

## REGULATION OF FRESHWATER COMMUNITY STRUCTURE AT MULTIPLE INTENSITIES OF DRAGONFLY PREDATION<sup>1</sup>

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**Abstract.** We examined the role played by predaceous dragonfly nymphs, *Celithemis fasciata* (Odonata: Libellulidae), in the regulation of the community structure of a benthic macroinvertebrate assemblage in Par Pond, an 1100-ha reservoir in South Carolina. Effects of predation intensity on species richness, evenness, and density were evaluated by adding zero, two, four, and eight large dragonfly nymphs (antepenultimate and penultimate instars) to previously sieved (0.85-mm mesh) bottom sediment containing benthic macroinvertebrates. Predator and prey assemblages were then placed in individual field microcosms that consisted of polyethylene trays surrounded by underwater screens (mesh <2 mm diagonally) and suspended 15 cm below floating platforms. Twelve replicates of each treatment level were run during each of three 6-wk experimental periods: April–May 1980, August–October 1980, and January–February 1981. In addition, colonization of microcosms by invertebrates was quantified, and samples from natural, unenclosed benthic fauna were collected seasonally along a transect for comparison with experimental assemblages. We tested whether predators enhanced, depressed, both increased and decreased, or had no effect on the complexity of the community structure. The dual effect of predation on community structure is predicted by Connell's "intermediate disturbance hypothesis."

Results showed that dragonfly nymphs can significantly influence the structure of the benthic community. However, the results did not show that invertebrate predation is the sole or even the primary regulator of community structure. Species richness was significantly greater at intermediate treatment levels (thus supporting Connell's general hypothesis), but the increase was not great (a range of  $\approx 10\%$ ). The mechanisms by which species richness is maximized at intermediate intensities of predation are not entirely evident, but are probably a combination of prey refuges and nonselective predation with patch switching. In contrast, species evenness, as measured by equitability and by Simpson's index, was greatest at the highest predation level (which does not support the intermediate disturbance hypothesis). Dragonflies appeared to exert a greater influence on prey density than on community diversity.

**Key words:** *benthic; Celithemis fasciata; Chironomidae; community; dragonfly; intermediate disturbance hypothesis; microcosm; Odonata; predation; reservoir; South Carolina; species diversity.*

### INTRODUCTION

Despite extensive research on populations and guilds of freshwater invertebrates, ecologists have not completely identified the mechanisms responsible for the spatial and temporal differences in community structure that are characteristic of benthic habitats. In contrast, the roles that aquatic predators (e.g., Dodson 1970) and temporal heterogeneity (Hutchinson 1961) play in structuring limnetic communities are much better established. Richerson et al. (1970) have proposed that contemporaneous disequilibrium also plays an important role. The evidence now accumulating from lentic experiments (e.g., Gurzeda 1960, Kajak 1963, Hall et al. 1970, Benke 1976, 1978, Thorp and Bergey 1981a, b) and lotic experiments (e.g., Peckarsky 1979, Peckarsky and Dodson 1980a, b, Allan 1982) is clarifying the relative importance of biotic and abiotic factors in regulating the structure (richness, evenness, and density) of benthic communities.

The field experiment discussed here focused on the question, Are invertebrate predators important regu-

lators of community structure in the benthic littoral zone of Par Pond, a reservoir in the southeastern United States? That is, do these aquatic predators contribute significantly to the maintenance of ecological diversity, and do they effectively moderate oscillations in prey population size? In particular, do intermediate intensities of predation by dragonfly nymphs maximize species richness, evenness, and/or density in a manner consistent with the intermediate disturbance hypothesis: "diversity is higher when disturbances are intermediate on the scales of frequency and intensity . . ." (Connell 1978).

Previous field experiments have demonstrated that invertebrate predators have important roles in some freshwater systems (see review in Peckarsky 1982). Studies of marine intertidal zones (e.g., Paine 1966, Dayton 1971) have elegantly shown that benthic invertebrates, as keystone species, can maintain high levels of prey diversity. Hall et al. (1970) suggested that lentic invertebrate predators affect the ratio of the two dominant benthic organisms, the midge *Chironomus* and the mayfly *Caenis*. Benke (1978) concluded that the primary determinant of community structure and production of aquatic insects was an interaction between refuge level and predation rate by invertebrates such as dragonflies.

<sup>1</sup> Manuscript received 11 January 1983; revised 19 July 1983; accepted 26 July 1983.

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In the reservoir studied here, dragonfly and damselfly nymphs (Odonata) are the large, numerically dominant invertebrate predators of benthic macroinvertebrates (Thorp and Bergey 1981a, b, Cothran and Thorp 1982, Thorp and Diggins 1982). From laboratory studies it is known that odonates exhibit a non-stabilizing, Type II functional response (sensu Holling 1959) to changes in prey density (e.g., Johnson 1973, Thompson 1975, Akre and Johnson 1979, Gresens et al. 1982). The effects of dragonflies on prey density and species composition in the field have been examined in ponds (Benke 1976), large pens (Benke 1978), and small, submerged aquaria (Benke et al., *in press*). The results are consistent with a hypothesis that prey are saved from local annihilation by refuges and by high prey turnover rates.

In our study we manipulated the abundance of nymphs of the dragonfly *Celithemis fasciata* Kirby (Odonata: Libellulidae) in field microcosms and examined the effects on prey density, richness, and evenness. This species was selected because of its presence throughout most of the reservoir, its numerical dominance within the Anisoptera of the study site, and its diet of benthic prey. Results for *C. fasciata* are, we believe, generally applicable to other odonates since this species is a good generalist (J. H. Thorp, *personal observation*), as are most other lentic odonates (Pritchard 1964, Thompson 1978).

The manipulation of invertebrate predators in field experiments is exceedingly difficult and requires a compromise among naturalism, replicability, and capacity to identify causal relationships. Previous field experiments have manipulated the density of invertebrate predators by seining ponds (Hall et al. 1970), controlling colonization of large field enclosures (Benke 1978), or selectively adding predators to submerged aquaria (Benke et al., *in press*). In contrast, we utilized an original design of field microcosms (sensu Giesy and Odum 1980), which we believed was a more appropriate method for determining the importance of dragonfly nymphs in regulating the benthic community within our large reservoir (see Thorp and Cothran [1982] for justifications and design details). These microcosms simulated natural conditions and provided replicability sufficient to show differences among experimental treatments. Although we believe that our method was valid for its purpose, it, like any experimental manipulation, produced conditions that were not completely natural. Conclusions based on data from these experiments must be tempered accordingly.

## METHODS

### *Equipment design*

Portions of the benthic community were compartmentalized in microcosms (polyethylene refrigerator trays  $20.3 \times 14.6 \times 6.4$  cm) suspended 15 cm below the water surface from a floating platform. Each platform consisted of a buoyant styrofoam sheet, a var-

nished wood frame that supported the mass of the apparatus when it was out of water, and underwater screens made of window screening with mesh  $<2$  mm diagonally. These five-sided screens fitted snugly around the sides of the microcosms and by extending to the surface, reduced unwanted emigration and immigration of odonates. Platforms were fixed to poles at depths of 1.5–2.0 m, in areas where minimal vegetation contacted the microcosms. Further details are given in Thorp and Cothran (1982).

### *Naturalness of microcosms*

To demonstrate the validity of using floating field microcosms to simulate natural benthic conditions, we determined whether colonization of microcosms occurred and whether communities within microcosms and within natural bottom areas were qualitatively similar. The nature and extent of colonization was determined by placing terrestrial sand (similar to the sediment composition in our treatment microcosms but without aquatic invertebrates) in floating microcosms that were identical with treatment microcosms. We recorded the number of taxa and individuals found during three successive 2-wk intervals for each of three seasonal experiments. At the end of each seasonal experiment, the natural bottom fauna was sampled with an Ekman grab along a transect in an area at 1 m depth adjacent to the platforms.

Results of these colonization studies showed that during periods of both high and low recruitment the natural prey species for dragonflies were continually supplemented by immigration (Thorp and Cothran 1982). This was critical because without immigration the experiment would have been a simple feeding study rather than a community-regulation experiment.

Macroinvertebrate communities of microcosms and of bottom samples were quantitatively and qualitatively similar (Thorp and Cothran 1982). Some differences in results were expected, of course, because bottom samples (1) had not been manipulated prior to sampling, (2) were from a more heterogeneous habitat, and (3) were greater in volume than the microcosms (surface areas of transects and microcosms were equal). Despite variations in conditions, there were no significant yearly differences between experimental microcosms and bottom samples in total invertebrate density or in density of Chironomidae. But there were significantly fewer taxa in microcosms than in bottom samples. Detailed analyses are given in Thorp and Cothran (1982).

### *Experimental procedures*

To measure quantitative and qualitative effects of dragonfly nymphs on the density and diversity of benthic macroinvertebrates, we manipulated the abundance of dragonflies in experimental microcosms. Floating platforms were located in the west arm of Par Pond (an 1100-ha reservoir in Barnwell County, South

TABLE 1. Effects of dragonfly nymphs on abundance of macroinvertebrates in each microcosm. Six-week experiments were run during three periods with zero, two, four, or eight *Celithemis fasciata* added to previously sieved field microcosms (0.0296 m<sup>2</sup> surface area) suspended in the water column.  $n = 12$  microcosms per treatment for first two periods, 9 per treatment for last period. Trichoptera = *Oecetis*, *Orthotrichia*, *Oxyethira*, *Polycentropus* and *Leptoceris*. Odonata = *Celithemis fasciata*, *C. elisa*, *C. ornata*, *Erythemis simplicicollis*, *Pachydiplax longipennis* and Zygoptera (mostly *Enallagma* spp.). Chironomidae = *Ablabesmyia*, *Labrundinia*, *Corynoneura*, *Brillia*, *Cricotopus*, *Psectrocladius*, *Glyptotendipes*, *Limnochironomus* (= *Dicortendipes*), *Polypedilum*, *Rheotanytarsus*, and *Tanytarsus*; in lesser abundance were *Procladius*, *Eukiefferiella*, *Chironomus*, *Cryptochironomus*, *Endochironomus*, *Harnischia*, *Lauterborniella*, *Parachironomus*, *Paralauterborniella*, *Paratendipes*, *Phaenopsectra* (= *Tribelos*), *Pseudochironomus*, and *Cladotanytarsus*. Other taxa found in lesser abundance include Tabanidae, Lepidoptera, Hirundinea, *Hydra*, and Coleoptera (*Peltodytes*, *Hydroporus*, *Berosus*).

	Overall	Number of predators per microcosm			
		0	2	4	8
April–May 1980					
		Number per microcosm ( $\bar{x} \pm 1$ se)			
Total number of taxa	...	17.6 ± 0.8	18.6 ± 0.6	19.0 ± 0.8	17.7 ± 0.7
Total no. individuals	...	141 ± 16	144 ± 12	133 ± 15	107 ± 7.3
Turbellaria	3.6 ± 0.4	4.2 ± 0.9	5.1 ± 1.0	3.2 ± 0.6	1.9 ± 0.6
Oligochaeta	13.8 ± 0.8	14.3 ± 2.0	15.2 ± 1.4	15.2 ± 1.3	10.7 ± 1.6
Amphipoda: <i>Hyaella</i>	39.2 ± 3.7	52.5 ± 8.8	47.3 ± 6.5	36.4 ± 7.7	20.6 ± 1.7
Trichoptera	5.4 ± 0.8	7.5 ± 2.5	4.2 ± 1.1	5.3 ± 1.0	4.7 ± 1.5
Ephemeroptera: <i>Caenis</i>	14.1 ± 2.3	9.2 ± 3.8	16.3 ± 4.4	15.7 ± 6.5	15.3 ± 3.4
<i>Callibaetis</i>	1.8 ± 0.2	2.1 ± 0.4	1.7 ± 0.3	2.2 ± 0.3	1.1 ± 0.3
Odonata (total)	4.6 ± 0.5	5.3 ± 1.1	5.5 ± 0.8	4.9 ± 1.0	3.0 ± 0.7
<i>Celithemis</i> ≥ 2.5 mm*	...	0.1 ± 0.1	1.2 ± 0.3	1.6 ± 0.2	3.2 ± 0.4
All odonates ≥ 2.5 mm	...	...	...	...	...
Ceratopogonidae	4.9 ± 0.4	4.6 ± 0.8	5.1 ± 0.9	4.8 ± 0.7	5.0 ± 0.9
Chironomidae (total)	41.9 ± 3.2	40.8 ± 7.9	42.7 ± 5.6	43.6 ± 7.3	40.6 ± 4.8
<i>Ablabesmyia</i>	15.5 ± 2.2	17.4 ± 5.8	18.1 ± 4.9	14.5 ± 3.3	12.0 ± 3.3
August–October 1980					
Total number of taxa	...	17.2 ± 0.7	19.7 ± 0.7	18.1 ± 0.8	17.9 ± 0.7
Total no. individuals	...	203 ± 12	210 ± 14	219 ± 19	186 ± 11
Turbellaria	0.4 ± 0.1	0.5 ± 0.2	0.3 ± 0.1	0.3 ± 0.2	0.5 ± 0.2
Oligochaeta	21.0 ± 1.3	19.9 ± 2.2	23.2 ± 3.0	19.6 ± 3.2	21.3 ± 2.3
Amphipoda: <i>Hyaella</i>	35.4 ± 4.3	34.5 ± 7.8	39.8 ± 8.8	41.8 ± 12	25.6 ± 5.2
Trichoptera	1.2 ± 0.2	0.6 ± 0.2	1.6 ± 0.4	1.9 ± 0.4	0.8 ± 0.3
Ephemeroptera: <i>Caenis</i>	3.6 ± 0.6	3.4 ± 0.6	5.1 ± 2.1	3.0 ± 0.5	3.2 ± 0.7
<i>Callibaetis</i>	3.1 ± 0.3	3.4 ± 0.5	2.8 ± 0.6	3.5 ± 0.6	2.6 ± 0.6
Odonata (total)	17.2 ± 1.0	17.6 ± 1.8	16.8 ± 2.3	19.1 ± 1.6	15.3 ± 1.9
<i>Celithemis</i> ≥ 2.5 mm	...	0.3 ± 0.1	1.2 ± 0.2	2.3 ± 0.2	3.3 ± 0.6
All odonates ≥ 2.5 mm	...	1.7 ± 0.3	2.7 ± 0.5	3.5 ± 0.5	4.7 ± 0.7
Ceratopogonidae	3.2 ± 0.5	2.6 ± 1.2	3.3 ± 1.1	2.8 ± 0.6	4.3 ± 1.3
Chironomidae (total)	118 ± 6.2	120 ± 14	115 ± 15	127 ± 11	112 ± 9.7
<i>Ablabesmyia</i>	88.1 ± 6.1	96.3 ± 14	79.8 ± 14	96.3 ± 11	80.0 ± 9.8
January–February 1981					
Total number of taxa	...	18.8 ± 0.6	20.1 ± 1.0	19.4 ± 0.6	18.9 ± 0.8
Total no. individuals	...	107 ± 13	133 ± 22	137 ± 11	104 ± 10
Turbellaria	0.4 ± 0.1	0.8 ± 0.3	0.1 ± 0.1	0.4 ± 0.2	0.2 ± 0.2
Oligochaeta	4.4 ± 0.7	6.0 ± 2.3	4.3 ± 1.5	4.0 ± 0.7	3.3 ± 0.8
Amphipoda: <i>Hyaella</i>	18.5 ± 1.5	15.1 ± 2.2	19.4 ± 1.9	22.3 ± 4.5	16.6 ± 2.6
Trichoptera	0.3 ± 0.1	0.3 ± 0.2	0.4 ± 0.2	0.1 ± 0.1	0.2 ± 0.1
Ephemeroptera: <i>Caenis</i>	17.6 ± 2.4	17.2 ± 0.6	22.2 ± 5.9	19.2 ± 1.7	11.6 ± 4.0
<i>Callibaetis</i>	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.4 ± 0.2	0.2 ± 0.1
Odonata (total)	3.8 ± 0.4	1.6 ± 0.6	3.2 ± 0.5	3.3 ± 0.5	7.0 ± 0.7
<i>Celithemis</i> ≥ 2.5 mm	...	0.2 ± 0.1	1.6 ± 0.2	2.8 ± 0.4	6.3 ± 0.7
All odonates ≥ 2.5 mm	...	0.3 ± 0.2	2.0 ± 0.3	2.9 ± 0.4	6.3 ± 0.7
Ceratopogonidae	5.0 ± 0.6	5.7 ± 1.5	4.7 ± 0.9	5.9 ± 1.3	3.8 ± 0.9
Chironomidae (total)	67.3 ± 5.1	58.0 ± 4.9	76.7 ± 14	78.6 ± 11	56.0 ± 7.5
<i>Ablabesmyia</i>	12.8 ± 1.8	10.1 ± 1.4	15.2 ± 5.8	15.1 ± 3.9	10.7 ± 2.4
Yearly (1980–1981)					
Turbellaria	1.6 ± 0.2	1.9 ± 0.5	2.0 ± 0.5	1.4 ± 0.3	0.9 ± 0.3
Oligochaeta	13.9 ± 0.8	14.1 ± 1.6	15.1 ± 1.8	13.7 ± 1.7	12.5 ± 1.6
Amphipoda: <i>Hyaella</i>	32.2 ± 2.2	35.8 ± 5.0	37.0 ± 4.4	34.7 ± 5.2	21.3 ± 2.2
Trichoptera	2.5 ± 0.4	3.3 ± 1.1	2.2 ± 0.5	2.7 ± 0.5	2.1 ± 0.7
Ephemeroptera: <i>Caenis</i>	11.3 ± 1.2	9.3 ± 2.3	13.8 ± 2.6	12.0 ± 2.7	9.8 ± 1.9
<i>Callibaetis</i>	1.8 ± 0.2	2.1 ± 0.3	1.7 ± 0.3	2.2 ± 0.3	1.4 ± 0.3
Odonata (total)	9.0 ± 0.7	8.7 ± 1.4	9.0 ± 1.4	9.6 ± 1.4	8.6 ± 1.2
Ceratopogonidae	4.3 ± 0.3	4.2 ± 0.7	4.3 ± 0.6	4.3 ± 0.5	4.4 ± 0.6
Chironomidae (total)	76.6 ± 4.1	74.4 ± 8.5	78.2 ± 8.7	83.3 ± 8.3	70.8 ± 7.1
<i>Ablabesmyia</i>	41.1 ± 3.9	44.1 ± 8.8	39.7 ± 7.7	44.4 ± 8.1	36.4 ± 6.9

\* The numbers of *Celithemis* with head widths ≥ 2.5 mm that were recovered during this period are an underestimate because the technique initially used to remove microcosms from screened enclosures failed to remove all dragonflies perched on the screen above the plastic tray. Head widths for total Odonata were not measured during this period, because problems with immigration, which developed in later periods, did not occur during this first test period.

Carolina) in an area designated in previous studies (Thorp and Bergey 1981a, b) as Station VI. Water-quality measurements were made for an adjacent area by Giesy and Tessier (1979). On the basis of pilot studies, the length of each experiment was set at 6 wk. We believed this was sufficiently long for treatment effects from antepenultimate and penultimate instar nymphs to be shown, but was sufficiently short to hinder younger instars from growing enough to individually significantly affect the community. The 6-wk studies were run three times: April–May 1980, August–October 1980, and January–February 1981. Each of four floating platforms contained 12 microcosms consisting of three replicates of each of the four treatments described below, for a total of 12 replicates per treatment in each experimental period (except in January–February, when a platform overturned in a storm, reducing replicates to nine per treatment).

To begin each experiment, we collected benthos with an Ekman grab from areas near the experimental site and sieved (0.85-mm mesh) the samples in the laboratory to remove unwanted large predators (e.g., dragonflies and beetle larvae). The remaining material and additional sediment were added to polyethylene refrigerator trays to a depth of  $\approx 2$  cm. The trays were placed in the screened microcosms. Two or three sprigs of aquatic vegetation (*Bacopa caroliniana*) were added to each microcosm to increase habitat heterogeneity and to provide additional perch sites for the dragonfly *Celithemis fasciata*. Treatments received zero, two, four, or eight *C. fasciata* nymphs. The numbers were chosen to bracket natural benthic densities for total odonates in this area (Thorp and Bergey [1981b]). All dragonfly nymphs had initial head widths of at least 2.5 mm, but most were  $> 3.5$  mm (antepenultimate and penultimate instars).

It was not possible to maintain the original numbers of large dragonflies throughout the experiments, because of (1) increases due to the growth of small dragonflies that were present initially or that colonized later (a problem only during August–October), or (2) decreases due to the emergence of adults (a problem during April–May) and to natural mortality (probably including cannibalism). More important, however, we maintained the rank (highest to lowest) in numbers of large dragonflies among treatments (see Table 1, heading: *Celithemis*  $\geq 2.5$  mm). The numbers of other predatory macroinvertebrates in the microcosms also fluctuated. Since it was not possible to monitor changes in numbers of predators within microcosms, we used the initial treatment level as an independent variable in the final analysis and assumed an among-treatment error equivalent to the variation caused by changes in predator numbers.

At the end of each experiment, microcosms were returned to the laboratory and preserved in ethyl alcohol, stained with Phloxine B, and sieved (United States Standard Number 60: 0.25-mm mesh); animals

were sorted and identified to genus in most cases. From samples containing large numbers of Chironomidae, 50–60 midges were selected randomly for identification. The number of midges in each genus was corrected as follows: total number of genus A = (number of genus A in subsample)  $\times$  (total number of Chironomidae  $\div$  number of Chironomidae in subsample). Head capsule lengths for all chironomids except those in the subfamily Tanypodinae were measured at  $400\times$  from the base of the dorsum of the head to the base of the antennal tubercle. The length for members of the Tanypodinae was measured as the distance from the base of the dorsum of the head to the base of the mandibles, since the antennae are retractable in this subfamily. An a priori decision was made to ignore certain taxonomic groups that either were transient (e.g., Cladocera) or were rare prey for dragonfly nymphs (e.g., Gastropoda).

Data were analyzed by ANOVA, general linear regression (GLM), and Pearson's product-moment correlation coefficients with the Statistical Analysis System (SAS; Barr et al. 1979). Assumptions of linearity were tested for lack of fit (Draper and Smith 1966). Parametric analyses were generally used since the *F* distribution (utilized in ANOVA and in the GLM procedure) is "relatively unaffected by lack of data normality and heterogeneity of variance . . ." (Kirk 1968: 63), and the data deviated only slightly from normality. Results were generally the same whether or not the data were log transformed. Unless otherwise noted, the term "significant" refers, henceforth, to statistical results with alpha levels of .05 or less. Three measures of community structure were utilized: (1) species richness (number of taxa per sample), (2) evenness, as measured by *D*, a modification of Simpson's index of diversity ( $D = 1 - \sum p_i^2$  [Simpson 1949], where  $p_i$  is the proportion of individuals of species *i* in the community), and (3) evenness or equitability, as calculated by  $E = H'/H'_{\max}$ , where *H'* is the Shannon-Wiener function, and  $H'_{\max} = \log_{10}$  no. species in the community (Hough 1936). All three measures have been employed frequently in benthic studies. (For a comparison of the uses for different indexes, see Pielou [1969]).

We focused on a null hypothesis and two reasonable alternative hypotheses, which in turn can be subdivided for separate effects on diversity and density of the total benthic assemblage. The null hypothesis is that dragonfly nymphs have no significant impact on community structure. A significant ANOVA result would lead to rejection of this null hypothesis. The first alternative hypothesis is that predators either depress or enhance indexes of community structure, but do not do both. A significant negative linear regression would support the prediction of depression. A positive regression would support the prediction of enhancement. The second alternative hypothesis is that predators have both positive and negative effects. To test this hypothesis, we fitted second- and third-order polynomial

exceed that expected by chance alone, the susceptibility of highly motile *Hyalella* to predation and the general trend for most taxa to decrease at the eight-predator level (Table 1) suggest that this significant linear relationship was a real phenomenon. Densities of the eight major groups listed above varied significantly from season to season, but in no case was there significant interaction between date and treatment level.

#### *Effects on prey size*

The effect of dragonfly predators on head length of Chironomidae was examined as a rough indicator of changes in secondary productivity among prey species. Size in the combined taxa was significantly affected by date and by predator treatment; however, the interaction was nonsignificant (Appendix). Although the maximum individual midge size occurred in the two-predator treatment, size was neither a significant linear nor a significant curvilinear function of predation level (Appendix). Sizes of the 11 most abundant midge genera varied significantly over time, but only the predatory *Ablabesmyia* and the detritivore *Corynoneura* varied significantly over treatments. These two midges were, respectively, the first and third most abundant genera.

#### DISCUSSION

With a few notable exceptions, most theories on biological control of freshwater communities are based on (1) extrapolations from laboratory experiments, (2) speculations or anecdotal observations from descriptive field studies, or (3) field experiments involving populations of one or, at most, a few prey species (see review in Peckarsky [1982]). These studies are useful in their own right, but field experiments of large assemblages or whole communities are the most pertinent in the present context, and there are fewest of them. Results from the few lentic experiments of the effects of invertebrate predators on benthic communities in general correspond with the results presented here, although most of these community studies identified significant predator-related effects only on component species rather than on the entire assemblage. Kajak and Kajak (1975) found that the biomass of the main predators in their systems slightly exceeded the biomass of the prey. In the presence of increased predation from the amphipod *Crangonyx*, the number of prey decreased. When the number of invertebrate predators was altered in a classic pond study by Hall et al. (1970), the biomass of benthic organisms (excluding the large invertebrate predators) indicated little response to predation in 1965. But later, the ratio of the two dominant benthic organisms, the midge *Chironomus* and the mayfly *Caenis*, was found to have been affected by predation (the mayfly became more abundant). In a related lotic study, stonefly predators in experimental cages, as compared with cages having no stoneflies or having restricted numbers of stoneflies,

significantly increased the attrition of mayfly prey (Peckarsky and Dodson 1980b).

Our results clearly show that nymphs of the dragonfly *Celithemis fasciata* can influence the structure of the benthic community. But the results do not suggest that invertebrate predation is the sole or even the primary mode of community regulation in the littoral zone of this reservoir. One might have expected species richness, species evenness, density, and/or secondary productivity to reflect strongly the intensity of dragonfly predation. In fact, although species richness was significantly greater at intermediate treatment levels, the differences seem proportionately small (range of  $\approx 10\%$ ). Immigrant predators, however, may have diminished the possibly large treatment effects of the original dragonflies. Alternatively, the necessary brevity of the experiments may have obscured the full effects of predation. In retrospect, it was perhaps naive to have expected dramatic effects of predation on species richness over relatively short periods. Without monitoring the community continuously for a much longer period (years or even decades), it might be difficult to evaluate the biological significance of this 10% change in species richness.

In contrast with the effects of dragonflies on species richness, species evenness (as measured by equitability  $E$  and by a modification of Simpson's index of diversity  $D$ ) was enhanced by higher predation, although the range was again small ( $\approx 14\%$ ). Conversely, size variation in midges, a common prey of dragonflies, was not noticeably affected by predation, which suggests that secondary productivity also was not influenced significantly.

Predators appeared to have their largest effect on prey density; densities were lowest in the eight-dragonfly treatment (18–32% less than the maximum values and 3–24% less than values from the zero-dragonfly treatment). In other field experiments, dragonflies emerging early have been shown to affect prey abundance (especially for midges in the subfamily Tanyptodinae; Benke 1978). Furthermore, since odonates have a large daily consumption capacity and a standing stock frequently two to three times that of their prey, they have both a numerical and a physiological potential for regulating the prey assemblage (Benke 1976, Benke et al., *in press*). The presence of some refuges from odonate foraging (Benke 1978) is probably a major factor preventing extinction of any given prey species. Ultimately, an evaluation of the degree to which invertebrate predators as a whole are important in community regulation will require knowledge of the relative roles of other biotic and abiotic factors in this process.

#### *Mechanisms of potential regulation by dragonflies*

The degree to which predators are important as regulators of community structure appears to be a con-

sequence of three factors: (1) the nature of competitive relationships in the prey assemblage (assuming that the prey species are resource limited in the particular habitat), (2) the feeding specificity of the predator, and (3) the equilibrium or nonequilibrium state of the system. Odonates, as feeding generalists (Pritchard 1964, Thompson 1978), might maintain higher diversity if they preferentially consume the dominant species within a competitive hierarchy (see related discussion in Lubchenco and Gaines [1981]). A laboratory study (M. L. Cothran and J. H. Thorp, *personal observation*) suggests that *Celithemis* nymphs prefer certain prey species but do not exclude other prey from their diet. Thompson (1978) concluded, however, that other odonates consume prey in roughly the same proportions as the proportions of the preys' occurrences in the field. Neither study suggests that preferential consumption of a dominant prey is the mechanism by which odonates contribute to community regulation. If the preferred prey species is not the competitively dominant one, or if nymphs feed selectively on a balanced competitive network, then predation will not promote higher species richness (Lubchenco and Gaines 1981), except when patch switching is involved (see below). This aspect of the predator-prey relationship cannot be resolved until further information on benthic communities becomes available.

Dragonflies might promote higher diversity if they switched among alternative prey on the basis of the relative abundance of the prey, or if they showed a Type III functional response (*sensu* Holling 1959). However, the Type II functional response characteristic of dragonfly nymphs (Gresens et al. 1982, Cothran and Thorp 1984) would not dampen oscillations in prey abundance. Moreover, we found no evidence of switching when *Celithemis fasciata* was given a choice between the midge *Chironomus tentans* and the cladoceran *Daphnia magna* (Cothran and Thorp 1984). Akre and Johnson (1979), however, concluded that the damselfly *Anomalagrion hastatum* switched between the motile *Daphnia* and the more sessile *Simocephalus* cladoceran species.

A final mechanism by which dragonfly nymphs could contribute to community regulation is through equivalent (i.e., nonselective) predation in combination with patch switching (see related discussion in Hanski [1981]). To be effective, this mechanism would necessitate: (1) a clumped prey dispersion (often the case in the benthos; Elliott 1973), (2) large within-patch variability in relative abundances of species (indicated in previous studies of Par Pond; Thorp and Bergey 1981b), and (3) aggregation of predators on temporarily dense prey patches (such movement can be inferred from Crowley [1979]). By heavily exploiting prey patches before emigrating, dragonfly nymphs may create local disequilibrium and thereby interrupt processes of competitive exclusion. By this mechanism, maximum diversity would occur at intermediate frequencies or in-

tensities of dragonfly predation, since intermediate levels would allow sufficient time for colonization and population regrowth, but would be too brief for extensive competitive exclusions.

#### *Relationship to the intermediate disturbance hypothesis*

This latter idea, embodied in the intermediate disturbance hypothesis (Connell 1978), has received widespread theoretical support (Hutchinson 1961, Paine 1966, Richerson et al. 1970, Caswell 1978, Connell 1978, Huston 1979, Sousa 1979, Lubchenco and Gaines 1981) and is rapidly gaining popularity, despite the dearth of hard experimental evidence to support it (exceptions are papers such as Sousa [1979]). Field experiments in which predators are either present or excluded (i.e., two treatments) are not adequate to support this hypothesis, since at least four treatment levels are required to test a second-order polynomial model of diversity on disturbance intensity. Results of our field microcosm experiments support this hypothesis, provided that species richness is the criterion and that variation of 10% constitutes a biologically significant effect. Our data, however, do not support the hypothesis if evenness (*E* or *D*) is the criterion used for changes in community diversity. The small range of richness values among treatments suggests that predation, or at least predation by dragonflies, is not the only factor contributing to regulation of the benthic assemblage.

#### SUMMARY

We have experimentally demonstrated that the dragonfly *C. fasciata* can influence, but probably not completely regulate, the structure of the benthic macroinvertebrate community within the littoral zone of a reservoir. Since locality and depth greatly affect the relative numerical dominance of dragonfly species (Thorp and Bergey 1981b, Thorp and Diggins 1982), it is probable that the portion of community regulation attributable to predation results not from a single keystone species (*sensu* Paine 1966) but from either a guild of odonates or predators in general. The means by which species richness is maximized at intermediate intensities of dragonfly predation is not completely evident, but a combination of prey refuges and nonselective predation with patch switching seems the most probable mechanism. The effect of these factors is to create local disequilibrium in the competitive exclusion process. Our data further suggest that dragonflies exert a greater influence on prey densities than on community diversity. Predation is, however, but one of many means by which communities are regulated, and it is not equally important in all systems at all times.

#### ACKNOWLEDGMENTS

We are most grateful to Dave Mayack, Bob Henry, and Ron Blessing, who provided advice and labor that helped in the construction of the microcosms. We are pleased to acknowledge the statistical and computer advice of John Pinder

and Gus Cothran. The work of Jean Coleman in drafting the figures, and the help of the secretarial pool at Savannah River Ecology Laboratory in preparing the manuscript, is appreciated. We thank Carolyn West and Kim Shoemaker for helping sort and identify some of the samples. A portion of this study was presented during a symposium on predator-prey relationships in freshwater and marine benthic communities, held at the 1981 meeting of the Ecological Society of America; discussions with symposium participants helped crystallize our thoughts for the final manuscript. Reviews of an earlier draft of this manuscript by Arthur Benke, Alan Covich, David Hart, Richard Hauer, and several anonymous reviewers improved this paper. These reviewers, however, do not necessarily agree with all the conclusions present in this paper. Research support came from contract DE-AC09-76SR00819 between the University of Georgia and the United States Department of Energy.

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APPENDIX

Analysis of variance (ANOVA) and general linear model (GLM) procedures for the effects of date (April-May, August-October, and January-February) and predation level (treatment = 0, 2, 4, or 8 dragonfly larvae/microcosm) on benthic prey species richness, equitability as measured by  $E = H'/H'_{max}$  (Hough 1936), evenness as measured by a modification of Simpson's index of diversity ( $D = 1 - \sum p_i^2$  [Simpson 1949]), and density (total organisms per microcosm tray), and on size (head length) of Chironomidae.

Source	df	Type IV SS	F	P	Source	df	Type IV SS	F	P
<i>Dependent variable: species richness</i>					ANOVA				
Date	120	40.0051	3.18	.0452	Treatment	130	0.0442	5.50	.0205
Treatment	120	61.7556	3.27	.0234	Lack of Fit	130	0.0047	0.29	.7510
Date x Trt	120	15.1465	0.40	.8771	GLM (2nd-order polynomial regression)				
GLM (linear regression)					Overall	129		2.74	.0682
Treatment	130	0.4190	0.06	.8031	Treatment	129	0.0051	0.64	.4268
GLM (2nd-order polynomial regression)					Trt x Trt*	129	0.0002	0.02	.8781
Overall	129		3.16	.0456	<i>Dependent variable: density</i>				
Treatment	129	35.0964	5.44	.0212	ANOVA				
Trt x Trt*	129	40.3796	6.26	.0136	Date	120	188996.41	43.65	.0001
Lack of fit	129	21.4438	3.39	.0680	Treatment	120	20118.08	3.10	.0291
<i>Dependent variable: E</i>					Date x Trt	120	4938.97	0.38	.8904
ANOVA					GLM (linear regression)				
Date	120	0.7207	87.58	.0001	Treatment	130	9094.44	2.54	.1132
Treatment	120	0.0338	2.74	.0457	GLM (2nd-order polynomial regression)				
Date x Trt	120	0.0206	0.84	.5444	Overall	129		2.88	.0596
GLM (linear regression)					Treatment	129	5637.44	1.60	.2078
Treatment	130	0.0339	3.56	.0615	Trt x Trt*	129	11183.89	3.18	.0769
GLM (2nd-order polynomial regression)					<i>Dependent variable: chironomid size</i>				
Overall	129		1.97	.1437	ANOVA				
Treatment	129	0.0001	0.01	.9346	Date	5098	664.75	9.19	.0001
Trt x Trt*	129	0.0038	0.40	.5298	Treatment	5098	425.87	3.93	.0084
<i>Dependent variable: D</i>					Date x Trt	5098	187.71	0.87	.5197
ANOVA					GLM (linear regression)				
Date	120	0.5713	77.51	.0001	Treatment	5108	60.92	1.68	.1955
Treatment	120	0.0412	3.72	.0133	GLM (2nd-order polynomial regression)				
Date x Trt	120	0.0267	1.21	.3079	Overall	5107		1.96	.1416
GLM (linear regression)					Treatment	5107	42.11	1.16	.2817
Treatment	130				Trt x Trt*	5107	81.16	2.23	.1351

\* Trt x Trt = a term within the polynomial equation equal to the squared value of x (number of predators).