Littoral invertebrate abundance in bluegill spawning colonies and undisturbed areas of a small pond

CLAY L. PIERCE,[1] KAREN ANN MUSGROVE, JEAN RITTERPUSCH, AND NANCY E. CARL
Department of Zoology, University of Maryland, College Park, MD, U.S.A. 20742

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Bluegill (*Lepomis macrochirus*) spawning activity creates benthic disturbances in the littoral zone of ponds and lakes. We assessed invertebrate densities and biomass in bluegill spawning colonies and nearby undisturbed areas before and after the onset of nest construction in a small pond. Juvenile fish abundance and prespawning sediment particle size distributions were also quantified. These data were used to evaluate whether bluegill spawning activity affects the abundance of benthic invertebrates. Densities and biomass of most macroinvertebrate taxa were similar before and just after nest construction. Insects tended to be more abundant in undisturbed areas 6 weeks after nest construction, while oligochaetes were more abundant in spawning areas. Total macroinvertebrate densities and biomass did not differ significantly on any sampling date. Microinvertebrates (principally cladocerans and copepods) were much more abundant in undisturbed areas before spawning. Copepods and ostracods were more abundant in spawning areas after nest construction. Juvenile fish abundances were similar before spawning, but were significantly greater in undisturbed areas after spawning began. Macrophyte inhibition, reduced invertebrate colonization, differential predation pressure from juvenile fish, and other potential effects of spawning activity may account for some of these patterns.

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La fraye du Crapet arlequin (*Lepomis macrochirus*) entraîne des modifications du benthos dans la zone littorale des lacs et des étangs. Nous avons mesuré la densité et la biomasse des invertébrés aux sites de fraye des colonies de crapets et dans les régions intactes environnantes d'un petit étang, avant et après le début de la construction des nids. L'abondance des poissons immatures et la répartition selon la taille des particules sédimentaires ont également été quantifiées avant la fraye. Ces données ont permis d'évaluer les effets de la fraye des crapets sur l'abondance des invertébrés benthiques. La densité et la biomasse de la plupart des taxons sont demeurées semblables avant et juste après la construction des nids. Les insectes avaient tendance à être plus abondants dans les régions intacts 6 semaines après la construction des nids, alors que les oligochètes étaient plus abondants aux sites de fraye. La densité et la biomasse totales des macroinvertébrés ne différaient pas significativement d'une journée à une autre. Dans les zones avoisinantes, les microinvertébrés (surtout les cladocères et les copépodes) étaient beaucoup plus abondants avant la construction des nids. Les copépodes et les ostracodes étaient plus abondants aux sites de fraye après la construction des nids. L'abondance des poissons immatures était la même aux sites de fraye et dans les zones avoisinantes avant la fraye, mais significativement plus abondante dans les zones avoisinantes après le début de la fraye. Certains de ces résultats peuvent être attribuables à l'inhibition des macrophytes, à une colonisation moins grande d'invertébrés, à une pression de prédation différentielle par les poissons immatures et à d'autres effets de la fraye.

[Traduit par la revue]

Introduction

Fish influence aquatic communities in ways other than through direct predation, including nutrient enrichment (Hrbáček *et al.* 1961; Lamarra 1975; Durbin *et al.* 1979), alteration of prey behaviour (see references in Dill 1987), and habitat disturbance (Hildebrand 1971; Orth 1975; Reidenauer and Thistle 1981; Cowell 1984; Carpenter and McCreary 1985; Fletcher *et al.* 1985). Evidence accumulating from a wide variety of systems suggests that natural disturbances, such as habitat disruption by other organisms, may play an important role in the structure and function of communities (Sousa 1984; Pickett and White 1984).

Bluegill (*Lepomis macrochirus*) spawning activity creates disturbances (Fig. 1) in the littoral zone of ponds and lakes. Males construct nests in shallow water by vigorously displacing large amounts of sediment and debris (Bain and Helfrich 1983), leaving circular depressions (Morgan 1951; Avila 1976). Nests are located in tightly packed clusters (referred to as colonies), which may contain from a few to several hundred nests (Dominey 1980, 1981; Gross 1982). Actual spawning periods are brief and highly synchronized within colonies (Dominey 1981), but males occupy nests for several days afterward to guard eggs and larvae (Gross 1982). This sequence is repeated several times during the breeding season, which lasts from 1 to 3 months during the spring and summer (Beard 1982).

As has been reported elsewhere (Miller 1963; Avila 1976), we have observed that bluegills establish spawning colonies in the same locations year after year at our study site. Thus, the benthic communities within these colonies experience a yearly and prolonged habitat disturbance. The purpose of this study was to assess invertebrate densities and biomass in spawning colonies before and after the onset of nest-building activity, and to compare those with abundances in nearby undisturbed areas. Our results provide a test of the hypothesis that bluegill spawning activity affects benthic invertebrates and a descriptive base from which further testable hypotheses can be drawn.

Study site

Our study was conducted in Farm Pond, located on the Patuxent Wildlife Research Center (U.S. Fish and Wildlife Service) (39°2′ N, 76°47′ W) in Prince George's County, Maryland, U.S.A. Farm Pond has a surface area of 0.33 ha and a maximum depth of 2 m, and receives periodic discharges from a small spring-fed reservoir nearby. Water temperatures at 0.3 m ranged from 6°C at 07:00 in mid-March to 27°C at 19:00 in early June. Dissolved oxygen concentrations at the same depth ranged from 12.1 mg/L at 07:00 in mid-March to 4.4 mg/L at

[1]Present address: Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montréal, Que., Canada H3A 1B1.

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FIG. 1. A small spawning colony in Farm Pond. Nests are 30–35 cm in diameter.

07:00 in early June. The littoral zone of the pond supports a dense band of rushes (*Eleocharis quadrangulata*) from the shoreline to about the 0.5-m depth contour, with water shield (*Brasenia schreberi*) extending out to roughly the 1-m contour. Macrophyte growth appears much less dense in spawning areas, presumably due to substrate disturbance (Carpenter and McCreary 1985). Decaying macrophytes and leaf fall from trees around the shoreline contribute to a heavy accumulation of detritus on the bottom. Bluegills and largemouth bass (*Micropterus salmoides*) are abundant, and are the only fish species found in Farm Pond.

Methods

We sampled from two spawning colonies that were large for this pond, discrete, and easily accessible. Both colonies were located between the shoreline and the 0.5-m depth contour, and contained 20–40 densely packed nests. They were roughly 35 m apart, and both were surrounded by undisturbed areas. These adjacent undisturbed areas served as controls for comparison with the spawning areas. Each spawning colony and adjacent undisturbed area was treated as a block in statistical analyses.

We sampled benthic invertebrate populations in these areas on three dates during 1984: 18 March, 28 April, and 8 June. Male bluegills began nest construction between 22 and 26 April. Thus, invertebrates were sampled just over a month before spawning activity, a few days after the onset of nest construction, and 6 weeks into the breeding season. During this period no nests were observed in the adjacent undisturbed areas, and nests within the colonies appeared to be constantly maintained by male bluegills.

Macroinvertebrates were sampled with a Hess sampler (Southwood 1978) (area sampled = 0.035 m^2, mesh size = 0.5 mm). Aquatic macrophytes were pulled or cut off at the substrate, and all vegetation, detritus, and associated organisms were transferred to the sample bag. This was followed by 20 forceful sweeps of the water in the cylinder by hand to standardize sampling effort. Five samples were taken from each of the two spawning colonies and two undisturbed areas on each date (i.e., 20 total samples per date). Microinvertebrates were sampled with inverted-funnel samplers (Brakke 1976) (area sampled = 0.013 m^2) placed in sampling areas for 24 h prior to macroinvertebrate sampling. Three such samples were taken from each area on each date (i.e., 12 total samples per date). All samples were taken randomly at depths of approximately 0.2–0.4 m, and preserved in the field with 70% ethanol.

Macroinvertebrate samples were washed in a No. 35 sieve (0.5-mm mesh), and the macroinvertebrates were separated from detritus by sugar flotation (Anderson 1959). Specimens were identified, counted, and measured for conversion to biomass with published regressions (Benke 1972; Smock 1980). Taxa were subsampled before measuring when they numbered more than 40 per sample. Vegetation and detritus from each sample were dried (60°C, 48 h) and weighed after thorough washing. These data were examined as potential covariates in the statistical analyses. Microinvertebrate samples were subsampled by 2.5, 5, 10, 20, or 30% depending on sample densities. Cladocerans were identified to genus and copepods (virtually all were cyclopoids) were identified as either adults–copepodites or nauplii. All specimens within subsamples were identified and counted in a plankton wheel, and the first 10 in each taxon were measured for conversion to biomass with published regressions (Dumont *et al.* 1975). Densities and biomass within the Cladocera and Copepoda were pooled for analysis.

We monitored juvenile fish abundance by placing unbaited minnow traps in sampling areas, yielding catch per unit effort comparisons between spawning and undisturbed areas. Six traps were set for 12 h in each area on the day before invertebrate sampling dates. Captured fish (all were bluegills) were counted and released.

We determined the sediment particle size distributions from three core samples (diameter = 9 cm, depth = 8 cm) taken in each area on 22 March, before the onset of spawning activity. Detritus was removed by hand sorting, coarse sieving (16 mm), and differential settling in a water column. Samples were wet-sieved, dried (60°C, 48 h), and weighed. Sediment fractions were classified according to Cummins (1962): very fine sand, silt, and clay (< 0.125 mm); fine sand (0.125–0.25 mm); medium sand (0.25–0.5 mm); coarse sand (0.5–1 mm); very coarse sand (1–2 mm); fine gravel (2–4 mm); medium gravel (4–8 mm); coarse gravel (8–16 mm).

The invertebrate response variables analyzed were numbers per sample and biomass per sample of several major taxa. A two-way ANOVA (block × treatment) was performed on each response variable for each date, and data were transformed ($\log_e (x + 1)$, $(x + 0.5)^{1/2}$, or $(x + 0.5)^{1/4}$ to stabilize variances according to recommendations in Allan (1984). (Preliminary analyses indicated that detritus was not a significant source of variation in any taxon, so it was not included in ANOVAs.) To test for differences in sediment particle size distribution, we used modified ANOVAs for continuous proportions (Stephens 1982). All analyses were performed using the GLM procedure of SAS (Ray 1982).

Results

There were no significant differences in densities of individual macroinvertebrate taxa between spawning and undisturbed areas before the onset of spawning (Table 1). Biomass of chironomids was significantly greater in spawning colonies on the first sampling date, but biomass of all other macroinvertebrate groups was similar between areas (Table 2). Total macroinvertebrate densities and biomass were also similar before spawning (Fig. 2).

Shortly after the onset of spawning, total macroinvertebrate densities and biomass remained similar between areas (Fig. 2). However, densities of tabanids were significantly greater in undisturbed areas (Table 1). By the 6th week of spawning activity, densities of mayflies and damselflies, and biomass of chironomids, damselflies, and beetles were significantly greater in undisturbed areas (Tables 1, 2). Densities of oligochaetes were greater in spawning areas on this date (Table 1). Total macroinvertebrate densities and biomass remained statistically similar after 6 weeks of spawning activity (Fig. 2).

Before spawning activity, densities of cladocerans and copepods, and biomass of cladocerans were significantly higher in undisturbed areas (Tables 1, 2). Dominated by these two groups on the first sampling date, total microinvertebrate densities and biomass were also higher in undisturbed areas (Fig. 2).

After the onset of spawning, there were no significant differences in density or biomass of total microinvertebrates

TABLE 1. Invertebrate densities (number/m^2) in spawning and undisturbed areas

	18 March 1984		28 April 1984		8 June 1984	
	Spawning	Undisturbed	Spawning	Undisturbed	Spawning	Undisturbed
Chironomidae	461 (242–855)	293 (276–412)	3 447 (2819–4214)	3 701 (2331–5868)	4 964 (3059–8042)	7 033 (4681–10 560)
Ceratopogonidae	39 (0–165)	7 (0–24)	168 (82–301)	119 (71–185)	184 (70–387)	326 (216–470)
Tabanidae	55 (2–185)	34 (10–71)	10 (0–25)**	66 (30–119)	8 (0–20)	3 (0–12)
Ephemeroptera	9 (1–20)	4 (0–16)	102 (60–160)	104 (66–156)	22 (4–51)*	123 (43–299)
Zygoptera	18 (2–42)	19 (3–42)	15 (5–28)	22 (3–54)	6 (0–26)*	50 (13–120)
Anisoptera	28 (11–49)	47 (23–77)	20 (6–38)	7 (0–17)	9 (0–22)	32 (11–60)
Coleoptera	15 (3–33)	12 (2–24)	220 (107–397)	219 (118–369)	88 (55–133)	170 (90–290)
Trichoptera	6 (0–16)	26 (7–55)	4 (0–12)	23 (2–58)	25 (2–66)	37 (8–86)
Oligochaeta	1 998 (1004–3950)	3 075 (1221–7680)	213 (94–448)	265 (67–876)	602 (199–1721)**	77 (19–203)
Cladocera	11 583 (4535 – 29 399)**	56 805 (25 695 – 125 468)	52 356 (28 586 – 95 840)	43 985 (19 960 – 96 813)	23 070 (10 053 – 52 811)	8 114 (4182 – 15 679)
Copepoda	10 591 (5667 – 19 733)***	39 045 (28 201 – 54 046)	222 184 (78 453 – 628 978)	116 654 (71 967–189060)	72 305 (36 361 – 143 704)*	22 710 (14 028 – 36 736)
Ostracoda	26 (0–150)	106 (0–669)	27 279 (9725 – 61 842)*	7 151 (2121 – 18 064)	36 843 (14 092 – 79 872)	13 126 (3719 – 34 107)
Rotifera	7 080 (2860 – 17 359)	8 136 (3095 – 21 188)	29 801 (14 253 – 62 219)	36 171 (21 187 – 61 712)	84 325 (36 157 – 196 528)	69 822 (25419 – 191 553)
Acari	0	0	206 (0–1607)	162 (0–1113)	2353 (110 – 12 075)	109 (0–1112)

NOTE: Data are back-transformed means with 95% confidence intervals in parentheses. Asterisks indicate significant differences between areas: *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$.
[a]Prespawning sample.
[b]Postspawning sample.

TABLE 2. Invertebrate biomass (mg dry mass/m^2) in spawning and undisturbed areas

	18 March 1984		28 April 1984		8 June 1984	
	Spawning	Undisturbed	Spawning	Undisturbed	Spawning	Undisturbed
Chironomidae	156.9 (96.5–246.5)*	77.7 (52.3–110.9)	965.7 (720.4–1291.5)	834.9 (533.2–1298.6)	1411.0 (909.3–2181.1)*	3385.9 (2317.0–4941.7)
Ceratopogonidae	0.6 (0–1.5)	0.1 (0–0.4)	8.1 (4.9–11.8)	5.1 (2.8–7.6)	10.5 (3.4–19.6)	15.9 (9.4–23.5)
Tabanidae	64.4 (10.0–180.5)	47.3 (10.7–114.0)	10.6 (0–34.4)	63.0 (7.0–189.7)	13.7 (0–42.0)	2.2 (0–8.2)
Ephemeroptera	2.6 (0–5.6)	0.6 (0–2.0)	48.2 (27.7–72.8)	45.0 (34.1–57.0)	2.4 (0–6.2)	6.5 (0.7–13.1)
Zygoptera	25.4 (1.7–67.5)	25.9 (4.0–62.3)	6.5 (0–16.5)	33.3 (3.7–89.9)	0.2 (0–0.8)**	30.8 (6.0–73.1)
Anisoptera	345.4 (63.5–1070.7)	749.6 (206.6–1952.2)	115.2 (11.5–392.6)	38.4 (0–149.8)	29.6 (0–111.5)	101.0 (0–467.0)
Coleoptera	10.7 (0–29.5)	9.7 (0–29.7)	31.2 (4.2–80.2)	10.2 (6.5–14.4)	5.3 (1.2–10.1)**	58.0 (14.3–146.0)
Trichoptera	39.9 (0–158.3)	217.3 (35.9–905.8)	21.9 (0–90.3)	47.4 (0–195.8)	1.1 (0–2.6)	23.0 (0–92.6)
Oligochaeta	3798.1 (1863.5–7710.8)	7464.5 (2751.3–20 168.2)	181.5 (71.9–410.3)	257.7 (59.0–905.8)	331.6 (79.8–1166.4)	78.9 (13.0–428.8)
Cladocera	19.3 (8.9–41.5)*	61.1 (23.4–159.1)	256.0 (130.7–501.4)	333.3 (67.5–1644.4)	56.8 (33.8–95.3)	31.2 (4.9–196.1)
Copepoda	36.1 (12.7–82.4)	78.4 (40.5–138.0)	173.6 (115.6–251.1)	135.2 (39.9–343.9)	72.3 (19.6–193.0)*	10.6 (2.6–29.6)
Ostracoda	0.01 (0–0.03)	0.02 (0–0.1)	175.5 (67.1–380.9)	61.2 (18.2–154.6)	248.7 (92.4–549.5)	88.0 (22.8–241.2)
Rotifera	0.5 (0.2–1.1)	0.6 (0.2–1.5)	2.4 (1.0–5.7)	2.8 (1.8–4.4)	5.3 (2.0–14.3)	3.9 (1.4–10.7)
Acari	0	0	0.8 (0–48.3)	0.4 (0–10.4)	2.4 (0.1–40.3)	0.1 (0–0.4)

NOTE: Data are back-transformed means with 95% confidence intervals in parentheses. Asterisks indicate significant differences between areas: *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$.
[a]Prespawning sample.
[b]Postspawning sample.

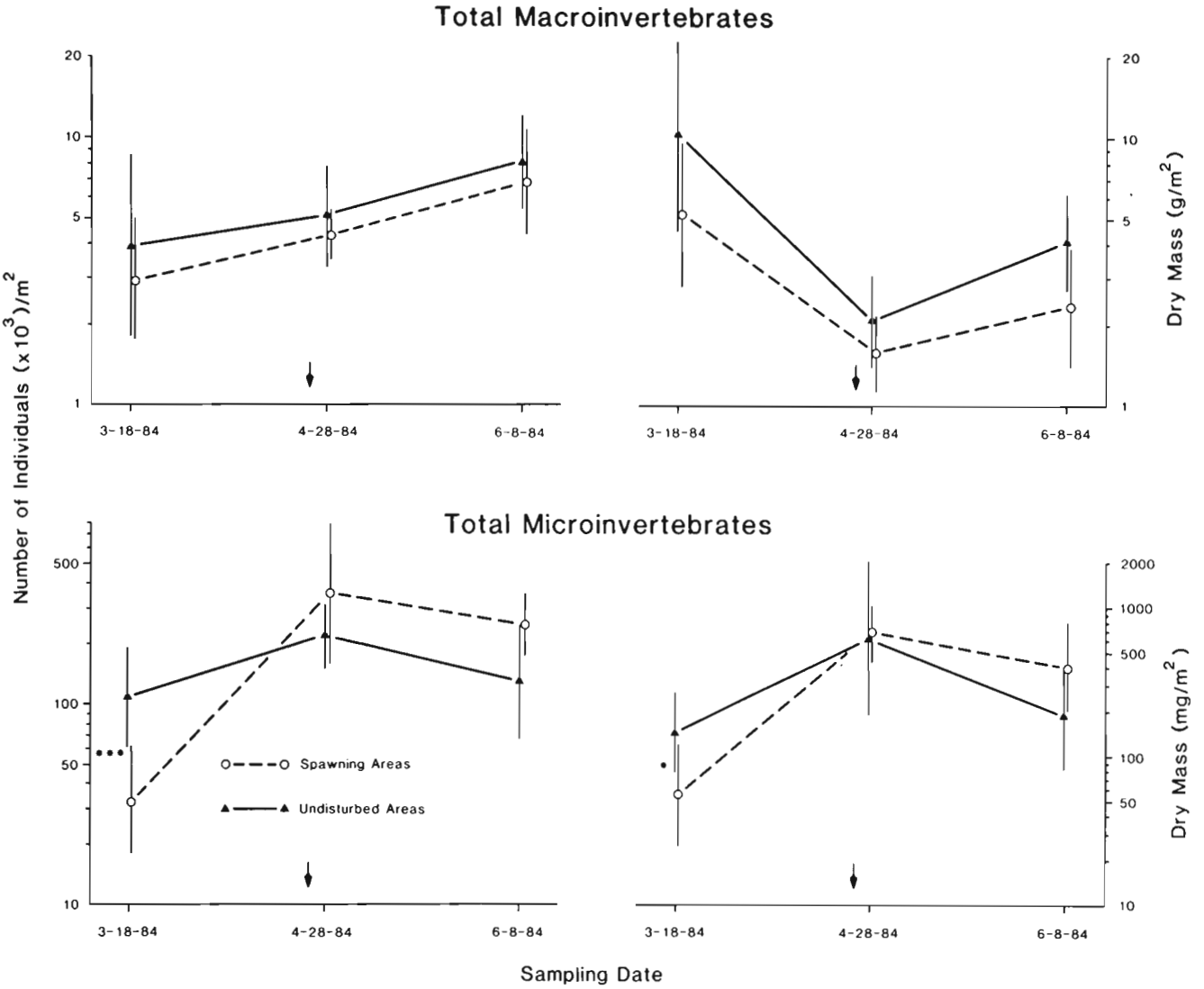

FIG. 2. Densities and biomass (back-transformed mean ± 95% CI) of total macro- and micro-invertebrates in spawning and undisturbed areas. Symbols are labeled in the lower left panel. Densities are shown in the left panels, biomass in the right panels. Macroinvertebrates include the insects and oligochaetes. Microinvertebrates include the microcrustaceans, rotifers, and mites. Arrows indicate the onset of spawning activity. Asterisks indicate significant differences between areas: * $0.05 > P > 0.01$, *** $P < 0.001$.

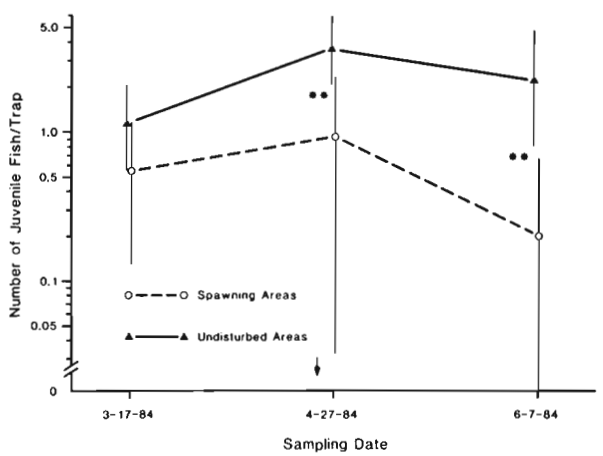

FIG. 3. Juvenile fish abundance (back-transformed mean ± 95% CI) in spawning and undisturbed areas. Arrow indicates the onset of spawning activity. Asterisks indicate significant differences between areas: ** $0.01 > P > 0.001$.

between areas (Fig. 2). However, ostracod densities were significantly higher in spawning areas just after initiation of spawning (Table 1), and densities and biomass of copepods were significantly greater in spawning areas on the third sampling date (Tables 1, 2).

Relative abundances of juvenile fish were similar between areas before spawning activity, but were significantly greater in undisturbed areas shortly after spawning began (Fig. 3). Abundances remained higher in undisturbed areas 6 weeks into the breeding season (Fig. 3).

The sediment particle size distributions in spawning and undisturbed areas were not significantly different prior to nest construction ($F_{7,70} = 0.84$, $P > 0.05$) (Table 3). The upper 8 cm of sediment in both areas consisted primarily of medium sand and finer particle sizes (Table 3).

Discussion

Considering the nature and duration of the disturbance to benthic habitats in spawning colonies, we were surprised that there were relatively few significant differences in invertebrate

TABLE 3. Sediment particle size distributions in spawning and undisturbed areas before the onset of spawning activity

	<0.125 mm	0.125–0.25 mm	0.25–0.5 mm	0.5–1.0 mm	1–2 mm	2–4 mm	4–8 mm	8–16 mm
Spawning	33.5	20.1	34.8	8.1	1.5	0.7	0.7	0.6
Undisturbed	38.7	25.9	26.8	4.1	1.5	1.1	1.0	0.9

NOTE: Data are back-transformed mean percent composition (by weight).

abundance between spawning and undisturbed areas after spawning began. Hildebrand (1971) found that substrate disturbance from spawning coho salmon markedly decreased both numbers and biomass of stream macroinvertebrates relative to fish-free controls. This effect was attributed to dislodgement and subsequent downstream drift. Carpenter and McCreary (1985) demonstrated that centrarchid nesting activities produced and maintained small-scale macrophyte zonation patterns based on differential colonization rates of plant species. Orth (1975) described large-scale destruction of estuarine eelgrass beds by foraging activities of rays. Eelgrass removal resulted in reduction of diversity and abundance of the associated macroinvertebrate fauna. However, Cowell (1984) and Fuller and Cowell (1985) found that simulated effects of *Sarotherodon aurea* nest construction on benthic invertebrates in a subtropical lake were minimal. In this system, invertebrates recolonized disturbed areas very rapidly. Similarly, Reidenauer and Thistle (1981) found that marine benthic copepod communities returned to normal very quickly following disturbance by stingray foraging activities. Our results and these other studies suggest that habitat disturbances by fish do not drastically alter invertebrate communities if the disturbed areas are relatively small and in close proximity to undisturbed areas that can serve as source pools for recolonization. The bluegill spawning colonies we sampled were small (20–40 nests) compared with some that have been reported in the literature (~500 nests) from larger lakes (Dominey 1980; Gross 1982). Systems with colonies of widely varying size would be ideal for testing whether effects of disturbance vary with colony size, and whether center to edge differences are more pronounced in larger colonies. We would expect greater disturbance effects in larger colonies, with effects being less pronounced toward the edges.

Another aspect of the scale of investigation also appears to have important consequences. Our study compared abundances in undisturbed areas with the general area within spawning colonies, averaging over any microscale differences between and within individual nests. Recent evidence suggests that such microscale differences exist within colonies (J. H. Thorp, personal communication), implying that future discussions of this phenomenon should clearly outline the scale.

Our results point to two broad trends that suggest testable hypotheses for further study. The first of these is that densities and biomass of insects tended to be lower in spawning areas relative to undisturbed areas after the onset of spawning activity (Tables 1, 2). Direct physical and habitat disturbance may account for some of these differences. Macrophyte removal in spawning colonies probably accounts for some of the reduction in damselfly abundance (Rabe and Gibson 1984), and possibly other taxa as well. Nest construction and maintenance is likely to dislodge invertebrates from their benthic refugia, making them more vulnerable to predation. Habitat alteration and fish activity in colonies may also reduce invertebrate colonization of these areas, both by larvae and ovipositing adults.

The second trend is that microinvertebrate abundances tended to differ in the opposite direction after onset of spawning, i.e., greater densities and biomass in spawning areas (Tables 1, 2). Juvenile fish distributions may play a role in this regard. Nesting male bluegills actively chase other fish away from spawning colonies, especially juvenile and other non-nesting bluegills (Dominey 1981; Bain and Helfrich 1983). Juveniles are also known to favor heavily vegetated areas in response to predation risk (Werner *et al.* 1983). Both of these observations suggest that juveniles should be more abundant in undisturbed areas than in spawning areas, and our trap data confirm this (Fig. 3). Juveniles feed heavily on microinvertebrates (Keast 1985), and have been shown to significantly reduce abundances (Bohanan and Johnson 1983). Nesting males will eat conspicuous prey such as terrestrial insects on the surface, but do not actively feed (Avila 1976). In effect, the territorial behavior of nesting male bluegills may result in protection of microinvertebrates from juvenile fish predation in spawning colonies.

The initial sampling date served not only as a control for short-term disturbance effects, but also provided an indication of whether disturbance effects persist from year to year. Differences between the two areas on the first date imply that spawning activity of the previous summer may affect invertebrate abundance in the following spring. Such historical effects may account for the greater abundances of cladocerans and copepods in undisturbed areas prior to establishment of nests (Tables 1, 2). Although substrate particle size distributions were similar between areas (Table 3), dead macrophytes were less prominent in spawning areas due to nesting activities during previous years. This may have resulted in less suitable habitat, as has been shown when living macrophytes are experimentally removed (Rabe and Gibson 1984).

Spawning activity may affect the benthic invertebrate community in a variety of ways that may either complement or oppose each other. For example, physical alteration of the habitat might make it less suitable for certain species, but reduced predation from nonspawning fish could result in higher survivorship. Thus, "damping out" of opposing effects is one potential explanation for our finding few significant differences between spawning and undisturbed areas. Low statistical power due to high variances is another potential reason. Allan (1984) has recently analyzed this pervasive problem in benthic studies and recommended 10 samples per treatment as a minimum level of replication. Our study just met this level (five replicates × two blocks per treatment), but greater replication would be desirable. Clearly, well-replicated experimental manipulations will be necessary to unravel these possibilities.

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