

A TEN YEAR STUDY OF THE ODONATE ASSEMBLAGE OF BAYS MOUNTAIN LAKE, TENNESSEE

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Bays Mountain Lake (NE Tennessee, USA) is a 15 ha shallow, eutrophic impoundment with relatively stable water level and well-developed littoral vegetation. Between July, 1977, and June, 1987, larval Odonata were sampled monthly by sweep-net from five habitats in the lake. Several lines of evidence developed from these data indicate that this assemblage has a persistent structure, relatively low variabilities of population densities, and is stable. The evidence includes long-term persistence of the dominant taxa, typical standard deviations of the logarithm of population sizes, high and significant year-to-year rank concordance, and few significant correlations of log density with time. Only three species shifted strongly in relative abundance during the ten-year study: *Dromogomphus spinosus* colonized the lake during this period; *Celithemis fasciata* was only abundant during the first two years; and *Tetragoneuria cynosura* declined over the period ($r = -0.81$, $P < 0.01$). Some of the ecological mechanisms underlying the constancy and stability of this odonate assemblage have been identified from diet analyses, laboratory behavior studies, and field enclosure experiments. Prominent among these mechanisms are interference competition (including mutual predation) among larvae, and predation and competition by insectivorous fish.

INTRODUCTION

Ecologists have long been intrigued by the challenge of identifying mechanisms responsible for persistence and stability of natural communities. More recently, the neglected but more fundamental need to assess and measure the persistence and stability of natural communities has become apparent. CONNELL & SOUSA (1983), reviewing the evidence for stability and persistence, emphasized that the necessary long-term density records over at least several generations for two or more species

in a community are rare, especially where the mechanisms of interaction have been demonstrated with field experiments.

In this paper we present a ten-year record of monthly population size estimates for thirteen taxa (including 16 species) that comprise more than 99% of individuals in the odonate assemblage of Bays Mountain Lake. The other 13 species recorded as larvae from Bays Mountain Lake (JOHNSON & CROWLEY, 1980b: tab. I) were encountered so infrequently, especially in the spring samples that we will focus on here, that we lack confidence in estimates of population size; for March/April estimates, the total estimate for all 13 other species averages less than 1% of the total odonate population size. We focus primarily on average population sizes in March and April, just before spring emergence. We consider the year-to-year variability (or constancy, including persistence; see HOLLING, 1973) of these data to reflect the opposing effects of the disturbance regime (i.e., intensities and frequencies of environmental perturbations; see CROWLEY, 1977) and of stability (i.e., resistance, insensitivity to disturbance; and resilience, ability to recover from disturbances; see PIMM, 1984). Following this view, we evaluate the effectiveness of any underlying resistance and resilience in withstanding disturbances via four different measures of year-to-year variability: persistence of taxa within generations, correlations of log population sizes with year, standard deviations of logarithms of population sizes, and a test of population rank-concordance across years. Finally we review evidence from field experiments and laboratory behavior studies that suggest which mechanisms might be responsible for the apparent stability of this assemblage.

Table I

Correlations of \log_{10} abundances (March/April) with year (1978-1987) for larval Odonata of Bays Mountain Lake. Taxa are listed in an order corresponding to their average rank abundance in March/April

Rank	Taxon	r	P*
1	<i>Enallagma traviatum</i>	- 0.19	n.s.
2	<i>Enallagma signatum</i>	- 0.53	n.s.
3	<i>Tetragoneuria cynosura</i>	- 0.81	< 0.01
4	<i>Celithemis elisa</i>	+ 0.29	n.s.
5	<i>Enallagma divagans</i>	- 0.50	n.s.
6	<i>Ischnura posita</i> & <i>I. verticalis</i>	+ 0.65	< 0.05
7	<i>Libellula luctuosa</i> & <i>L. incesta</i>	- 0.42	n.s.
8	<i>Enallagma basidens</i>	+ 0.13	n.s.
9	<i>Celithemis fasciata</i>	- 0.66	< 0.05
10	<i>Dromogomphus spinosus</i>	+ 0.70	< 0.05
11	<i>Argia fumipennis violacea</i>	+ 0.34	n.s.
12	<i>Macromia alleghaniensis</i> & <i>Didymops transversa</i>	- 0.65	< 0.05
13	<i>Lestes vigilax</i>	+ 0.39	n.s.

* Note that the Dunn-Sidak correction for multiple comparisons, $\alpha' = 1 - (1 - \alpha)^{1/k}$, where k is the number of comparisons (i.e., 13) would require $\alpha' = 0.004$ for individual taxa to insure an overall $\alpha = 0.05$. By this conservative criterion, none of the observed correlations would be considered significant (URY, 1976).

STUDY AREA

Since 1977, we and our students have been studying the lentic littoral zone communities of Bays Mountain Park (City of Kingsport, Sullivan County, Tennessee, USA ; 82° 37'W, 36° 31'N), with a particular emphasis on ecological relationships of the dominant macroinvertebrate predators, larval Odonata. Bays Mountain Lake is a 15 ha shallow eutrophic impoundment in a forested watershed at 550 m elevation. It was formed by construction of a dam in 1916, drained and re-filled during 1966-1967, stocked with fish (notably bluegill sunfish, *Lepomis macrochirus*, redear sunfish, *L. microlophus*, and largemouth bass, *Micropterus salmoides* (Osteichthyes : Centrarchidae)) in 1968, and fertilized to enhance fish production during 1969-1974. During this study the lake has been dimictic, with ice cover for at least one month each winter, and an anoxic hypolimnion (below 4 m) by mid-summer.

The spillway-type dam stabilizes the water level and has facilitated the development of littoral vegetation, especially submersed macrophytes (*Najas flexilis* and *Vallisneria americana*), emergent rushes (*Eleocharis quadrangulata* and *E. ovata*), and floating-leaved lotus (*Nelumbo lutea*). Other littoral habitats include extensive allochthonous detritus along certain shores, and small sand deposits near the mouths of two inlet streams. JOHNSON & CROWLEY (1980b) present a map of Bays Mountain Lake and estimates of the area covered by each littoral habitat type. These areas have changed little during the study.

A total of 46 species of Odonata have been reported from Bays Mountain Park (JOHNSON *et al.*, 1980), and 35 of these have been identified as larvae in monthly sweep-net collections (JOHNSON & CROWLEY, 1980b), including 28 from Bays Mountain Lake. Recent larval collections have added another species to these totals, *Didymops transversa* (Anisoptera : Macromiidae), small specimens of which may have been confused with *Macromia alleghaniensis* in earlier collections (K. J. TENNESSEN, pers. comm.).

METHODS

In July, 1977, we established 9 permanent sampling stations in Bays Mountain Lake : one for floating-leaved lotus, and two for each of the other four habitats. A second lotus station was added in July, 1980, and two more submersed-macrophyte stations in July, 1982. Since July, 1977, one standard 1-m sweep-net sample (0.33 m²) has been collected from each station near the middle of each month (except December, 1982, and January and February of most years). Samples were searched in the field, and all odonate larvae were preserved in 70% alcohol, measured (headwidth), and identified to the lowest feasible taxon using a dissecting microscope, available keys (especially WESTFALL, 1984), and reference collections. Because of uncertainty in the identification of early instars, the following taxa have been combined for this analysis : *Ischnura verticalis* and *I. posita* ; *Libellula luctuosa* and *L. incesta* ; and *Macromia alleghaniensis* and *Didymops transversa*.

The population size of each taxon in Bays Mountain Lake was estimated monthly by (1) obtaining the mean number of larvae per sweep for each habitat, (2) multiplying by 3 to

estimate mean number per m², (3) multiplying by the area covered by a given habitat (JOHNSON & CROWLEY, 1980b: tab. I), and (4) summing these products over all five habitats. Each monthly estimate is based on 9 (1977-1980), 10 (1980-1982) or 12 (1982-1987) sweep-net samples. These calculations differ only slightly from those in previous analyses of parts of this data set (see JOHNSON & CROWLEY, 1980b; CROWLEY & JOHNSON, 1982a; JOHNSON, 1986).

The persistence of populations within this odonate assemblage was determined by direct application of CONNELL & SOUSA's (1983) definition of persistence, which requires that the population be present except possibly for intermittent periods not exceeding one generation.

To evaluate year-to-year constancy of population sizes and relative abundances, we focused on data from March and April of each year. This is a time of year, just prior to the onset of adult emergence, when population estimates are relatively unaffected by year-to-year variance in the magnitude and timing of recruitment, when most individuals have already survived through the vulnerable early instars, when most are large enough to be identified with confidence, and when population size is not changing dramatically. To further reduce the variance due to sampling error, we used averages of the March and April estimates in the stability analysis and in Figure 3. To determine whether there were significant trends of abundance through time, we calculated correlations of the logarithm of average population size versus year.

Following CONNELL & SOUSA (1983), we used the standard deviation of the logarithms (base 10) of March/April population estimates ($1 + N \times 10^{-3}$) separated by at least the length of a generation to measure variability of population size and to permit comparisons with variabilities of other natural populations. For populations with univoltine (annual) life cycles (most of the taxa in our study; see JOHNSON *et al.*, 1980; JOHNSON & CROWLEY, 1980b), these calculations were straightforward. For the three that are at least predominantly semivoltine – *Tetragoneuria cynosura*, *Dromogomphus spinosus*, and *Macromia alleghaniensis* – separate standard deviations were calculated from years 1, 3, 5, 7, and 9 and from years 2, 4, 6, 8, and 10, and the two were averaged.

A stable community should tend to maintain a relatively consistent pattern of relative abundances of taxa through time, an expression of persistent structure (GROSSMAN, 1982; GROSSMAN *et al.*, 1982). Though Kendall's rank concordance test (DANIEL, 1978) and the interpretation of results it generates has led to some confusion and debate in the recent ecological literature (e.g., GROSSMAN *et al.*, 1985), this approach does permit a straightforward test of the persistent-structure prediction. We calculated the rank-concordance coefficient *W* and evaluated its statistical significance to compare rank structure of our 13 dominant taxa across the ten years of March-April data.

RESULTS

Larval population estimates for 13 odonate taxa, based on 9-12 monthly sweep-net samples from five littoral-zone habitats in Bays Mountain Lake, are presented in Figures 1-13. Note that most taxa (10 of 13) have been recorded in these samples during all ten consecutive years of this study; the other three (*Celithemis fasciata*, Fig. 9; *Dromogomphus spinosus*, Fig. 10; and *Lestes vigilax*, Fig. 13) have been recorded in nine of the ten years. The status of two populations has changed dramatically: *Celithemis fasciata* was abundant during the first two years, but has been very rare since July, 1979 (Fig. 9); and *Dromogomphus spinosus* was quite rare (or absent) during the first few years, but has become relatively abundant in the last five years (Fig. 10). But since low-density populations might

occasionally fail to be sampled by chance alone, the temporal patterns of abundance do not assure that any of these populations was completely absent from Bays Mountain Lake at any time during this period. Overall the larval odonate assemblage of Bays Mountain Lake can be considered persistent : it is composed of essentially the same set of species year after year, with no species absent for longer than one generation (CONNELL & SOUSA, 1983).

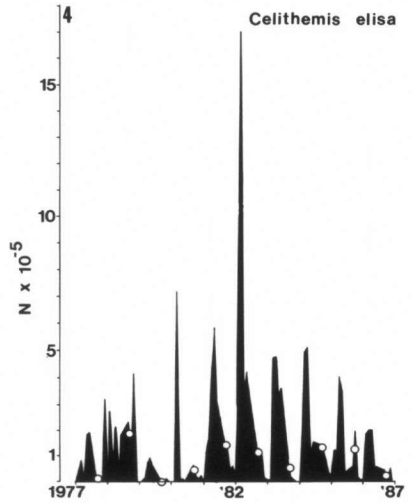
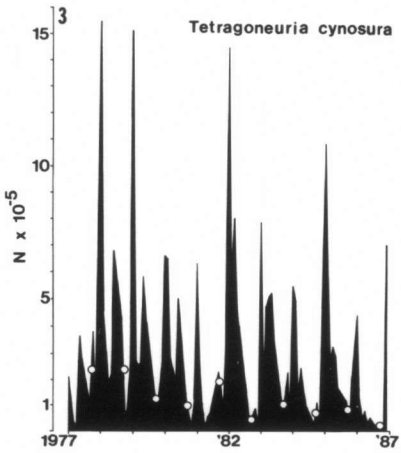
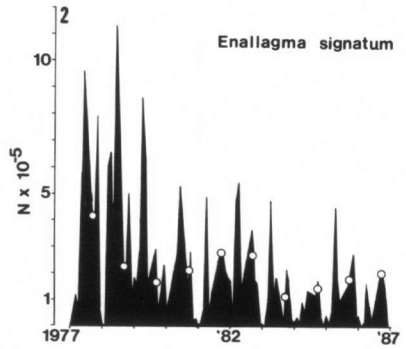
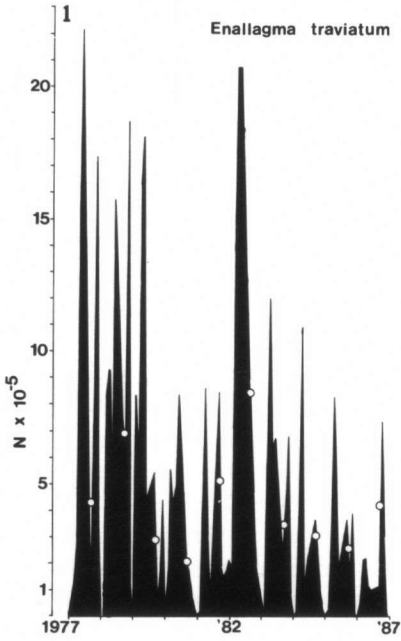
Most of these taxa (8 of 13) show no apparent trend of abundance with time (Tab. I). If critical values of α are corrected for the effects of multiple comparisons using the Dunn-Sidak method (URY, 1986), none of the 13 correlations are significant. But, considered one at a time, 5 are significant. They include populations whose changing patterns of abundance were apparent above (*Celithemis fasciata* and *Dromogomphus spinosus*), as well as *Ischnura* (increasing, Fig. 6), the macromiids (decreasing, Fig. 12) and *Tetragoneuria cynosura* (decreasing, Fig. 3).

Figure 14 compares the standard deviations of logarithms of odonate population sizes separated by one generation to the frequency distribution reported by CONNELL & SOUSA (1983 : fig. 1A). These taxa exhibit generation-to-generation variability in population size typical of the populations reviewed by CONNELL and SOUSA [$X^2_g = 5.37$, $P > 0.10$]. The two that were most variable, *Celithemis fasciata* and *Dromogomphus spinosus*, have clearly changed their status within this assemblage as discussed above and represent exceptions to the overall stable pattern. Another two, *Macromia alleghaniensis* and *Lestes vigilax* are also the least abundant of the taxa included in this study ; their populations would therefore have experienced greater demographic variability, and estimates of their population sizes may have been subject to more sampling error as well.

There is highly significant concordance of ranks for relative abundance (Figure 15 ; KENDALL'S $W = 0.753$, $P < 0.001$). Thus the larval odonate assemblage within Bays Mountain Lake retains detectably persistent rank structure, despite the undoubted importance of environmental disturbance.

DISCUSSION

Our analysis suggests that the larval odonate assemblage of Bays Mountain Lake meets some objective criteria for persistence and stability. The same 13 taxa, comprising more than 99% of individuals in this assemblage, were present in at least nine of the ten years (Figs 1-13). Their population sizes exhibit generation-to-generation variability (Fig. 14) that is comparable to that of the populations reviewed by CONNELL & SOUSA (1983). Two populations have experienced dramatic status changes during this ten-year study (Figs 9 & 10) ; but correlations between population size and time, when corrected for multiple comparisons, yielded no significant temporal trends (Tab. I). Furthermore, these relatively stable populations form an assemblage with a highly concordant structure of ranked abundances among years (KENDALL'S $W = 0.753$), a value for concordance that is among the highest published for aquatic assemblages (Tab. II).



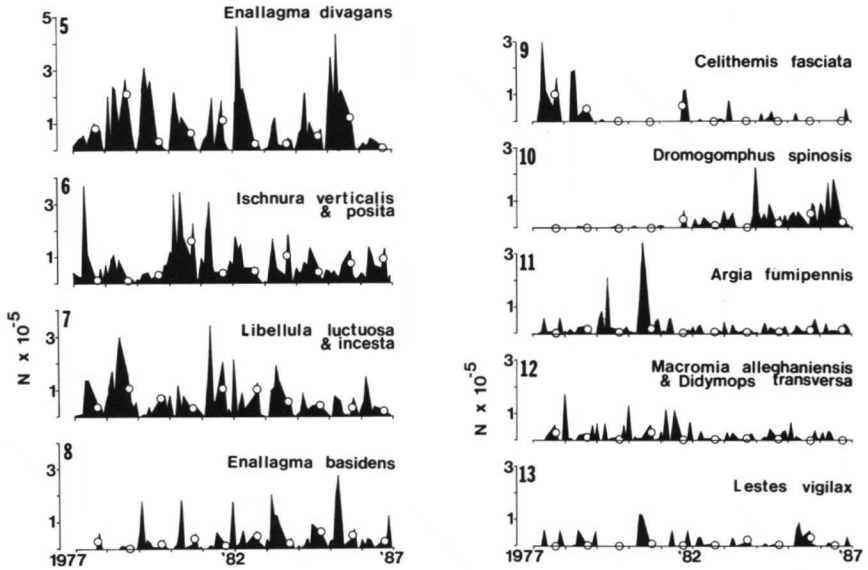


Fig. 1-13. Monthly estimates of larval population sizes in Bays Mountain Lake for each of thirteen odonate taxa, July 1977 through June 1987. Circles indicate the average of March and April estimates for each year. Figure numbers correspond to the ten-year means of rank abundance in March/April.

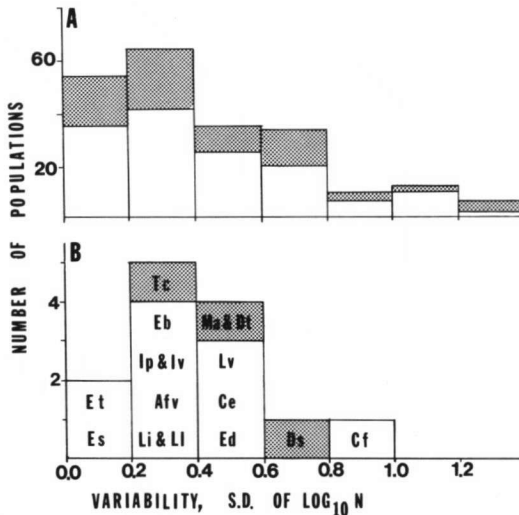


Fig. 14. Comparison of generation-to-generation variability in population size for (B) the odonate taxa of Bays Mountain Lake (March/April, 1978-1987) with (A) the set of populations reviewed by CONNELL & SOUSA (1983). Shading indicates species with life cycles greater than one year.

Table II
 Concordance of rank abundance through time for taxa comprising certain aquatic assemblages

KENDALL'S W	P	Assemblage	Taxa	Samples	Years	Reference
0.831	< 0.001	desert stream fish (lower)	7	14	14	(MEFFE & MINCKLEY, 1987)
0.816	< 0.05	coral reef fish	42	16	2	(TALBOT <i>et al.</i> , 1978)
0.775	< 0.01	desert stream benthos (summer)	12	3	3	(MEFFE & MINCKLEY, 1987)
0.757	< 0.01	desert stream benthos (spring)	12	4	4	(MEFFE & MINCKLEY, 1987)
0.753	< 0.001	lake dragonflies (spring)	13	10	10	(this study)
0.709	< 0.025	desert stream benthos (fall)	12	3	3	(MEFFE & MINCKLEY, 1987)
0.705	< 0.001	desert stream fish (canyon)	7	14	14	(MEFFE & MINCKLEY, 1987)
0.678	< 0.001	'major' stream fish (spring)	18	4	12	(YANT <i>et al.</i> , 1984) *
0.677	< 0.005	marine copepods	30	7	9	(MCGOWAN & WALKER, 1985)
0.634	< 0.001	desert stream fish (upper)	7	12	12	(MEFFE & MINCKLEY, 1987)
0.632	< 0.005	desert stream benthos (winter)	12	4	4	(MEFFE & MINCKLEY, 1987)
0.612	< 0.001	rocky intertidal fish	9	13	2	(GROSSMAN, 1982)
0.327	< 0.01	'resident' stream fish (fall)	9	12	12	(HERBOLD, 1984) *
0.121	n.s.	'Abundant' stream fish (fall)	10	12	12	(GROSSMAN <i>et al.</i> , 1982) *
0.090	n.s.	'opportunistic' stream fish (fall)	6	12	12	(HERBOLD, 1984) *

* alternate interpretations for the same assemblage.

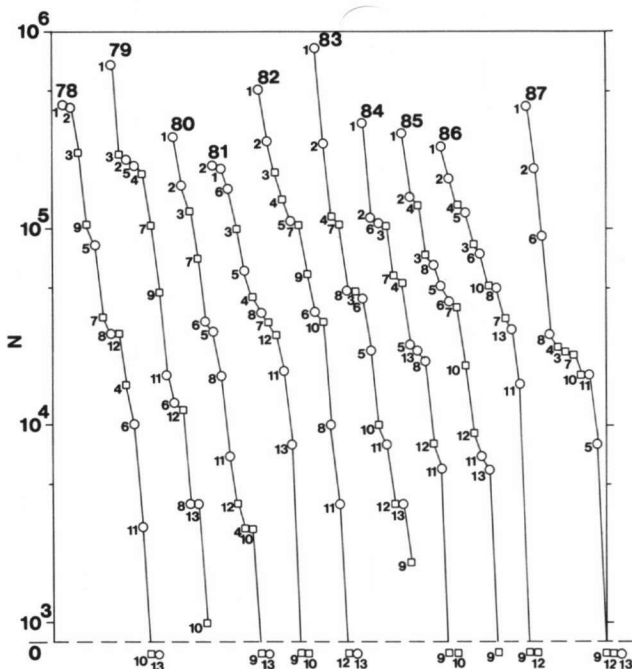


Fig. 15. Dominance-diversity curves show the larval population size (log scale) of each odonate taxon for March/April of each year, 1978-1987. Zygoptera are represented by circles ; Anisoptera, by squares. Taxa are identified by numbers corresponding to their ten-year mean ranks as in Figures 1-13.

In light of the evidence for persistence and stability presented above, what mechanisms may account for the observed stability of this assemblage? In the remainder of the paper, we summarize results of recent studies that provide some answers to this question and conclude with a diagrammatic conception of how the mechanisms fit together.

Three findings from descriptive field studies (JOHNSON *et al.*, 1980 ; JOHNSON & CROWLEY, 1980a, 1980b ; CROWLEY & JOHNSON, 1982 ; MERRILL & JOHNSON, 1984) are particularly relevant to this discussion. (1) The odonate assemblage of fish-free Ecology Pond is distinctly different from that coexisting with insectivorous fish in Bays Mountain Lake ; but the odonates capable of coexisting with fish may nonetheless be strongly influenced by fish predation. (2) There is broad overlap in habitat, season, and diet among the dominant populations of Bays Mountain Lake (i.e., *Enallagma traviatum*, *E. signatum*, *E. divagans*, *Tetragoneuria cynosura* and *Celithemis elisa*) ; thus one might expect intense competition within this guild if resources were both limiting and depletable. (3) Mutual predation is an important phenomenon among (and within) the dominant anisopteran populations.

Figure 16 shows the 'strong' links (PAINE, 1980) in the food-web for the littoral zone of Bays Mountain Lake based on diet studies (WATSON, 1985 ; BOHANAN & JOHNSON, 1983 ; MOORE, 1985 ; MARTIN, 1986) as well as field enclosure experiments (BOHANAN & JOHNSON, 1983 ; CROWLEY *et al.*, 1987a ; JOHNSON *et al.*, 1984, 1985, 1987 ; PIERCE *et al.*, 1985 ; T. H. MARTIN, pers. comm.). Note that there is broad overlap in the diets of tanypodine midges, larval odonates, and small sunfish. These taxa may be expected to experience exploitation competition, if the availability of prey resources were ever limiting and at least locally depletable by the odonates. From the perspective of odonate populations, it is possible that competition with small sunfish may be as important as predation by large sunfish. JOHNSON (1986) used an eight-year record of size-frequency distributions from monthly sweep-net data to suggest that *Tetragoneuria cynosura* experiences very high mortality between mid-July and mid-August, a period when they appear to be especially vulnerable to predation by larger dragonfly larvae, including conspecifics (MERRILL & JOHNSON, 1984), and by large redear sunfish (MARTIN, 1986).

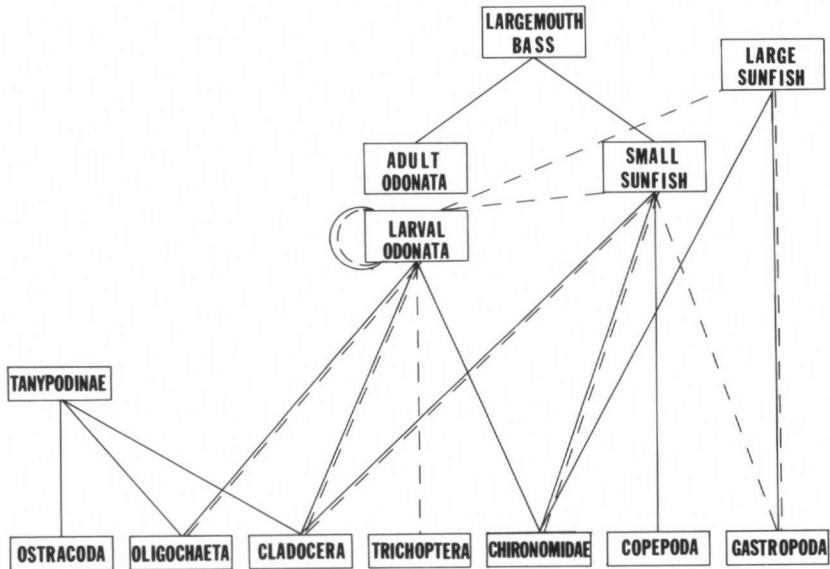


Fig. 16. Strong links in the food web of the littoral zone of Bays Mountain Lake. Solid lines indicate prey comprising at least 10% of the diet of predators (BOHANAN & JOHNSON, 1983 ; MERRILL & JOHNSON, 1984 ; MOORE, 1985 ; WATSON, 1985 ; MARTIN, 1986 ; and some unpublished studies). Dashed lines indicate statistically significant depletion of prey populations by natural densities of predators in *in situ* enclosure/exclosure experiments (BOHANAN & JOHNSON, 1983 ; CROWLEY *et al.*, 1987a ; JOHNSON *et al.*, 1984, 1985, 1987 ; PIERCE *et al.*, 1985 ; MARTIN, pers. comm.).

A series of *in situ* enclosure experiments designed to detect both intraspecific and interspecific competition among larval odonate populations at approximately natural biomass densities (CROWLEY *et al.*, 1983; JOHNSON *et al.*, 1984, 1985; PIERCE *et al.*, 1985) found that exploitation competition was not an important phenomenon within the enclosures. A combined analysis of the evidence for prey depletion from the four published experiments (JOHNSON *et al.*, 1987) suggests that odonate predation resulted in prey population depletion for only three taxa (oligochaetes, large cladocerans, and small trichopteran larvae; see Figure 16), representing only one-third of the biomass in typical odonate diets.

These odonate competition experiments have detected some interference competition. In one experiment (JOHNSON *et al.*, 1985), conducted in September 1981, there was clear-cut evidence that smaller larvae of both *Tetragoneuria cynosura* and *Celithemis elisa* suffered density-dependent mortality attributable to predation by larger size-classes of the same species. Intraspecific predation was at least as intense as that between species. In two other experiments involving damselfly (*Enallagma*) larvae (JOHNSON *et al.*, 1984; PIERCE *et al.*, 1985) interference effects were detected for one of each pair of species; the effects were more subtle — changes in individuals' mass for a given head-width.

A set of three field enclosure experiments conducted during the summer of 1984, focused on the effects of interference among and within year-classes of the semivoltine *Tetragoneuria* population (CROWLEY *et al.*, 1987a). The results of these experiments not only reiterated the importance of predation on small larvae by larger conspecifics, but also suggested that 'feeding interference' is an important phenomenon among the larger larvae. Together with laboratory behavior studies to be described below, these field experiments have tended to strengthen our inference (Fig. 17), based originally on diet analyses, that aggressive interactions among odonate larvae can strongly influence larval odonate assemblages (cf., BENKE, 1978; BENKE *et al.*, 1982; ROBINSON & WELLBORN, 1987; but see BAKER, 1986).

Other field experiments have focused on the interaction between larval odonates and sunfish. The first of these was a simple fish-exclusion experiment, conducted in the spring of 1980 (BOHANAN & JOHNSON, 1983). It did not find any influence of fish predation on odonate densities, probably because the three-month experiment did not include the odonate-recruitment season. But it did provide evidence that sunfish predation, attributed to the small size-class that frequents the shallow habitats studied, could significantly reduce the densities of some important odonate prey — chironomid midge larvae, and chydorid cladocerans.

An *in situ* enclosure experiment (MOORE, 1985) explicitly designed to detect competition between small sunfish and two year-classes of *Tetragoneuria cynosura* found that fish depletion of dragonfly prey resources may inhibit dragonfly growth. Moreover, the first-year-class *Tetragoneuria* suffered significantly higher mortality when enclosed with *both* larger dragonflies *and* small fish (45% survival) than with either separately (76% and 73% respectively) or with neither (72%). Since the

dragonflies that died were too large to have been eaten by these very small fish, we attribute this result to an indirect effect of fish on dragonfly behavior and distribution.

As field diet data (MERRILL & JOHNSON, 1984) provided evidence of broad diet overlap and mutual predation among larvae, and our field enclosure experiments failed to detect exploitation competition (JOHNSON *et al.*, 1984, 1985 ; PIERCE *et al.*, 1985 ; JOHNSON *et al.*, 1987), we focused on interference and aggressive encounters among odonates in the laboratory. Experiments with different size-classes of mid- to late-instar *Ischnura* (MCPEEK & CROWLEY, 1987 ; CROWLEY *et al.*, 1988) suggests that interference competition may cause larval feeding inhibition largely attributable to a reduction in search time due to the time spent monitoring the activity of other larvae. And a study of first-year-class *Tetragoneuria* behavior in the presence and absence of larger conspecifics (CROWLEY *et al.*, 1987a) found that the small larvae tend to 'freeze' in the presence of large ones, especially under visible light.

A comparison (PIERCE *et al.*, 1985) of the behavior of the dominant damselfly species in fish-free Ecology Pond (*Enallagma aspersum*) and Bays Mountain Lake (*Enallagma traviatum*) tested hypotheses based on observed differences between the species composition of the odonate assemblages of these two locations (JOHNSON & CROWLEY, 1980a). As predicted, the species that coexists with fish in the lake moved less often and was better hidden by the substrate under daylight conditions. These behaviors were also associated with less vulnerability to fish predation. However, the field enclosure experiment designed to test the further hypothesis that the more active species would be more successful in competition in the absence of fish predation did not have the expected result — instead of winning a 'scramble' for resources, the more active *E. aspersum* seem to have suffered from more interference competition due to more frequent encounters.

Preliminary results of *in situ* enclosure experiments in progress (T. H. MARTIN, pers. comm.) suggest that competition and/or predation by small sunfish may have an important effect on both the population density and individual growth rates of the first-year-class of *Tetragoneuria* during summer recruitment ; and that predation by large sunfish reduces survival of the larger size-classes of dragonflies. A second experiment currently underway using large enclosures (2.6 m²) shows that *Tetragoneuria* life-history is influenced by density-dependent phenomena : In enclosures without second-year-class dragonfly larvae, about half of the first-year-class individuals surviving to September from the high-egg-density treatments were in intermediate instars characteristic of a semivoltine life-history ; but all of those from the low-egg-density treatments had attained the penultimate instar and would be expected to complete univoltine life-histories. This result suggests that density-dependent interactions within the cohort (probably 'feeding interference') is a very important phenomenon. Behavioral observations on first-year-class larvae are planned to elucidate the mechanism responsible.

In Figure 17, we illustrate the effects of ecological phenomena observed for odonate larvae at Bays Mountain Lake on the dynamics of an individual odonate

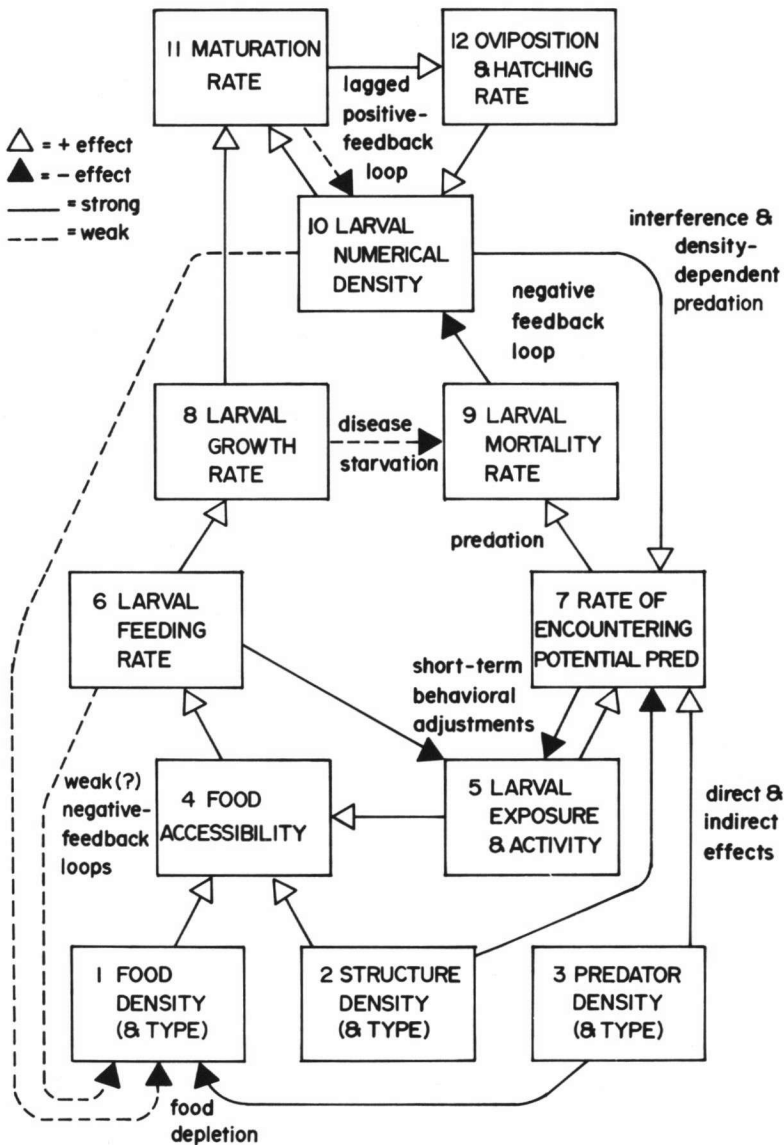


Fig. 17. Hypothetical interactions among vital rates and other factors determining the dynamics of odonate populations. Open arrowheads indicate positive feedbacks ; solid arrowheads, negative feedback. Solid lines indicate what we consider to be strong effects ; dashed lines, weak effects. Potentially important feedback loops are discussed in the text.

population. The interactions among vital rates and other factors influencing odonate population dynamics generate negative feedback loops that may account for the observed stability and persistence of these populations, despite environmental disturbances. The lagged positive feedback loop 10-11-12 is constrained by a larval negative feedback loop 7-9-10 that results from intraspecific interference, density-dependent predation, or both (CROWLEY *et al.*, 1987b). The absence of consistent food depletion (JOHNSON *et al.*, 1987) weakens the impact of negative feedback loops based on intraspecific food exploitation (e.g., 1-4-6 and 1-4-6-8-11-12-10), but fish may substantially deplete the odonate food supply (e.g., see HALL *et al.*, 1970).

Odonate larvae may trade off feeding rate against better concealment from predators by adjusting their spatial distribution and movements (HEADS, 1986); these short-term behavioral adjustments generate two other negative feedback loops, 5-4-6 and 5-7. Larval growth rate and mortality rate interact to determine maturation rate, presumably a close correlate of fitness in these species (e.g., see FINCKE, 1982). Thus some species seem to have evolved to maximize maturation rate by enhancing growth, despite a high potential mortality cost when predators are present (the "fast life-style" of SIH (1986)); others seem to have evolved to maximize maturation rate by effectively avoiding predators at the expense of slow growth (the "slow life-style" of SIH, 1986; see JOHNSON & CROWLEY, 1980a).

Much work remains before we can hope to achieve a thorough understanding of the mechanisms responsible for the apparent stability and persistence of the larval odonate assemblage at Bays Mountain Lake, or of comparable assemblages elsewhere. For example, a neglected but important part of an empirical stability analysis is characterizing the disturbance regime and the resistance to disturbances inherent in the assemblage. Major sources of year-to-year variation in larval density may include shifts in density or age-structure of predators and of prey populations; seasonal weather effects on flight season, ice cover, macrophyte density and water temperature; and effects of parasites and diseases. Because the resistance of a population to a given disturbance may reflect interactions among many inherent and environmental factors, the ecological "dose-response" relationship associated with a disturbance regime should prove very difficult to characterize. Manipulative field experiments seem to offer the best hope of measuring resistance and resilience to disturbances of known time and magnitude. These and sensitivity analyses of relatively realistic computer models (e.g., CROWLEY *et al.*, 1987b) may help identify the most ecologically important types of disturbance from the above list, and long-term monitoring of the factors responsible may then permit at least rough quantitative predictions of the resulting dynamics.

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