Odonatologica 9 (4): 297-308 December 1, 1980

HABITAT AND SEASONAL SEGREGATION AMONG COEXISTING ODONATE LARVAE

D.M. JOHNSON[1] and P.H. CROWLEY[2]

[1]Department of Biological Sciences, East Tennessee State University, Johnson City, Tennessee 37601, United States

[2]T.H. Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506, United States

Received April 14, 1980 / Accepted April 22, 1980

Larvae of 35 spp. have been collected in sweep-net samples from the littoral zone of a lake and a pond at Bays Mountain Park, Tennessee, USA. Several spp. are apparently restricted to the fish-free pond (*Anax junius, A. longipes, Libellula cyanea, Tramea lacerata, Archilestes grandis, Lestes eurinus, Enallagma aspersum*); others (*Aeshna umbrosa, Erythemis simplicicollis, Plathemis lydia*) are found predominantly in the pond. — Bays Mountain Lake contains several spp. of insectivorous fish. Its odon. assemblage is dominated by spp. that utilize submersed macrophyte and allochthonous detritus habitats; 6 of these account for about 90% of the larvae in the lake (*Tetragoneuria cynosura, Celithemis elisa, C. fasciata, Enallagma divagans, E. signatum, E. traviatum*). Seasonal segregation of life histories probably reduces competition among these dominant spp.; habitat segregation may be more important among the less abundant spp.

INTRODUCTION

Odonate larvae are general predators (THOMPSON, 1978a, 1978b), often abundant relative to the prey populations that apparently limit their densities (BENKE, 1976; LAWTON, 1971; PEARLSTONE, 1973); despite this seemingly high potential for competition, larvae of many species commonly coexist (BENKE & BENKE, 1975). We have recently suggested (JOHNSON & CROWLEY, 1980) that habitat segregation and seasonal segregation of life histories are the niche partitioning mechanisms largely responsible for maintaining large assemblages such as the 46 species collected at Bays Mountain Park, Sullivan County, Tennessee (JOHNSON, CONEY & WESTFALL, 1980). This paper describes how the larvae of those Bays Mountain species are utilizing lentic habitats within the park, to what extent they segregate into different habitats, and how the most abundant species are seasonally segregated.

STUDY AREA

Bays Mountain Park is a 525 ha forested watershed in the Ridge and Valley Province of the southern Appalachian Mountains in Sullivan County, northeastern Tennessee (82° 37' W, 36° 31' N). It is maintained as a nature preserve and educational facility by the City of Kingsport. Aquatic habitats within the park include several small streams and two man-made lentic habitats: Bays Mountain Lake and Ecology Pond (Fig. 1).

Bays Mountain Lake (formerly Kingsport Reservoir) is a shallow eutrophic lake with a surface area of 15 ha at an elevation of 550 m. It was formed in 1916 by construction of a dam across Dolan Branch. The lake was drained in 1966 to repair the dam, allowed to re-fill in 1967, and stocked with fish in 1968. Fish now known to be living in the lake are largemouth bass, *Micropterus salmoides*; bluegill sunfish, *Lepomis macrochirus*; redear sunfish, *Lepomis microlophus*; warmouth, *L. gulosus*; mosquito fish, *Gambusia affinis*; channel catfish, *Ictalurus punctatus*; and yellow bullhead, *I. natalis*. The bluegill dominates both total fish numbers and biomass. Littoral vegetation has become abundant in recent years as a result of a stable water level, fertilization (1969-1974) to increase fish production, and dispersal of seeds by migratory waterfowl attracted to winter food plots. During the two years of our study the lake has been dimictic, with ice-cover for at least one month in the winter and an anoxic hypolimnion (below 4 m) by mid-summer.

Ecology Pond has a surface area of 0.58 ha and maximum depth of 1.5 m. It was formed by construction of an earthen dam in 1969 and was drained, dried out, and re-filled in 1972. A vertical outflow pipe has prevented colonization by fish; the only abundant vertebrate predator is the redspotted newt, *Notophthalmus viridescens*.

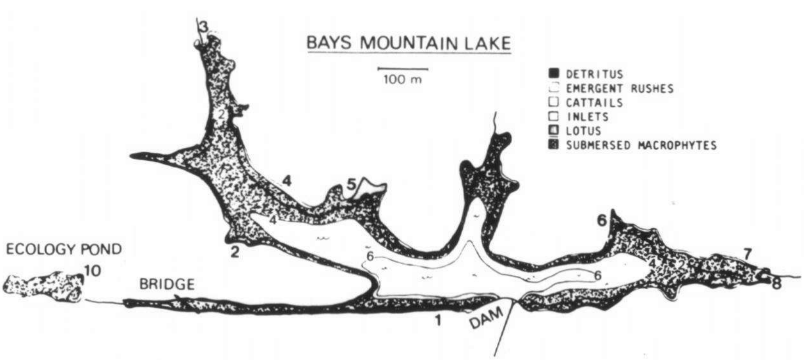

Fig. 1. A map of lentic habitats at Bays Mountain Park, Sullivan County, Tennessee, showing depth contours (in meters), the distribution of littoral habitats in July, 1979, and the location of ten sampling stations.

METHODS

In July, 1977, we established ten regular sampling stations at sites representing six distinct types of littoral lentic habitats at Bays Mountain Park (Fig. 1): (1) the northeastern corner of Ecology Pond (Station 10), a site dominated by allochthonous detritus in most seasons but overgrown by the submersed macrophyte *Najas flexilis* from August through October; — (2) allochthonous detritus, primarily deciduous leaves accumulating in shallow water near shaded shores (Stations 1 & 9); — (3) the submersed macrophytes *Vallisneria americana* and *Najas flexilis*, covering much of the lake bottom except where anoxic conditions exist for part of the summer at depths greater than 4 m (Stations 2 & 6); — (4) sandy substrates deposited by inlet streams (Stations 3 & 8), characterized by bare sand, some detritus, a submersed carpet-like growth of *Scirpus* sp., and emergent *S. purshianus*; — (5) long stems and floating leaves of American Lotus, *Nelumbo lutea*, dominating one cove (Station 5); and — (6) emergent spike-rushes *Eleocharis quadrangulata* and *E. ovata*, forming dense stands along some shores (Stations 4 & 6).

A total of 210 standard sweep-net samples was obtained by monthly sampling of these stations between July, 1977, and June, 1979. (Ice cover prevented sampling in January, 1978, and in February of both years.) Each standard sweep covered approximately 1/3 m^3 by drawing a triangular dip-net 1/3 m wide along the bottom for a distance of about 1 m. Samples were usually sorted immediately by placing the debris in white enamel pans and manually searching for living odonates; during cold weather some samples were returned to the laboratory in buckets and refrigerated until they were sorted. Larvae removed from the samples were preserved in 70% alcohol until they were identified and measured.

Larvae were identified by consulting a list of adults captured at Bays Mountain Park (JOHNSON, CONEY & WESTFALL, 1980), using published keys (GARMAN, 1927; NEEDHAM & HEYWOOD, 1929; NEEDHAM & WESTFALL, 1955; GLOYD & WRIGHT, 1959), rearing specimens to adulthood after photographing their caudal lamellae (Crowley, unpublished), and consulting with M.J. Westfall, Jr. (University of Florida). Some early-instar individuals could be identified only to genus, and very small libellulids only to family. Each larva was measured using a stereomicroscope with an ocular micrometer to determine head width (maximum distance across the eyes) and wing-pad length (from the posterior dorsal edge of the mesothorax to the tip of the rear wing-pad). For the more abundant species, clusters of points on a graph of head width against wing-pad length were used to assign individuals in instars.

In April, 1978, an emergence screen was placed at each sampling station. Screens were made by stapling aluminium window screening to two wooden dowels driven into the substrate. The screens are 60 cm wide and 70 cm tall, extending from the substrate to at least 30 cm above the water. Exuviae were removed from these screens once each week, preserved in 70% alcohol, and identified to species. These collections should not be considered quantitative estimates of the numbers emerging from each habitat, because there is great variation in the availability of alternate emergence sites; but they do provide useful information concerning the seasonal pattern of emergence for the more abundant species.

In order to estimate the area covered by each type of habitat, we drew vegetation maps of Bays Mountain Lake and Ecology Pond in the summer of 1979 (Fig. 1). Aerial photographs were used to determine the shape of the shoreline. Thirty transects were run across Bays Mountain Lake and ten across Ecology Pond by stretching wire marked in 12.5 ft (3.8 m) intervals along the surface with the aid of floating plastic jugs. Depth soundings at 25 ft (7.6 m) intervals along these transects were used to sketch in approximate depth contours. Additional measurement of one-meter contour were obtained from John Rupley, Jr. (unpublished). When a map (scale, 1 inch = 200 ft) of the shoreline and depth contours was complete, the distribution of each type of vegetation was sketched in from estimates obtained during a canoe trip around the perimeter of the lake in July, 1979. The submersed macrophyte zone was terminated at the 4 m depth contour based on observations by SCUBA divers in August, 1978; the hypolimnion below this depth is anoxic during most of the summer. We then traced the map onto graph paper (20 squares per inch) on which each square represented 10 ft^2. The number of squares covered by each habitat was used to estimate its real extent in m^2.

The total numbers collected in each habitat were converted to estimates of population densities (m^{-2}) by dividing by the number of samples from each habitat type (42 for most habitats, 21 for American Lotus and Ecology Pond) and multiplying by 3 (each sweep sampled about 1/3 m^2). The total number of individuals using each habitat was estimated by multiplying these densities by the area covered by each habitat; for this calculation we assumed that odonates do not utilize the submersed macrophytes at depths greater than 2 m (Johnson, unpublished).

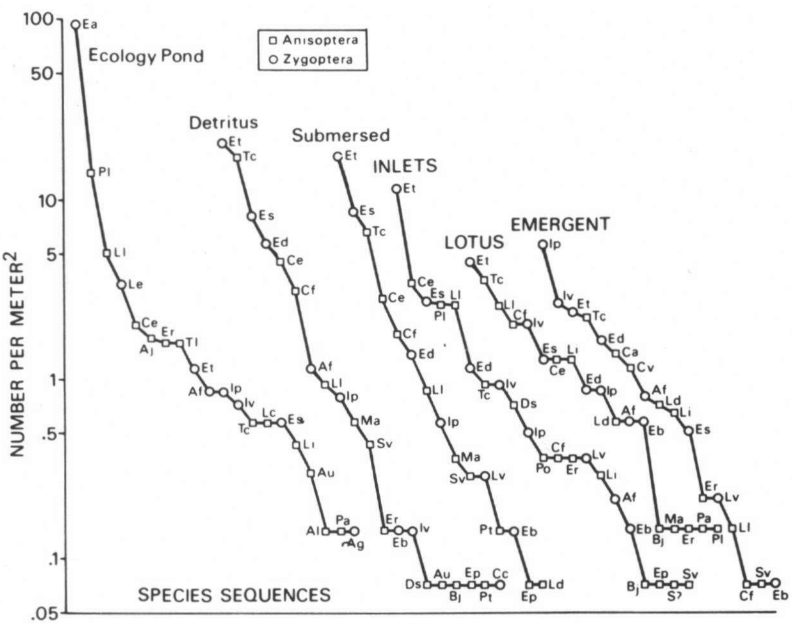

Fig. 2. The average density of larvae of each species of odonate in each habitat, based on monthly sweep-net samples taken between July, 1977, and June, 1979. Species are ranked by density within each habitat, and the curves displaced horizontally to avoid overlapping. Species abbreviations are listed in Table I.

RESULTS

A total of 3236 odonate larvae were collected in the 210 sweep-net samples from July, 1977, through June, 1979. Those too small to be identified with certainty (37 *Celithemis*, 101 *Libellula*, 23 Libellulidae, 6 *Enallagma*, and 37 *Ischnura*) have been distributed among the species that they might have been in proportion to the abundances of identified individuals of each species in each habitat. The relative abundances of the species by habitat are shown in Figure 2. Table I presents the estimated total population size of each species and the proportion utilizing each habitat type; from these data, the numbers of individuals or population densities can be readily obtained. Estimated population sizes for all species in Bays Mountain Lake and in Ecology Pond are ranked in Figure 3.

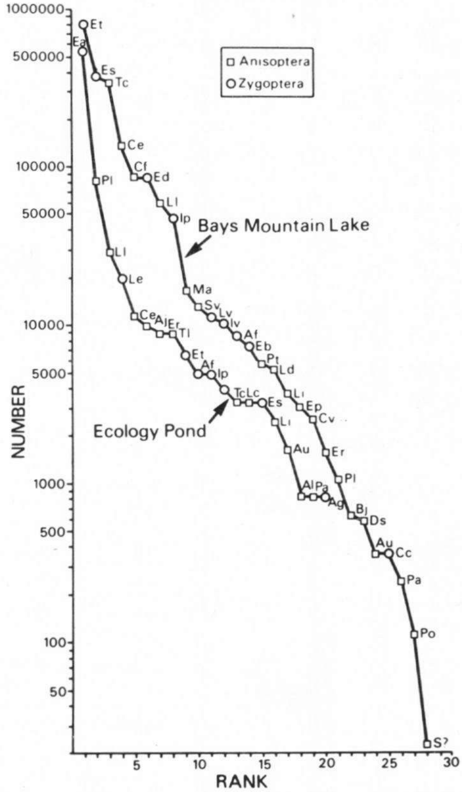

Fig. 3. The ranked abundances of larvae of each species of odonate in Ecology Pond and Bays Mountain Lake. Average densities in each habitat (Fig. 2) were multiplied by the area covered by that habitat (Fig. 1, Tab. I), and these products were summed to estimate the population size for each species. Species abbreviations are listed in Table I.

Six species dominate the submersed macrophyte and allochthonous detritus habitats in Bays Mountain Lake (Fig. 2) and account for 90% of all individuals in the lake (Fig. 3): *Tetragoneuria cynosura*, *Celithemis elisa*, *C. fasciata*, *Enallagma divagans*, *E. signatum* and *E. traviatum*. Figures 4 and 5 summarize the life histories of these species, based on measurements of individuals collected in sweep-net samples and exuviae found on emergence screens for all habitats combined.

The life histories of the three *Enallagma* species that dominate Bays Mountain Lake are compared in Figure 4. Apparent interspecific differences with respect to mean instar (sensu BENKE, 1970) may also be interpreted as size differences because the criteria for assigning individuals to instar were essentially identical for all three species (Crowley, unpublished). *E. divagans* emerges earliest in the spring, develops synchronously, and is about two instars larger than *E. traviatum* throughout most of the year. *E. traviatum*

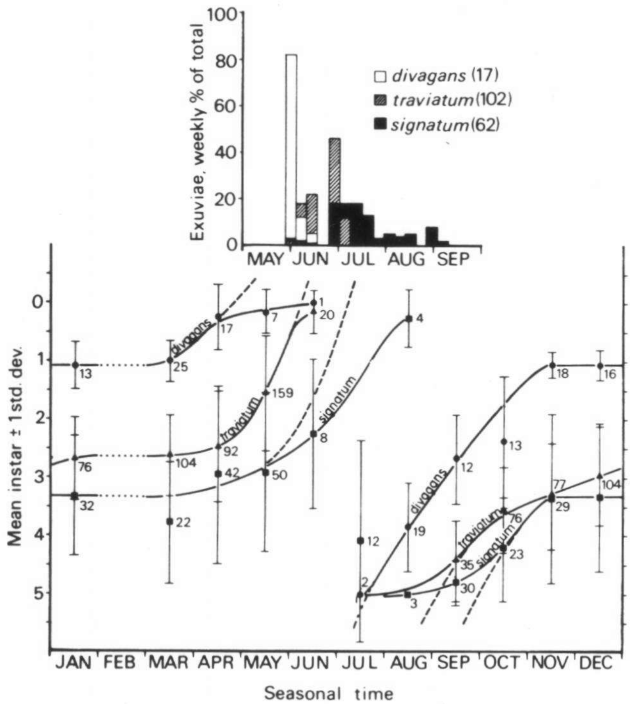

Fig. 4. A comparison of the life histories of three *Enallagma* species which dominate Bays Mountain Lake, based on measurements of larvae collected in monthly sweep-net samples. A number besides each mean indicates the number of individuals used to calculate the mean instar. Instars are numbered in reverse order: 0 = final instar, 1 = penultimate instar, etc. Dashed lines show the trend expected if means were not influenced by emergence from the final instar or recruitment into catchable sizes. The upper panel shows the emergence pattern for each species based on exuviae collected on screens at ten stations (total numbers of exuviae in parentheses).

emerges somewhat earlier than *E. signatum*, but these species do not have such synchronous development, and there is considerable size-overlap during the autumn. *E. traviatum* apparently continues to grow later into the winter than the other two species, resuming growth one instar larger than *E. signatum* in the spring.

Comparison of *Tetragoneuria* and *Celithemis* life histories (Fig. 5) is complicated by the fact that *T. cynosura* has a two-year life cycle in Bays Mountain Lake; also it is difficult to distinguish *C. elisa* and *C. fasciata* in the early instars. *Tetragoneuria* emerges early in the spring, and the new year-class of larvae grows rapidly throughout the summer. Their development seems to slow down in September, they overwinter in the U-3 (ante-antepenultimate) instar, and do not appear to resume growing until the following June. Second-year larvae spend most of the summer in the penultimate instar, molt into the final instar in September and October, and emerge the following spring. Since *Celithemis* emerges in June and July, its larvae are considerably smaller than *Tetragoneuria* in the late summer. They grow rapidly and catch up with the first year-class of *Tetragoneuria* by September, so that both species overwinter in the same instar. *Celithemis* starts growing earlier in the spring and emerges in mid-summer after only one year of development. Data from the emergence screens indicate that *C. elisa* emerges a few weeks earlier on average than *C. fasciata*.

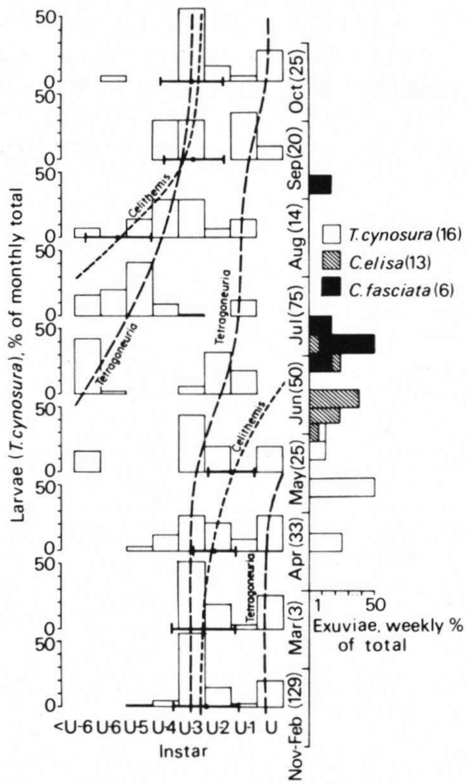

Fig. 5. A comparison of the life histories of *Tetragoneuria* and *Celithemis* in Bays Mountain Lake, based on measurements of larvae collected in monthly sweep-net samples. Histograms represent the percentage of *Tetragoneuria* larvae in each instar during each month (or months): parenthetical numbers indicate the number of *Tetragoneuria* larvae included in each histogram; and a line of long dashes shows the typical development of a *Tetragoneuria* cohort through its two-year life cycle. Solid dots represent mean instars (± 1 S.D.) of *Celithemis* larvae collected during each time period; and a line of short dashes shows the typical development of a *Celithemis* cohort through a one--year life cycle. Emergence patterns along the right margin are based on exuviae collected on screens at ten stations (total numbers in parentheses).

DISCUSSION

Forty-six species of odonates have been collected at Bays Mountain Park (JOHNSON, CONEY & WESTFALL, 1980), but we have found only thirty-five of them in our sweep-net samples of lentic habitats. Among the species not found as larvae, the following are usually associated with lotic habitats: *Cordulegaster maculata, Hagenius brevistylus, Stylogomphus albistylus, Calopteryx maculata, Lestes rectangularis, Argia moesta, Enallagma civile* and *E. exsulans.* Their larvae are probably utilizing streams within the park or the nearby Holston River, which flows along the northern side of Bays Mountain. The species not found as larvae that are characteristic of lentic habitats are very rare in the adult collections and are probably living undetected in the sampled habitats: *Tramea carolina, Amphiagrion saucium,* and *Anomalagrion hastatum.*

Among the species found in our sweep-net collections, seven are restricted to Ecology Pond: *Anax junius, A. longipes, Libellula cyanea, Tramea lacerata, Archilestes grandis, Lestes eurinus,* and *Enallagma aspersum.* For three others, more than 80% of their estimated population size (Tab. I) is found in the pond: *Aeshna umbrosa, Erythemis simplicicollis,* and *Plathemis lydia.* Many of these species are known to be relatively active visual predators whose feeding behavior is probably incompatible with the presence of insectivorous fish (KIME, 1974; SHERK, 1977; NESTLER, 1978; JOHNSON & CROWLEY, 1980). These ten habitat specialists account for about 90% of the individuals in Ecology Pond. It seems reasonable to suppose that species common in the lake have access to Ecology Pond; yet only four of the six most abundant species have been collected there at all (Tab. I), and their combined numbers account for only 3% of the total. Since the internal physical structure of Ecology Pond is similar to that in the lake (allochthonous detritus and submersed macrophytes), we attribute the unique odonate assemblage found in the pond ultimately to the absence of fish predation, which permits more active odonates to eliminate by competition or predation the species that dominate in the lake. Though these differences in distribution may also result at least in part from differences in oviposition behavior, we suspect that oviposition preferences may themselves reflect a correlation between physical characteristics of the body of water (e.g. size) and the probable intensity of fish predation (i.e. small or temporary ponds may have fewer insectivorous fish).

Since our information about Ecology Pond odonates is based on one sweep-net sample per month from only one location, we do not have sufficient data to suggest what mechanisms facilitate coexistence of species within the pond. However, one case of seasonal segregation among species of the family Lestidae is particularly striking (cf. also JOHNSON, CONEY &

Table I

Habitat utilization by odonate larvae, based on 210 monthly sweep-net samples between July, 1977 and June, 1979. The first column of numbers presents the total number of larvae collected in all samples that were identified to species; parenthetical numbers are totals augmented by assignment of individuals whose identities were not certain. The second column presents an estimate of the total population size in lentic habitats at Bays Mountain Park, calculated by summing the products of average density in each habitat (Fig. 2) and area covered by that habitat (Fig. 1 and first row below). Other columns indicate the proportion of each species' population utilizing each habitat type.

	Abbreviation and Species	No. collected	Total population	Ecology Pond surface (m²)	Bays Mountain Lake: *habitats* and surface a (m²) *detr*	*subm*	*inlet*	*lotus*	*emerg*
				5840	5160	38700	316	1740	2310
Af	*Argia fumipennis violacea* (Hag.)	40	13800	0.364	0.428	0	0.005	0.072	0.132
Cc	*Chromagrion conditum* (Hag.)	1	368	0	1.000	0	0	0	0
Ea	*Enallagma aspersum* (Hag.)	653	545000	1.000	0	0	0	0	0
Eb	*E. basidens* Calv.	11	7470	0	0.099	0.740	0.006	0.133	0.022
Ed	*E. divagans* Sel.	144	87700	0	0.336	0.600	0.004	0.017	0.043
Es	*E. signatum* (Hag.)	290(292)	382000	0.009	0.110	0.870	0.002	0.006	0.003
Et	*E. traviatum* Sel.	757(761)	804000	0.008	0.131	0.840	0.004	0.010	0.007
Ip	*Ischnura posita* (Hag.)	92(117)	45900	0.109	0.088	0.482	0.003	0.032	0.284
Iv	*I. verticalis* (Say)	59(71)	14800	0.282	0.050	0	0.020	0.235	0.413
Ag	*Archilestes grandis* (Ramb.)	1	835	1.000	0	0	0	0	0
Le	*Lestes eurinus* Say	24	20000	1.000	0	0	0	0	0
Lv	*L. vigilax* Hag.	12	11700	0	0	0.948	0.010	0	0.043
	Z y g o p t e r a (total)	*2094(2137)*	*1930000*	*0.305*	*0.098*	*0.568*	*0.003*	*0.010*	*0.017*
Ds	*Dromogomphus spinosus* Sel.	11	594	0	0.620	0	0.380	0	0
Ps	*Progomphus obscurus* (Ramb.)	5	113	0	0	0	1.000	0	0
Au	*Aeshna umbrosa* Wlk.	3	2040	0.819	0.181	0	0	0	0
Aj	*Anax junius* (Dr.)	12	10000	1.00	0	0	0	0	0
Al	*A. longipes* Hag.	1	835	1.000	0	0	0	0	0
Bj	*Basiaeschna janata* (Say)	3	639	0	0.576	0	0.036	0.388	0
Ma	*Macromia alleghaniensis* Wllmsn	14	17000	0	0.173	0.812	0	0.015	0
Ep	*Epicordulia princeps* (Hag.)	3	3160	0	0.117	0.876	0.007	0	0
S?	*Somatochlora* sp	1	23	0	0	0	1.000	0	0
Tc	*Tetragoneuria cynosura* (Say)	405	358000	0.009	0.247	0.711	0.001	0.017	0.014
Ce	*Celithemis elisa* (Hag.)	162(193)	149000	0.078	0.155	0.723	0.007	0.015	0.021
Cf	*C. fasciata* Kirby	73(88)	88800	0	0.178	0.779	0.001	0.039	0.002
Cv	*C. verna* Pritchard	15(16)	2640	0	0	0	0	0	1.000
Er	*Erythemis simplicicollis* (Say)	21(22)	10800	0.852	0.068	0	0.011	0.023	0.046
Ld	*Ladona deplanata* (Ramb.)	15	5410	0	0	0.511	0	0.184	0.305
Lc	*Libellula cyanea* Fabr.	1(4)	3340	1.000	0	0	0	0	0
Li	*L. incesta* Hag.	9(24)	6320	0.397	0	0	0.014	0.354	0.236
Ll	*L. luctuosa* Burm.	38(122)	89400	0.327	0.054	0.557	0.009	0.050	0.004
Pa	*Pachydiplax longipennis* (Burm.)	2	1080	0.771	0	0	0	0.229	0
Pt	*Perithemis tenera* (Say)	3	5900	0	0.062	0.938	0	0	0
Pl	*Plathemis lydia* (Dr.)	129(138)	84600	0.987	0	0	0.010	0.003	0
Sv	*Sympetrum vicinum* (Hag.)	12	13500	0	0.164	0.822	0.002	0	0.012
Tl	*Tramea lacerata* Hag.	10(11)	9180	1.000	0	0	0	0	0
	A n i s o p t e r a (total)	*948(1108)*	*863000*	*0.192*	*0.162*	*0.600*	*0.004*	*0.024*	*0.018*
	Odonata (total)	**3042(3245)**	**2800000**	**0.270**	**0.118**	**0.578**	**0.003**	**0.014**	**0.017**

a) Areas not included in this row are: 57735 m² of depths greater than 4 m, 44120 m² of submersed macrophytes at depths of 2-4 m, and 214 m² of cattails *Typha* sp.

b) This figure represents the area covered by submersed macrophytes at depths less than 2 m, the part of this habitat assumed to be utilized by odonate larvae.

WESTFALL, 1980): *Lestes eurinus* grows rapidly in late summer and fall, overwinters as a relatively large larva, and emerges in June; *Archilestes grandis* overwinters in the egg stage, grows very rapidly in early summer and emerges in July. We are not sure when the *Archilestes* eggs hatch in the spring; but it is clear that, if the larvae of these two species encounter each other at all, they are in very different size categories.

The most abundant odonates in Bays Mountain Lake co-occur in the extensive submersed macrophyte and allochthonous detritus habitats (Tab. I, Fig. 2). Seasonal segregation of life histories reduces size-overlap among the dominant *Enallagma* species throughout much of the year (Fig. 4), and between *Tetragoneuria* and *Celithemis* during periods of most rapid growth (Fig. 5). Since studies of odonate diet show that large larvae can eat larger prey (CHUTTER, 1961; KIME, 1974; THOMPSON, 1975), we infer that seasonal segregation reduces diet overlap. Nevertheless, BENKE (1978) found that *Epitheca* (= *Tetragoneuria*) and *Celithemis* species with clearly segregated life histories were engaged in significant interspecific interactions, and he suggests that these might include predation on the smaller species by the larger ones. Clearly, diet analyses will be required to determine the real significance of seasonal segregation for the interaction of odonate species coexisting in our study area.

Little is known about the intensity of competitive and predatory interactions between Anisoptera and Zygoptera. It would be particularly useful to know if the relative abundances of these suborders within lentic habitats reflect general differences in competitive abilities or in susceptibilities to particular invertebrate predators or insectivorous fish (cf. JOHNSON & CROWLEY, 1980). Figure 4 can in effect be superimposed on Figure 5 by adjusting for instar-specific differences in head width, permitting a direct examination of size overlap among the dominant Anisoptera and Zygoptera. When this is done, we find that the most abundant anisopteran, *Tetragoneuria cynosura*, overlaps the *Enallagma* species very little during summer and fall. Its spring emergence and early oviposition result in larvae that hatch early and grow through the "zygopteran" size-classes during the summer, effectively exploiting the time gap between *Enallagma* generations that is apparent in Figure 4. On the other hand, the *Celithemis* species experience considerable overlap with *Enallagma divagans*, suggesting that niche partitioning among these species depends on non-size-related differences in diet, microhabitat use, or other factors.

Except for the several most abundant species depicted in Figures 4 and 5, seasonal patterns of body size (instars) and population densities appeared relatively erratic and were difficult to establish. The seasonal variability may reflect differences in weather between the two years, intralittoral movements cued by fluctuating water temperature, the relatively fine temporal subdivision attempted (monthly, implying relatively few individuals per time period), or other factors. The preliminary results do indicate some intriguing differences among the Zygoptera regarding late season growth: By comparing the monthly size distributions, we find that *Enallagma aspersum, E. traviatum* and *Ischnura posita* apparently continue growing at least in late November and perhaps December, whereas *E. divagans, E. signatum* and *I. verticalis* do not (cf. also Fig. 4). A more thorough documentation of larval seasonality at Bays Mountain park must await further data.

From Table I and Figure 2 it is clear that the odonate assemblage utilizing the emergent rushes differs strikingly from the assemblage in submersed macrophytes or allochthonous detritus: Two species of *Ischnura* are dominant, *Enallagma signatum* is much less abundant than elsewhere, and *Celithemis verna* seems to replace *C. fasciata.* Some of these differences may be attributed to the presence of microhabitats associated with the distinctive vertical structure of this vegetation, or to the absence of microhabitats characteristic of the submersed macrophytes. Another important characterisitic of the emergent rushes may be better protection from fish predation, particularly nearest the shore; some of the species found here are also found in Ecology Pond (Tab. I, Fig. 2).

The less abundant habitat types, inlets and lotus, have odonate assemblages that seem to be mixtures of those in the more abundant habitats. This is probably because they share habitat characteristics with the other sites: Detritus, submersed macrophytes, and some vertical structure are features of both habitats. Only a few cases of apparent specialization on these habitats stand out: The burrower *Progomphus obscurus* is clearly restricted to the sandy substrates near inlet streams, and *Dromogomphus spinosus* reaches higher densities there than in detritus (Tab. I, Fig. 2); *Libellula luctuosa* is relatively abundant in inlet and lotus habitats as well as in Ecology Pond, thus achieving a relatively high rank in Bays Mountain Lake (Fig. 3) despite low densities in the more abundant habitats (Fig. 2).

Since the submersed macrophyte habitat covers such an extensive area (Fig. 1) and is occupied by so many odonate species (Tab. I), one might consider any species not found there to be a habitat specialist. In addition to emergent and inlet specialists noted above, the following species have been collected from Bays Mountain Lake, but not from the submersed macrophytes: *Aeshna umbrosa, Basiaeschna janata, Erythemis simplicicollis, Libellula incesta, Plathemis lydia, Argia fumipennis violacea,* and *Chromagrion conditum.*

ACKNOWLEDGEMENTS

We thank DAVID TAYLOR and JOHN RUPLEY, Jr. for sharing unpublished data used in mapping the lake; ROBERT BOHANNAN, CLIFF CONEY, KAROL LYNN JOHNSON, JOHN RODGERS and ROBERT MERRILL for assistance with the field work; KAREN NOEL, TERESA NOEL and ALLAN WILSON for help with measurements and data analysis; TOM BOWMAN and the staff of Bays Mountain Park for helping in many ways; and MINTER WESTFALL, Jr. for patiently teaching us the subtleties of odonate taxonomy. This research has been supported by grants from the National Science Foundation (DEB 78-17518 and DEB 78-02832).

REFERENCES

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., 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.

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.

GARMAN, P., 1927. *Guide to the insects of Connecticut.* Conn. Geol. Nat. Hist. Survey No. 39.

GLOYD, L.K. & M. WRIGHT, 1959. *In*: W.T. Edmondson, [Ed.], Freshwater biology, 2nd ed. Wiley, Chichester.

JOHNSON, D.M. & P.H. CROWLEY, 1980. Odonate "hide-and-seek": habitat-specific rules? *In*: W.C. Kerfoot, [Ed.], The evolution and ecology of zooplankton populations. (Am. Soc. Limnol. Oceangr. Spec. Symp. 3). Univ. Press New Engl., Hanover.

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.

KIME, J., 1974. *Ecological relationships among three species of aeshnid dragonfly larvae (Odonata: Aeshnidae).* Ph. D. thesis, Univ. Washington, Seattle.

LAWTON, J.H., 1971. Maximum and actual field feeding-rates in the larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). *Freshwat. Biol.* 1: 99-111.

NEEDHAM, J.G. & H.G. HEYWOOD, 1929. *A handbook of the dragonflies of North America.* Thomas, Springfield.

NEEDHAM, J.G. & M.J. WESTFALL, 1955. *A manual of the dragonflies of North America (Anisoptera).* Univ. Calif. Press, Berkeley.

NESTLER, J.M., 1978. Resource allocation by 3 co-occurring genera of Anisoptera (Odonata) nymphs from Lake Isaqueena, South Carolina. *Bull. ecol. Soc. Am.* 59: 56.

PEARLSTONE, P.S.M., 1973. The food of damselfly larvae in Marion Lake, British Columbia. *Syesis* 6: 33-39.

SHERK, T.E., 1977. Development of the compound eyes of dragonflies (Odonata). I. Larval compound eyes. *J. exp. Zool.* 201: 391-416.

THOMPSON, D.J., 1975. Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of Daphnia magna by Ischnura elegans. *J. Anim. Ecol.* 44: 907-916.

THOMPSON, D.J., 1978a. Prey size selection by larvae of the damselfly, Ischnura elegans (Odonata). *J. Anim. Ecol.* 47: 769-785.

THOMPSON, D.J., 1978b. The natural prey of larvae of the damselfly, Ischnura elegans (Odonata: Zygoptera). *Freshwat. Biol.* 8: 377-384.