	768	1056	1110
Ostracoda	F	150	567	312
Oligochaeta	G	736	415	131
Burrowing midges	G	1086	2565	787
Sprawling midges	G	1908	1662	628
Climbing midges	G	145	216	94
Trichoptera	G	35	20	26
Odonata	G	120	103	133
Misc. insects	G	26	20	16
Acari	F	57	55	13
(Cyclopoida) <sup>1</sup>	F	1719	6748	5797
Nematoda) <sup>1</sup>	G	13	5	0
Undetectable <sup>2</sup>				
Hydrozoa	G	19	3	0
Turbellaria	G	26	17	7
Hirudinea	G	0	17	7
Gastropoda	G	6	1	11
Not potential				
Rotifera	F	92	1482	705
Collembola	G	1	2	0
Hemiptera	G	0	4	7
Diptera pupae	G	40	107	28
Pelecypoda	G	79	26	12
Osteichthyes	G	1	2	6
Amphibia	G	0	0	2

<sup>1</sup> Taxa found in another study of anisopteran fecal pellets in this habitat R.E. Bohanan, pers. comm.).

<sup>2</sup> Soft-bodied taxa which could not be detected in fecal pellets if they were eaten.

or  $P_{jk}$  are the proportion of the diets of populations  $i$  or  $j$  in that category (HURLBERT, 1978). These indices incorporate estimates of resource abundance in a way that weights utilization of a rare resource more than utilization of a common one. They were chosen because they yield values proportional to expected encounter frequencies per unit of available resource among individual larvae (cf. also CROWLEY & JOHNSON, 1982). The expected value of  $L$  is 1.0 if the two populations involved were exploiting resource categories in the proportions available. Values greater than 1.0 reflect a common tendency to

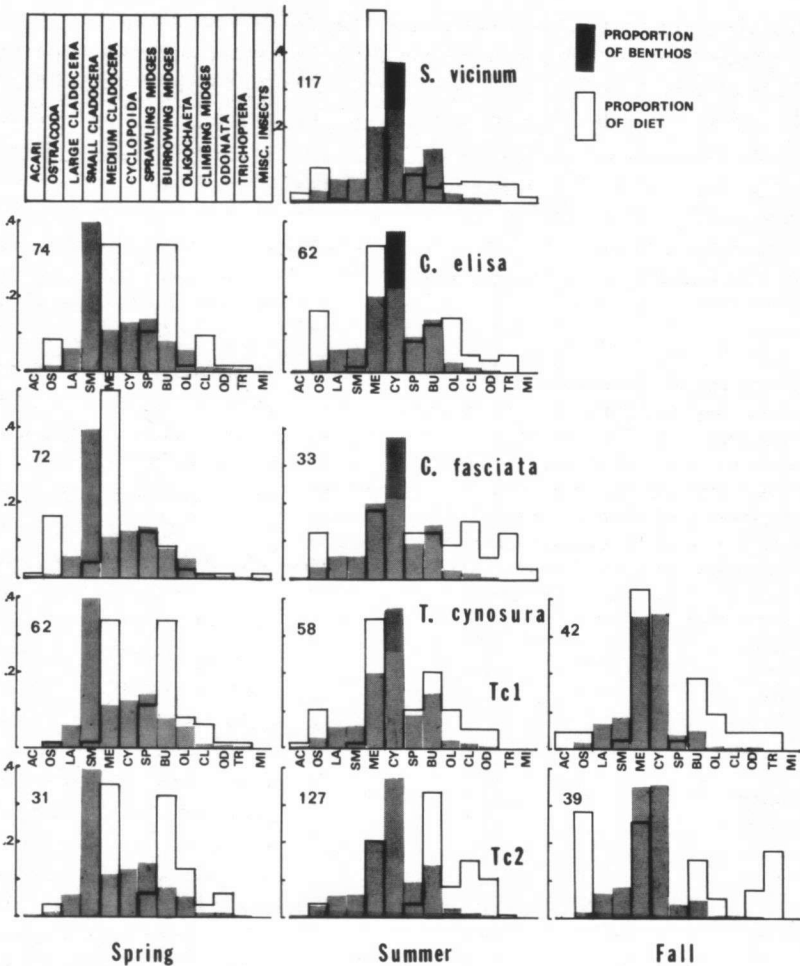


Fig. 2. Proportional representation of potential and detectable prey categories (Tab. II) in the detritus of Bays Mountain Lake (Tab. III) compared to the diets of late-instar larval Anisoptera collected in similar habitats (Tab. I) by season. The number of items identified for each diet is also indicated.

exploit certain resource categories disproportionately.

Values of dietary overlap and specialization for all pairs of populations co-occurring within each season are presented in Figure 3. The populations are arranged along each axis according to their mean instar rankings (cf. Fig. 1) so that any reduction of overlap caused by size differences will yield a decline from the back diagonal (specialization within populations) toward the front right

corner (the pair of populations with greatest size differences). All values in Figure 3 are greater than 1.0, reflecting the general similarity among diets seen in Figure 2. Three of the highest index values involve *C. fasciata* during summer: Cf-Tc2, Cf-Ce, Cf-Sv. The other high values are: Ce-Sv in summer, and Tc2-Tc1 in fall.

Dietary overlap and specialization tended to be least in spring and greatest in fall (Fig. 3). There is little suggestion of reduced overlap due to size differences among populations in either spring or summer. *Celithemis fasciata* appears to have been the most specialized species in both spring and summer. In spring this is largely attributed to its utilization of relatively rare ostracods as well as medium

cladocerans. In summer this is due to its eating more of the relatively rare climbing midges, odonates, trichoptera and miscellaneous insects (Fig. 2). Trichopteran larvae also account for most of the high specialization indices of *Celithemis elisa* and *Sympetrum vicinum* during summer. Both year-classes of *Tetragoneuria cynosura* had unusually high specialization values in fall (Fig. 3), when the first year class specialized on water mites; and the second year-class, on ostracods. Both ate more odonate and trichopteran larvae than might have been expected from estimates of their abundances.

Values of Hurlbert's L presented in Figure 3 should be proportional to encounter frequencies experienced

Table IV

Statistical significance of diet differences among anisopteran populations within seasons at Bays Mountain Lake. G-tests of Independence with 13 degrees of freedom were performed on observed frequencies of prey categories in fecal pellets (Tab. 1). Abbreviations for populations are as follows: Tc2, second year-class of *Tetragoneuria cynosura*; Tc1, first year-class of *T. cynosura*; Ce, *Celithemis elisa*; Cf, *C. fasciata*; Sv, *Sympetrum vicinum*. The number of prey items in each diet is enclosed in parentheses

SEASON	Population	Cf	Ce	Tc1	Tc2
SPRING	Tc2 (31)	ca	ns	ns	
	Tc1 (62)	**	ns		
	Ce (74)	**			
	Cf (71)				
SUMMER	Sv (117)				
	Tc2 (127)	***	*	***	*
	Tc1 (58)	*	ns	ns	
	Ce (61)	ca	ns		
	Cf (33)	ns			
FALL	Tc1 (42)				
	Tc2 (39)	ca			

ns,  $P \geq 0.1$ ; ca,  $0.1 > P \geq 0.05$ ; \*,  $0.05 > P \geq 0.01$ ; \*\*,  $0.01 > P \geq 0.001$ ; \*\*\*,  $P < 0.001$

by an individual of one population with each other individual of its own population (specialization index) and with each member of co-occurring populations (overlap indices) per unit of resource. To the extent that  $L_{ij}$  expresses the average tendency of individuals to attempt to use the same unit of resource, weighting  $L_{ij}$  by the abundance of population  $j$  (Fig. 1) indicates the overall impact of  $j$  on  $i$  (cf. Fig. 4).

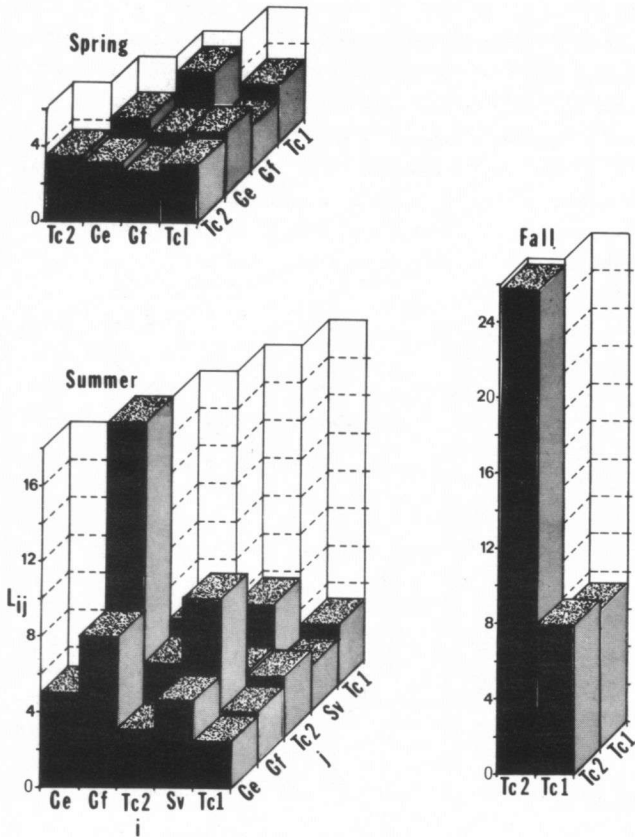


Fig. 3. Seasonal indices of dietary overlap (inter-population) and specialization (intra-population) among species (or year-classes) of larval Anisoptera co-occurring in allochthonous detritus habitats at Bays Mountain Lake.  $L_{ij} = \sum P_{ik} P_{jk} / R_k$  (HURLBERT, 1978) is based on proportional representation of prey categories in fecal pellets ( $P_{ik}$  and  $P_{jk}$ ) and benthos ( $R_k$ ) which are presented in Fig. 2. The species (or year-class) abbreviations are: Sv, *Sympetrum vicinum*; Cf, *Celithemis fasciata*; Ce, *C. elisa*; Tc1, first year-class of *Tetragoneuria cynosura*; Tc2, second year-class of *T. cynosura*.

By this measure, members of the second year-class of *Tetragoneuria cynosura* experienced more frequent encounters with other anisopteran larvae than members of any other population (Fig. 4), and a large proportion of those encounters (75%) were intra-specific. The intensity of these interactions was relatively low in spring, but much higher in summer and fall. The first year-class individuals for *T. cynosura* experienced less intense interactions, with 68% involving conspecifics. *Sympetrum vicinum* experienced the least impact for the whole year by being in our collections for such a short period of time. Relative

encounter frequencies in summer were higher for *S. vicinum* (64% of them intra-specific) and *Celithemis fasciata* (only 35% intra-specific, but 57% intra-generic) than for *C. elisa* which seems to have experienced relatively little impact.

Relatively high frequencies of intra-specific encounters could be an important selective pressure within these populations whenever they are food-limited. The intensity of resulting interactions might be reduced if individuals in different instars exploited different prey categories (cf. ENDERS, 1976). To determine whether this might have been an important phenomenon within the populations studied, we calculated indices of dietary overlap and specialization using data for each instar for which at least 12 prey items had been identified (Tab. 1). Figures 5, 6 and 7 provide relatively weak evidence that overlap is reduced by size differences among instars within species. Trends were in the expected direction for all species in spring (Fig. 5); but the magnitude of the reduction is small. During summer (Fig. 6) trends were more ambiguous, though each species had one instar with especially high specialization (*S. vicinum*, 2; *C. elisa* and *C. fasciata*, 0; and *T. cynosura*, 2), yielding a fairly large reduction in overlap when compared to other instars.

*Tetragoneuria cynosura* was the only species present in our collections during fall. The larger instars (0 and 1) representing the second year-class exhibited high indices of specialization and overlap, with a reduction among instars which was

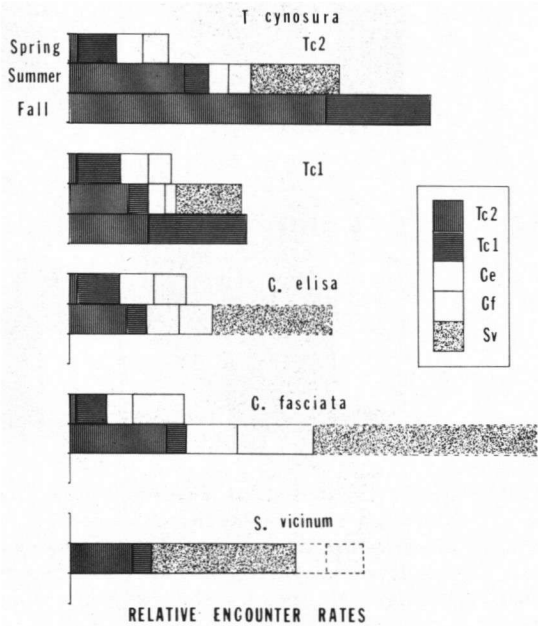


Fig. 4. Relative encounter rates with other larval Anisoptera experienced by members of each species (or year-class) within allochthonous detritus habitats at Bays Mountain Lake.  $\sum L_{ij} N_j$ , where  $L_{ij}$  is the index of dietary overlap (or specialization) with members of population  $j$  from Fig. 3, and  $N_j$  is the number of individuals collected from population  $j$  during each season (Fig. 1 and Tab. 1). Calculated encounter rates between *Celithemis* and *Sympetrum* during summer are enclosed in dashed lines to indicate that those populations were collected during different parts of that season and may not have actually encountered each other to this extent.

The larger instars (0 and 1) representing the second year-class exhibited high indices of specialization and overlap, with a reduction among instars which was

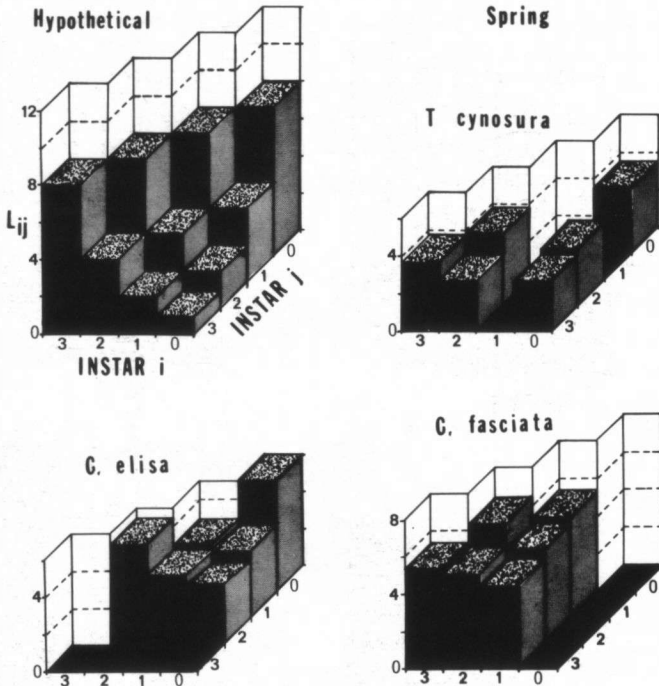


Fig. 5. Indices of dietary overlap (and specialization) among (and within) instars of larval Anisoptera species co-occurring in allochthonous detritus habitats of Bays Mountain Lake, during spring. A reduction of niche overlap with increasing size differences would appear as a decline from the rear diagonal (intra-instar specialization) toward the right front corner. The "hypothetical" diagram arbitrarily illustrates a 50% reduction of  $L_{ij}$  for each unit difference in instar number.

trivial compared to the total (Fig. 7). But overlap between these instars and that representing the first year-class (3) was considerably less, and was approximately equal to the niche specialization within the smaller instar (Fig. 7). Most of the differences between year-classes apparent in Figure 7 are attributed to the fact that the larger instars ate an unusually high number of relatively rare trichopteran larvae, as well as ostracods and odonates (Fig. 2).

## DISCUSSION

The ecological significance of the high dietary overlap described in this study (Figures 3, 5, 6 & 7) depends upon the importance of competition for food within the community being studied (PIANKA, 1974; WEINS, 1977; HAIRSTON, 1980; SCHOENER, 1982). In a competitive community, extensive overlap suggests intense competition which may be the predominant influence on

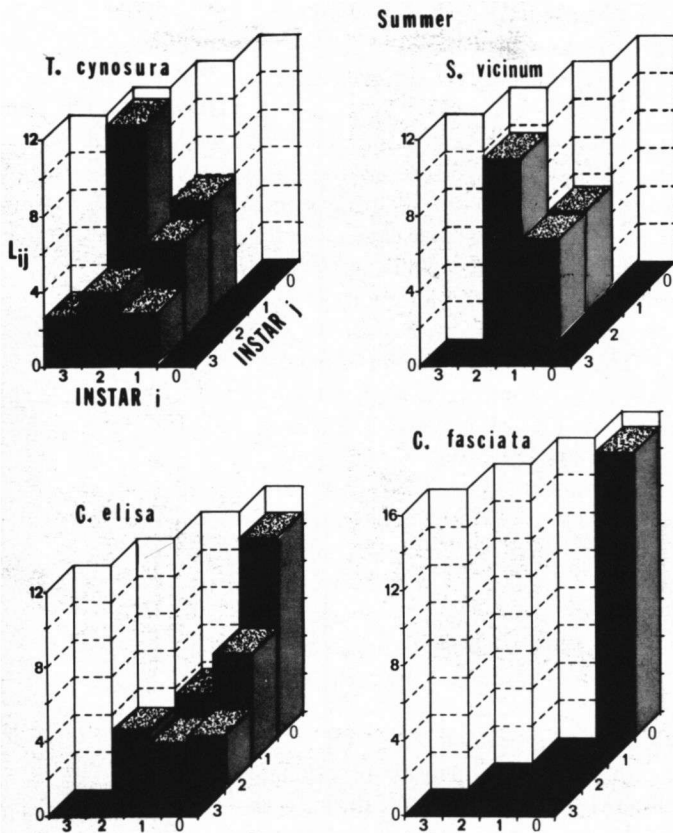


Fig. 6. Indices of dietary overlap (and specialization) among (and within) instars of larval Anisoptera species co-occurring in allochthonous detritus habitats of Bays Mountain Lake during summer. (For further explanation cf. caption of Fig. 5).

community structure. In a non-competitive community, overlap may have little effect. Slight differences observed under non-competitive circumstances might be the basis for important resource partitioning during "lean seasons" or "ecological crunches".

No evidence to date suggests that competition for food is an important phenomenon within the larval odonate assemblage at Bays Mountain Park. CROWLEY & JOHNSON (1982) describe patterns of niche overlap with regard to habitat and seasonality which are consistent with the existence of both resource partitioning (competition coefficients estimated from  $L_{ij}/L_{ii}$  which are less than 1.0) and ecological shift (declining specializations and overlaps through time) among the most abundant populations. Could competition for food be

responsible for observed ecological shifts?

Consider the case of *Celithemis fasciata*, a population involved in ecological shifts reducing niche overlap with respect to both habitat and seasonality from July 1977 through June 1980 (CROWLEY & JOHNSON, 1982, tab. 8). One consequence of its shift was a dramatic reduction of niche overlap with its congener, *C. elisa*. The present analysis detected very high dietary overlap between these two populations during summer ( $L_{ij} = 8.02$ , Fig. 3). But our estimates of relative encounter frequency in the detritus habitat (Figure 4) found that *C. elisa* accounted for only a small proportion (22%) of *C. fasciata* interactions with other large dragonfly larvae. The observed shift tended to increase habitat overlap with *T. cynosura*, a population with which there was less dietary overlap (Fig. 3) but, due to its greater abundance, resulted in a large estimated proportion (43%) of encounters (Fig. 4). We conclude that competition for food could not readily account for this niche shift. However, it is possible that the prey assemblage and consequent diets in the submersed macrophyte habitat differed from those observed in the detritus.

A recent field experiment (MORIN, 1984) found a ten-fold higher density of odonate larvae within fish-exclusion cages during one growing season in a North Carolina farm pond. This suggests that odonate densities in the presence of fish were considerably below their "carrying capacity" and would therefore be expected to be influenced relatively little by competition for prey. A study of diets of sunfish (*Lepomis* spp.) in Bays Mountain Lake (Thomas H. Martin, pers. comm.) has found that small instars of Anisoptera larvae were frequently eaten, especially *Tetragoneuria cynosura* by redear sunfish (*L. microlophus*) in summer, and *Celithemis* spp. by bluegill sunfish (*L. macrochirus*) in late fall. Thus it is possible that densities of the larval populations we studied were also reduced to levels where competition for food was not important.

On the basis of production estimates, BENKE (1976) concluded that the larval

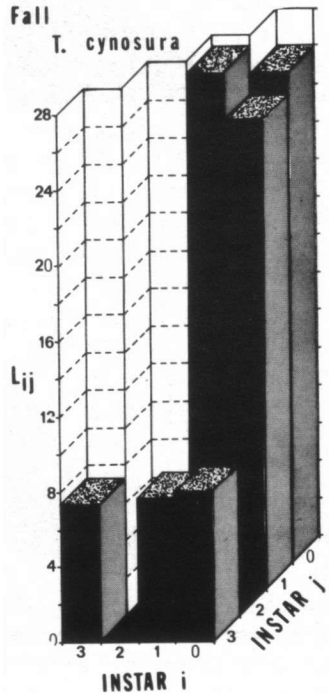


Fig. 7. Indices of dietary overlap (and specialization) among (and within) larval instars of *Tetragoneuria cynosura* co-occurring in allochthonous detritus habitats of Bays Mountain Lake during fall. (For further explanation cf. caption of Fig. 5).



anisopteran biomass observed in Dick's Pond was supported by very high turnover of prey populations restricted to refuges. His subsequent large-pen field experiment (BENKE, 1978) found strong interactions between seasonally segregated early-emerging species on the one hand, mainly *Epitheca* (= *Tetragoneuria*) *cynosura* and *Ladona deplanata*, and late-emerging ones on the other, primarily *Celithemis fasciata*. These results might appear to suggest that competition was important despite size differences caused by seasonal segregation. However, Benke considered it more plausible that the results were attributable to mutual predation among odonate larvae. This interpretation is consistent with results of another in situ experiment (BENKE et al., 1982) conducted in small enclosures at Dick's Pond under conditions of severe food limitation.

One result of *Tetragoneuria cynosura*'s having a two-year development period in Bays Mountain Lake was that large second year-class individuals were present throughout summer when all four species were hatching and growing through vulnerable early instars. The later emerging *Celithemis* and *Sympetrum* populations were also present as late-instar larvae during spring and part of summer when first year-class *T. cynosura* were smallest and most vulnerable. Small odonate larvae were an important component (5.4%) of the diets of the late-instar larvae studied, and 7.4% of the larvae had eaten at least one odonate. These values are very similar to those reported by BENKE (1978): 3% and 6.8% respectively. He found that most Anisoptera mortality in Dick's Pond could be accounted for by this level of mutual predation.

Recent laboratory and field experiments on competition among odonate larvae at Bays Mountain Park (PIERCE, 1982; JOHNSON et al., 1984a; JOHNSON et al., 1984 b) found no evidence of exploitation competition; but interference competition was detected in some cases. Reviews by FOX (1975) and POLIS (1981) suggest that intraspecific predation, a consequence of size differences within populations, is an important phenomenon influencing predator population dynamics. Non-lethal aggressive interactions among odonate larvae should also be influenced by the size differential between participants (BAKER, 1980, CROWLEY, 1984).

Co-occurrence of populations of generalized predators such as odonate larvae provides opportunities for aggressive interactions including mutual predation both within and among species. We agree with BENKE (1978) that "interference" competition may be a more important consequence of size differences among co-occurring larvae than reduction of "exploitation" competition due to dietary niche partitioning.

#### ACKNOWLEDGEMENTS

We thank TOM BOWMAN and his staff at Bays Mountain Park for their cooperation; WILLIAM

M. BECK, Jr (Florida A & M University) for assistance in identifying midge larvae; CLIFF CONEY and ROBERT BOHANAN for assistance in identifying microcrustaceans; PHILIP H. CROWLEY (University of Kentucky) for advice concerning niche-overlap indices; and TOM MARTIN for writing the computer program to calculate them. ART BENKE, ORA JOHANSSON and PHIL CROWLEY made particularly useful comments on early drafts of the manuscript. GEORGE BICK and SID DUNKLE also offered useful suggestions on style. This research was supported in part by National Science Foundation Research Grants (DEB 78-17518, DEB 79-05490, and DEB 81-04425) to Dan M. Johnson. Part of it was submitted to East Tennessee State University in partial fulfillment of the requirements for a Master of Science degree by the senior author.

#### REFERENCES

- ANDERSON, R.O., 1959. A modified flotation technique for sorting bottom fauna samples. *Limnol. Oceanogr.* 4: 223-225.
- BAKER, R.L., 1980. Use of space in relation to feeding areas by zygopteran nymphs in captivity. *Can. J. Zool.* 58: 1060-1065.
- BAKER, R.L. & H.F. CLIFFORD, 1981. Life cycles and food of *Coenagrion resolutum* (Coenagrionidae: Odonata) and *Lestes disjunctus disjunctus* (Lestidae: Odonata) populations from the boreal forest of Alberta, Canada. *Aquatic Insects* 3: 179-191.
- BENKE, A.C., 1970. A method for comparing individual growth rates of aquatic insects with special reference to the Odonata. *Ecology* 51: 328-331.
- BENKE, A.C., 1972. *An experimental field study on the ecology of coexisting larval odonates*. Ph. D. thesis, Univ. Georgia.
- 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.
- BENKE, A.C., P.H. CROWLEY & D.M. JOHNSON, 1982. Interactions among coexisting larval Odonata: an in situ experiment using small enclosures. *Hydrobiologia* 94: 121-130.
- BOEHMS, C.N., 1971. *The influence of temperature upon embryonic diapause and seasonal regulation in *Sympetrum vicinum* (Hagen) (Odonata: Libellulidae)*. Ph. D. thesis Univ. N. Carolina, Chapel Hill.
- BRASSE, D.F., 1976. Modification of the Whiteside-Williams Pattern Sampler. *J. Fish. Res. Bd Can.* 33: 2861-2863.
- BROOKS, J.L., 1959. Cladocera. In: W.T. Edmondson, [Ed.], *Freshwater biology*, 2nd ed., pp. 587-656, Wiley, New York.
- CHUTTER, F.M., 1961. Certain aspects of the morphology and ecology of the nymphs of several species of *Pseudagrion* Selys (Odonata). *Arch. Hydrobiol.* 57: 430-463.
- CLOAREC, A., 1977. Alimentation de larves d'*Anax imperator* Leach dans un milieu naturel (Anisoptera: Aeshnidae). *Odonatologica* 6: 227-243.
- CORBET, P.S., 1954. Seasonal regulation in British dragonflies. *Nature, Lond.* 174: 655.
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- CORBET, P.S., 1980. Biology of Odonata. *A. Rev. Ent.* 25: 189-217.
- CROWLEY, P.H., 1984. Evolutionarily stable strategies for larval dragonflies. In: S. Levin & T. Hallam, [Eds.], *Lecture notes in biomathematics*, Vol. 54, pp. 55-74. Springer, Berlin-Heidelberg-New York.
- CROWLEY, P.H. & D.M. JOHNSON, 1982. Habitat and seasonality as niche axes in an odonate community. *Ecology* 63: 1064-1077.

- CUMMINS, K.W. & W.P. COFFMAN, 1978. Table 22a. Summary of ecological and distributional data for Chironomidae (Diptera). In: R.W. Merritt & K.W. Cummins, [Eds]. An introduction to the aquatic insects of North America, pp.370-376, Kendall/Hunt, Dubuque.
- ENDERS, F., 1976. Size, food-finding and Dyar's constant. *Environ. Ent.* 5: 1-10.
- FISCHER, Z., 1967. Food composition and food preference in larvae of *Lestes sponsa* (L.) in a static water environment. *Polskie Archwum Hydrobiol* 15: 59-71.
- FOLSOM, T.C. & N.C. COLLINS, 1982. Food availability in nature for the larval dragonfly *Anax junius* (Odonata: Aeshnidae). *Freshw. Invert. Biol.* 1: 33-40.
- FOX, L.R., 1975. Cannibalism in natural populations. *A. Rev. Ecol. Syst.* 6: 87-106.
- GERKING, S.D., 1957. A method of sampling the littoral macrofauna and its application. *Ecology* 38: 219-226.
- GRIFFITHS, D., 1970. Observations on the food of dragonfly nymphs from a bog water in North Norway. *Entomologist's mon. Mag.* 106: 41-47.
- HAIRSTON, N.G., 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* 61: 817-826.
- HURLBERT, S.H., 1978. The measurement of niche overlap and some relatives. *Ecology* 59: 67-77.
- HUTCHINSON, G.E., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Natur.* 83: 145-159.
- INGRAM, B.R., 1976. Life histories of three species of Lestidae in North Carolina (Odonata: Zygoptera). *Odonatologica* 5: 231-244.
- INGRAM, B.R. & C.E. JENNER, 1976. Life histories of *Enallagma hageni* (Walsh) and *E. aspersum* (Hagen) (Zygoptera: Coenagrionidae). *Odonatologica* 5: 331-345.
- JOHANSSON, O.E., 1976. *Ecological studies on co-existence amongst damselfly larvae (Odonata: Zygoptera) in the Norfolk Broads*. Ph. D. thesis, Univ. East Anglia.
- JOHANSSON, O.E., 1978. Co-existence of larval Zygoptera (Odonata) common to the Norfolk Broads (U.K.) I. Temporal and spatial separation. *Oecologia* 32: 303-321.
- JOHNSON, D.M., C.C. CONEY & M.J. WESTFALL, 1980. The Odonata of Bays Mountain Park, Sullivan County Tennessee. *J. Tenn. Acad. Sci.* 55: 73-76.
- JOHNSON, D.M. & P.H. CROWLEY, 1980a. Odonate "Hide-and-seek": habitat specific rules? In: W.C. Kerfoot, [Ed.], Evolution and ecology of zooplankton communities, pp. 569-579, Univ. Press New England, Hanover, N.H.
- JOHNSON, D.M. & P.H. CROWLEY, 1980b. Habitat and seasonal segregation among coexisting odonate larvae. *Odonatologica* 9: 297-308.
- JOHNSON, D.M., R.E. BOHANAN, C.N. WATSON & T.H. MARTIN, 1984a. Coexistence of *Enallagma divagans* and *Enallagma traviatum* (Zygoptera: Coenagrionidae) in Bays Mountain Lake: an in situ enclosure experiment. *Adv. Odonatol.* 2. (In press).
- JOHNSON, D.M., P.H. CROWLEY, R.E. BOHANAN, C.N. WATSON & T.H. MARTIN, 1984b. Competition among larval dragonflies: a field enclosure experiment with *Tetragoneuria* and *Celithemis elisa* (Odonata: Anisoptera). *Ecology*. (In press).
- KIME, J.B., 1974. *Ecological relationships among three species of aeshnid dragonfly larvae (Odonata: Aeshnidae)*. Ph. D. thesis, Univ. Wash., Seattle.
- KORMONDY, E.J. & J.L. GOWER, 1965. Life history variations in an association of Odonata. *Ecology* 46: 882-886.
- LAWTON, J.H., 1970. Food and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *J. Anim. Ecol.* 39: 669-689.
- LAWTON, J.H., 1971. Maximum and actual feeding-rates in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). *Freshw. Biol.* 1: 99-111.
- LAWTON, J.H., B.A. THOMPSON & D.J. THOMPSON, 1980. The effects of prey density on survival and growth of damselfly larvae. *Ecol. Ent.* 5: 39-51.
- LUTZ, P.E., 1968a. Life history studies on *Lestes eurinus* Say. *Ecology* 49: 576-579.

- LUTZ, P.E., 1968b. Effects of temperature and photoperiod on larval development in *Lestes eurinus*. *Ecology* 49: 637-644.
- LUTZ, P.E., 1974a. Effects of temperature and photoperiod on larval development in *Tetragoneuria cynosura*. *Ecology* 55: 370-377.
- LUTZ, P.E., 1974b. Environmental factors controlling duration of larval instars in *Tetragoneuria cynosura*. *Ecology* 55: 630-637.
- LUTZ, P.E. & C.E. JENNER, 1964. Life history and photoperiodic responses of nymphs of *Tetragoneuria cynosura* (Say). *Biol. Bull. Woods Hole* 127: 304-316.
- MERRILL, R.J., 1981. *A comparison of the diets of dragonfly larvae (Odonata: Anisoptera) coexisting in an allochthonous detritus habitat*. M. Sc. thesis, East Tennessee St. Univ.
- MORIN, P.J., 1984. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina farm pond. *Ecology* 65: 53-60.
- NEEDHAM, J.G. & M.J. WESTFALL, 1955. *A manual of the dragonflies of North America (Anisoptera) including the Greater Antilles and the provinces of the Mexican border*. Univ. California Press, Berkeley-Los Angeles.
- NESTLER, J.M. 1980. *Niche relationships of the Anisoptera of Lake Isaqueena*. Ph. D. thesis, Clemson Univ.
- PAULSON, D.R. & C.E. JENNER, 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. *Ecology* 52: 96-107.
- PEARLSTONE, P.S.M., 1973. The food of damselfly larvae in Marion Lake, British Columbia. *Synesis* 6: 33-39.
- PIANKA, E.R., 1974. Niche overlap and diffuse competition. *Proc. natn. Acad. Sci. U.S.A.* 71: 2141-2145.
- PIERCE, C.L., 1982. *The relationship of behavior to competition and predation in two larval odonate populations*. M. Sc. thesis, Univ. Kentucky.
- POLIS, G.A., 1981. The evolution and dynamics of intraspecific predation. *A. Rev. Ecol. Syst.* 12: 225-251.
- PRITCHARD, G., 1964. The prey of dragonfly larvae in ponds in northern Alberta. *Can. J. Zool.* 42: 785-800.
- ROSS, Q.E., 1967. *The effect of different naiad and prey densities on the feeding behavior of Anax junius (Drury) naiads*. M. Sc. thesis, Cornell Univ.
- SAWCHYN, W.W. & C. GILLOTT, 1975. The biology of two related species of coenagrionid dragonflies in Western Canada. *Can. Ent.* 107: 119-128.
- SCHOENER, T.W., 1982. The controversy over interspecific competition. *Am. Scient.* 70: 586-595.
- SOKAL, R.R. & F.J. ROHLF, 1981. *Biometry*, 2nd ed. Freeman, San Francisco.
- THOMPSON, D.J., 1978. Prey size selection by larvae of the damselfly, *Ischnura elegans*. *J. Anim. Ecol.* 47: 769-785.
- THOMPSON, D.J., 1982. Prey density and survival in damselfly larvae: field and laboratory studies. *Adv. Odonatol.* 1: 267-280.
- WEINS, J.A., 1977. On competition and variable environments. *Am. Scient.* 65: 590-597.
- WHITESIDE, M.C. & C. LINDEGAARD, 1980. Complementary procedures for sampling small benthic invertebrates. *Oikos* 35: 317-320.
- WHITESIDE, M.C. & J.B. WILLIAMS, 1975. A new sampling technique for aquatic ecologists. *Verh. internat. Ver. Limnol.* 19: 1534-1539.
- WILSON, D.S., 1975. The adequacy of body size as a niche difference. *Am. Nat.* 109: 769-784.
- WRIGHT, M., 1943. The effect of certain ecological factors on dragonfly nymphs. *J. Tenn. Acad. Sci.* 18: 172-196.