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COMMUNITY RESPONSES TO VARIABLE PREDATION: FIELD STUDIES WITH SUNFISH AND FRESHWATER MACROINVERTEBRATES¹

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Abstract. I studied the impact of variable predation by bluegill sunfish on macroinvertebrate prey in a North Florida lake. Underwater time-lapse cinematography and censuses of bluegill abundances in shallow, middepth, and deep habitats permitted estimation of predation intensity and variability within and among lake habitats. I then incorporated predation rates typical of the middepth zone in caging experiments where predation fluctuated in one treatment and remained constant in another. Prey community structure was subsequently monitored for 1 yr under variable, constant, ambient, and no predation regimes.

Patchy, temporally variable predation characterized middepth and deep lake habitats, whereas in the shallow zone predation was relatively constant and homogeneous. Predation varied significantly every 2–4 wk in the middepth zone, but varied little between consecutive weeks or days. Caging experiments revealed that variable predation altered prey community composition and increased the mean size and size range of some prey (e.g., Odonata) as compared to the constant predation treatment. Prey abundances also appeared more heterogeneous among cages (patches) and varied more temporally under a variable predation regime. However, total prey abundance, species abundance, and within-patch spatial heterogeneity did not differ among predator treatments. In general, the macroinvertebrate community exposed to variable predation more closely approximated the natural middepth zone community than that from the constant predation regime. Previous studies of fish predation on macroinvertebrate communities have concentrated on shallow littoral habitats, but these results suggest that conclusions drawn from shallow habitats may not be representative of all lake zones. Variable predation may occur in many systems, and may contribute substantially to the spatial heterogeneity, temporal inconstancy, and species composition of prey communities.

Key words: *biological disturbance; bluegill; caging experiment; community structure, fish; freshwater; lakes; Lepomis macrochirus; macroinvertebrates; predation; sunfish; variation.*

INTRODUCTION

One of the striking features of natural populations and communities is their temporal and spatial variability. Abundances fluctuate dramatically over various time scales and spatial distributions are characteristically heterogeneous (DenBoer 1981, Titmus 1983). Some of the heterogeneity observed in natural communities may be attributable to inappropriate sampling (Downing 1979, Titmus 1983), but many patterns are a consequence of variation in climate (Andrewartha and Birch 1954), resource abundance (Wiens 1976), or disturbance (Denslow 1985). Many ecologists view variation in ecological processes as noise that obscures simpler phenomena, as stochastic events that destabilize communities, or as disturbances that interrupt deterministic biological interactions (see Chesson and Case 1986, DeAngelis and Waterhouse 1987,

for reviews). Yet theory suggests that environmental variation can also redirect community dynamics, creating patterns analogous to those produced by deterministic processes (Chesson 1986). For example, in some systems stochastic disturbance promotes spatial heterogeneity and community diversity (see Pickett and White 1985 for review). But interest in disturbance has focused largely on catastrophic physical phenomena (e.g., Connell 1978, Sousa 1979, Wethy 1985, and many others), whereas the ramifications of variable, noncatastrophic biotic disturbances, like predation, remain largely unexplored (Chesson 1978).

The possible importance of variation in predation was recognized early (Huffaker 1958, Hutchinson 1961). Since then, theoretical investigations have suggested that variation in predation might increase the temporal fluctuations and spatial heterogeneity of prey populations, and promote the diversity and persistence of communities (see Chesson and Case 1986, Woolhouse and Harmsen 1987, for review). Despite theoretical insights, few empirical studies have dissected predation into its specific components (e.g., mean, intensity, vari-

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ation) to examine the independent effect of each. If predators are mobile, predation can be highly localized in time and space, introducing a large component of variance to the patterns of prey mortality (Ayling 1981, Duggins 1983, Menge 1983, Keough 1984, Robles 1987, and others). Prey distributions may also be indirectly affected by predators if prey aggregate to social or physical refugia, or, in the case of cryptic prey, disperse to minimize predation (see Endler 1984, Sih 1987, for review). Although variable predation may be manifest in observable community responses, confirmatory empirical evidence is scant and primarily correlative (but see Gutierrez et al. 1980, West 1986, Fairweather 1988). Thus, the influence of variable predation on the structure of natural communities remains in question.

Perhaps nowhere are the effects of predation more evident than in freshwater lentic ecosystems (see Sih et al. 1985, Kerfoot and Sih 1987, for review). Although predatory interactions among freshwater invertebrates are well documented (see Bay 1974, Peckarsky 1984, for review), the cascading effects (sensu Paine 1980) of predation by fishes appear to be the overriding mechanism structuring the planktonic and benthic communities in lakes and ponds (Zaret 1980, Healey 1984, Kerfoot and Sih 1987). Manipulations of fish abundance in ponds and lakes result in dramatic changes in benthic community structure, notably the loss of large, mobile invertebrates and a decrease in the mean size of benthic infauna (see Macan 1977, Healey 1984). In particular, experimental manipulations of bluegill sunfish (*Lepomis macrochirus*) by Crowder and Cooper (1982), Bohanan and Johnson (1983), Gilinsky (1984), and Morin (1984a, b) demonstrate that bluegills significantly alter the species compositions and density of infaunal and epiphytic macroinvertebrates (but see Thorp and Bergey 1981). Their results suggest that bluegills are "keystone predators" (sensu Paine 1966) because they are size selective and consume disproportionately more invertebrate predators than nonpredators. However, seasonal, ontological, and individual differences in bluegill habitat use, diet, and foraging frequency are marked (Mittelbach 1981, Bartell 1982, Werner et al., 1983, Butler 1988a), creating temporal and spatial variation in prey mortality. Thus, the bluegill sunfish-macroinvertebrate system provides an interesting opportunity to study the relationship between variation in predation and prey community structure.

In this study, I document the patterns of bluegill predation in a north Florida lake and evaluate the impact of a variable predation regime on macroinvertebrate community structure. Observations of bluegill predation and manipulations of bluegill abundances were employed to test whether: (1) bluegill predation varies at scales relevant to the structure of natural prey communities, (2) variability in bluegill predation contributes to spatial or temporal variability in prey populations, (3) variable predation creates prey commu-

nities that are different than those resulting from constant predation, and (4) a variable predation regime is a better analog to natural predation regimes than the conventionally employed constant predation regime.

SITE DESCRIPTION

The study was conducted in Dog Lake, an oligotrophic 12-ha lake in the Apalachicola National Forest, 15 km southwest of Tallahassee, Leon County, Florida. The maximum depth of Dog Lake is 7 m, and water visibility varies from 2 to 8 m. The lake bottom is covered by a patchy, vegetated understory of bladderwort (*Utricularia floridana*), interspersed with spike rush (*Eleocharis elongata*) and areas of open sand or silt. *Panicum hemitomon* (maiden-cane), the sole emergent plant in the lake, is dense and homogeneously distributed along the lake margin at depths <1.5 m, patchily distributed from 1.5–6 m in depth, and absent in the deep (>6 m), central portion of the lake (Butler 1988b). Thus, three distinct habitats or zones, defined by water depth and *Panicum* density, are evident in Dog Lake: (1) a shallow, heavily vegetated lake margin (shallow), (2) an intermediate depth, patchily vegetated zone (middepth), and (3) a deep zone with no emergent vegetation (deep). These habitats correspond to the upper, middle, and lower infralittoral zones. For brevity, I use the terms shallow, middepth, and deep throughout the text.

STUDY ORGANISMS

Mosquitofish (*Gambusia affinis*), starhead topminnows (*Fundulus nottii*), bluegill sunfish (*Lepomis macrochirus*), and largemouth bass (*Micropterus salmoides*) are the only fishes present in Dog Lake. Topminnows and mosquitofish occur along the shallow (i.e., <0.5 m) lake margins, whereas the centrarchid fishes are distributed throughout the lake. This study focused on bluegills, the most abundant and widely distributed fish in Dog Lake and other north Florida lakes (Werner et al. 1978, M. J. Butler IV, *personal observation*). Preliminary analyses of bluegill (60–125 mm total length; TL) stomach contents indicated that in Dog Lake nearly 95% (by mass) of their diet is macroinvertebrates (M. J. Butler IV, *personal observation*). Because bluegills were abundant, ubiquitous, and fed primarily on benthic invertebrate prey, they were believed to be a major predator of macroinvertebrates in Dog Lake, as they are in many North American lakes (Keast and Welsh 1968, Mittelbach 1984a and others).

The abundances of the 31 genera of macroinvertebrates collected from Dog Lake (Table 1) are consistent with those reported from other lentic waters in the southeastern United States (Thorp and Bergey 1981, Gilinsky 1984, Morin 1984a). Detailed life history information is not available for many of these insects; most are reported to be univoltine or bivoltine, but many may be multivoltine in Florida (Sweeney 1984). Periods of emergence and reproductive activity are also

prolonged in North Florida's warm temperate climate, creating broadly overlapping larval cohorts and a more seasonally persistent taxonomic structure than at higher latitudes (Butler 1984).

METHODS

Bluegill distribution among lake habitats

To estimate the large-scale patterns of bluegill predation among habitats and seasons, I monitored bluegill abundance and distribution in three habitats (shallow, middepth, deep) every 4–6 wk from May 1986 to July 1987. Observations were made using SCUBA between 1200 and 1600 along three 100–250 m underwater transects, one within each habitat; new transects were established for each census. While swimming along each transect, I stopped every 10 m to record the number of bluegills (40–125 mm TL) observed in a 36 m³ volume (2 m either side of the transect, 0–3 m off the bottom, and 0–3 m in front of the observer). Ten metres was estimated to be the minimum distance between which independent diver observations could be made, and thus constitute the minimum "patch size" for these observations. At shorter intervals, fish sometimes swam ahead of the diver before veering away, which would have decreased the independence of observations. Up to 25 bluegill could be accurately counted at one time, so abundances exceeding 25 were recorded as "> 25." These data provided estimates of bluegill (1) abundance, (2) variability in abundance, (3) patchiness, and (4) mean crowding (density per patch) as a function of habitat and season.

I used two-factor Analyses of Variance (ANOVA) to compare bluegill abundance and the variability in their abundance (i.e., patchiness) among habitats and seasons. Means and variances were calculated for the observations made along each transect during a monthly census, yielding 10 summer (May–October 1986; April–July 1987) and 2 winter (January–February 1987) replicates. Residuals (plotted against expected values) were inspected for homogeneity of variance and data were $\ln(x + 1)$ transformed before the analysis. Bonferroni (Dunn's) multiple comparison tests were used to investigate differences among specific habitats.

Bluegill spatial distributions within habitats and seasons were determined from the mean index of dispersion (i.e., Morisita's Index of Dispersion) calculated for each transect. Values of I exceeding unity indicate a patchy distribution, less than unity a regular distribution, and unity a random distribution. I also examined the pattern of bluegill patchiness in each habitat as a function of spatial scale by plotting Morisita's index for observations grouped into intervals of 10, 20, 30, 40, and 50 m along each transect. This method and similar methods used to measure population dispersion are reviewed by Ludwig and Reynolds (1988). Finally, I estimated the intensity of predation in a "patch" by calculating Lloyd's index of mean crowding

TABLE 1. Macroinvertebrate prey types collected from the benthos and from artificial plants in Dog Lake, Leon County, Florida. The most common macroinvertebrates are indicated by *.

Cnidaria	<i>Hydra americana</i>
Platyhelminthes	Turbellaria
	<i>Dugesia tigrina</i> *
Annelida	Oligochaeta
	<i>Aulodrilus americanus</i> *
	<i>Dero digitata</i>
Arthropoda	Hydracarina
	<i>Hydrodroma despiciens</i> *
	<i>Arrenurus</i> sp.*
	<i>Limnesia</i> sp.
Insecta	Ephemeroptera
	<i>Callibaetis</i> sp.*
	<i>Caenis pretiosus</i>
	<i>Leptophlebia</i> sp.
	Odonata
	Anisoptera
	<i>Pantala</i> sp.
	Zygoptera
	<i>Enallagma signatum</i>
	<i>Enallagma</i> sp.
	Trichoptera
	<i>Polycentropis</i> sp.*
	<i>Oxythira</i> sp.*
	<i>Oecetis</i> sp.
	Coleoptera
	Hydrophilidae
	<i>Berosus peregrinus</i>
	Diptera
	Chironomidae*
	<i>Ablabesmyia manilus</i>
	<i>Alluandomyia</i> sp.
	<i>Bezzia</i> sp.
	<i>Chironomus</i> sp.
	<i>Dicrotendipes</i> sp.
	<i>Glyptotendipes</i> sp.
	<i>Parachironomus</i> sp.
	<i>Paratanytarsus</i> sp.
	<i>Procladius</i> sp.
	<i>Pseudochironomus</i> sp.
	<i>Tanytarsus</i> sp.
	<i>Thienemannomyia</i> sp.
	<i>Zavreliella</i> sp.

for each transect and census; I considered each observation (spaced at 10-m intervals along a transect) a single patch 36 m³ in volume.

Bluegill predation in the middepth zone

I examined the spatio-temporal patterns of bluegill predation in the middepth zone in detail because (1) preliminary observations suggested that predation varied most there, (2) the middepth zone comprised the largest area in Dog Lake, and (3) no information relative to fish predation frequency, intensity, etc., was available for this habitat. Thus, bluegill foraging activity was monitored in the middepth zone over an 18-

mo period (long-term film data) using underwater time-lapse cinematography. Two permanent observation sites were filmed (Minolta 601 supereight time-lapse movie camera equipped with an underwater housing) simultaneously approximately every 2 wk (biweekly) from December 1985–June 1987. The film sites were situated 50 m apart at 3 m depth \approx 100 m from shore. Both observation areas included open lake bottom (covered by short understory plants) and *Panicum* patches. Each camera filmed a 1-m³ area for 24 h, exposing 1 frame every 20 s, yielding \approx 2000 daylight observations (frames) per site and census date (a total of \approx 240 000 observations during the study). A clock in an underwater housing was placed within camera range at each site to provide a record of time. Bluegills are generally inactive at night (Keast and Welsh 1968, M. J. Butler IV, *personal observation*) so observations were made between sunrise and sunset. I analyzed films frame by frame and recorded the number of bluegills present and feeding per observation (frame). Feeding bluegills were distinguished by their flared gills and orientation to a substrate, as confirmed by diver observations (Butler 1988a). In June 1987, I attempted to film both middepth sites once a week for 4 wk to estimate short-term variability in bluegill predation (short-term film data); exposures were made every 40 s for 48 h. To film for 48 h, a longer interval between observations (i.e., 40 vs. 20 s) was necessary because of limits imposed by film length. One camera failed during these filmings, so between-site comparisons in bluegill predation could not be made for this data set.

To analyze film data I summed observations within hours, yielding the total number of bluegill present and the number feeding per cubic metre per hour, two separate but presumably correlated estimates of predation. Bluegills were abundant in some observations and absent in others, so data were $\ln(x + 1)$ transformed and the residuals inspected to ensure homogeneity of variance. No bluegills were observed in the middepth zone from October–March (roughly corresponding to changes in water temperature above or below 20°C), so I omitted the winter 1985 and 1986 film data, creating two separate data sets for analysis: March–September 1986 and April–June 1987. On four occasions in 1986 (1 April, 3 and 15 May, 5 August) one of the two cameras failed. To avoid open cells in the 1986 data analysis, I estimated the missing data using the weighted marginal means and reduced the error degrees of freedom accordingly; the 1987 data were complete. The number of bluegills present per observation and the number feeding per observation served as dependent variables in four separate three-factor (Date \times Site \times Time-of-Day) ANOVAs; experimentwise error rate = 0.0125. The Time-of-Day factor had two levels, crepuscular (2 h before/after sunset/sunrise) and midday (2 h before/after 1200 EST). Hours within the Time-of-Day factor were the replicates in this design. In another set of analyses, I omitted the April, May, and August data

(where camera failure created incomplete data sets) and grouped biweekly censuses by month in a hierarchical design (three-factor nested ANOVA; site crossed with biweekly censuses and month, biweekly censuses nested within month) to estimate the variability of predation among months and the site \times month interaction. The short-term (June 1987), single-site film data describing the number of bluegill per cubic metre and the number feeding per cubic metre were analyzed in two three-factor nested (Week, Day nested within Week, Time-of-Day nested within Day) ANOVAs. Variance components were estimated for each factor and interaction in these analyses; experimentwise error rate = 0.025. These data (long- and short-term time-lapse observations) provided a detailed description of bluegill predation in the middepth zone at two sites over several temporal scales (i.e., season, month, biweek, week, day, and time-of-day).

Variable predation caging experiment

Treatments.—The importance of bluegill predation frequency on macroinvertebrate community structure was tested in a caging experiment in the middepth zone of Dog Lake. Three treatments were randomly applied to nine experimental cages (three replicates per treatment): (1) no predation, (2) constant predation, and (3) variable predation. I also monitored three partially caged areas to measure the effects of ambient predation while controlling for some cage effects (see Cage Design). Bluegill exclusion served as the no predation treatment, providing an estimate of prey community structure independent of predation. I established a constant predation treatment by including four bluegills (50–150 mm TL) in each of three cages. In the remaining three cages I varied bluegill abundances approximately every 2 wk to create a variable predation regime (Fig. 3). Bluegill densities were identical among variable treatment cages but fluctuated with time according to natural fluctuations I observed in the time-lapse films; densities ranged from 0–12 bluegills/cage. A 2-wk interval was chosen because: (1) it was the shortest interval at which I could monitor natural predation and manipulate predation regimes, and (2) bluegill predation in Dog Lake varies significantly at 2-wk intervals (see Bluegill Predation in the Middepth Zone). I increased bluegill densities in the variable treatment cages by seining fish from the shallow littoral zone and immediately adding them to the cages. To decrease bluegill densities, I opened cage entrances and (using SCUBA) chased bluegills from the cages. Whenever I entered the variable treatment cages I also visited the constant and no predation cages to check bluegill abundances and control disturbance among treatments.

Cage design.—In November 1985, I constructed the nine full-cages (3 \times 3 \times 2 m high with tops) out of 1.5-cm mesh Vexar screen, supported by eight polyvinyl chloride poles (3 cm diameter; 2.5 m tall) driven 0.5 m into the substrate. Aluminum lawn edging was

driven 10 cm into the substrate around the bottom edge of the cages to seal the bottoms. The large mesh allowed free passage of water and invertebrates, yet restricted the movement of all fish except fry (i.e., <15 mm TL). Permitting invertebrates to move in and out of the cages insured natural recolonization (see Cage Effects section), but may moderate predation treatment effects. A smaller mesh would have curtailed invertebrate movement, creating isolated prey populations and an exaggerated predator effect. The three partial-cages were similar to the full-cages except that only a 0.25-m tall mesh fence was lashed around the bottom of the polyvinyl chloride poles. Several preliminary cage controls were tested and the final design was a compromise between mimicking full-cage effects and allowing an accurate assessment of ambient predation; more complete cages attracted fish. Although partial-cages did not exhibit all the effects inherent in full-cages, they recreated some cage effects (see Cage Effects section).

Cages were arrayed parallel to the northeast shore of Dog Lake 10–15 m apart at 5 m depth. Large (9 m²) cages were chosen because this size defines an area larger than the largest bluegill school I observed in Dog Lake (≈4 m²), is less likely to affect bluegill behavior than small cages, and reduces cage effects relative to small cages. To control for initial differences in *Panicum* density at cage sites and differences arising from the destructive sampling of natural plants, I counted and removed the *Panicum* from each cage by cutting the stems at the substrate surface. One hundred artificial plants were then added to each cage to approximate original *Panicum* densities (mean number of *Panicum* per cage site = 128, SD = 76). The artificial plants mimicked the structure of the unbranched *Panicum* stems, were readily colonized by periphyton and macroinvertebrates, and were easily sampled and replaced (Butler 1988b).

Sampling design.—To assess the effect of the treatments on benthic and epiphytic community structure, I sampled the benthos and artificial plants within cages monthly from June 1986–November 1986. Partial-cages were sampled once every 3 mo to monitor natural prey communities. Because bluegills are not present in the middepth zone in winter (see Bluegill Distribution Among Lake Habitats), treatments were not applied from October–March. However, pre- and post-treatment samples were taken during the spring of 1986 (March and May) and winter of 1987 (January and February). Divers used corers (7.5 cm diameter) and a portable 1-m² grid to locate and collect 5 cm deep benthic samples from eight randomly chosen locations within each cage. No location was sampled more than once and, to minimize edge effects, cores were not taken within 0.5 m of cage walls. Species accumulation curves from preliminary samples indicated that eight cores sampled 75–85% of the species in the benthic community (Butler 1988b). A larger sample of species was

not possible unless >20 cores were taken per cage, which was not logistically feasible. Preliminary sampling and a two-factor nested ANOVA (factor 1 = cage; factor 2 = rows of cores within a cage; error term = cores within rows) also revealed that benthic prey abundances varied more between core samples taken within cages ($F = 0.89$; $df = 4,12$; $P > .05$; 88% of variance explained), than between cages ($F = 0.07$; $df = 1,12$; $P > .05$; 9% of variance explained). Thus, sampling effort was concentrated within cages (eight cores per cage), rather than between cages (three replicates per treatment) to reduce sampling error. Core samples were preserved in 10% buffered formalin and stained with rose bengal. In the laboratory, samples were washed through a 500- μ m sieve (United States Standard Sieve Series Number 35) and the remaining macroinvertebrates identified and counted.

In addition to core samples, four artificial plants were collected from each cage on each sample date. Four plant samples per cage was sufficient to collect ≈75% of the species present in Dog Lake (Butler 1988b). Artificial plants were made of polypropylene rope (0.5 cm diameter; 0.5 m long) cast in 4-cm³ concrete bases. Although shorter than *Panicum*, the yellow, artificial plants resembled the cylindrical, single-stalked natural plants. Preliminary experiments comparing macroinvertebrate colonization of real vs. artificial plants indicated that real plants may attract slightly more macroinvertebrates per plant (mean = 8.8, SD = 4.1) than artificial plants (mean = 7.3, SD = 5.2; $F = 3.05$; $df = 1,64$; $P = .06$). Nonetheless, relative comparisons among artificial plants collected from treatment cages were possible. Plants were collected arbitrarily from each cage, individually sealed in plastic bags, and transported to the laboratory where they were rinsed in a 500- μ m sieve. The macroinvertebrates retained in the sieve were counted and identified under a dissecting microscope. After sampling a cage, replacement plants were added to keep plant densities constant; individual plants were not resampled for at least 2 mo to permit recolonization. To assess the specific effect of bluegill predation on large, predatory invertebrate size distributions, the head widths of odonate larvae collected from plant samples were measured using a dissecting microscope fitted with an ocular micrometer.

Cage effects.—Cage effects, which are well documented in the marine benthic literature (e.g., Virnstein 1978) were evaluated by comparing light levels, water flow, macroinvertebrate densities (benthos and plants), and macroinvertebrate colonization of artificial plants in full- and partial-cages (Butler 1988b). Full-cages significantly decreased water flow at the substrate-water interface (ANOVA; $F = 7.13$; $df = 3,29$; $P < .005$). Light levels were also lower in full-cages, but similar to uncaged, heavily vegetated areas (ANOVA: $F = 882.68$; $df = 2,78$; $P < .05$). Full-cages significantly increased the total number of macroinvertebrates on plants (t test; $t = 3.35$; $df = 28$; $P < .01$), but decreased

benthic macroinvertebrate abundances, compared with those collected in partial-cages (t test; $t = 2.39$; $df = 9$; $P = .04$). Macroinvertebrate colonization rates (total number of individuals and species) on plants (two two-factor ANOVAs; cage and colonization day were the two factors; $P > .05$) and the number of species on plants ($t = 0.90$; $df = 31$; $P > .05$) or in the benthos ($t = 0.30$; $df = 9$; $P > .05$) were similar in full- and partial-cages. Because some cage effects were detected, only full-cage treatments (where cage effects were common to all treatments) were used to test statistical hypotheses. Thus, comparisons among the three experimental treatments were not confounded with cage effects. General comparisons between full-cage treatments and the partially caged ambient predation sites are based only on descriptive statistics (e.g., means and variances) and may be biased by cage effects.

Hypotheses and statistical analyses.—Variation in predation may affect prey community structure in many ways, and several possibilities were evaluated for benthic and epiphytic macroinvertebrates using various statistical methods. Below I present specific hypotheses and the statistical tests that address each.

1. *Total macroinvertebrate and taxonomic abundances are unaffected by predation regime and month.*—Differences in the number of macroinvertebrates or taxa ($\ln[x]$ transformed to standardize treatment variances) were analyzed using univariate two-factor (Treatment, Month) repeated-measures ANOVAs. In these analyses, cages served as replicates and the mean number of individuals (or taxa) per core (or plant) were the dependent variables; means were computed from within-cage samples. I used orthogonal contrasts to determine if the variable and constant predation treatments differed significantly.

2. *Macroinvertebrate community composition is unaffected by predation regime or Month.*—A two-factor Multivariate Analysis of Variance (MANOVA) was used to detect whether the abundances of the eight most numerous taxonomic groups in Dog Lake (Hydracarina, Chironomidae, Ephemeroptera, Odonata, Oligochaeta, Planaria, Trichoptera, and a Miscellaneous grouping) differed significantly among predator treatments or months of the year. A repeated-measures MANOVA was not used because it did not permit enough degrees of freedom to test treatment effects. The two-factor MANOVA can be justified on biological grounds in that sequential replicates were essentially independent because different core locations and plants were sampled on each occasion, and macroinvertebrate colonization is so rapid that recolonization would have been completed within the 4–6 wk sampling interval. Following the MANOVA, a discriminant function analysis identified those species groups whose abundances contributed significantly to differences among treatments and months. I used the discriminant function correlations (loadings) and partial F values (which essentially partition out the covariance

between variables) to determine the individual contribution of the species groups to the discriminant function. The larger the discriminant function correlation or partial F value for a particular variable, the greater that variable's contribution to the overall discriminant function. These two measures are less subject to predictor intercorrelations than are standardized discriminant weights or univariate F values (Dillon and Goldstein 1984). Only data accumulated from artificial plants were analyzed because cores contained too few individuals and species groups. In general, the multivariate approach is more informative for community analyses than diversity indices or multiple univariate ANOVAs on each species because: (1) it avoids the ambiguity of species richness and diversity indices relative to shifts in dominance among species, (2) the likelihood of a type I error is reduced, and (3) multivariate tests emphasize the community as the unit of response and are sensitive to correlated changes in species abundances (see Morin 1983).

3. *The spatial distribution of prey within or among cages is unaffected by predation regime or month.*—Within-cage patchiness was addressed by comparing, among treatments, the within-cage variances (i.e., variance among samples) in the number of macroinvertebrates found in cores and plants in two two-factor (Treatment \times Month) ANOVAs. To examine the variation in prey abundances between cages (i.e., variation among patches), two one-factor ANOVAs were used, one for core data and the other for plant data. I used the variance among cages computed for each monthly sample as a source of replication in this second set of ANOVAs because no spatial replication was available. However, using time-series samples as replicates decreases the sensitivity of the analysis. Despite differences in macroinvertebrate abundances among months, no Treatment \times Month interactions were detected in the two-factor repeated measures ANOVA discussed in section 1. Thus, in this particular analysis, differences among treatments can be attributed to treatment conditions, not differential treatment responses over time. Experimentwise error rates of $\alpha = 0.025$ were employed in both sets of ANOVAs, and variable and constant predation treatment effects were directly compared with orthogonal contrasts.

4. *Temporal fluctuations in prey abundance are unrelated to predation regime.*—I addressed this hypothesis by comparing (one-factor ANOVA), among treatments, the mean change (calculated from replicate cages) in macroinvertebrate densities between consecutive monthly samples. Core and plant data were analyzed separately, and orthogonal contrasts used to compare the effects of the variable and constant predation treatments.

5. *Size distributions of large invertebrate predators are unaffected by predation regime.*—I compared the size distributions of the odonates, the largest macroinvertebrate predators in Dog Lake, in two ways. First,

I examined treatment effects on the head widths of odonates in a one-factor ANOVA; a Bonferroni multiple comparison test was used to test for differences among treatments. Time was not used as a factor in this analysis because odonates were not very abundant; instead odonates were grouped by treatment over time. Again, omitting time as a factor in the design decreases the sensitivity of the analysis because treatment effects on odonate instars could not be independently evaluated. I also compared the impact of bluegill predation on the size range of large invertebrate prey collected in the three predator treatments using a two-sample nonparametric test of dispersion (Moses Distribution-Free Ranklike Test).

RESULTS

Bluegill distribution among lake habitats

Bluegill abundances were significantly related to both habitat ($F = 8.62$; $df = 2,30$; $P < .001$) and season ($F = 12.05$; $df = 1, 30$; $P = .001$). In summer, bluegills were more abundant in shallow and middepth habitats than in the deep, unvegetated zone (Bonferroni test; $P < .01$; Table 2). No bluegills were seen in middepth or deep sites during the winter. Habitat ($F = 5.74$; $df = 2,30$; $P = .008$), season ($F = 14.10$; $df = 1,30$; $P < .001$), and their interaction ($F = 4.42$; $df = 2,30$; $P = .02$) had strong effects on bluegill patchiness (i.e., variation in bluegill density along transects). During the summer, bluegill distributions were 3–5 times as patchy (clumped) in the middepth zone as in the deep or shallow regions of the lake (Table 2). Comparisons of bluegill patchiness among habitats and spatial scales also revealed that bluegills were most patchily distributed in the middepth zone, particularly at the smallest scale of 10 m (Fig. 1). Similarly, the number of bluegills per

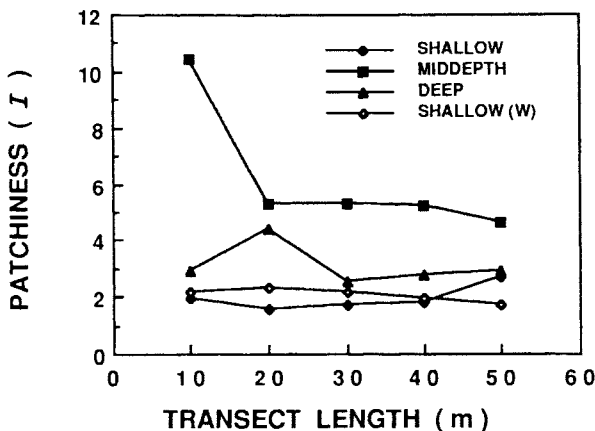


FIG. 1. Morisita's Index of Patchiness (I) describing bluegill distributions at five spatial scales (transect lengths) in the shallow, middepth, and deep zones of Dog Lake. Data presented are from observations made from May–October 1986 in all three habitats, and during the winter (W; January and February 1987) in the shallow zone; there were no fish in the middepth or deep zones in winter.

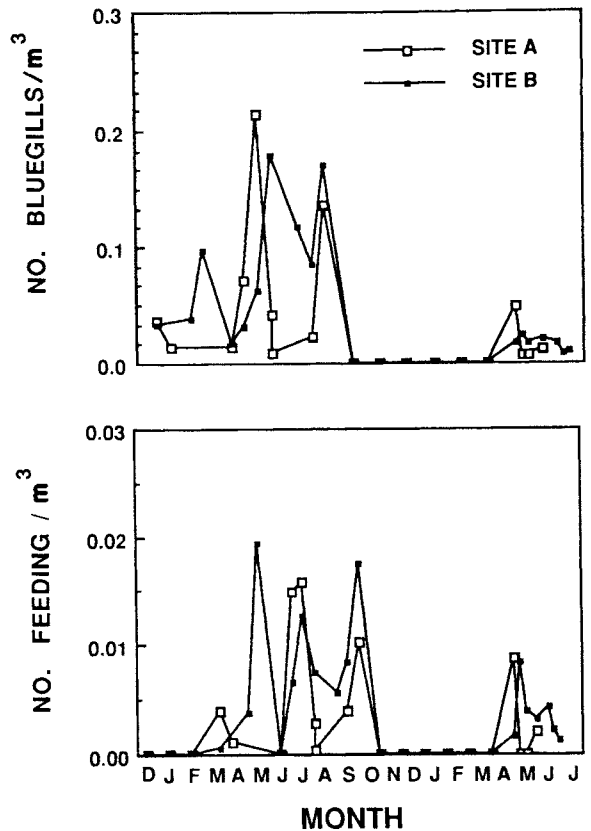


FIG. 2. The total number of bluegills present per m^3 per hour and the total number feeding per m^3 per hour at two sites in the middepth zone of Dog Lake from December 1985–July 1987. Data were obtained using time-lapse cinematography; totals per hour are based on 180 observations/h taken every 20 s during daylight.

patch (i.e., Lloyd's index of crowding) was highest for groups of fish observed in the middepth habitat and lowest in deep water (Table 2). These data suggest (and diver observations corroborate) that bluegills traveled in dense schools in the middepth zone during the summer, creating a locally patchy and intense predation regime. No bluegill predation occurred in the middepth or deep zones during winter because bluegills moved to shallow water. The patchy distribution of fish in the deep habitat was similar to that in the middepth zone, but bluegills were less abundant there and usually travelled in smaller shoals. In the heavily vegetated shallow habitat, bluegill densities (hence predation) were relatively homogeneous both spatially and temporally.

Bluegill predation in the middepth zone

No predation occurred in the middepth zone during winter (Fig. 1), but once bluegill moved into the middepth habitat in late March, predation increased until the breeding season began in late May (Fig. 2). Predation peaked in July and remained high throughout the summer until bluegills abruptly vacated the mid-

TABLE 2. Various indices describing bluegill abundances and distribution in shallow, middepth, and deep Dog Lake habitats during the summer and winter.

Season	Habitat	Number bluegill obs.		Lloyd's index of crowding		Morisita's index of dispersion		Total no. obs.	Total no. fish
		\bar{X}	(SD)	\bar{X}	(SD)	\bar{X}	(SD)		
Summer	shallow	5.54	(5.33)	9.36	(7.36)	1.96	(0.76)	145	844
	middepth	3.44	(1.67)	26.46	(11.88)	10.43	(8.59)	153	507
	deep	1.05	(1.64)	4.51	(8.04)	2.93	(1.77)	108	124
Winter	shallow	2.30	(0.14)	4.65	(0.10)	2.16	(0.18)	27	61
	middepth	0		0		0		31	0
	deep	0		0		0		26	0

depth zone in October (Fig. 2). More detailed analysis of the long-term time-lapse film data yielded similar results. In 1986 and 1987, the number of bluegills per cubic metre differed between biweekly censuses and between film sites when viewed at 2-wk intervals (i.e., site \times biweekly interaction), although in 1986 differences among censuses were marginal (Table 3). Similar trends were evident in the analyses describing the number of bluegills feeding per cubic metre (Table 3). Strong month, biweekly, and site \times biweekly effects were also evident in the analyses that included month as a factor

(Table 4). Thus, in addition to the biweekly and site \times biweekly effects detected in the main analysis, predation also varied significantly among months. Results from the analysis of the short-term (June 1987) film data indicate that the number of bluegills present or feeding per cubic metre differed little between weeks, days, or time-of-day (Table 5). Thus, a substantial portion of the variation in bluegill predation in the mid-depth zone can be attributed to differences between months (13–23%), biweekly censuses (12–26%), and between sites every 2 wk (14–28%; Tables 3 and 4).

TABLE 3. Results of four three-factor ANOVAs testing the effects of Biweekly observation intervals, Sites within the middepth zone, and Time-of-Day on two separate dependent variables in 1986 and 1987. Data were taken from underwater time-lapse films. Eight degrees of freedom were subtracted from the 1986 error term because eight missing observations were estimated.

Number of bluegill present per m ³ per hour										
1986										
Source	df	MS	F	P	Variance explained (%)	df	MS	F	P	Variance explained (%)
Biweekly (B)	10	395.16	2.25	.03	9	3	65.03	12.17	<.01	26
Site (S)	1	69.14	0.14	.72	3	1	7.03	0.18	.70	7
Time-of-day (T)	1	344.05	1.75	.22	1	1	0.78	0.12	.75	0
B \times S	10	502.11	2.86	<.01	26	3	39.53	7.40	<.01	28
B \times T	10	196.77	1.12	.37	2	3	6.28	1.18	.35	0
S \times T	1	174.73	0.91	.36	0	1	3.78	0.26	.65	5
B \times S \times T	10	192.65	1.10	.39	3	3	14.78	2.77	.08	16
Error	36	175.61			56	16	5.34			18

Number of bluegill feeding per m ³ per hour										
1986										
Source	df	MS	F	P	Variance explained (%)	df	MS	F	P	Variance explained (%)
Biweekly	10	3.657	1.72	.11	5	3	2.031	4.33	.02	12
Site	1	0.920	0.21	.65	2	1	0.031	0.02	.89	5
Time-of-day	1	0.557	0.32	.58	1	1	0.281	0.77	.44	1
B \times S	10	4.321	2.03	.05	14	3	1.448	3.09	.06	15
B \times T	10	1.757	0.83	.61	2	3	0.365	0.78	.52	2
S \times T	1	0.011	0.00	.96	4	1	0.281	0.21	.68	8
B \times S \times T	10	3.411	1.61	.14	17	3	1.365	2.91	.07	28
Error	36	2.125			55	16	0.469			29

TABLE 4. Short-term film analysis of the number of bluegill present and the number feeding at two middepth zone sites in Dog Lake in June, July, and September 1986 and April and May 1987.*

Number of bluegill present per m ³ per hour					
Source	df	MS	F	P	Variance explained (%)
Site	1	0.084	0.60	.44	3
Month	4	1.929	13.56	<.01	23
Biweekly	5	0.622	3.67	<.01	10
Site × month	4	0.128	0.90	.47	3
Site × biweekly	5	0.648	4.56	<.01	26
Hours (error)	80	0.142			37

Number of bluegill feeding per m ³ per hour					
Source	df	MS	F	P	Variance explained (%)
Site	1	0.000	0	.97	1
Month	4	0.350	6.20	<.01	13
Biweekly	5	0.224	3.96	<.01	14
Site × month	4	0.053	0.94	.44	0
Site × Biweekly	5	0.139	2.46	.04	14
Hours (error)	80	0.056			49

* Data were analyzed in a three-factor nested ANOVA; site was crossed with biweekly censuses (2-wk) and month, biweekly censuses nested within month, and hours nested within biweekly census (replicates).

Among-site differences in bluegill predation (i.e., site × biweekly census interaction) only occurred at 2-wk intervals, presumably because differences between sites "averaged out" over longer time periods as fish repeatedly visited the sites. Predation also varied considerably over short time scales (e.g., within and among hours of the day), but no significant differences were detected between days or weeks.

Variable predation caging experiment

To ascribe differences between the two predation treatments (constant vs. variable) to differences in the variability of predation and not mean predation, I calculated and compared the number of predation days the treatments experienced between each sample date (i.e., monthly). "Predation days" was defined as the number of bluegills present per square metre per day in the treatment cages. Because bluegill abundances within cages were censused at least biweekly, accurate estimates of predation intensity and variability were possible (Fig. 3). The mean predation levels experienced by the constant (0.49 bluegills·m⁻²·d⁻¹) and variable (0.47 bluegills·m⁻²·d⁻¹) predation treatments were similar (*T'* = 0.09; df = 5; *P* > .05), whereas the variance in the variable treatment (*s*² = 0.047) was significantly

(*F*_{max} test: *F* = 42.45; df = 6,6; *P* < .005) greater than that in the constant predation treatment (*s*² = 0.001). Thus, any difference in prey community response to these two treatments must be associated with differences in the variability of predation, not mean predation.

1. *Total macroinvertebrate and taxonomic abundances are unaffected by predation regime.*—Densities of macroinvertebrates and taxa depended on month (*P* < .001; Tables 6 and 7), but not predator treatment (*P* > .05). Some species-specific responses may have been obscured in this analysis because individual species densities were low and had to be lumped into larger taxonomic groups (e.g., Oligochaeta, Anisoptera, Zygoptera, etc.) for analysis. Overall, macroinvertebrate abundances (both benthic and epiphytic) tended to be higher in the variable and ambient predation treatments, and an order of magnitude higher on plants than in the benthos (Fig. 4). Total macroinvertebrate and species abundances on plants generally increased from May–January (Fig. 5), whereas benthic abundances remained relatively constant until October when they increased (Fig. 5). Winter increases in macroinvertebrate abundances corresponded with the movement of bluegills from the middepth zone and the cessation of experimental treatments (bluegills were removed from all cages during the winter).

2. *Macroinvertebrate community composition is affected by predation regime or month.*—The epiphytic macroinvertebrate community was altered by both predator treatment (*P* < .01) and month (*P* < .001; Table 8). Discriminant function analysis indicated that differences detected by the MANOVA corresponded to differences in the abundances of odonates, trichop-

TABLE 5. Results of two three-factor nested ANOVAs testing the effects of Week, Day, and Time-of-Day on two separate dependent variables. Data are from short-term films.

Number of bluegill present per m ³ per hour					
Source	df	MS	F	P	Variance explained (%)
Week	3	0.016	0.23	.87	4
Day	4	0.035	0.51	.73	6
Time-of-day	8	0.134	1.96	.08	22
Error	32	0.069			68

Number of bluegill feeding per m ³ per hour					
Source	df	MS	F	P	Variance explained (%)
Week	3	0.072	0.63	.60	2
Day	4	0.315	1.17	.34	2
Time-of-day	8	0.043	0.38	.92	16
Error	32	0.115			80

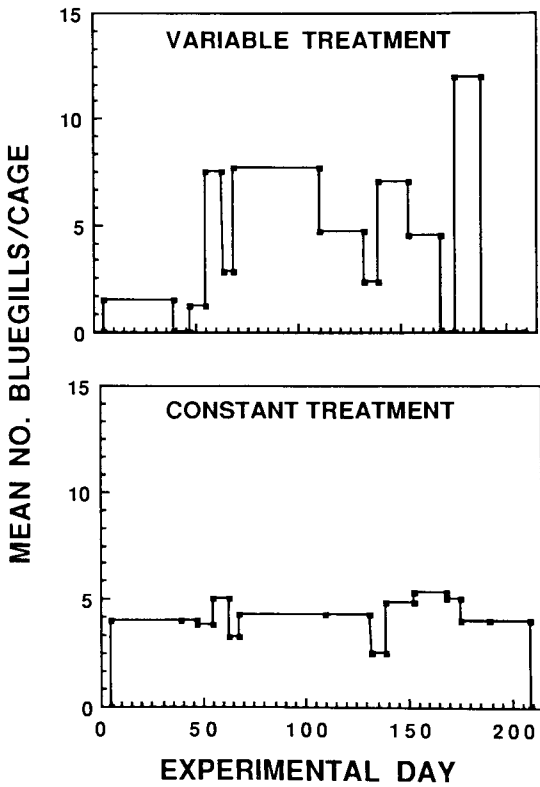


FIG. 3. The mean number of bluegills per cage in the variable and constant predation treatments during the 1986 experiment (three cages per treatment). Bluegill densities fluctuated significantly more in the variable treatment, but mean densities (for the duration of the experiment) did not differ.

terans, and oligochaetes (Table 9). Turbellarians, chironomids, ephemeropterans, and the miscellaneous prey category were negatively correlated with the abundances of mites, odonates, trichopterans, and oligochaetes (Table 9). Three of the last four prey categories consist largely of predaceous species (i.e., mites, odonates, trichopterans) and individuals in all four are either large or very active; these are uncommon traits where fish are abundant (Macan 1977, Healey 1984). Discriminant function correlations computed for the month factor were mostly negative, with no clear trends among prey taxa.

Densities of the three prey groups most affected by the predator treatments (trichopterans, odonates, oligochaetes) were altered in complex ways, with changes in trichopteran abundances dominating the overall response (Fig. 6). Trichopteran densities were similar in the no predation and variable predation treatments (overall means ± 1 SE: 4.13 ± 0.87 individuals/plant vs. 4.20 ± 0.79 individuals/plant), but lower in the constant predation treatment (2.25 ± 0.45 individuals/plant). Trichopteran densities in the different predator treatments became more disparate with time (Fig. 6). Odonate abundances peaked in late summer (Fig. 6) and mean (± 1 SE) densities in the variable, constant,

and no predation treatments were $0.37 (\pm 0.08)$, $0.51 (\pm 0.16)$, and $0.69 (\pm 0.15)$ individuals per plant, respectively. Few oligochaetes were collected from plants in the variable (mean ± 1 SE: 0.17 ± 0.10 individuals/plant) and constant (0.10 ± 0.05 individuals/plant) predation treatments, but their densities tripled (0.36 ± 0.12 individuals/plant) where fish were absent.

3. *The spatial distribution of prey within or among cages is unaffected by predation regime or month.*—Predation did not affect the within-cage variation in macroinvertebrate abundance in the benthos or on plants (Tables 6 and 7). However, the distribution of epiphytic macroinvertebrates changed significantly over time; benthic distributions were unaltered (Tables 6 and 7). The greatest variation in macroinvertebrate densities on plants and in the benthos occurred in the variable predation treatment and the least in the constant predation treatment (Fig. 7A). Although the ambient predation sites were not included in the analysis

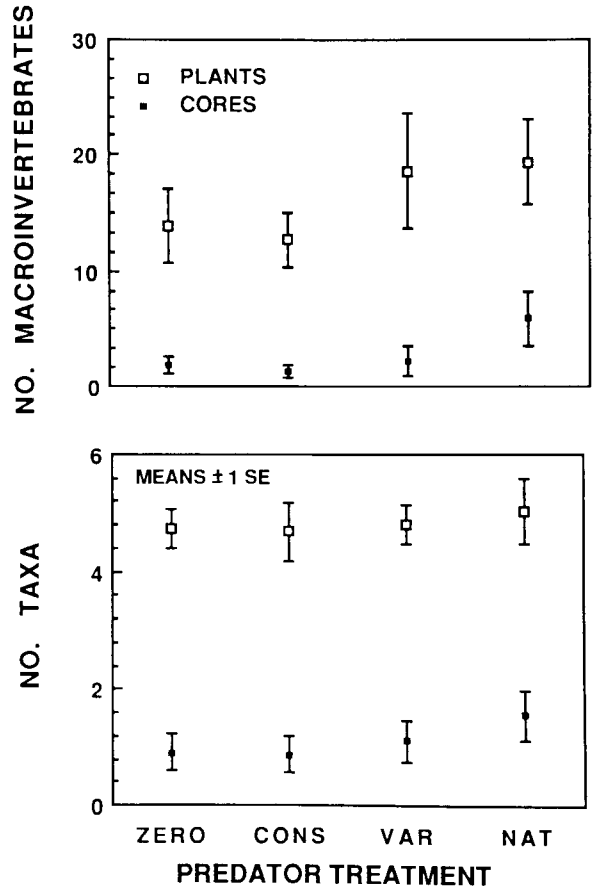


FIG. 4. Results of the field caging experiment testing the effects of no predation (ZERO), constant predation (CONS), and variable predation (VAR) treatments on the total number of macroinvertebrates and number of taxa collected per artificial plant and benthic core sample. Data collected from the ambient predation (i.e., natural predation; NAT) sites are provided for comparison.

TABLE 6. Results of four two-factor repeated measures ANOVAs testing the effects of bluegill predation treatments, months, and the treatment × month interactions on the mean and variance of the number of macroinvertebrates and species in plant samples.

Source	Mean no. macroinvertebrates/plant					Mean no. species/plant				
	df	MS	F	P	Approx. power*	MS	F	P	Approx. power	
Treatment (T)	2	0.410	1.13	.39	<0.20	0.0097	0.27	.78	0.70	
Error	5	0.362				0.0363				
Month (M)	5	3.034	41.56	<.01	0.99	0.9871	38.42	<.01	0.99	
T × M	10	0.110	1.51	.19	0.35	0.0317	1.23	.32	<0.35	
Error	25	0.073				0.0257				

Source	Variance, no. macroinvertebrates/plant					Variance, no. species/plant				
	df	MS	F	P	Approx. power	MS	F	P	Approx. power	
Treatment (T)	2	0.500	0.10	.90	<0.20	0.2258	2.43	.20	0.20	
Error	5	4.909				0.0929				
Month	5	8.561	7.17	<.01	0.95	1.4508	2.55	.06	0.45	
T × M	10	1.859	1.56	.18	0.40	0.6593	1.16	.37	<0.35	
Error	25	1.193				0.5683				

* The power of these analyses to detect differences among treatments of ≥ 1 SD.

(see Methods: Case Effects) the within-cage variation in prey densities at these sites equalled that in the variable predation treatment (benthic macroinvertebrates) or fell between those recorded in the constant and variable predation treatments (epiphytic macroinvertebrates; Fig. 7A).

Between-cage (among-patch) variation in the number of prey on plants ($F = 1.86$; $df = 2,15$; $P > .05$) or in the benthos ($F = 0.93$; $df = 2,12$; $P > .05$) did not differ significantly among the three predator treatments. However, orthogonal contrasts specifically comparing the constant and variable predation treatments suggest that between-cage variation in epiphytic prey densities may have been greater under a variable,

as opposed to a constant, predation regime ($T' = 1.76$, $df = 15$, $P = .09$; Fig. 7B). Ambient predation in Dog Lake created between-cage variation in prey numbers most similar to that in the variable predation treatment (Fig. 7B).

4. *Temporal fluctuations in prey abundance are unrelated to predation regime.* — Differences among treatments in the month-to-month fluctuations of epiphytic macroinvertebrates were marginally nonsignificant ($F = 3.02$; $df = 2,15$, $P = .08$), whereas fluctuations in benthic macroinvertebrate abundances were insignificant ($F = 0.02$; $df = 2,12$; $P > .05$). Orthogonal contrasts comparing the variable and constant predation treatments revealed a similar pattern, suggesting that

TABLE 7. Results of four two-factor repeated measures ANOVAs testing the effects of bluegill predation treatments, months, and the treatment × month interactions on the mean and variance of the number of macroinvertebrates and species in core samples.

Source	Mean no. macroinvertebrates/core					Mean no. species/core				
	df	MS	F	P	Approx. power	MS	F	P	Approx. power*	
Treatment (T)	2	1.1100	3.62	.11	0.25	0.3409	1.89	.24	<0.20	
Error	5	0.3067				0.1801				
Month (M)	4	1.5893	8.15	<.01	0.55	0.9730	8.88	<.01	0.91	
T × M	8	0.1472	0.75	.64	<0.20	0.1680	1.53	.21	<0.20	
Error	20	0.1950				0.1096				

Source	Variance no. macroinvertebrates/core					Variance no. species/core				
	df	MS	F	P	Approx. power	MS	F	P	Approx. power*	
Treatment (T)	2	4.1208	2.66	.16	<0.20	0.0527	0.09	.91	<0.20	
Error	5	1.5491				0.5757				
Month	4	1.7994	1.59	.22	<0.20	0.9262	3.79	.02	0.35	
T × M	8	0.3746	0.33	.94	<0.20	0.5189	2.13	.09	<0.20	
Error	20	1.1312				0.2442				

* The power of these analyses to detect differences among treatments of 1 SD.

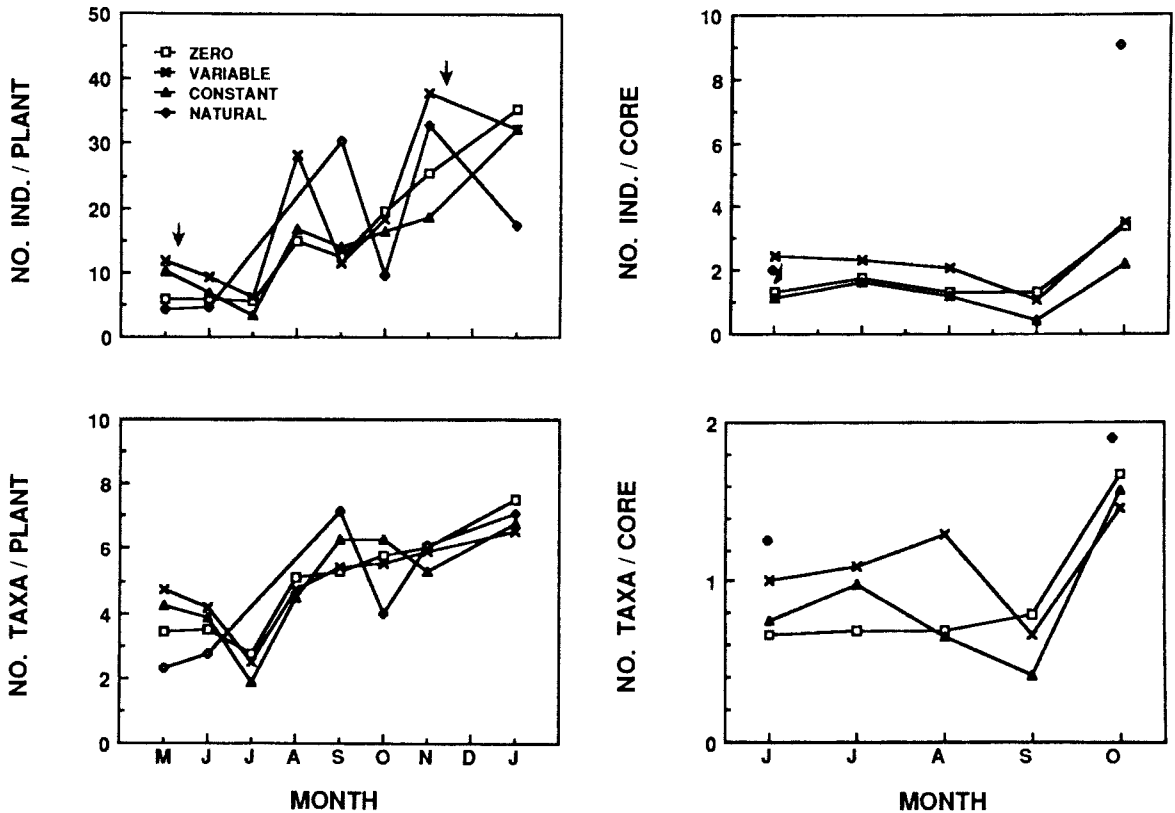


FIG. 5. The mean number of macroinvertebrates (top panels) and number of taxa (bottom panels) per artificial plant (left panels) and benthic core (right panels) plotted as a function of experimental treatment (zero, variable, and constant predation) and sample date. Data from the ambient (natural) predation sites are provided for comparison. The arrows in the top left panel indicate when the experiment was initiated and terminated.

prey abundances on plants may have fluctuated more where predation was variable ($T' = 1.89$, $df = 15$, $P = .08$; Fig. 7C). Temporal fluctuations in epiphytic prey densities were greatest in the ambient and variable predation treatments, and least where predation was constant or absent (Fig. 7C). No significant temporal changes in benthic prey were detected ($T' = 0.20$, $df = 15$, $P > .05$).

5. *Size distributions of large macroinvertebrate predators are unaffected by predation regime.*—Odonates differed in size among treatments (ANOVA: $F = 4.37$;

TABLE 9. Standardized discriminant function coefficients (Coeff.), discriminant function correlations (Corr.) or loadings, partial- F values (F), and significance levels (P) for each of the eight macroinvertebrate prey categories analyzed in the two-factor (predation regime, month) MANOVA.*

Prey type	Predation regime			
	Coeff.	Corr.	F	P
Turbellaria	-0.8905	-0.2320	2.17	.13
Hydracarina	0.1891	0.0648	0.09	.92
Oligochaeta	0.8762	0.3457	4.02	.03
Diptera	-0.3126	-0.2702	1.21	.31
Odonata	0.6219	0.3038	3.47	.05
Trichoptera	0.6708	0.1668	6.46	<.01
Ephemeroptera	-0.4515	-0.3190	1.48	.25
Miscellaneous	0.2613	-0.1966	0.37	.69

Prey type	Month			
	Coeff.	Corr.	F	P
Turbellaria	-0.5036	-0.4339	15.93	<.01
Hydracarina	-0.8110	-0.4514	5.41	<.01
Oligochaeta	-0.1638	-0.0014	2.26	.08
Diptera	-0.1460	-0.1224	8.80	<.01
Odonata	0.4869	-0.0180	6.37	<.01
Trichoptera	-0.7429	-0.5872	7.39	<.01
Ephemeroptera	0.3553	-0.0863	1.13	.37
Miscellaneous	-0.0140	-0.0406	0.36	.87

TABLE 8. Summary of MANOVA testing the effects of blue-gill predation regime, month, and their interaction on eight macroinvertebrate prey categories. Roy's largest root, Hotelling's trace, Pielou's criterion, and Wilks' lambda were calculated in the MANOVA and yielded identical conclusions; values of Wilks' lambda are shown for example.

Source	Hy-pothesis df	Error df	Approx. F value	Wilks' lambda	P
Predation	16	46	2.58	0.2776	<.01
Month	40	103	6.02	0.0052	<.01
Interaction	80	154	1.14	0.0522	.24

* Corresponding values for the nonsignificant (MANOVA) predation regime \times month interaction term are not provided.

df = 2,91; $P < .025$; $P < .001$ in all three multiple comparison tests). The largest individuals were found in the no predation treatment (mean head width ± 1 SE: 12.9 ± 0.9 mm) and the smallest in the constant predation treatment (8.9 ± 0.8 mm; Fig. 8); head width in the variable predation was 10.8 ± 1.2 mm. The variance in odonate sizes was greater in the no predation treatment ($P = .01$; Moses Ranklike Test; Hollander and Wolfe 1973: 92-99), and possibly in the variable predation treatment ($P = .09$), than in the constant predation treatment (Fig. 8). Size ranges were similar in the variable and no predation treatments (P

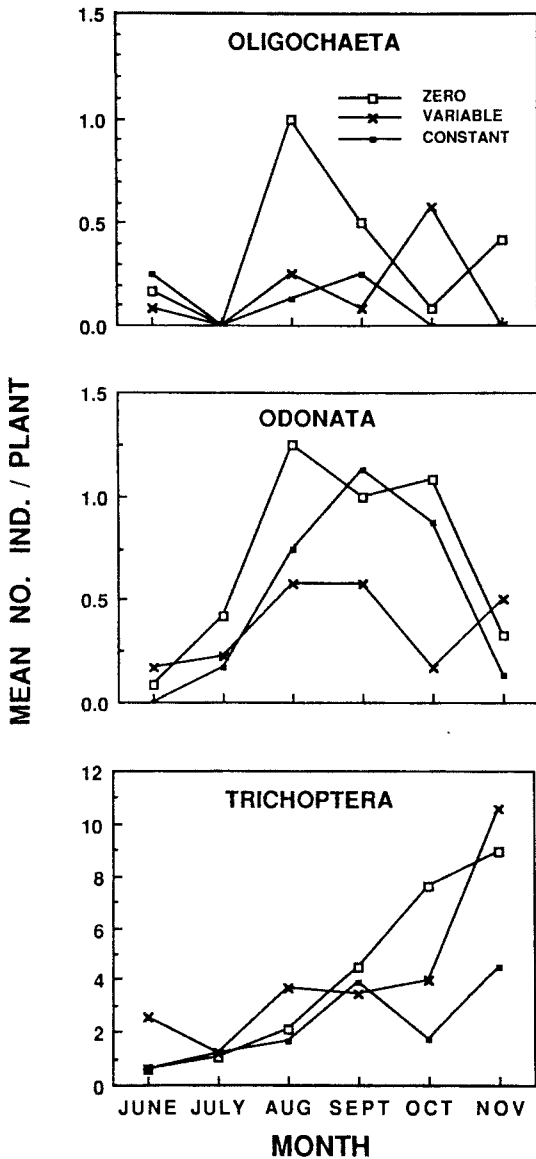


FIG. 6. The mean number of Oligochaeta, Odonata, and Trichoptera collected per artificial plant plotted for each predator treatment (zero, variable, and constant bluegill predation) and month.

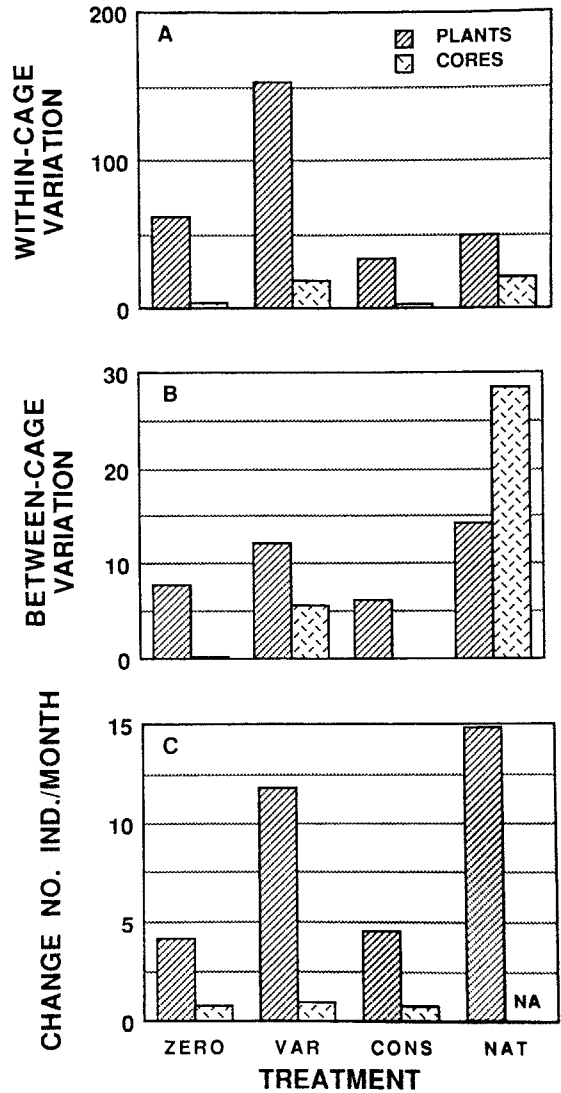


FIG. 7. The effect of experimental treatment (zero, variable, and constant predation; ZERO, VAR, and CONS, respectively) on the within-cage variation (top panel), between-cage variation (middle panel), and the variation among monthly samples (bottom panel) in the number of macroinvertebrates collected on artificial plants and in benthic cores. Natural (NAT) background values calculated from samples collected at the ambient predation sites are presented for comparison; NA = value not available because the sampling intervals exceeded 1 mo.

> .10). These trends in odonate size distributions (i.e., means and variances) among treatments also held for both odonate genera in Dog Lake. The largest, *Pantala*, a dragonfly found on plants and in detritus, were collected from the variable (mean head width ± 1 SE: 11.8 ± 6.1 mm) and no predation (11.7 ± 6.1 mm) treatments. Where predation was constant, *Pantala* were smaller and had a more uniform size distribution (headwidth 10.2 ± 3.9 mm). Similarly, the plant-climbing damselfly *Enallagma*, was largest and most

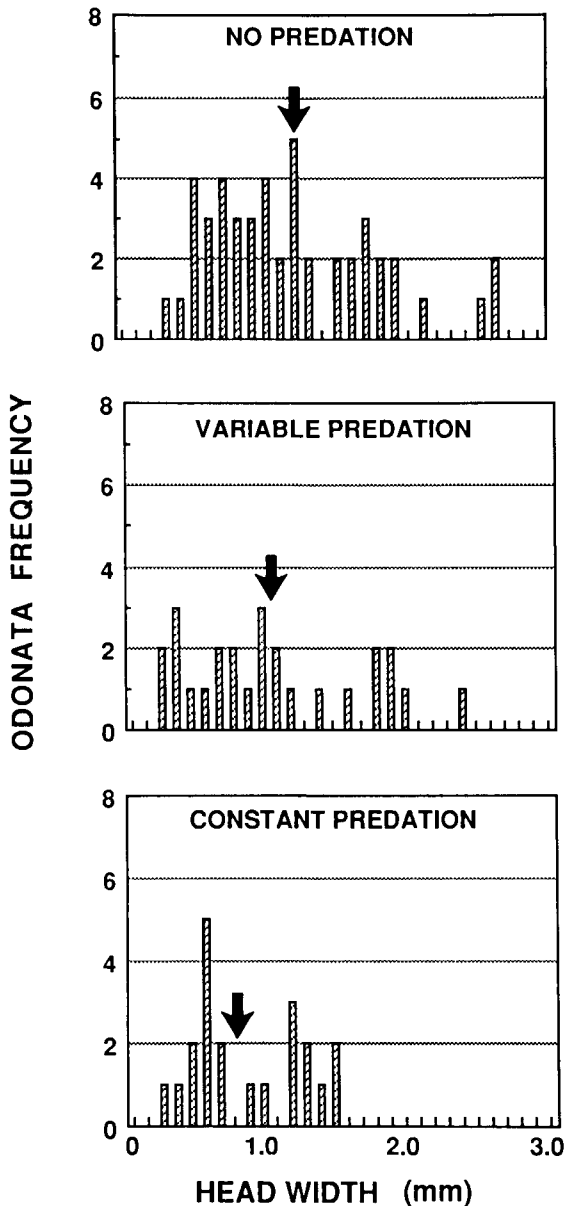


FIG. 8. Odonate size frequency distributions for individuals collected from artificial plants and benthic cores in the no predation ($n = 47$), variable predation ($n = 26$), and constant predation ($n = 21$) treatment cages. Arrows indicate the mean sizes in each treatment.

variable in size in the no predation (headwidth 11.2 ± 5.2 mm) and variable predation treatments (10.5 ± 6.1 mm), compared to their size distribution in the constant predation treatment (7.8 ± 3.5 mm).

DISCUSSION

Patterns of predation in lentic systems

Detailed observation of bluegill foraging suggests that predation rates within Dog Lake differed markedly among habitats and seasons, creating spatial and tem-

poral gradients in predation intensity. During the summer, bluegills were dense and evenly dispersed in the vegetated, shallow zone, creating a rather homogeneous predation regime. A patchy, locally intense predation regime existed in middepth and deep water habitats where emergent vegetation was patchy or nonexistent, and bluegills usually shoal (i.e., travelled and fed as a group). Predation was particularly intense within patches in the middepth zone, as indicated by the high mean crowding indices there and the fact that bluegill feeding rates increase with shoal size (Mittelbach 1984b, Butler 1988a). Bluegill predation also varied significantly among sites in the middepth zone with a periodicity of 2–4 wk. These differences did not persist over longer durations because sites were repeatedly visited by foraging fish, which eventually reduced the between-site variation in predation. However, the onset of winter abruptly altered these patterns. No bluegills were observed in the middepth and deep sites once water temperatures dipped below 15°C. Instead, bluegills concentrated in the warmer, shallow zones where they were active and continued to feed (although their feeding rates were probably reduced in the cool water). Macroinvertebrate colonization data support the notion that predation rates dropped in winter because macroinvertebrate densities and sizes were greatest during winter in all habitats, including the shallow zone where fish were dense (M. J. Butler, *unpublished manuscript*). Similar winter effects were noted in Gilinsky's (1984) study of a littoral zone in North Carolina. These seasonal patterns of fish abundance stand in contrast to those observed at higher latitudes. In cool temperate regions, winter lake water temperatures are greatest in the hypolimnion, so fish overwinter in deep water and feed sporadically (Hall and Werner 1977). Thus, drawing conclusions from studies conducted solely during the summer in the shallow littoral zones of northern lakes may provide an overly simplistic view of the patterns of fish predation, and perhaps macroinvertebrate community structure in lentic systems.

Variable predation and prey community structure

Variable predation by bluegills created macroinvertebrate communities unlike those resulting from constant predation, and generally mimicked natural conditions in Dog Lake better than a constant predation regime. In fact, in every test for a predator effect (significant or nonsignificant), the variable predation treatment mean exceeded that of the constant predation treatment, a statistically improbable result (Binomial test; $N = 12$; $P = .0002$). Variable predation had perhaps its most marked effect on macroinvertebrate community composition. Changes in the abundances of various taxa were complex and intercorrelated, and prey size distributions, an often overlooked component of community structure, were altered along with species abundances. Large or active invertebrates were pref-

entially eaten by bluegills, increasing the relative abundances of smaller, more sedentary species (Gilinsky 1984, Morin 1984a, b, Pierce et al. 1985). Three prey categories (oligochaetes, odonates, and trichopterans) responded strongly to predators, but interpreting treatment effects based on species abundances alone can be misleading. For example, odonates were most dense where bluegills were excluded, a result attributable to predation by bluegills, but odonate abundances were also higher in the constant predation treatment than the variable predation treatment. This result would be difficult to interpret if it were not known that only small odonates persisted under constant predation, whereas a variety of sizes remained where predation was variable. This implies that variable predation by size-selective predators expands prey size distributions, perhaps because temporally variable predation may also be spatially heterogeneous (depending on the frequency and duration of predation at that locale). If predation is infrequent or of short duration, the entire area may not be searched by predators, and even preferred prey may escape predation via temporary spatial refugia. Thus, large odonates may persist where predation is variable and in turn may inflict heavy mortality on smaller odonates (Morin 1984a, Pierce et al. 1985), driving down total odonate abundance. This scenario suggests that the effects of variable predation may cascade through the system via second-order predators or other indirect mechanisms, precipitating complex changes in community composition.

Variable predation had no significant effect on within-patch (cage) heterogeneity in prey abundances, but it appeared to enhance the between-patch variation and temporal fluctuations in prey numbers on plants. Further evidence demonstrating the significance of fluctuating predation in maintaining prey spatial heterogeneity is provided by the fact that the variability in prey abundances among cages and treatments was greater during the experiment than before or after it. Similar populations subject to stochastic sources of mortality (e.g., variable predation) can randomly diverge, increasing the among-population variation in abundance (see DeAngelis and Waterhouse 1987 for review). Perhaps the increased between-patch variation in prey numbers observed where predation varied is an example of this phenomenon. Independent confirmation of the effect of predation on prey spatial heterogeneity is limited, but a few studies suggest that predators can increase heterogeneity in prey populations. I found evidence for this effect when I manipulated gyrenid beetle densities in macrophyte patches and discovered that bluegills reduced mean prey densities and increased the variance to mean ratio of the prey distribution (M. J. Butler IV, *personal observation*). Similar results have been obtained in very different systems. For example, predatory whelks consume barnacles and increase their patchiness on Australian rocky shores (Fairweather 1988), while aphid

distributions in California alfalfa fields are made more heterogeneous by ladybird beetle predation (Gutierrez et al. 1980).

Temporal fluctuations in prey abundance may also be magnified where predation is variable, as appeared to be the case for the epiphytic macroinvertebrates in this study. One might expect that prey densities would fluctuate most in a variable predation treatment, because bluegill densities were continually altered in those cages. But it is important to note that (1) I manipulated bluegill density in the variable treatment in response to changes in natural densities observed in the lake, and (2) that the resultant fluctuations in prey densities were nearly identical to those observed in nature. Thus, monthly fluctuations (i.e., short-term variance) in prey abundances in the middepth zone of Dog Lake were a direct consequence of variation in bluegill predation. Although the generality of this result remains to be tested, it is nonetheless consistent with theory. Prey population fluctuations should be most dramatic where disturbance (e.g., predation) is frequent and variable, and where the temporal scale of disturbance equals or exceeds prey generation (i.e., recolonization) rates (Levins 1968). These conditions are met in the middepth zone of Dog Lake where shoals of foraging bluegill visit patches and macroinvertebrates subsequently recolonize them within ≈ 2 wk. This type of between-patch variation, believed to result from random inter-patch prey migration, within- and between-individual variation in predator foraging tactics, and interpatch environmental stochasticity (Chesson 1978), stabilizes unstable predator-prey population dynamics and promotes coexistence of predators and prey (see Murdoch and Oaten 1975, Chesson and Case 1986).

Although my experimental design was appropriate as an initial attempt to investigate the consequences of variable predation per se, it did not allow me to distinguish effects arising from changes in predation intensity from those attributable to changes in predation frequency. Because the predation regime employed in the variable predation treatment was meant to mirror that in Dog Lake, it varied in both frequency and intensity. I usually altered bluegill presence (i.e., frequency of predation) in the variable treatment cages every 2 wk, but sometimes (depending on natural predation rates observed in the lake) bluegill abundances remained constant in those cages for up to 6 wk. Similarly, the intensity of bluegill predation fluctuated between 0 and 12 fish per cage. Thus, as in nature, predator frequency and intensity were confounded in this treatment. To my knowledge the relative effects of predation frequency and intensity have not been explicitly addressed, but if predation is viewed as a form of disturbance (e.g., Ayling 1981, Duggins 1983), then theoretical predictions may be drawn with reference to interhabitat differences in lentic predation regimes and the intermediate disturbance hypothesis. The intermediate disturbance hypothesis (Connell 1978, Lub-

chenco 1978) predicts that species diversity will be maximized at intermediate frequencies of disturbance. Like any disturbance, if predation is very frequent relative to the life-span of the prey, it essentially becomes a constant source of mortality. Constant, size-selective predation decreases prey densities and creates a more homogeneous distribution of mostly small, inactive prey, conditions characteristic of shallow littoral zones (Macan 1977, Gilinsky 1984). In middepth littoral zones, the diversity of prey sizes and the spatio-temporal heterogeneity of the community are enhanced by intermediate frequencies of predation. One might also suspect that in the deep zone where fish are generally absent macroinvertebrates would be larger and more homogeneously distributed, and that predator-prey interactions among invertebrates might be more prevalent. Similar predictions might be tenable based on disturbance intensity. Populations exposed to severe disturbances are more susceptible to local extinction (Leigh 1981) and these effects may be manifest at the community level. Intense predation by fishes reduces total macroinvertebrate abundances and, via the consumption of rarer species, species diversity (Healey 1984). Of course, frequency of predation may interact with predation intensity to allow diverse prey communities to persist under intense but patchy disturbances (see Pickett and White 1985). Perhaps this is the case in deeper lentic habitats where fish tend to shoal and the abundances of certain prey types (e.g., active predators) and size classes (e.g., large individuals) depend largely on the patchy nature of predation. For now we can only speculate as to the relative importance of various components of predation to prey community structure, but future research should move beyond simple tests of general predator effects (e.g., effect of different predator species or numbers of predators) and incorporate more experiments testing the independent effects of predation intensity, frequency, and duration.

Predation and prey recolonization

Macroinvertebrate colonization, like predation, differs among habitats and seasons (M. J. Butler, *unpublished manuscript*), and may interact with predation in structuring lentic prey communities. The major source of new recruits in most lakes is the shallow littoral zone, and macroinvertebrates usually disperse to other habitats from there (see Sheldon 1985 for review). Differences in prey abundance or community composition among habitats or seasons can be generated by recruitment processes, but within habitats or seasons rapid colonization reduces the variance in prey distributions and minimizes differences in community composition (M. J. Butler, *unpublished manuscript*). In fact, colonization is so quick that defaunated plants and benthos are completely recolonized in 2–3 wk (Cowell 1984; M. J. Butler, *unpublished manuscript*), a time scale strikingly similar to that where predation

varies most (see Results: Bluegill Predation in the Mid-depth Zone). Thus, variation in predation by fishes coupled with rapid macroinvertebrate recolonization of denuded patches creates a chaotic system of prey reduction and reestablishment that may be critical in maintaining the heterogeneity inherent in lentic macroinvertebrate communities. In fact, rapid recolonization can be adaptive where the probability of mortality (e.g., predation) is temporally and spatially stochastic (Parsons 1982), and in patchy environments it may be necessary for long-term community persistence (Murdoch and Oaten 1975, Hastings 1977, Caswell 1978).

Prey recolonization capabilities can also have serious ramifications for the design of caging experiments testing predation. For example, rapid macroinvertebrate recolonization in Dog Lake probably moderated the impact of predation in my experiment because macroinvertebrates could easily pass through the large mesh (1.5 cm) of my cages. While this would not bias comparisons among treatments, it resulted in a more conservative, and realistic, test of predator effects. Confining predators and prey within small enclosures generally strengthens treatment responses, but extrapolating those results to natural systems where predators and prey are mobile may be difficult and inappropriate (Virnstein 1977).

In summary, our perception of the role fish predation plays in lentic macroinvertebrate communities may be oversimplified because we generally have not incorporated geographic, seasonal, and habitat-specific differences in predation in our conceptual models. Most studies have been conducted in shallow, densely vegetated littoral zones where fish predation is pronounced, but relatively homogeneous. However, in the middle and deep infralittoral zones clumped predators create a patchy, intense predation regime that varies across similar regions within habitats. This variable predation regime, in contrast to the more conventional constant predation treatment, may enhance the spatial and temporal heterogeneity of prey populations and significantly alter prey community structure. In systems strongly influenced by predators, variation in predation, independent of mean predation effects, may be an important component contributing to structure and heterogeneity in prey communities.

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