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Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake

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Synopsis

Young-of-the-year fish communities in naturally vegetated sites were compared with those inhabiting nearby sites where lakeshore development (i.e., construction of homes, boat docks, and beaches) reduced nearshore macrophyte species richness and abundance. The study was conducted in a 2266 hectare, glacially formed, eutrophic lake in northwestern Iowa during the summers of 1987 and 1988. Study sites were divided into 3 depth zones, and fishes were collected by seining (0–1 m), plexiglass traps (1–2 m), and a nonclosing Tucker trawl (2–3 m). Species richness and total fish abundance were consistently greater in natural than in developed sites in both nearshore (0–1 m) and intermediate (1–2 m) depth zones, but differed little between natural and developed sites in the offshore (2–3 m) depth zone. Nearly 50% of the species sampled, including yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus,* inhabited limnetic areas as larvae before migrating inshore as juveniles. Eighteen of the 20 fish species collected as juveniles were in greater abundance in natural than in developed sites. Smallmouth bass *Micropterus dolomieui* was the only game species consistently found in equal or greater abundance in developed sites. Within all sites, juvenile fishes were generally most abundant where macrophyte abundance and species richness were greatest. Findings from this study demonstrate the importance of nearshore aquatic vegetation to fishes during their first summer of life. If nearshore vegetation beds of lakes continue to be regarded as a nuisance and indiscriminately removed, important fish nursery habitat will be lost. The short-term result will likely be reduced year-class strength of vegetation-dependent species. More importantly, the long-term effects will be changes in fish community richness and composition which will, in turn, alter the lake's fishery.

Introduction

Unaltered shorelines of many shallow lakes in the midwestern United States are characterized by dense stands of emergent and submerged aquatic vegetation. Aquatic macrophytes play an important role in the complex interrelationships among nutrients, plankton, periphyton, macroinvertebrates, and fish (Wetzel 1983, Engel 1985, De Nie 1987, Janecek 1988). Aquatic vegetation is used by many freshwater fish species during one or more of their life periods: as spawning substrates (Breder & Rosen 1966, Becker 1983, Janecek 1988), as protective cover from predators (Brown & Colgan 1982, Savino & Stein 1982, 1989, Werner et al. 1983, Keast 1985, Mittelbach 1986, Gotceitas &

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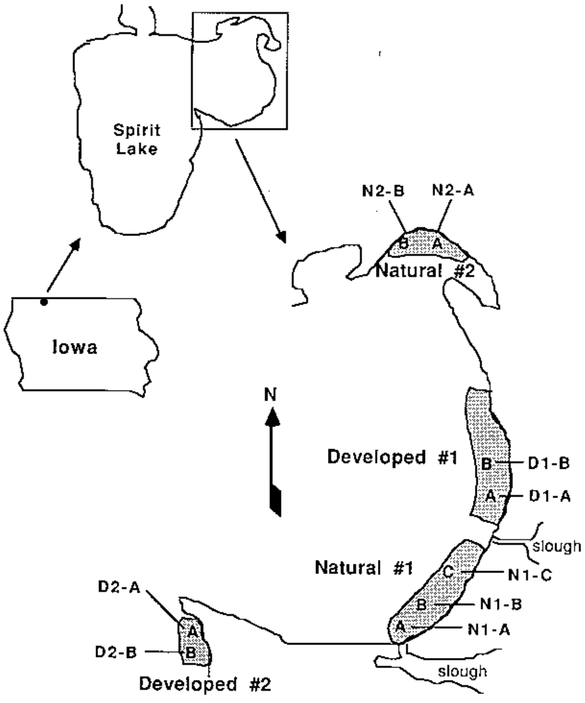

Fig. 1. Geographic location of Spirit Lake and the locations of the 4 study sites and nine 100 m sampling blocks within the lake's northeast bay. (N = natural, D = developed; 1 and 2 refer to replicate sites; and A, B, and C refer to specific 100 m sampling blocks). Figure not drawn to scale.

Colgan 1987, Werner & Hall 1988, Gotceitas 1990), and as feeding sites (Janecek 1988).

Nearshore vegetation beds, however, may conflict with recreational pursuits such as swimming and boating. Consequently, many lakefront property owners remove nearshore vegetation without considering the potential effects on fish communities. Such is the case at northwest Iowa's Spirit Lake, where extensive recreational use and development of the lake's shoreline have eliminated or altered native emergent and submerged vegetation from all but about 10% of the shoreline. The lake's northeast bay is the last area with unaltered aquatic vegetation beds (Fig. 1).

Little information currently exists on the use of vegetated nearshore areas by young-of-the-year fishes, in part because of sampling difficulties in such habitats (Kahl 1963, Higer & Kolipinski 1967, Kushlan 1981). Thus, for Spirit Lake and other lakes experiencing rapid recreational development, information on the use of nearshore aquatic vegetation by fish larvae and juveniles is needed to provide insight into both the short- and long-term effects of extensive vegetation removal on lake fish communities.

The objective of this study was to compare species richness, composition, and relative abundance of young-of-the-year fish assemblages at two naturally vegetated sites with those of two previously similar sites (Sigler 1948) now altered by shoreline development (i.e., construction of homes, boat docks, and beaches).

Study area

Spirit Lake, a 2266 ha, glacially formed, eutrophic lake is the largest natural lake in Iowa (Fig. 1). Maximum depth varies between 7 and 8 m, with secchi disk visibility during summer typically less than 2 m. Thirty-four species inhabit Spirit Lake and its associated sloughs. The recreational fishery is based on black bullhead *Ictalurus melas,* yellow perch *Perca flavescens,* walleye *Stizostedion vitreum vitreum,* muskellunge *Esox masquinongy,* largemouth bass *Micropterus salmoides,* smallmouth bass *Micropterus dolomieui,* bluegill *Lepomis macrochirus,* and black crappie *Pomoxis nigromaculatus.* Walleye and muskellunge reproduce poorly in the lake but are stocked regularly by the Iowa Department of Natural Resources in response to high angler demand.

Study sites

Nine 100 m blocks were established randomly within four study sites for fish and vegetation sampling during the summers of 1987 and 1988 (Fig. 1). The two developed sites [Developed # 1 (D1) and Developed # 2 (D2)] were in the past characterized by vegetation communities similar to those of the two natural sites [Natural # 1 (N1) and Natural # 2 (N2)] (Sigler 1948). Sites D1, D2, and N2 each had two 100 m sampling blocks (D1-A, D1-B; D2-A, D2-B; N2-A, N2-B), whereas N1 had 3 such blocks (N1-A, N1-B, N1-C) (Fig. 1).

Methods

Nearshore macrophyte sampling

A descriptive survey of the macrophyte beds that characterized natural and developed sites was conducted. Transects were established perpendicularly to shore every 10 m within each 100 m sampling block to facilitate both vegetation and fish sampling. Beginning at the water's edge, macrophyte species richness, composition, relative abundance, and substrate type were determined at 10 m intervals along 4 randomly selected transects, within each of the 100 m sampling blocks, until a water depth of approximately 1.5 m was reached. A relative abundance value of 1 (scarce), 2 (common), or 3 (abundant) was assigned to each plant species present in a 4 m^2 quadrat placed at the 10 m intervals along each selected transect. Overall macrophyte abundance was calculated at 10 m intervals for each 100 m block by summing the species-specific relative abundance values for all plants located at that distance from shore. These values were then averaged for all 100 m sampling blocks within a site to provide an index of relative macrophyte abundance for that site.

Fish sampling

To facilitate fish sampling, littoral areas were divided into three depth zones (0–1, 1–2, and 2–3 m), and fish were collected in these zones by seining, plexiglass traps, and a nonclosing Tucker trawl, respectively. Seining and trapping were conducted with reference to transects, established perpendicularly to shore, within each 100 m sampling block.

Seining in the nearshore (0–1 m) depth zone was conducted with a 9.1 m × 1.2 m, 0.318 cm mesh common-sense seine. Random selection of shoreline transect markers (numbered 1–9) dictated where seine hauls would begin within a block during each sampling period, with the condition that consecutive transects would not both be used. Three seine hauls were made weekly within each block between 22 June and 11 August in 1987 and between 23 May and 5 August in 1988.

Plexiglass trap design was modified from Breder (1960). Traps measured 0.31 × 0.31 × 0.61 m and were constructed of 0.64 cm plexiglass. Two rigid conduit straps were bolted to the back of each trap, one above the other. At each set location, a 3.81 cm diameter steel conduit pole was driven firmly into the lake bottom. With the pole in place, a trap was mounted to the pole by the pair of conduit straps. This construction allowed traps to slide down the pole, fill with water, and sink to a predetermined depth. A bolt through the pole kept the trap at the desired depth (midway between the surface and the bottom) and oriented in the chosen direction, (parallel to shore). The throat opening was set at 1 cm early in the summer and was increased to 2 cm in July to accommodate larger juvenile fishes. For a complete description of trap construction and manner of setting, see Bryan (1989).

Within each 100 m sampling block, 10 traps were set in pairs along alternating transects: one at a water depth of 1.0 m and another farther offshore at a water depth of 1.5 m. Traps were set for a 24 h period each week from 6 June to 6 August, 1988.

A nonclosing Tucker trawl was used to collect fishes inhabiting the (2–3 m) depth zone. The trawl had a 1.2 × 1.2 m opening and mesh size of 1800 μm, which tapered back into a plankton collection bucket. The trawl was towed behind a 7 m jet boat at 1.3–1.8 m s^{-1}. All samples were collected after dark (2100–2400 h), parallel to shore, and following the 2 m contour line.

Trawling was conducted every two weeks in 1987 between 22 June and 4 August. Because this sampling schedule proved inadequate for accurately describing the successional appearance of fish larvae offshore, sampling was conducted weekly between 11 May and 4 August in 1988. A flow meter positioned in the mouth of the trawl allowed determination of water volume sampled during each tow. Densities of all fish species captured were estimated for both years.

Total numbers of each species captured by seining and trapping were recorded in the field, and subsamples of each species were preserved in 10% formalin to verify identification in the laboratory. All fish captured by trawling were immediately preserved. Auer's (1982) key for fish larvae was used to identify all specimens.

In addition to the fish sampling described, clear water conditions during the spring of 1988 enabled us to make visual observations of spawning activity for several fish species.

Data analysis

Catch-per-unit-effort (CPUE) was used to describe the relative abundance of fishes at each site from weekly samples. For all species except black bullheads, CPUE from seining was the number of fish captured per 3 seine hauls within a given sampling block and week. Because black bullheads schooled throughout most of their first summer, number of schools per 100 m sampling block was recorded rather than number of individual fish captured per seine haul. This was done to reduce sampling bias associated with such a highly clumped distribution. Catch-per-unit-effort for traps was the number of fish captured per 5 traps set in a particular block at a specified depth. Catch-per-unit-effort for the Tucker trawl was the number of fish captured per 4000 m^3 of water sampled at each site. Catch data were transformed by taking logarithms of CPUE values plus one, and analyzed using analysis of variance (ANOVA) in which the time factor (weeks) was regarded as a repeated measure (Cochran & Cox 1957, p. 293). All ANOVAs were performed using the Statistical Analysis System (SAS) General Linear Models (GLM) procedure (SAS Institute Inc. 1985). The mean square error for sites nested within shore-type (natural or developed) was used to test for the effect of shore-type (1,2 df) on fish abundance (CPUE). Weekly comparisons were made by sorting the CPUE data by week and then running the analysis described above on each week's data. Student's t-tests and the Friedman nonparametric two-way analysis of variance by ranks (Daniel 1978, p. 224) were used to compare differences in overall macrophyte abundance between natural and developed shore-types. The Friedman test was used to evaluate differences in both macrophyte and fish species richness between shore-types. A separate analysis was conducted for each depth zone and sampling gear. Data from 1987 and 1988 were analyzed separately for seining and trawling because of additional weeks sampled in 1988.

Results

Nearshore macrophyte communities

Emergent vegetation, consisting of hardstem bulrush *Scirpus acutus,* common cattail *Typha latifolia,* and narrow-leaved cattail *Typha angustifolia,* was present only in natural sites. In addition, 3 species of submerged macrophytes – flat-stemmed pondweed *Potamogeton zosteriformis,* longleaf pondweed *Potamogeton nodosus,* and coontail

Table 1. Mean (N = 9) water depth and associated mean (N = 2) macrophyte species richness and relative abundance in natural and developed sites of Spirit Lake, Iowa, 1988.

Meters from shore	Mean water depth (cm)	SE	Species richness				Species abundance				$p > t^a$
			Natural		Developed		Natural		Developed		
			x̄	SE	x̄	SE	x̄	SE	x̄	SE	
10	66.6	4.0	12.5	1.5	7.5	0.5	20.8	2.2	10.8	1.3	0.056
20	92.8	7.1	12.5	0.5	8.0	0.0	22.5	2.5	14.0	1.5	0.100
30	108.5	7.9	11.0	1.0	7.0	0.0	20.0	4.0	12.8	0.8	0.217
40	114.1	5.2	10.5	1.5	7.0	1.0	18.5	4.5	11.3	1.3	0.261
50	124.7	5.4	10.5	1.5	6.0	1.0	18.2	3.8	10.0	1.0	0.176

[a] Probability of a greater t-value from a student's t-test with 2 df comparing species abundance between natural and developed sites.

Ceratophyllum demersum – were found only in natural sites. One species, horned pondweed *Zannichellia palustris,* was found only in site N2. In general, *Potamogeton* spp. dominated the submerged macrophyte communities in all sites, but muskgrass *Chara contraria,* wild celery *Vallisneria americana,* and naiad *Najas flexilis* were also common. Macrophyte species richness was greater in site N2 than in N1 at all distances from shore sampled (Friedman nonparametric two-way analysis of variance by ranks: $X_r^2 = 5.00$, 1 df, $p = 0.025$), whereas no such trend was apparent between the two developed sites ($X_r^2 = 0.20$, 1 df, $p = 0.655$). However, overall species richness was greater at natural than developed sites at all distances from shore sampled ($X_r^2 = 5.00$, 1 df, $p = 0.025$) (Table 1). Sand and gravel were the dominant substrate types in all sampling blocks.

In addition to greater species richness, site N2 had the greatest macrophyte abundance of the 4 study sites at all distances from shore sampled ($X_r^2 = 13.56$, 3 df, $p = 0.004$), which caused greater variability in mean macrophyte abundance values for natural compared to developed shore-types. Nevertheless, natural sites produced greater mean macrophyte abundance values at all depths sampled ($X_r^2 = 5.00$, 1 df, $p = 0.025$). This difference between shore-types decreased with increasing distance from shore (Table 1).

Considering macrophyte distribution, emergent species at site N2 were well-established near the shore in many areas, whereas emergent vegetation at site N1 (primarily hardstem bulrush) was not well established within 15 m of the shore because of prevailing winds resulting in greater wave action. Distribution of the submerged macrophytes was similar between the two natural sites and between the two developed sites, but differed between natural and developed shore-types. Alterations of macrophyte beds in developed sites were observable to a distance of 60–80 m offshore, but were most pronounced within 20–30 m of shore.

Seining

Young-of-the-year fish species richness was greater in natural than in developed sites in all weeks sampled in 1987 ($X_r^2 = 6.00$, 1 df, $p = 0.014$) and in all but the first week in 1988 ($X_r^2 = 6.40$, 1 df, $p = 0.011$) (Fig. 2). In addition, summer fish species richness differed significantly ($t = 13.00$, 2 df, $p = 0.006$) between natural (18 species at both sites) and developed (12 and 11 species) shorelines. Twelve species were regularly captured in natural sites compared with 6 in developed sites, and longnose gar *Lepisosteus osseus,* northern pike *Esox lucius,* yellow bullhead *Ictalurus natalis,* banded killifish *Fundulus diaphanus,* green sunfish *Lepomis cyanellus,* and black crappie were found only at natural sites. Two additional species – common carp *Cyprinus carpio* and bluntnose minnow *Pimephales notatus* – were abundant in natural sites but rare in developed sites during years when these species were common in the northeast bay.

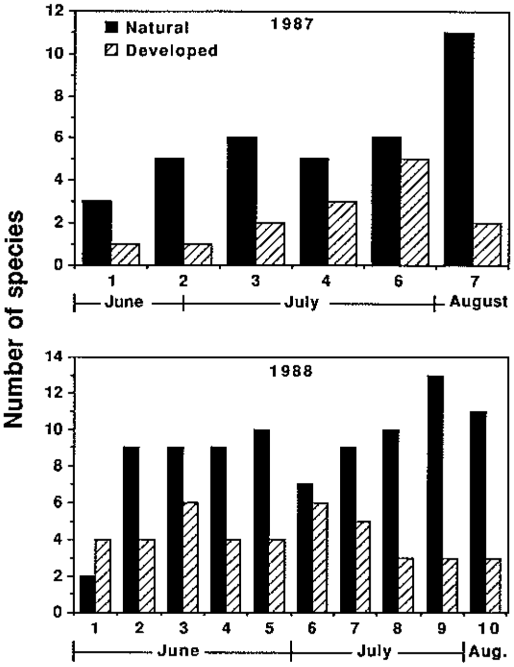

Fig. 2. Number of young-of-the-year fish species collected each week by shoreline seining in natural and developed sites of Spirit Lake, Iowa, 22 June – 11 August 1987 and 30 May – 5 August 1988.

Mean weekly total fish abundance was greater in natural than in developed sites in all weeks sampled during both summers. Differences during most weeks were not statistically significant, however,

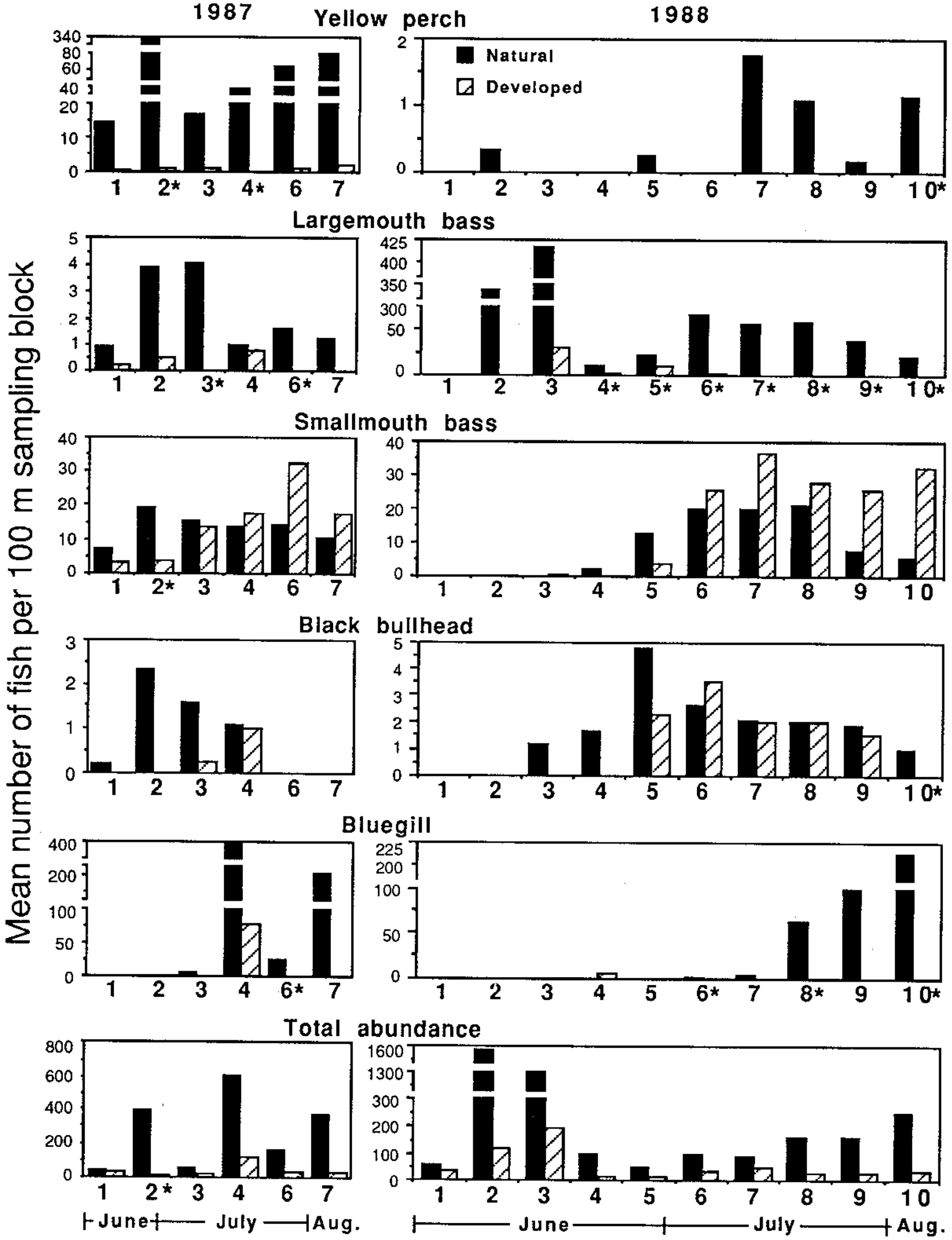

Fig. 3. Mean weekly CPUE of game species and total fish abundance sampled by shoreline seining in natural and developed sites of Spirit Lake, Iowa, 22 June – 11 August 1987 and 30 May – 5 August 1988. Note scale change on each graph. * = significant difference ($p \leq 0.05$) between means determined by ANOVA with 1, 2 df.

because of great variation in CPUEs between like shore-types (Fig. 3.). Young-of-the-year from 5 of the 8 fish species constituting Spirit Lake's sport fishery (yellow perch, largemouth bass, smallmouth bass, black bullhead, and bluegill) were collected on a weekly basis during both years of the study. Despite large differences in year-class strength for both yellow perch and largemouth bass between 1987 and 1988, their distribution, as determined by CPUE, clearly showed a marked preference by both species for natural shorelines. Likewise, bluegill were rarely collected from developed sites but were a dominant species in natural sites during July and August. Although initially found in greater abundance in natural sites, smallmouth bass was the only game species consistently found in greater abundance in developed sites.

An important forage species, spottail shiner *Notropis hudsonius,* was common in nearshore waters of natural sites in June of 1987 ($\bar{x}$ CPUE = 8, SE = 1.5, N = 25), but none were sampled from developed sites that year. In June of 1988, abundance of spottail shiners in natural sites was also greater ($\bar{x}$ = 401, SE = 270, N = 15) than that in developed sites ($\bar{x}$ = 37, SE = 295, N = 12), but this difference was significantly greater ($p \leq 0.05$) in week 5 only, because of great variation in CPUEs resulting from the clumped (schooling) distribution of this species. Young-of-the-year spottail shiners apparently moved offshore as juveniles, because few were collected at any site after the end of June. The smaller CPUE of spottail shiners in 1987 compared to 1988 was mainly the result of missing peak abundance inshore, as sampling did not begin until 22 June in 1987. Bigmouth buffalo *Ictiobus cyprinellus* were also abundant in natural sites during June of 1988 ($\bar{x}$ = 158, SE = 27.5, N = 25) but were less abundant in developed sites ($\bar{x}$ = 38, SE = 30.1, N = 20) at this time. This species was likely missed altogether in 1987 because of the late initiation of sampling. Common carp were collected only in 1988. Mean weekly CPUE values for carp were greater in natural sites in 7 of the 9 weeks in which they were sampled, and they were significantly greater ($p \leq 0.05$) in weeks 2, 3, and 5. In both years, walleye *Stizostedion vitreum vitreum* and darter spp. (*Etheostoma nigrum, E. exile,* and *Percina caprodes*) were occasionally collected in small numbers from natural sites, but few were taken from developed sites by seining.

Extensive black bullhead spawning was visually observed in the emergent macrophyte zone of natural sites in 1988. All nests observed were placed against at least one clump of bulrush and were in a water depth of 0.75 to 1.5 m. Although both developed sites were concurrently checked for bullhead spawning, no such activity was observed.

Trapping

Plexiglass traps revealed species richness and abundance patterns similar to those determined by seining. No additional species were collected in traps that were not sampled by seining. Young-of-the-year fish species richness was greater in natural than in developed sites in all but 2 of the weeks sampled ($X_r^2 = 4.00$, 1 df, $p = 0.046$). Trapping also indicated that summer fish species richness was higher at natural (11 and 9 species at sites N1 and N2) than developed (3 and 6 species at sites D1 and D2) shorelines; however, this difference was not significant ($t = 3.05$, 2 df, $p = 0.093$). As indicated by both trapping and seining data, differences in species richness between natural and developed sites became greater as the summer progressed. Largemouth and smallmouth bass were the two most regularly captured species in all sites throughout the summer. Bigmouth buffalo, black crappie, bluegill, and green sunfish *Lepomis cyanellus* were found exclusively in natural sites.

Mean weekly CPUEs for largemouth bass were significantly greater in natural than in developed sites ($p \leq 0.05$) in the 5th week of sampling only. Mean CPUEs for bluegill were significantly greater ($p \leq 0.05$) in natural sites in weeks 7, 8, and 9. Conversely, mean weekly CPUEs for smallmouth bass were greater in developed sites during all weeks sampled and were significantly greater ($p \leq 0.05$) in developed sites in weeks 3, 4, and 6. Mean weekly total fish abundance was significantly greater ($p \leq 0.05$) in natural sites in weeks 7, 8, and 9. This was mainly due to large catches of bluegill from natural sites during these weeks.

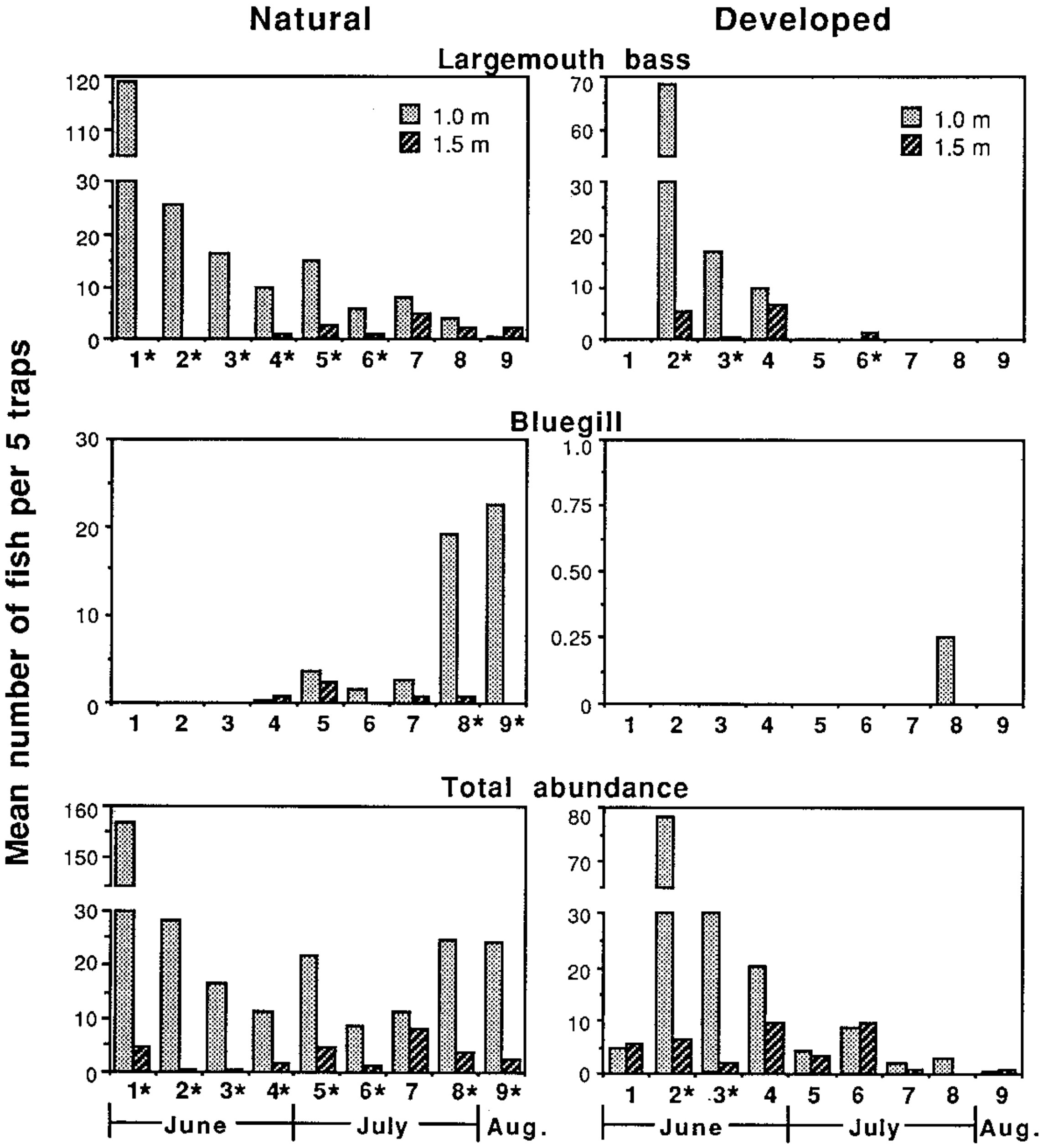

Fig. 4. Mean weekly CPUE of largemouth bass, bluegill, and total fish abundance sampled by plexiglass traps in natural and developed sites of Spirit Lake, Iowa, 6 June – 6 August 1988. Note scale change on each graph. * = significant difference ($p \leq 0.05$) between means determined by ANOVA with 1, 2 df.

In natural sites, mean weekly total fish abundance was significantly greater ($p \leq 0.05$) at a water depth of 1.0 versus 1.5 m during 8 of the 9 weeks sampled. Similarly, largemouth bass abundance was greater ($p \leq 0.05$) from traps set at 1.0 versus 1.5 m for the first 6 consecutive weeks this species was collected. Largemouth bass abundance did not differ significantly between depths during weeks 7, 8, and 9, which likely reflected a dispersal to deeper waters in late summer (Fig. 4). Conversely, smallmouth bass showed no clear water depth preference as smallmouth abundance was similar be-

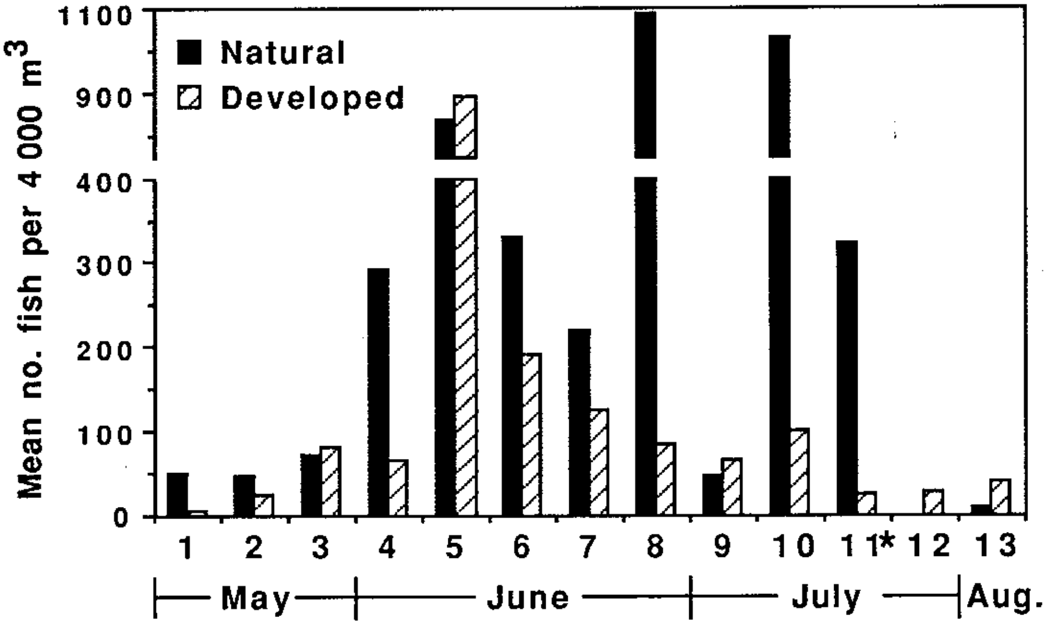

Fig. 5. Mean weekly CPUE of all young-of-the-year fish species collected by trawling in inshore open waters of natural and developed sites in Spirit Lake, Iowa, 11 May – 4 August 1988. Neither natural site was sampled on week 12. Site N2 was not sampled on week 13. * = significant difference ($P \leq 0.05$) between means determined by ANOVA with 1, 2 df.

tween water depths during most weeks sampled. Bluegill abundance was not significantly different between depths during the first 4 weeks that they were collected (weeks 4–7); however, during weeks 8 and 9, bluegill abundance was significantly greater ($p \leq 0.05$) in 1.0 than in 1.5 m of water. Mean summer CPUE values for yellow perch, largemouth bass, common carp, spottail shiner, bluegill, and total fish abundance were all significantly greater ($p \leq 0.05$) at a depth of 1.0 versus 1.5 m. Finally, the total of infrequently collected species was captured more often at 1.0 than at 1.5 m ($p = 0.036$) as well.

In contrast to natural sites, mean weekly total fish abundance in developed sites was significantly greater ($p \leq 0.05$) at a water depth of 1.0 versus 1.5 m during only 2 of the 9 weeks sampled. Likewise, largemouth bass abundance was greater ($p \leq 0.05$) in 1.0 m during weeks 2 and 3 only (Fig. 4). Although catches of smallmouth bass were generally greater at 1.0 versus 1.5 m of water, they were significantly greater ($p \leq 0.05$) during weeks 2 and 3 only. Few bluegill were collected in traps at developed sites. Mean summer CPUE values were greater at a water depth of 1.0 versus 1.5 m for all species collected in developed sites except common carp; however, these differences were significant for largemouth bass ($p < 0.001$), smallmouth bass ($p = 0.002$), and total fish abundance ($p = 0.001$) only.

Trawling

Fifteen fish species in the larval to early juvenile life periods were collected from trawling in nearshore openwaters during the study. The more frequent trawling of 1988 showed that weekly species richness was similar between natural and developed sites throughout the summer ($X_r^2 = 1.45$, 1 df, $p = 0.229$). Furthermore, summer fish species richness did not differ significantly between natural (1987: 4 and 5 species, 1988: 11 and 12 species) and developed (1987: 7 and 5 species, 1988: 12 and 13 species) sites. Walleye, yellow perch, darter spp. (*Etheostoma nigrum, E. exile,* and *Percina caprodes*), bigmouth buffalo, black crappie, common carp, freshwater drum, *Aplodinotus grunniens*, and bluegill were the most common species collected in both natural and developed sites in 1988.

With the exception of bluegill, mean weekly densities of each fish species sampled in 1987 and 1988 did not differ significantly between natural and developed sites. The more intensive sampling of 1988 produced mean weekly total fish densities that were greater in natural than in developed sites during 8 of the 13 weeks sampled, but significantly greater ($p \leq 0.05$) only for week 11 (Fig. 5). Large catches in natural sites during late June and July (including week 11) consisted almost entirely of bluegill. Excessive vegetation prevented sampling at natural sites on week 12 and at site N2 on week 13.

Discussion

Throughout the summer months, nearshore areas of natural sites, which were characterized by diverse submerged and emergent macrophytes, had greater young-of-the-year fish species richness and abundance than did adjacent developed sites. The young-of-the-year fish species dominating natural sites of Spirit Lake have been found in great abundance in densely vegetated habitats of other lakes as well (Keast 1985, Ridenhour 1960). Barnett & Schneider (1974), Holland & Huston (1985), Keast (1985), and Conrow et al. (1990) agree that shallow water vegetation beds provide critical habitat for the establishment of diverse young-of-the-year fish assemblages, and are particularly important to fishes during their juvenile life period. Human activities which eliminate vegetation beds where juvenile fishes avoid predation and feed during their first summer of life, may reduce juvenile survival (Di Costanzo 1957) and future recruitment into the fishery (Holland & Huston 1985).

Because bottom substrates and shoreline slopes differed little between natural and developed sites, and because Spirit Lake's northeast bay was once vegetated similarly throughout (Sigler 1948), present differences in young-of-the-year fish assemblages between natural and developed sites can be primarily attributed to aquatic vegetation removal and increased recreational activities associated with shoreline development.

Smallmouth bass and darter species seemed to be the most tolerant of vegetation removal; they dominated the 0–1 m depth zone of developed sites where extensive vegetation removal had occurred. Other investigations (Coble 1975, Becker 1983) have indicated that sandy, rocky areas largely devoid of macrophytes provide suitable habitat for these fish species. Conversely, the absence of longnose gar, northern pike, yellow bullhead, banded killifish, green sunfish, and black crappie, and the relative scarcity of yellow perch, largemouth bass, bluegill, spottail shiners, and bluntnose minnows, suggest that developed sites are less suitable for these species than were the more diversely and densely vegetated natural sites.

Observations of black bullhead spawning demonstrated the importance of emergent vegetation to this species in Spirit Lake. Because we found no nests of yolksac young at developed sites and because no young appeared there for 2 weeks after swim-up at natural sites, evidence suggests that young-of-the-year black bullheads did not inhabit developed shorelines until old enough to disperse to them from vegetated spawning grounds. Forney (1955) also suggested that black bullhead spawning was associated with emergent and submerged vegetation beds in Clear Lake, Iowa, and that schools found in unvegetated areas had probably dispersed there from vegetated sites.

The greater abundance of fishes in 1.0 versus 1.5 m of water in natural sites may be explained by two factors. First, aquatic vegetation surveys conducted during this study revealed that macrophyte richness and abundance were greatest at a water depth of nearly 1.0 m in all sites, creating the most structurally complex microhabitat available (Table 1). This water depth was typically found 20 m offshore. Such habitats provide diverse and abundant prey assemblages for young fishes (Krecker 1939, Gerrish & Bristow 1979, Keast 1985). Second, large piscivorous fish were more abundant on the offshore side of the emergent vegetation beds (at a water depth of about 1.5 m) than they were on the nearshore side (at a depth of about 1.0 m) (personal observation). Similar observations were made by Barnett & Schneider (1974). Dense vegetation in shallow waters offers young fish two key ingredients for survival – food and protection from predators.

The lack of a strong depth-related distribution of young fishes in the 1–2 m depth zone of developed sites is attributed to reduced vegetative cover at a depth of 1.0 m resulting from shoreline development and nearshore recreational activity. Reduced vegetative structure here had a pronounced effect on the distribution and abundance of vegetation-dependent species such as largemouth bass and bluegill, but had little affect on smallmouth bass which do not rely as heavily on vegetative cover.

Unlike the nearshore (0–1 m) and intermediate (1–2 m) depth zones, the offshore (2–3 m) areas did not exhibit marked differences in young-of-the-year fish species richness or abundance between natural and developed sites. At least two factors may explain this finding. First, the impacts of shoreline development simply did not extend this far offshore; hence, vegetation beds and substrate types differed little between natural and developed sites. Second, the early life history of the fishes themselves may largely explain the similarities found in this depth zone. Fishes collected by trawling were primarily larvae and young juveniles. Bluegill and yellow perch larvae have been shown to undergo habitat shifts from inshore spawning sites to open-water limnetic areas only to return to vegetated littoral areas as juveniles (Werner 1969, Whiteside et al. 1985, Post & McQueen 1988, Werner & Hall 1988). Our concurrent sampling of three different depth zones in Spirit Lake showed that walleye, yellow perch, darter spp., bigmouth buffalo, black crappie, common carp, freshwater drum, and bluegill were collected in abundance in the openwaters of the lake as larvae, appearing later in inshore samples as juveniles. Although such habitat shifts were most evident for bluegill and yellow perch, the abundance of other species offshore during larval development, and their subsequent appearance inshore as juveniles, suggest that species in addition to bluegill and yellow perch may avoid nearshore areas during early life. Conversely, the infrequent capture or absence of longnose gar, northern pike, spottail shiners, bluntnose minnow, yellow bullhead, banded killifish, largemouth bass, smallmouth bass, and green sunfish larvae in trawl samples suggests that these species remained inshore during larval development. Faber (1967) and Amundrud et al. (1974) documented similar successional appearances of percid and centrarchid larvae in limnetic areas of two northern Wisconsin Lakes and Lake Opinicon, Ontario, respectively. Evidently, patterns of habitat use by young fishes shown in Spirit Lake are widespread among midwestern lakes with similar fish communities.

If larvae remained in open-water areas as juveniles, their easy capture in an unstructured environment would eventually attract piscivorous fishes offshore to feed on them (Werner & Hall 1988). Thus, returning inshore to vegetation offers juveniles a new strategy for survival and a broader prey base associated with the seasonal growth of macrophytes (Keast 1985). Once inshore, intense predation pressures confine juvenile fishes to areas of abundant cover (Werner et al. 1977, Mittelbach 1986, Werner et al. 1983, Gotceitas & Colgan 1987, Werner & Hall 1988, Savino & Stein 1989). The diverse and abundant invertebrate food base associated with nearshore macrophytes allows for the development of dietary specialization both intra- and interspecifically (Werner et al. 1977, Keast 1985). The result is a diverse juvenile fish assemblage not found in areas with little vegetation or in open water (Conrow et al. 1990).

Holland & Huston (1985) warned that continued sediment deposition and subsequent loss of submerged vegetation beds in Mississippi River backwaters, a crucial fish nursery habitat, may adversely affect the recruitment of several important sport fish species in the river. Although the causes of vegetation loss may be different in inland lakes, effects on the fishery are potentially the same. If nearshore vegetation beds of lakes continue to be regarded as a nuisance and removed indiscriminately, important fish nursery habitat will be lost. The short-term result will likely be a reduced year-class strength of vegetation-dependent species.

More importantly, the long-term effects will be changes in fish community richness and composition which will, in turn, alter the lake's fishery.

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Fish imagery in art 33: Beal's *The Fish Bucket*

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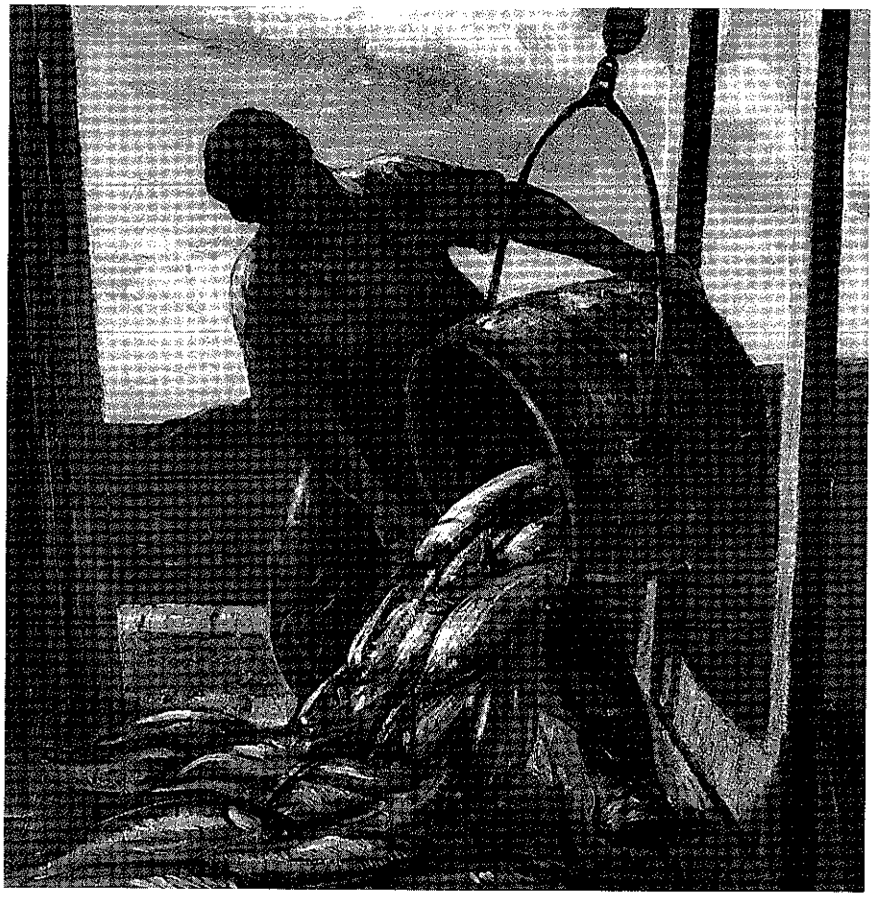
Gifford R. Beal (1879–1956) was a minor but popular artist whose art is transitional between the realistic art favored in 19th Century America and the abstract art of the 1940's and 1950's. He studied with William M. Chase who was famous for his lustrous paintings of fish as 'common objects'. Beal frequently chose as his subjects common people engaged in activities such as commercial fishing or tending circus animals. He had the good fortune to be related by marriage to Duncan Phillips who established the Phillips Collection in Washington, D.C. and collected Beal's paintings.



The Fish Bucket (oil on canvas, 61 × 61 cm, 1924) is from the Phillips Collection. Compositionally, the painting utilizes the classical triangular form, with the fisherman's head as the apex. Neither fish nor fisherman is painted in a realistic manner. Although there is some depth in the painting, created by the roundness of the fish barrel and fish pouring from it, the painting is modern in feeling, approaching abstraction.

Phillips, M. 1982. Duncan Phillips and his collection. W.W. Norton & Co., New York. 345 pp.