COEXISTENCE OF *ENALLAGMA DIVAGANS* AND ENALLAGMA TRAVIATUM (ZYGOPTERA : COENAGRIONIDAE) IN BAYS MOUNTAIN LAKE, TENNESSEE: AN *IN SITU* ENCLOSURE EXPERIMENT

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Enallagma divagans and *E. traviatum* coexist as larvae in Bays Mountain Lake (City of Kingsport, Sullivan County, Tennessee) where they are among the most abundant odonate populations in allochthonous detritus habitats. An *in situ* enclosure experiment, designed to detect both intraspecific and interspecific competition among larvae at approximately natural densities and size-distributions, was conducted during April 1982. *E. divagans* larvae experienced significantly better survival and biomass increases than *E. traviatum* during the one-month experiment, but neither response was density-dependent. The mean "condition" (the ratio of individual larval mass to the mass predicted by a regression of ln (mass) on ln (head width) for all individuals of each species measured during the experiment) of individual *E. divagans* larvae was density-dependent, with interspecific effects at least as important as intraspecific ones.

Fecal pellet analyses detected considerable dietary overlap and little evidence of resource partitioning among the surviving larvae; yet there was no evidence of exploitation competition. Only one of the principal prey populations (oligochaetes) was significantly reduced in the presence of damselflies compared to control enclosures. The density-dependent "condition" of individual *E. divagans* may be attributable to some form of interference competition.

INTRODUCTION

Odonate populations in eastern North America form diverse assemblages with an average of 25 species in the best-studied sites (CROWLEY & JOHNSON,

1982b). In an effort to understand the mechanisms facilitating coexistence in such assemblages, we have been studying the Odonata of Bays Mountain Park (City of Kingsport, Sullivan County, Tennessee) since 1977. Three species of *Enallagma* (Zygoptera : Coenagrionidae) — *E. traviatum*, *E. signatum*, and *E. divagans* — rank among the 6 most abundant populations of odonate larvae in Bays Mountain Lake (JOHNSON & CROWLEY, 1980a, Fig. 3). These species utilize similar habitats. Over 90% of their populations are found in submersed macrophyte or allochthonous detritus (JOHNSON & CROWLEY, 1980a, Table 1), with the greater densities in the latter habitat (JOHNSON & CROWLEY, 1980a, Fig. 2). Seasonal segregation of life histories (JOHNSON *et al.*, 1980, Fig. 1; JOHNSON & CROWLEY, 1980a, Fig. 4) could reduce niche overlap between *E. divagans*, a typical "spring" species (*sensu* CORBET, 1954), and the other 2 (*cf.* HUTCHINSON, 1959; JOHANNSSON, 1978; JOHNSON & CROWLEY, 1980b).

This paper will focus on the interaction of *E. divagans* with *E. traviatum*, the most abundant odonate population in Bays Mountain Lake. Despite the fact that *E. divagans* was an average of two instars larger than *E. traviatum* throughout most of the year, CROWLEY & JOHNSON (1982a) found that niche overlap on 2 dimensions (habitat and seasonality) was not less than overlap on habitat alone. Nevertheless, competition coefficients calculated from the 2-dimensional overlap indices were both less than 1.0, suggesting that the 2 species might coexist at equilibrium despite exploitation competition (HUTCHINSON, 1978).

The experiment reported in this paper, involving *Enallagma divagans* and *E. traviatum*, is one of several which have been conducted during the last 2 years in an effort to determine the importance of competition within the larval odonate assemblage in Bays Mountain Lake (PIERCE, 1982; PIERCE *et al.*, in press; JOHNSON *et al.*, 1985). It is designed to detect both intraspecific and interspecific competition at approximately natural densities with natural substrate and prey. Such experiments should help to clarify the relative importance of exploitation competition, interference competition, and predation as phenomena influencing the species composition and stability of this odonate assemblage (SCHOENER, 1983; CONNELL, 1983).

MATERIALS & METHODS

Experimental enclosures, described in detail elsewhere (CROWLEY *et al.*, 1983), were cylinders of nylon netting (mesh size 0.5 mm) 30 cm high with clear plastic dishes (area 324 cm^2) sealing the bottom. Enclosures were tied to stakes in shallow water (*ca.* 0.2 m depth) so that their open tops protruded above the surface. Substrate collected from dishes buried in allochthonous detritus for several days was placed into each enclosure after carefully removing all odonate larvae, but retaining potential prey populations. One group of 6 enclosures was placed in each of 3 detritus locations within Bays Mountain Lake during 22-24

March 1982. Three randomly selected samples of the substrate were preserved immediately to estimate initial densities of macrobenthic populations. Inverted-funnel samplers (*cf.* BRAKKE, 1976) placed overnight in 3 randomly selected larger enclosures (part of a separate experiment being run concurrently; see JOHNSON *et al.*, 1985) were used to estimate initial densities of microcrustacea and water mites. One dish was buried in each location to be sampled as an unenclosed "final open dish" at the conclusion of the experiment.

Enallagma larvae removed from enclosure substrate, and others collected by sweep-net in Bays Mountain Lake, were sorted into species and instar categories based on caudal gill morphology and head width measurements (P.H. CROWLEY, unpublished data). These were used to compose 15 nearly identical "doses" of each species which approximated ambient size-frequency distributions and had a total estimated "biomass" (sum of cubed head widths, see CROWLEY & JOHNSON, 1982a) approximately equal to half of that characteristic of the entire odonate assemblage for this habitat and season (from quantitative samples for April 1980, D.M. JOHNSON, unpublished data). Three randomly selected doses of each species were preserved immediately in 70% alcohol to provide estimates of actual initial biomasses (Table I). The others were randomly assigned to certain treatment combinations: single doses of *E. divagans* (Ed) or *E. traviatum* (Et) representing approximately half natural odonate biomass densities; and double doses of each species (EdEd and EtEt) or one of each species (EdEt) representing approximately natural odonate biomass densities. Odonates were not added to control enclosures (C). Each treatment was introduced to a randomly selected enclosure at each location during 24-25 March 1982.

Table I

Characteristics of larval "doses" used to establish initial odonate treatments. Means and standard errors based on 3 samples. The pooled mean was used as the estimate of initial biomass of both "doses".

Dose	Species	Number	Mean dry weight (mg)	Pooled mean (mg)
Ed	*E. divagans*	9 ± 0	14.26 ± 0.91	
				13.85
Et	*E. traviatum*	25 ± 0	13.44 ± 1.00	

The experiment was terminated during 29 April-1 May 1982, approximately 1 month after it began. On the afternoon preceding termination for each enclosure (or open dish), an inverted-funnel sampler (*cf.* BRAKKE, 1976), composed of two 7.5 cm diameter long-neck glass funnels attached to 60 ml collecting bottles by rubber stoppers, was placed on the substrate. Samplers were removed the following morning, and their contents concentrated and preserved in 70% alcohol. These samples were used to determine the density of microcrustaceans and water mites (see WHITESIDE & LINDEGAARD, 1980).

The enclosure was lifted slowly from the water and placed into a large metal tub. Open dishes were surrounded by nylon cylinders before lifting. Most odonate larvae were removed from the substrate and isolated in separate containers for collection of fecal pellets. The substrate was then preserved with formalin and returned to the laboratory where it was washed using 0.5 mm mesh screens and sorted by sugar flotation (ANDERSON, 1959). A complete census was made of all macrobenthic taxa recovered from each enclosure.

The response of benthic populations to experimental treatment was evaluated using analyses of variance and single degree of freedom orthogonal contrasts on log-transformed data ($y' = \ln (y + 1)$). Orthogonal contrasts were designed to detect temporal effects (Initial $<>$ Final, Control, Ed, EdEd, EdEt, EtEt, Et), enclosure effects (F $<>$ C, Ed, EdEd, EdEt, EtEt, Et), prey depletion (C $>$ Ed, EdEd, EdEt, EtEt, Et), odonate density effects (Ed, Et $>$ EdEd, EdEt, EtEt), odonate species effects (Ed, EdEd $<>$ Et, EtEt), and differences between the response to single-species and combined species predation (EdEt $>$ EdEd, EtEt). The statistical significance of contrasts for which the direction of the difference was predicted *a priori* were evaluated using one-tailed probability distributions.

Odonate larvae recovered by sugar flotation, as well as those removed for fecal pellet collection, were identified to species, measured (head width), and then dried to constant weight at 60°C. These data provide 3 measures of the response of odonates to experimental treatments: *Survival*, the proportion of introduced larvae of each species which survived to be recovered within each enclosure; *Biomass*, the ratio of final biomass of larvae of each species to the initial biomass introduced (Table I); and *Condition*, the ratio of individual larval mass to the mass predicted by a regression of ln (mass) on ln (head width) for all individuals of each species measured during the experiment (*E. divagans*, ln (mass) = 4.071 ln (head width) - 3.340; *E. traviatum*, ln (mass) = 2.271 ln (head width) -1.745).

Each variable was subjected to an analysis of variance and single degree of freedom orthogonal contrasts using the General Linear Model Procedures of the Statistical Analysis System (HELWIG & COUNCIL, 1979). (For the treatment with both species present, we will indicate which species' response we are discussing by listing it first — EdEt or EtEd). Orthogonal contrasts were designed to detect species effects (Ed, EdEd, EdEt $<>$ Et, EtEt, EtEd), density-dependence (Ed $>$ EdEd, EdEt and Et $>$ EtEt, EtEd), and differences between intraspecific and interspecific crowding (EdEt $>$ EdEd and EtEd $>$ EtEt). The statistical significance of effects for which the direction of difference was predicted *a priori* was evaluated with one-tailed probability distributions.

Fecal pellets produced by larvae collected at the end of the experiment were spread apart in mounting medium on microscope slides. They were scanned at 160X with a compound microscope, and prey fragments identified to the lowest taxon possible. The number of each taxon eaten was taken to be the minimum required to account for observed fragments. If any oligochaete chaetae were

identified we made the conservative assumption that only 1 individual had been eaten.

RESULTS

Comparison of initial and final instar-frequency distributions (Fig. 1) suggests that most damselfly larvae survived and molted at least once during the month-long experiment. Orthogonal contrasts (Table II) found that, when averaged over all treatments, the *Enallagma divagans* larvae had better survival (90%) than *E. traviatum* (76%). Inspection of Fig. 1 suggests that many of the *E. traviatum* that died were among the smaller instars introduced. Survival was not significantly density-dependent for either species (Table II).
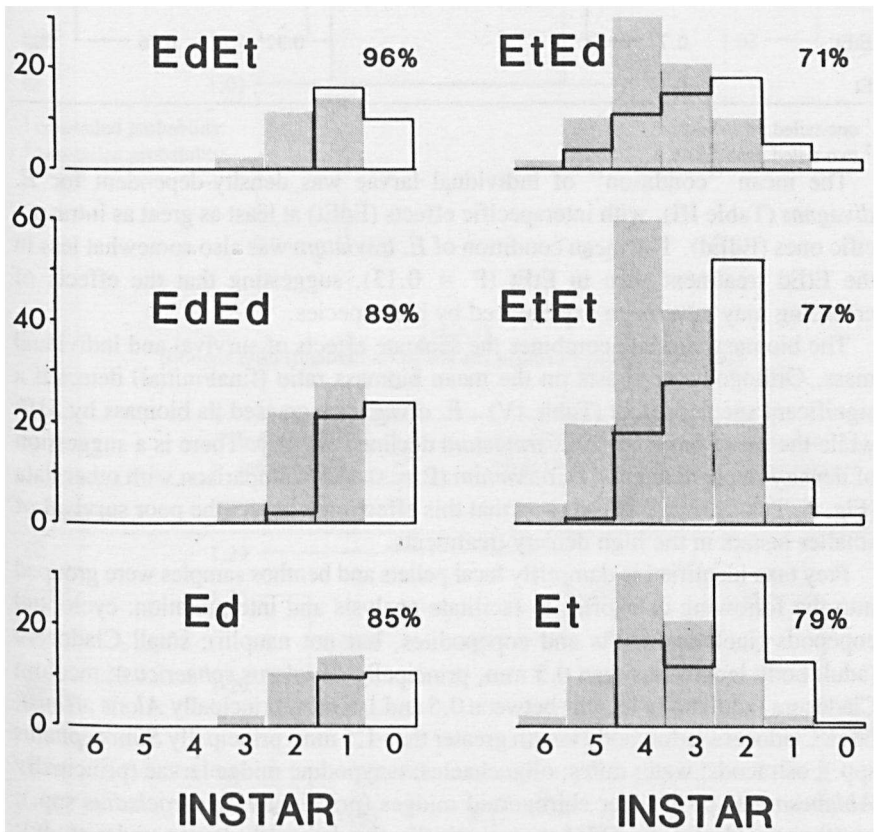

Fig. 1. A comparison of initial (shaded) and final (solid lines) larval instar-frequency distributions for *Enallagma divagans* (left) and *E. traviatum* (right) subjected to various odonate treatments. The mean percentage surviving the 1 month experiment in each treatment is indicated. Numbers are sums of data from 3 replicates of each treatment. Instars are numbered in reverse order (O = ultimate, 1 = penultimate, *etc.*).

Table II
Survival means and planned orthogonal contrasts.

Treatment	Interspecific > Intraspecific		Low Density > High Density		Species Differences	
	$\overline{X}$	P	$\overline{\overline{X}}$	P	$\overline{\overline{\overline{X}}}$	P
Ed	0.85					
EdEd	0.89			0.45[2]	0.90	
		0.25[1]	0.93			
EdEt	0.96					0.04[2]
EtEd	0.71					
		0.55[2]	0.74			
EtEt	0.77			0.32[1]	0.76	
Et	0.79					

[1] one-tailed probability
[2] two-tailed probability

The mean "condition" of individual larvae was density-dependent for *E. divagans* (Table III), with interspecific effects (EdEt) at least as great as intraspecific ones (EdEd). The mean condition of *E. traviatum* was also somewhat less in the EtEd treatment than in EtEt (P = 0.13), suggesting that the effects of crowding may have been experienced by both species.

The biomass variable combines the separate effects of survival and individual mass. Orthogonal contrasts on the mean biomass ratio (final/initial) detected a significant species effect (Table IV) - *E. divagans* increased its biomass by 31% while the mean biomass of *E. traviatum* declined slightly. There is a suggestion of density-dependence for *E. traviatum* (P = 0.12). Comparison with other data (Fig. 1, Tables II and III) suggest that this effect may reflect the poor survival of smaller instars in the high density treatments.

Prey taxa identified in damselfly fecal pellets and benthos samples were grouped into the following categories to facilitate analysis and interpretation: cyclopoid copepods (includes adults and copepodites, but not nauplii); small Cladocera (adult body length less than 0.5 mm, principally *Chydorus sphaericus*); medium Cladocera (adult body lengths between 0.5 and 1.5 mm, principally *Alona affinis*); large Cladocera (adult body length greater than 1.5 mm, principally *Simocephalus* spp.); ostracods; water mites; oligochaetes; tanypodine midge larvae (principally *Ablabesmyia* spp.); other chironomid midges (principally *Psectrocladius* spp.); ceratopogonid midges; Odonata (principally the damselfly larvae under study); miscellaneous insects (caddisflies, mayflies, beetles and dipteran pupae). The following categories were found in the benthos but not in damselfly fecal pellets: snails, sphaeriid clams, and planarid flatworms. They were excluded from analyses reported here.

Table III
Condition means and planned orthogonal contrasts.

Treatment	Interspecific > Intraspecific		Low Density > High Density		Species Differences	
	$\overline{X}$	P	$\overline{\overline{X}}$	P	$\overline{\overline{\overline{X}}}$	P
Ed	1.15					
EdEd	1.04			0.02^1	1.05	
		0.29^2	1.00			
EdEt	0.96					
						0.60^2
EtEd	0.99					
		0.13^2	1.03			
EtEt	1.07			0.48^2	1.03	
Et	1.03					

[1] one-tailed probability
[2] two-tailed probability

Table IV
Biomass ratio (final/initial) means and planned orthogonal contrasts.

Treatment	Interspecific > Intraspecific		Low Density > High Density		Species Differences	
	$\overline{X}$	P	$\overline{\overline{X}}$	P	$\overline{\overline{\overline{X}}}$	P
Ed	1.29					
EdEd	1.35			0.89^2	1.31	
		0.76^2	1.32			
EdEt	1.29					
						0.01
EtEd	0.86					
		0.93	0.87			
EtEt	0.88			0.12^1	0.94	
Et	1.10					

[1] one-tailed probability
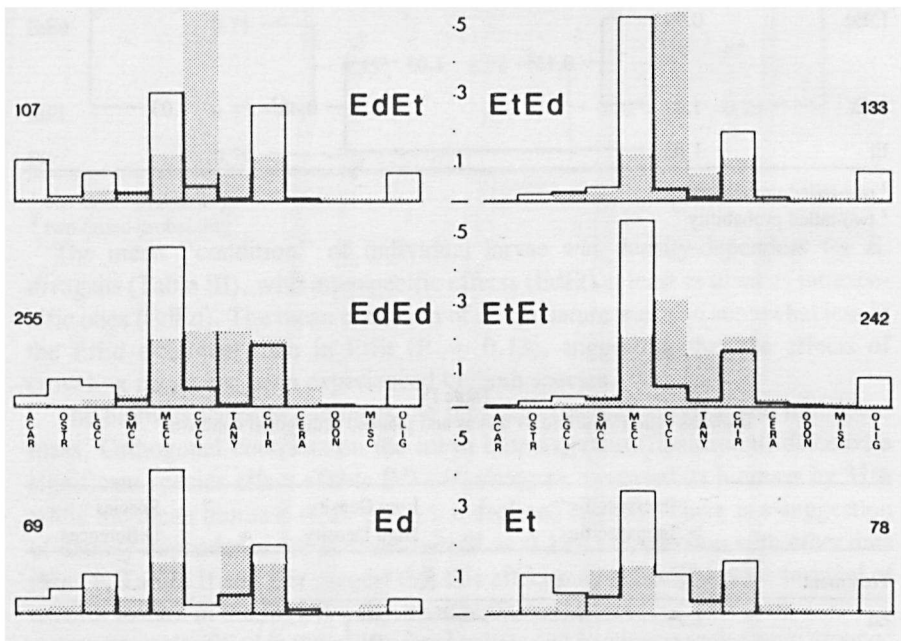[2] two-tailed probability

64

Fig. 2. Proportional composition of available benthos (shaded) and damselfly diets (solid lines) for *Enallagma divagans* (left) and *E. traviatum* (right) from various odonate treatments at the conclusion of a 1 month enclosure experiment. The number of items identified in fecal pellets to characterize each diet is indicated. Benthic groups are identified by the following acronyms: ACAR = water mites; OSTR = ostracods; LGCL = large cladocerans; SMCL = small cladocerans; MECL = medium cladocerans; CYCL = cyclopoid copepods; TANY = tanypodine midges; CHIR = non-tanypod chironomids; CERA = ceratopogonid midges; ODON = odonates; MISC = miscellaneous insects; OLIG = oligochaetes.

The relative abundances of potential prey categories from each odonate treatment were compared to the composition of larval diets (Fig. 2). The diets of the 2 species were strikingly similar: both ate disproportionate numbers of medium cladocerans, ostracods, oligochaetes, and (in most treatments) chironomid midges; and both ate fewer cyclopoid copepods, tanypodine midges and small cladocerans than might be expected from their abundance. Inspection of the original data sheets, on which most prey fragments were identified to genus, provided no evidence of diet partitioning within these grouped categories. When the 2 species were present in the same enclosures (EdEt & EtEd) there was very high dietary overlap. HURLBERT'S (1978) index of niche overlap, calculated from the proportions presented in Fig. 2, has a value (L = 11.8) much greater than that which would be expected if the two species were exploiting resources in direct proportion to abundance (L = 1.0).

The response of prey densities to experimental treatments is presented in Fig. 3. Most of these populations were unaffected by the experimental treatments. Only 1 prey population (oligochaetes) was reduced significantly in odonate treatments compared to control enclosures. Tanypodine midges showed a significant response to odonate species (less abundant when *E. traviatum* was present). They were also reduced in enclosures with both odonates (EdEt) compared to those with double doses of either species alone (EdEd, EtEt). Significant "enclosure" and "species" effects on odonates simply reflect the experimental manipulations.

DISCUSSION

The enclosure experiments were designed to determine whether competition might be an important phenomenon influencing the growth or survival of the larval damselflies which dominate detritus habitats of Bays Mountain Lake. Damselfly densities within enclosures were considerably higher than natural because they were chosen such that the double dose treatments would approximate the biomass of the total odonate assemblage. This element of our experimental design might be expected to force unusually intense competitive interactions if coexisting odonate populations normally partition resources (either prey or microhabitats) in ways that reduced niche overlap.

Comparison of the damselfly diets in Fig. 2 with those of dragonfly larvae collected in the same habitats (MERRILL, 1981; MERRILL & JOHNSON, 1984; JOHNSON *et al.*, 1985; BOHANAN & WATSON, in preparation) suggests little resource partitioning among sub-orders, though larger dragonfly larvae may be able to exploit some categories of prey (*i.e.* odonates and trichopterans) that are too large for smaller damselflies to handle (*cf.* THOMPSON, 1978). There is little evidence of prey resource partitioning between the two species of *Enallagma* studied (Fig. 2). Thus, if prey resources were limiting within the enclosures, one would expect to observe exploitation competition between the 2 damselfly populations indicative of the intensity of such interactions within the
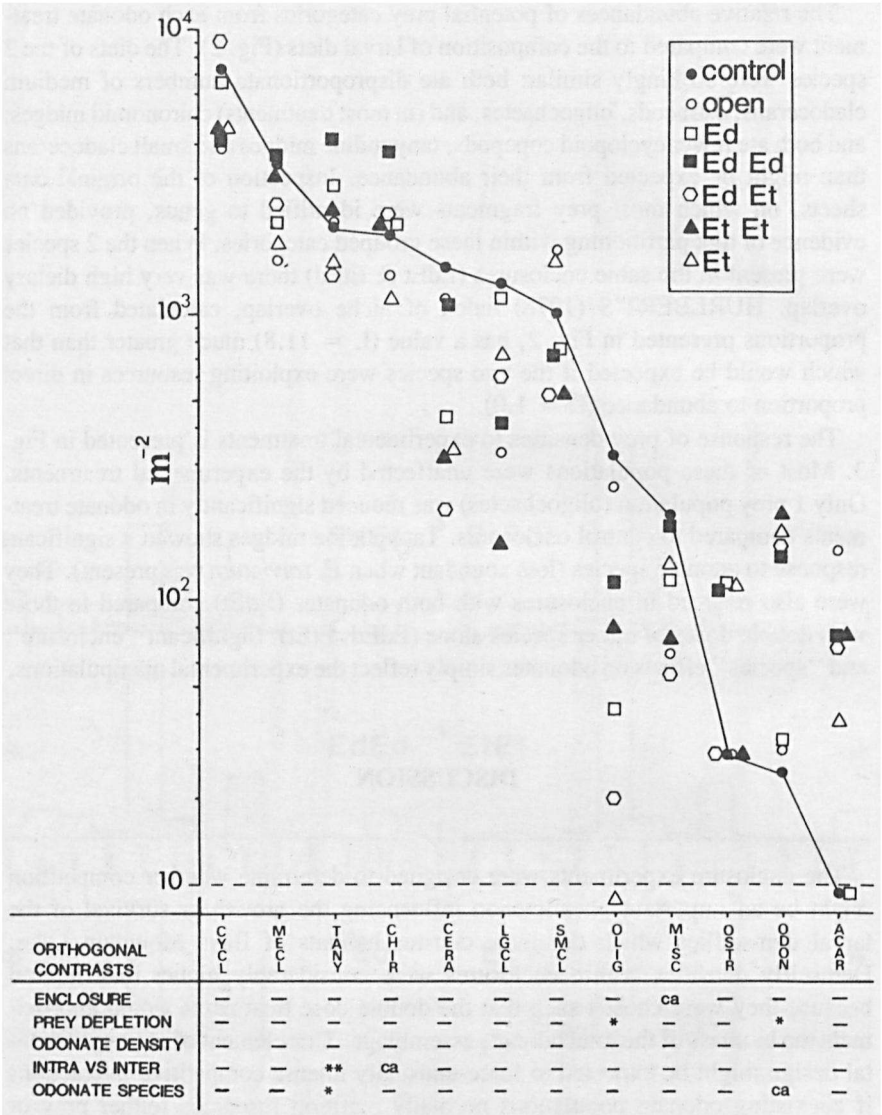
Legend:
- • control
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- ○ Ed Et
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- △ Et

Y-axis: m^{-2} with values 10^4, 10^3, 10^2, 10

ORTHOGONAL CONTRASTS	CYCL	MECL	TANY	CHIR	CERA	LGCL	SMCL	OLIG	MISC	OSTR	ODON	ACAR
ENCLOSURE	–	–	–	–	–	–	–	–	ca	–	–	–
PREY DEPLETION	–	–	–	–	–	–	–	*	–	–	*	–
ODONATE DENSITY	–	–	–	–	–	–	–	–	–	–	–	–
INTRA VS INTER	–	–	**	ca	–	–	–	–	–	–	–	–
ODONATE SPECIES	–	–	*	–	–	–	–	–	–	–	ca	–

Fig. 3. Mean population densities of each benthic group from enclosures (or open dishes) subjected to various treatments (see key) at the conclusion of a 1 month experiment. Acronyms are explained in Fig. 2. The significance of certain planned orthogonal contrasts is indicated: **, P ≤ .01; *, .01 < P ≤ .05; ca, .05 < P ≤ .10.

odonate assemblage as a whole. However, several lines of evidence suggest that damselfly larvae did not experience food-limitation within the enclosures:

1) Only 1 prey category (oligochaetes) was depleted significantly in odonate enclosures compared to controls. This is probably attributable to damselfly predation, because both species tended to eat oligochaetes disproportionately. But oligochaetes were not such an important component of damselfly diets that reduction of this one category would be expected to affect larval growth or survival.

2) Midge larvae, which probably account for more than 90% of the biomass consumed by *Enallagma* in these enclosures (assuming relative masses of prey categories similar to those reported by LAWTON (1970) and JOHANSSON (1976)), were present in approximately natural densities in all odonate treatments (Fig. 3).

3) The total biomass of *E. divagans* within the enclosures increased an average of 31% during the 1 month experiment (Table IV). While *E. traviatum* biomass declined slightly in two treatments, this seems to be attributable to mortality rather than to reduced growth rate (Fig. 1 and Table II). No evidence suggests that this mortality be attributed to starvation (see LAWTON *et al.*, 1980).

Much of the mortality experienced by larvae in this experiment was probably caused by intra-odonate predation (BENKE, 1978; BENKE *et al.*, 1982; MERRILL, 1981; MERRILL & JOHNSON, 1984; JOHNSON *et al.*, 1985). The broader instar distribution and concomitant larger proportion of relatively vulnerable smaller larvae of *E. traviatum* (Fig. 1) may account for its experiencing greater mortality (Table II).

These arguments suggest that exploitation competition for a limited food supply was not an important phenomenon within the experimental enclosures. The same conclusion was reached from similar enclosure experiments conducted with *E. aspersum* and *E. traviatum* in November 1981 (PIERCE, 1982; PIERCE *et al.*, in press), and with *Tetragoneuria cynosura* and *Celithemis elisa* (Anisoptera) in September 1981 and April 1982 (JOHNSON *et al.*, 1985).

However, BOHANAN & WATSON (in preparation) report high dietary overlap between odonate larvae and small sunfish (*Lepomis* spp. < 30 mm standard length). Since such potentially important competitors as small sunfish were excluded from enclosures used in the odonate competition experiments reported here (and cited above), exploitation competition could still be important in the natural community. Enclosure experiments conducted in September 1982 and April 1983 suggest that these groups may experience exploitation competition under approximately natural conditions in the detritus habitats of Bays Mountain Lake (JOHNSON *et al.*, 1983; and in preparation).

Despite the apparent lack of food-limitation, the mean "condition" of surviving *Enallagma divagans* was found to be significantly lower in the higher density (double dose) treatments (Table III). A comparable finding was reported for *E. aspersum* from similar enclosure experiments (PIERCE, 1982; PIERCE *et al.*, in press). This effect may be attributable to aggressive interactions resulting in interference competition among *Enallagma* larvae. Interference has occasionally been postulated to account for reduced individual growth rates for odonate larvae

in natural populations (MACAN, 1964, 1977; ROSS, 1967). Aggressive behavior has been demonstrated in the laboratory for both dragonflies (ROSS, 1971) and damselflies (BAKER, 1980, 1981; UTTLEY, 1980); and the factors influencing its evolution have been analysed from the perspective of game theory by CROWLEY (1984).

The intensity of interference competition might be reduced by differential utilization of microhabitats among larvae of different taxa and sizes (*cf.* JOHANNSSON, 1978). Therefore, one might expect such interactions to be intensified when only 2 species (and a limited range of size-classes) compose natural biomass densities, as in this experiment.

Even if experimental results were indicative of interaction intensity in the natural assemblage, it would be difficult to assess the long-term ecological consequences of reduced larval condition detected in a 1 month experiment. If the distribution of such effects were patchy in either space or time, one might expect the disadvantaged larvae to survive with only subtle effects on the timing of their development (*cf.* LAWTON *et al.*, 1980). But should such effects tend to persist, they might eventually influence larval mortality or fecundity (through reduced size of emerging adults). For the experiment reported here, the affected larvae were in either the final or penultimate instars (Fig. 1) and were expected to emerge in about one month (JOHNSON & CROWLEY, 1980a, Fig. 4). Thus it seems reasonable to suppose that the effects observed might persist to influence adult fecundity and thus larval population dynamics. Considering the relatively small (though statistically significant) magnitude of the observed effect (Table III), we are inclined to believe that its influence on population dynamics would be subtle.

The results of this and other recent experiments suggest that exploitation competition is not an important factor influencing larval odonate growth or survival within the detritus habitats of Bays Mountain Lake. Exclusion of other potential competitors (*i.e.* small sunfish) may have been partly responsible for alleviating food-limitation. Further experiments will be necessary to evaluate this possibility.

The interference competition observed between *E. divagans* and *E. traviatum* in this experiment does not seem sufficiently intense (or consistent through space and time) to be influencing the interaction of *Enallagma* populations within the lake as a whole. Nevertheless, results of this and other recent experiments suggest that some form of interference competition (either reduced individual mass or increased mortality) may often be experienced by members of this odonate assemblage. Further study of aggressive behavior and factors influencing larval encounter frequencies (*i.e.*, microhabitat utilization, dispersal, and feeding behavior) should contribute considerably to our understanding of this potentially important phenomenon.

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REFERENCES

ANDERSON, R.D. 1959. A modified 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. 1981. Behavioural interactions and use of feeding areas by nymphs of *Coenagrion resolutum* (Coenagrionidae: Odonata). *Oecologia 49*:353-358.

BENKE, A.C. 1978. On the significance of interactions among coexisting predators: a field experiment with dragonfly larvae. *J. Anim. Ecol.* *47*:335-350.

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.

BRAKKE, D.F. 1976. Modification of the Whiteside-Williams Pattern Sampler. *J. Fish. Res. Bd Can. 33*:2861-2863.

CONNELL, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat. 122*:661-696.

CORBET, P.H. 1954. Seasonal regulation in British dragonflies. *Nature (Lond.) 174*:655.

CROWLEY, P.H. 1984. Evolutionarily stable strategies for larval dragonflies. *In*: S. Levin & T. Hallam, Eds.. *Lecture Notes in Biomathematics*. Vol. 54, Springer/Verlag.

CROWLEY, P.H., & D.M. JOHNSON. 1982a. Habitat and seasonality as niche axes in an odonate community. *Ecology 63*:1064-1077.

CROWLEY, P.H., & D.M. JOHNSON. 1982b. Co-occurrence of Odonata in the eastern United States. *Adv. Odonatol. 1*:15-37.

CROWLEY, P.H., C.L. PIERCE, D.M. JOHNSON, & R.E. BOHANAN. 1983. An enclosure for experimental manipulation of lentic littoral and benthic communities. *J. Freshwater Ecol. 2*:59-66.

HELWIG, J.T., & K.A. COUNCIL. 1979. *SAS User's Guide*. 1979 Edition. SAS Institute Inc., Raleigh, N.C.

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. Nat. 93*:145-159.

HUTCHINSON, G.E. 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven, Conn.

JOHANNSSON, O.E. 1976. Ecological studies on co-existence amongst damselfly larvae (Odonata: Zygoptera) in the Norfolk Broads. Ph.D. Thesis, University of East Anglia.

JOHANNSSON, 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., & P.H. CROWLEY. 1980a. Habitat and seasonal segregation among coexisting odonate larvae. *Odonatologica 9*:297-308.

JOHNSON, D.M., & P.H. CROWLEY. 1980b. Odonate "hide and seek": habitat-specific rules? In: W.C. Kerfoot, Ed.. *The Evolution and Ecology of Zooplankton Communities.* University Press of New England, Hanover, N.H. 569-579.

JOHNSON, D.M., C.C. CONEY, & M.J. WESTFALL, JR. 1980. The Odonata of Bays Mountain Park, Sullivan County, Tennessee. *J. Tenn. Acad. Sci. 55*:73-76.

JOHNSON, D.M., R.E. BOHANAN, C.N. WATSON, & T.H. MARTIN. 1983. Exploitation competition between small fish and dragonfly larvae. *Bull. Ecol. Soc. Am. 64*:90.

JOHNSON, D.M., P.H. CROWLEY, R.E. BOHANAN, C.N. WATSON, & T.H. MARTIN. 1985. Competition among larval dragonflies: a field enclosure experiment. *Ecology 66* (in press).

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., B.A. THOMPSON, & D.J. THOMPSON. 1980. The effects of prey density on survival and growth of damselfly larvae. *Ecol. Ent. 5*:39-51.

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

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

MERRILL, R.J. 1981. A comparison of the diets of dragonfly larvae (Odonata: Anisoptera) coexisting in an allochthonous detritus habitat. M.S. Thesis, East Tennessee State University.

MERRILL, R.J., & D.M. JOHNSON. 1984. Dietary niche overlap and mutual predation among coexisting larval Anisoptera. *Odonatologica 13*: 387-406.

PIERCE, C.L. 1982. The relationship of behavior to competition and predation in two larval odonate populations. M.S. Thesis, University of Kentucky.

PIERCE, C.L., P.H. CROWLEY, & D.M. JOHNSON. Behavior of larval Odonata: implications for community structure. *Ecology* (in press).

ROSS, Q.E. 1967. The effect of different naiad and prey densities on the feeding behavior of *Anax junius* (Drury) naiads. M.S. Thesis, Cornell University.

ROSS, Q.E. 1971. The effect of intraspecific interactions on the growth and feeding behavior of *Anax junius* (Drury) naiads. Ph.D. Thesis, Michigan State University.

SCHOENER, T.W. 1983. Field experiments on interspecific competition. *Am. Nat. 122*:240-285.

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

UTTLEY, M.G. 1980. A laboratory study of mutual interference between freshwater invertebrate predators. Ph.D. Thesis, University of York.

WHITESIDE, M.C. & C. LINDEGAARD. 1980. Complementary procedures for sampling small benthic invertebrates. *Oikos 35*:317-320.