

**A Synoptic Review of the Ecology and Management
of Bluegill Sunfish (*Lepomis macrochirus*) with
Implications for Fishery Management in Wisconsin**



Photo by Dr. Derek Ogle

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Foreword- David J. Neuswanger

This literature review is a project of the Wisconsin Department of Natural Resources (WDNR) Panfish Standing Team. In Wisconsin, “panfish” traditionally have been regulated as a broad group that includes several taxa – the sunfishes (*Lepomis* spp.), crappies (*Pomoxis* spp.), and yellow perch (*Perca flavescens*). The Panfish Standing Team is responsible for assembling and summarizing technical information to advise the WDNR Fisheries Management Board on matters of statewide panfish management policy and practice.

Content of this review is structured by the primary rate functions influencing fish population density and size structure – reproduction and recruitment, movement and distribution, growth, and mortality. Scope of the review is limited to peer-reviewed journal articles, AFS special publications, and agency-approved research bulletins published through 2015 and deemed relevant to the ecology and management of inland lake populations of bluegill in Wisconsin. We strove to summarize enough vital elements from each major study to minimize the need for readers to routinely consult original works. This required us to include critical context with regard to study sites and methods in order to help readers decide if results are applicable to their work. To facilitate comprehension by curious anglers and to maximize relevancy for managers who currently regulate harvest in English units of measure, we converted numbers from metric to English whenever practical.

Though much remains to be learned, great strides have been made in understanding the ecology and management of bluegill. It is our hope that the Wisconsin DNR and other fishery management agencies in the upper Midwest will find this synopsis relevant and useful in developing and adjusting bluegill management policies and practices in the years ahead.

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Bluegill Reproduction and Recruitment

Abiotic Factors Affecting Bluegill Reproduction (Survival of Eggs/Larvae to Dispersal)

Water temperature strongly influences the onset, peak period, and duration of spawning for bluegill (*Lepomis macrochirus*). Bluegills may begin spawning when surface water temperatures reach 64°F (Scott and Crossman 1973). Snow et al. (1970) reported that bluegill spawning activity in Wisconsin begins in May at a water temperature of 67°F, peaks in June, and continues through early August. Beard (1982) found that actual spawning of bluegill did not occur at water temperatures less than 70°F and occurred only rarely at water temperatures greater than 80°F in three small winterkill lakes in northwestern Wisconsin, where he documented multiple bouts of spawning from late May through early August during seasons ranging between 31 days (4 bouts) and 112 days (11 bouts) long.

Bluegill nesting colonies are not randomly distributed relative to available habitat, and specific colony sites are used repeatedly (Avila 1976; Bartlett et al. 2010). Ehlinger (1997) reported significantly fewer bluegill nesting colonies and more nests per colony as the proportion of pelagic habitat (depth >13 feet) increased beyond 50% of total surface area in 12 small lakes (12-211 acres) in southern Wisconsin. Beard (1982) found that bluegills nested on substrates of muck, sand, and gravel in northwestern Wisconsin lakes; but they had a slight preference for areas of gravel mixed with sticks. In Lake Caroline, Virginia, Bain and Helfrich (1983) found that most bluegills nested at depths < 2 feet where the substrate in active nests was predominately coarse gravel (0.3-1.3 inch diameter) even though undisturbed substrate in the nesting area was mostly sand (0.005-0.02 inch diameter). Larval mortality decreased as the proportion of particles larger than 0.3 inch diameter increased in unguarded nests in Lake Caroline because larvae were less vulnerable to predators in the gravel interstices. In 356-acre glacial Lake Cochrane in South Dakota, Gosch et al. (2006) found the average depth of 15 bluegill spawning colonies was 3 feet, and all nest sites had gravel in close proximity to short, low-density *Chara* despite the availability of other substrates and macrophytes at various

densities. In summary, gravel seems to be a preferred substrate for bluegill nesting in most waters studied to date.

Water transparency influences the depth at which bluegills spawn. In mesotrophic Lake Opinicon, Ontario, nesting occurred at water depths ranging between 1.3 and 8.2 feet (Gross and Charnov 1980). In an extraordinarily clear glacial lake in Pennsylvania (102-acre Lake Giles; Secchi transparency \geq 33 feet), 45% of nesting colonies occurred at depths of 3 to 6 feet; but 30% of colonies were at depths $>$ 12 feet, and maximum colony depth was 19 feet (Olson et al. 2006). In Lake Giles, nesting depth increased during the spawning season as water temperature increased. On June 8 when littoral zone water temperature was uniformly 65°F to a depth of 11 feet, 88% of nests were less than 5 feet deep; but by June 23 (near the summer solstice), 59% of nests were 13 to 15 feet deep in 68 to 69°F water (Olson et al. 2008).

Ultraviolet radiation (UVR) in transparent lakes has an important negative effect on the survival of early life history stages of bluegill (Gutierrez-Rodriguez and Williamson 1999). In Lake Giles, Pennsylvania, nests less than 3 feet deep were predicted to suffer UVR-induced larval mortality of 55% under full exposure. However, shallow-nesting bluegills frequently chose overhanging trees or other shoreline structures to nest under, thus minimizing actual UVR exposure and reducing predicted larval mortality to only 19% at those depths (Olson et al. 2006). Researchers concluded that removal of shade-producing shoreline vegetation could greatly increase the risk of UVR-induced mortality in highly transparent lakes if suitable spawning habitat is not available in deep water as it was in Lake Giles. However, the risk of UVR-induced mortality in most Wisconsin lakes is much lower than in Lake Giles; lakes in the upper Midwest and northwestern Ontario typically have high levels of DOC which minimize UVR attenuation at bluegill spawning depths (Williamson et al. 1996). In summary, it seems unlikely that UVR will cause significant mortality of larval bluegills in most Wisconsin lakes.

Biotic Factors Affecting Bluegill Reproduction (Survival of Eggs/Larvae to Dispersal)

Male bluegills generally nest and breed with high synchrony in densely packed colonies (Snow et al. 1970; Gross and MacMillan 1981) containing as few as 4 and as many as 272 nests

(Neff et al. 2004) spaced 2 inches apart (Côté and Gross 1993). Neff et al. (2004) found that 4.5% of parental males built nests solitarily in Lake Opinicon – at least 3 feet away from their nearest neighbors. Solitary nesters were similar in size and age to colonial nesters; but they were in significantly better condition, and they obtained as many eggs from females as did dominant males nesting in the interior of colonies. Côté and Gross (1993) found that the fungus *Saprolegnia* sp. infected significantly more eggs in the nests of solitary males (38%) than of colonial nesters (19%), possibly because colonial males spent less time defending eggs from predators and more time fanning them, which reduces fungal infection.

Ehlinger et al. (1997) provided a summary of reproductive behavior in male bluegill, which exhibit two basic alternative reproductive strategies – parental and cuckolder. Gross and Charnov (1980) found parental males usually mature late in life (ages 7 or 8), compete aggressively with other parental males for interior positions within nesting colonies, build and defend nests, and care for developing offspring. Cuckolder males mature early and do not build or tend nests even if parental males are removed. Instead, they steal fertilizations from parental males in one of two ways: As young “sneakers” (primarily ages 2 and 3), they dart in and out of nests to join parental males in fertilizing the eggs of visiting females. As older “satellites” (primarily ages 4 and 5) they hover over nests mimicking female appearance and behavior in order to gain access to spawn alongside actual females. Ehlinger et al. (1997) discovered that mature cuckolder males differed from mature parental males in morphology (size-adjusted body shape) and physiology – cuckolder males allocating significantly more of their total body mass to testes (5.6%) than parental males (1.2%). Mature males could be categorized reliably as cuckolders if testis mass accounted for 3% or more of total body mass. Differences between male types in Lake Opinicon, Ontario were conserved when their progeny were reared in Illinois ponds (Ehlinger et al. 1997). Highly variable growth rates among bluegills in those ponds significantly affected the timing and proportion of males maturing as parentals; but the proportion maturing as cuckolders (~20%) was relatively constant, raising the possibility of a heritable basis for observed variation in male reproductive behavior and associated morphological and physiological traits.

Population size structure influences maturation and reproductive behavior of male bluegills. In Illinois ponds, Aday et al. (2002) found that peak spawning activity in a population of stunted bluegills (all nesting males < 6.3 inches) occurred three to four weeks later than in two populations of non-stunted bluegills (all nesting males \geq 7.1 inches). In Illinois experimental ponds stocked with bluegills from Lake Opinicon, Ontario, Jennings et al. (1997) found that in the presence of relatively large parental males, smaller parental males had low gonadosomatic index (GSI) values, rarely nested, and failed to spawn. But in the absence of relatively large parental males, smaller parental males had high GSI values, nested frequently, spawned successfully, and provided parental care. Gross and Charnov (1980) found that male bluegills with mature testes in Lake Opinicon grew significantly less in the season of capture than equal-aged males with immature testes. But the hypothesis that a maturation-linked decline in growth rate leads to reduced size structure upon overexploitation of large parental bluegills was not tested directly by Jennings et al. (1997). Casselman and Montgomerie (2004) found that sperm concentration in ejaculates was significantly higher in the older, dominant males nesting in the interior of colonies in Lake Opinicon. Oplinger et al. (2013) tested whether growth, age at maturity, and energy investment into maturation were maternally inherited traits by crossing males and females from both stunted and non-stunted Illinois populations. The authors found no evidence of maternal inheritance of these traits and conclude that they are influenced by environmental characteristics including existing male population structure and predation pressure.

Populations with higher standing stocks of bluegill may produce lower-density cohorts of offspring. In 38 Midwestern bass-bluegill ponds ranging between 0.5 and 6.0 acres in area, Novinger and Legler (1978) reported that bluegill populations with standing stocks of 100-150 pounds/acre produced the maximum densities of offspring by fall. In ponds with lower and higher standing stocks, densities of age-0 bluegills recovered in fall rotenone samples were considerably lower. Schneider (1999) documented low spawning activity in a lightly exploited and dense population of large adult bluegills in Blueberry Pond, Michigan – a relatively shallow, clear, weedy, 20-acre private lake with an extremely high density of large bluegill (204 per acre \geq 8 inches). He observed very little spawning activity and very low recruitment despite finding that Blueberry Pond bluegills of variable size and condition exhibited normal reproductive

potential after being transferred into experimental ponds at low density (8-31 adults per pond, drained after four months to count all age-0 bluegills). During three years of monitoring, relatively few bluegill nests were seen in Blueberry Pond (100-200 per year), and only three male bluegills were ever observed guarding nests. Schneider (1999) estimated that only 2% of the adult bluegills even attempted to spawn in Blueberry Pond. Because these fish demonstrated the capacity to spawn at expected levels when removed from their high-density environment, Schneider discussed the possibility that social inhibition may have repressed bluegill reproduction in Blueberry Pond. It was not determined if this inhibition was strictly behavioral or if it also affected maturation of testes (not measured) until the fish were transferred to a less crowded environment.

Nest predation influences sunfish nesting behavior and survival of eggs and larvae. Bain and Helfrich (1983) found that fish were far more important than invertebrates as predators on bluegill larvae in Lake Caroline, Virginia, where 83% of all fish caught hovering near nesting colonies with bluegill larvae in their guts were 1.5- to 5.0-inch bluegills. In a study of high-density bluegill populations exhibiting stunted growth in Michigan ponds, Breck (1996) found a high rate of recruitment failure due primarily to predation by juvenile bluegills on eggs and larvae in the nest and on fry leaving the nest. Predation on bluegill nests from the water column was primarily by conspecifics (94%) in Lake Opinicon (Gross and MacMillan 1981), though pumpkinseed (*Lepomis gibbosus*) also consumed bluegill eggs and larvae.

Gross and MacMillan (1981) found significant substrate-level predation by snails (11%, mostly *Viviparous georgianus*) and fishes (7%, mostly *Ictalurus* spp.) in Lake Opinicon, where brood losses from peripheral nests were at least three times greater than from interior nests. They proposed that brood predation has been an important selective pressure in the evolution of colonial nesting behavior in bluegill. In Michigan ponds stocked with 1.2 crayfish per square yard (*Orconectes virilis* and *O. rusticus*), Dorn and Mittelbach (2004) found that crayfish activity destroyed all bluegill nests in small colonies (≤ 15 males) during a four-week period. When crayfish enclosures were introduced, bluegills selected nesting locations only inside the enclosures suggesting that bluegills can discriminate between safe and risky nesting environments.

Fishery managers have long suspected that the bottom-feeding activity of common carp (*Cyprinus carpio*) adversely affects centrarchid nesting success. Wolfe et al. (2009) challenged conventional thought of negative interaction between carp and bluegill by stocking adult bluegills in enclosures with and without common carp and found that bluegills spawned just as well in either case. Carp were observed feeding throughout their enclosures, yet densities of larval and early juvenile bluegills were similar in enclosures with and without carp. However, Forester and Lawrence (1978) found a 67% reduction in bluegill standing stock in ponds with common carp in comparison to control ponds that did not contain carp, although it is not confirmed whether this was the result of reduced nesting success or other factors.

Managing Bluegill Reproduction

Becker (1983) stated that stunting (overpopulation, often from excessive recruitment, leading to slow growth rate and high natural mortality prior to reaching angler-acceptable size) of bluegills was considered the biggest fish management problem in Wisconsin. Beard (1982) suggested suction-pump removal of bluegill eggs and fry from colonial nests as a potential method to eliminate year classes prior to dispersal in lakes smaller than 100 acres – a limit based on perceived logistical constraints. Despite acknowledging that bluegills often spawn until early August, Beard hypothesized (but did not test) that near-weekly destruction of colonial nests during the usual June peak in spawning activity and fry dispersal might eliminate bluegill year classes.

Beyerle and Williams (1967) applied enough copper sulfate crystals to theoretically kill all bluegill eggs and fry at nest sites in four Michigan lakes between 80 and 200 acres, starting at the onset of spawning activity (May 18) and ending when all spawning activity ceased (August 9). Mean fall capture rate of age-0 bluegill, though highly variable, was slightly *higher* in treatment lakes the year after treatment than the year before treatment; and mean age-0 CPE was only marginally lower in treatment lakes than in control lakes. Investigators concluded that poisoning of eggs and fry at nest sites did not kill many (if any) more bluegills than would have died naturally during the first year of life. Also, they questioned whether nest-site poisoning

would be worth such intense effort (new nesting colonies were created continuously during their chemical control operations) if compensatory survival should occur in subsequent years.

Factors Affecting Bluegill Recruitment (Survival of Dispersed Larvae to Stock Size)

Abiotic factors

Studies of the recruitment advantages of early versus late spawning in bluegill have produced highly variable results that often appear to be linked to temperature changes. Bluegill year-class strength was negatively related to date of first fry dispersal during 1971-1974 in three small winterkill lakes in northwestern Wisconsin, where the strongest cohorts were produced in years when fry began dispersing before late June (Beard 1982). Similar results were reported by Cargnelli and Gross (1996) for the 1993 year class of bluegills in Lake Opinicon, Ontario, where early-season fry (hatched during the first trimester) represented only 17% of total fry production but comprised 40% of recruits in spring of 1994. However, Garvey et al. (2002) reported disproportionately low survival of early-season sunfish fry to the fall juvenile stage in Lake Opinicon in 1998 – a year when water temperatures declined sharply from 70°F to 64°F immediately following the peak of larval abundance in late May. Schneider and Lockwood (2002) documented very weak 1992 year classes of bluegill in 10 of 16 study lakes in southern Michigan following the 1991 eruption of Mount Pinatubo, Philippines, which decreased the number of degree-days exceeding 65°F in southern Michigan to just 58% of the norm in summer of 1992. In 14-acre Ridge Lake in east central Illinois, Santucci and Wahl (2003) also found that early-season bluegill fry experienced much higher mortality by fall than those spawned later, in this case due to increased exposure to predation and documented high consumption (58-93% of littoral zone bluegill fry) by abundant young largemouth bass (*Micropterus salmoides*), which averaged 179/acre \leq age 3 during 1987-1989. To confound matters further, a study in two experimental ponds (9 and 11 acres) with predators in Alabama found that larval sunfish (almost all bluegill) mortality rate was highest for 10-day cohorts produced during intermediate bouts of spawning and lowest for the earliest and latest fry cohorts (Partridge and DeVries 1999), which ultimately could lead to a bimodal length-frequency distributions of yearling bluegill. In summary, dynamic abiotic and biotic factors seem to influence the extent to which early- or late-

hatched bluegills are more likely to recruit in any particular year, ecosystem, or geographic region. Garvey et al. (2002) emphasized that management of stable, resilient populations requires an appreciation for the flexible responses of life histories – facilitated by prolonged spawning in the case of bluegill – to unpredictable environmental variation.

Predation by Percids

There are a variety of examples of walleye (*Sander vitreus*) demonstrating effectiveness in controlling bluegill recruitment through predation. When walleye assumed dominance in the fish community of 293-acre Escanaba Lake, Wisconsin during the late 1940s and early 1950s, angler catch rates for panfish were extremely low (Kempinger and Carline 1977). As estimated density of age-2-and-older walleyes declined from ~35/acre in the late 1950s to ~15/acre in the early 1960s, angler catch rates for panfish, including bluegills, increased to low but detectable levels of 0.04-0.06/hour. When walleye density rebounded to levels above 25/acre and northern pike (*Esox lucius*) became well established in the mid to late 1960s, angler catch rates for all panfish species crashed to pre-1955 levels. These co-occurring phenomena suggest that Escanaba Lake predators (particularly walleyes) exerted strong control over panfish recruitment. Kempinger and Carline (1977) believed that a small number of adult panfish were able to produce large numbers of juveniles to sustain high densities of predators in Escanaba Lake, but very few survived to adulthood.

In natural lakes, walleyes prey upon bluegills throughout the year. In 10-acre Camp Lake in northwestern Wisconsin, Beard (1982) reported that age-0 walleyes only 2.4 inches long began eating bluegills during the second or third week of July when early-cohort larval bluegills began appearing in the littoral zone. Age-0 bluegills occurred in a high proportion of stomachs of small stocked walleye fingerlings in mid summer, decreasing in frequency in late summer as age-0 bluegills became scarce or too large for age-0 walleyes to consume. In September and October of 1989, bluegills or unidentified *Lepomis* in Lake Mendota, Wisconsin comprised 74% of the total number of fish observed in age-0 walleye stomachs; by comparison yellow perch (*Perca flavescens*) comprised only 13% (Madenjian et al. 1991). The vulnerability of bluegills to predation by age-0 walleyes was especially important in determining the growth of walleyes

during their first growing season (Madenjian and Carpenter 1991). In 13-acre Jewett Lake in northeastern Michigan and three southern Michigan lakes with relatively simple fish communities, 36-37% of the fall walleye diet, by weight, was sunfish (mostly bluegill), which occurred in 20-35% of stomachs (Schneider and Breck 1997).

Walleyes tend to feed over winter and thus may contribute to age-0 bluegill overwinter mortality. Kelso (1972) reported maintenance rations for walleye of 28 mg/g/week (0.40 % body weight/day) at 39°F and 82 mg/g/week (1.17% of body weight/day) at 68°F. Therefore, walleyes must eat at least one-third as much in mid winter as they do in mid spring just to maintain body mass; no growth is expected at water temperatures < 54°F. Schneider and Breck (1997) stocked unstructured 0.5-acre experimental ponds with 1.1-inch bluegills (4,348-8,502/acre) and juvenile walleyes (19-45/acre) or adult yellow perch as predators every fall for four years. Overwinter mortality of age-0 bluegills averaged 10% in seven control ponds without predators, 39% in ponds with some type of predator, and 55% (range 25-89%) in ponds where walleye were the sole predator. Schneider and Breck (1997) concluded that juvenile walleye and adult yellow perch in sufficient biomass can consume enough age-0 bluegills during winter to help control stunting in bluegill. A similar conclusion was reached by Moffett and Hunt (1945) for yellow perch in 73-acre Cedar Lake in southern Michigan, where age-0 bluegills comprised 84% of total winter food volume in the stomachs of 185 perch.

Schneider and Breck (1997) found most (62%) of the 219 bluegills found in Michigan walleye stomachs were < 2 inches long, but maximum size of bluegills eaten increased with walleye length. As predicted by walleye mouth gape estimates, empirical consumption data from four Michigan lakes confirmed that 12-, 15-, and 20- inch walleyes ate bluegills up to 4 and 5 inches long. In laboratory experiments with water temperatures 64-70°F, light intensity 150-200 lx, and no simulated structure, Einfalt and Wahl (1997) reported that capture efficiencies of 4- to 8-inch walleyes exceeded 70% for bluegills < 1.0 inch but rapidly declined to < 20% for bluegills \geq 2.0 inches. Optimal size of bluegill as prey was 15-24% of walleye total length, though size of prey chosen decreased relative to predator size. Walleyes 4-5 inches long rarely ate bluegills > 1.6 inches, and 6- to 8-inch walleyes rarely ate bluegills > 2.0 inches. Given a choice between equal numbers of optimal-size gizzard shad (*Dorosoma cepedianum*), golden

shiners (*Notemigonus chrysoleucas*), and bluegills, juvenile walleyes consumed significantly more gizzard shad (76%) than bluegills (7%), suggesting that gizzard shad have the potential to function as a major buffer against predation by walleye on bluegill in waters with abundant young shad.

Predation by Esocids

In aquaria, northern pike 13-23 inches long selected cyprinids over centrarchids, and centrarchids ≥ 4 inches were rarely consumed (Beyerle and Williams 1968). Wahl and Stein (1988) stocked juvenile northern pike, muskellunge (*Esox masquinongy*), and tiger muskellunge (northern pike x muskellunge hybrid) into laboratory tanks with single-species groups of optimal-size prey, where all three esocid taxa captured bluegills less efficiently (0.14 capture per strike) than fathead minnows (*Pimaphales promelas*, 0.67) and gizzard shad (0.78). Experiments in Ohio impoundments confirmed that feeding and growth of fall-stocked juveniles of all three esocid taxa were less in a centrarchid-dominated system than in a system with soft-rayed or fusiform prey. Tomcko et al. (1984) found that only 14% and 26% of pond-stocked tiger muskellunge fingerlings captured optimal-size bluegills stocked at low prey density (1 per m²) and high prey density (5 per m²), respectively. Frequency of occurrence of bluegill in the diet of pond-stocked hybrid muskellunge was low regardless of macrophyte density or prior hybrid experience consuming live prey.

Predation by Largemouth Bass

Largemouth bass have been the focal predator in a bulk of the existing literature on predator-prey relationships related to bluegill, though most of these seminal studies were performed in the southern United States. Anderson (1978) and Novinger and Legler (1978) both documented an inverse relationship between the quality of largemouth bass and bluegill. These results demonstrated that in small impoundments abundant, but small, largemouth bass populations exerted enough predation pressure to control bluegill recruitment and create low density bluegill populations with higher size structure.

In 13 small South Dakota impoundments Guy and Willis (1990) found a positive relationship between largemouth bass catch per effort and bluegill PSD, while largemouth bass PSD was negatively correlated with bluegill PSD. Santucci and Wahl (2003) similarly documented high mortality of bluegill fry (58-93%) attributable largely to an abundant population of young largemouth bass, which averaged 179/acre \leq age in Ridge Lake, Illinois. Combined, these results suggest that an abundant population of small largemouth bass may have some effectiveness in controlling bluegill recruitment and increasing size structure, particularly in small lakes with relatively simple fish communities.

Rasmussen and Michaelson (1974) studied the fish community effects of imposing a 12-inch minimum length limit on largemouth bass at three small impoundments (20-30 acres) in northwestern Missouri in the late 1960s. Jamesport and Worth were clear and weedy, and bluegills were the only significant prey. Limpp was productive (Secchi visibility = 14 inches during summer phytoplankton blooms), with sparse macrophytes and a notable population of golden shiners. Despite high angler harvest of largemouth bass \geq 12 inches at all lakes, electrofishing capture rates of bass \geq 8 inches increased from 14-40/hour during pre-regulation years (N = 1-2) to 40-66/hour after imposition of the 12-inch minimum length limit (N = 3-5 years). There was a concurrent reduction in trap net capture rates of small and intermediate-size bluegill. With increasing competition for prey, bass growth rates declined, but bluegill growth rates either increased (Worth) or remained satisfactory (Jamesport and Limpp). Bluegill size structure (RSD-7) improved greatly in Worth Lake, but similar improvements were not observed at Jamesport and Limpp, where angler harvest was very high (averaged 156 bluegills/acre/year at Limpp) under liberal regulations (25 pounds plus one fish, daily). Thus, predation by increased numbers of small bass apparently reduced the density of intermediate-size bluegills and provided an opportunity for bluegills to grow to angler-preferred sizes in all three lakes, but improvements in bluegill population size structure were often unrealized because liberal regulations allowed high angler exploitation once bluegills reached quality size.

Managing Bluegill Recruitment

The use of largemouth bass as a predator on bluegill has been well documented in the United States and in smaller impoundments this simple predator-prey relationship can be efficiently managed to produce quality bluegill populations (Anderson 1978). Gabelhouse (1982) described a management approach referred to as “the panfish option” in which protection of largemouth bass under a 15 inch minimum length limit leads to a high density of small bass and effective predation on bluegill, ultimately resulting in bigger bluegill. Rasmussen and Michaelson (1974) provide a similar case study and found positive results with an even less restrictive length limit. The general strategy behind the “panfish option” has become widely accepted among fisheries professionals. Guy and Willis (1990) tested and found that this key relationship between bass and bluegill was similar in northern impoundments, lending credibility to application of the panfish option across a wide geographic area.

While largemouth bass effectiveness as a predator on bluegill is widely accepted in waterbodies with simple fish communities, several studies indicate that largemouth bass often fail to control bluegill recruitment in waters where more-preferred prey such as crayfish and young bullheads (*Ameiurus spp.*, Lewis and Helms 1964; Snow 1971), gobies (Azuma and Motomura 1998), or gizzard shad (Einfalt and Wahl 1997) can serve as buffer species when abundant. This may be an important consideration in choosing which predator to manage for when controlling bluegill recruitment is a goal.

The use of walleye to control panfish recruitment was suggested in New York State’s first Walleye Management Plan, in which Forney (1977) stated, “The walleye as a predator converts production of small fish into a larger, more desirable form and simultaneously reduces competition within the fish community which enables yellow perch, crappie and other pan fish to attain a harvestable size... Optimum yield from the fish community should take precedent over maximum yield of walleyes as a management objective in inland waters... Restricting walleye harvest to improve size and yield of pan fish is a legitimate objective in a mixed-species sport fishery.”

Goeman et al. (1990) noted that Minnesota lakes with naturally reproducing walleyes or successful walleye management programs tended to have abundant yellow perch and relatively few but fast-growing bluegills that attained sizes acceptable to anglers. They tried stocking walleyes (including large fall fingerlings at 1.0-33.5/acre) and adult yellow perch into small lakes (180-220 acres) with stunted bluegills. Fish community structure remained poor after several years of walleye stocking and surveys indicated that stocked walleye survival was low and likely limited by abundant small northern pike. They concluded that stocking yellow perch or walleye to control bluegills were not viable options in small lakes with high densities of slow-growing northern pike. It was recommended that attempts at community manipulation in these lakes focus on removal, harvest, or other manipulation of top predators in the fish community.

Schneider (1997) evaluated the introduction of bluegill into a simple walleye-perch community in 13-acre Jewett Lake. Walleye became the only primary piscivore in the fish community of Jewett Lake after its introduction in 1975 and successful reproduction starting in 1978. Several natural year classes of walleye were produced prior to appearance of the first large year classes of bluegill (probably introduced by anglers) in 1986 and 1987. As bluegill became established, total fish standing crop doubled to 63 pounds/acre, of which 52% was bluegill. Total mortality of bluegill from fall age-0 to fall age-1 was relatively high ($A = 0.92$) due to predation by walleye and yellow perch, allowing surviving bluegills to grow quickly from 1.4 to 4.3 inches in one year. At high average adult density (8.5/acre \geq 14 inches), walleye maintained community stability. Schneider (1997) concluded it may be feasible to use walleye as a tool to improve growth rate and size structure in populations of bluegill or yellow perch in small lakes.

Schneider and Lockwood (2002) tested several strategies for reducing bluegill recruitment in 12 bass-bluegill lakes in southern Michigan. One experimental treatment was to stock fingerling walleyes 4.7-6.8 inches long in three 75- to 100-acre lakes in 1990 at rates of 15-18 per acre. All fish species were protected from harvest through 1996. Bluegill population size structure improved greatly in all three lakes after a four-year lag. By 1995, average combined trap-net CPEs of 7- and 8-inch bluegills for all three lakes had increased from less than 9/net to more than 20/net. Some 9-inch bluegills were produced. There was no such change in four 170-

to 292-acre reference lakes (controls) where a 14-inch minimum length limit for largemouth bass took effect in 1993. This experiment suggests that walleyes can be more effective than largemouth bass in controlling bluegill recruitment and maintaining satisfactory bluegill size structure in complex fish communities of some upper Midwestern lakes.

Snow (1968) reported Wisconsin's first attempt to control recruitment of bluegills by stocking predators at high densities into Clear Lake in Sawyer County – a 77-acre lake with sand/gravel substrates, sparse macrophyte growth, and insufficient density of largemouth bass to control a population of severely stunted bluegill. Both walleye and muskellunge were stocked as possible panfish predators. Walleye introduction failed but muskellunge were successfully established. Bluegill growth rate remained slow indicating that the established muskellunge population was not an effective control. Because walleye were not successfully established it was not possible to make conclusions on their effectiveness at controlling bluegill recruitment. However, this study highlights an equally important consideration: that effectiveness of establishing certain predators may be limited more by habitat considerations than management effort or public desire.

Northern pike introduced at high densities (28-32 per acre) into two small Michigan lakes survived at a high rate (44-60%) but did not consume enough overabundant bluegills to grow at an average rate or to increase the growth rate of stunted bluegills (Beyerle 1971). Similarly, predation by stocked tiger muskellunge did not reduce density, increase growth rate, or improve size structure of slow-growing bluegills in Ridge Lake, Illinois (Storck and Newman 1992).

Implications for Managing Bluegill Recruitment in Wisconsin

Managing bluegill recruitment by limiting reproduction through mechanical (Beard 1982) or chemical means (Beyerle and Williams 1967) has proven to be ineffective or logistically infeasible. Predation may be the only practical and affordable way to reduce excessive bluegill recruitment in Wisconsin lakes, and previous studies have shown success is not universal. Among the available predators, there is little support from the literature that esocids will consume enough bluegills to affect bluegill population density or size structure. Similarly, there

are no documented cases of smallmouth bass (*Micropterus dolomieu*) controlling bluegill recruitment.

Predation by abundant largemouth bass often is sufficient to control recruitment of bluegill in relatively small lakes (Rasmussen and Michaelson 1974; Guy and Willis 1990; Santucci and Wahl 2003), but the relationship is more complicated when more-preferred prey (e.g., yellow perch, gizzard shad, and crayfish) are present that could buffer the predatory impact of bass on less-preferred bluegill. Challenges remain to identify thresholds of lake size, turbidity, and buffer species abundance, above which predation by largemouth bass will not likely control recruitment sufficiently to sustain satisfactory growth rates and population size structure of bluegill. Moreover, managers are faced with competing management goals when considering whether to manage largemouth bass for maximum predation potential or quality size.

Walleyes can be effective predators on bluegill and other panfish species, yet lakes must exhibit characteristics needed to sustain walleye at a sufficient abundance to provide predation. Most of Wisconsin's large, high profile lakes have complex aquatic communities with many species of prey that buffer the single-species impact of predation by largemouth bass, thus walleyes at moderate to high density have greater potential to consume enough juvenile bluegills throughout the year to reduce excessive recruitment and sustain adequate growth. However, as lakes get larger and fish communities more complex, the ability to control bluegill recruitment through predation may be masked by other environmental drivers as well as angler harvest. In general, stocking walleye as a means to control bluegill has had limited results, largely because stocking often fails to produce any kind of sizable adult walleye population, particularly in shallow clear lakes (Snow 1968; Goeman 1990). The availability of adequate thermal-optical habitat conditions as described by Lester et al. (2004) and Robillard and Fox (2006) may determine which lakes are suitable for walleye dominance and which may be irrevocably dominated by largemouth bass or northern pike where even moderate walleye densities cannot possibly be sustained (Santucci and Wahl 1993). More work is certainly needed to elucidate how and when largemouth bass and walleye predation effectively control bluegill recruitment, yet given the varying nature of Wisconsin lakes and other driving forces, the relationship will likely never be fully clear nor apply the same to all lakes.

Bluegill Movement and Distribution

Werner (1967) was the first to demonstrate that bluegill fry migrate from the littoral to the limnetic zone shortly after swim-up. In 27-acre Crane Lake, Indiana, bluegill fry remained pelagic for several weeks before returning to littoral zone macrophytes at lengths of 21-25 mm for the remainder of the summer.

In large lakes, larval sunfish (*Lepomis* spp.) that survive their migration out of the littoral zone do not become uniformly distributed throughout the limnetic zone. In 9,831-acre Lake Mendota, Wisconsin and 1,927-acre Lake Opinicon, Ontario, larval sunfish densities throughout the summer were substantially higher in shallow limnetic areas (near nesting colonies) than in deep areas far from shore (Post et al. 1995; Garvey et al. 2002). In Lake Opinicon, larval density at the deepest offshore site was only 8% of average inshore limnetic density. Shoup et al. (2014) used hydroacoustic methods to document daily migrations of juvenile bluegill into open water at night, and returning to near shore weedy habitat during the day. The authors found significantly less predators in open water and night, leading to the conclusion that these migrations were part of a response to predation.

Bluegills move among lakes in a connected chain. Substantial movement may not happen every year, but Parsons and Reed (2005) twice observed significant movement of adult bluegills among lakes of the Alexandria Chain in west central Minnesota. In 1993 and 1995, respectively, T-bar anchor tags from 27% of quality-size bluegills tagged in Le Homme Dieu and 36% of those tagged in Lake Victoria were returned by anglers fishing in other – usually immediately adjacent – lakes of the chain.

Bluegill Growth

Abiotic Factors Influencing Bluegill Growth

Abiotic factors are easily measured and recorded and therefore, many researchers have analyzed the relationship between different abiotic factors and bluegill growth. Tomcko and Pierce (2001) evaluated the relationship between bluegill growth rates and Secchi depth, total alkalinity, maximum depth, lake surface area, the shoreline development factor, percent littoral area and the mean maximum July air temperature in Minnesota lakes. They found that Secchi depth, maximum depth, and total alkalinity explained 16-33% of the variation in bluegill growth. Tomcko and Pierce (2001) found that littoral area and total alkalinity were positively related to bluegill growth. Similarly, Hoxmeier et al. (2009) found that larger body size of juvenile bluegills was associated with low Secchi depth.

Waterbody type and yearly variation in climatic conditions affect bluegill growth rate. Back-calculating previous-year-only length increments of more than 18,000 bluegills from 113 Nebraska lake populations, Porath and Hurley (2005) found that annual growth of bluegills at ages 2 and 3 was significantly greater in shallow, weedy, natural sandhill lakes than in man-made flood control reservoirs, pits, and ponds. Sandhill lakes are almost entirely littoral; mean depths range between 3 and 10 feet, and average coverage by submersed macrophytes is 48% (Paukert et al. 2002a). Porath and Hurley (2005) believed this habitat provided a stable source of abundant invertebrate prey for juvenile bluegills, consistent with the observations of Schneider (1999) in Blueberry Pond, Michigan, where bluegills 1 to 3 inches long ate a variety of invertebrates (especially small midge larvae and nymphs of the mayfly *Caenis* sp.) often associated with the dense vegetation. Porath and Hurley (2005) detected significant among-year differences in annual length increments for bluegills ages 2 through 6 in sandhill lakes from 1994 through 2001, suggesting annual growth was influenced by changes in climatic conditions also. Hoxmeier et al. (2009) found temperature to be the most important overall factor in explaining bluegill size structure. Gerking (1966) found an expected positive correlation between bluegill growth rate and length of the growing season. These results may have implications for management even within an individual state such as Wisconsin.

Beitinger and Magnuson (1979) cited numerous studies reporting the final temperature preferendum for bluegills at approximately 88°F, bounded by lower and upper avoidance temperatures of 84 and 91°F. Consistent with those earlier observations, Beitinger and Magnuson (1979) found that laboratory-held bluegills from Lake Mendota, Wisconsin grew fastest at 86 and 88°F; and at 93°F bluegills had significantly lower food conversion efficiencies and growth rates than fish held at lower water temperatures. Kitchell et al. (1974) had assumed somewhat lower maximum and optimum temperatures for feeding (88 and 81°F, respectively) in their model of bluegill biomass dynamics. But they demonstrated that even a 5.4°F (3°C) increase in the annual temperature cycle could adversely affect bluegill biomass, despite the increased length of growing season, by elevating mid-summer water temperatures above the level considered optimal for growth.

Hoxmeier et al. (2009) looked at the effects of temperature, water transparency and prey availability on bluegill growth in Illinois reservoirs. They found that good growth and large body size were associated with warm, clear lakes and abundant prey. This suggests that bluegills were able to feed more efficiently in clearer water. These results were further supported by Aday et al. (2002) on an overlapping set of Illinois reservoirs.

Biotic Factors Influencing Bluegill Growth

Many biotic factors may influence bluegill growth including relative density of bluegills, age and size structure of bluegills, prey availability, competition, and predator abundance. In a series of experiments in nuclear reactor cooling pond in South Carolina, Belk (1995) found that variance in bluegill growth and age and size at maturity were due to environmental factors and not genetic variation. Possible environmental factors were resource availability, demographic structure, and size-selective predators. They concluded that the lack of genetically based differences in growth patterns might be due to the relatively young age of the pond.

In a study of bluegill in Illinois reservoirs, Hoxmeier et al. (2009) found that bluegill density and harvest mortality did not contribute much explanatory power to growth models and

that their effects might be mitigated by temperature, water quality and prey availability. However, many other studies have shown evidence of density dependent growth. Osenberg et al. (1988) found that climatic variability explained very little observed variation in nine Michigan lakes. Most variation in growth appeared to be related to density dependent competition for limited food resources Wiener and Hanneman (1982) compared the effects of population density on condition and growth of bluegills in northern Wisconsin lakes. They found that mean condition factors and back-calculated lengths were negatively correlated with relative density of bluegills. In keeping with those findings Beckman (1950) found a significant increase in bluegill growth rate following major winterkill events in four Michigan lakes, presumably a result of the suddenly decreased density of bluegill and other fish species. However, the improvement in growth rate lasted only one year following winterkill, suggesting that short term reductions in density may not have long-term gains in growth.

Breck (1997) measured growth rates of young-of-year bluegill in experimental ponds and simulated growth in a model. He found that growth rate decreased when the zooplankton density decreased below a certain threshold. The time of this growth reduction and the size of the fish at the end of the growing season were density dependent.

Competition with other species for food may have an effect on bluegill growth. Aday et al. (2003) examined the relationship between gizzard shad and bluegill. Growth rates of bluegill were increased in waters without gizzard shad, which may be due to higher benthic invertebrate densities. Bluegills were smaller in waters containing gizzard shad and higher turbidity. Increased turbidity may have negatively affected bluegill foraging.

Presence of predators and predation pressure have a positive effect on bluegill growth (discussed more in-depth in the “Factors Affecting Bluegill Recruitment” section of this literature review). Oplinger et al. (2011) tested response in growth rate of bluegill from stunted and non-stunted populations when stocked into ponds with and without largemouth bass. Presence of bass resulted in faster growth of bluegill from both population types, though fish from non-stunted populations maintained a larger growth advantage.

Given bluegills unique life history, in particular the various male maturation strategies, the presence or lack of large male bluegills may influence growth of the rest of the population (Ehlinger et al. 1997; Jennings et al. 1997, Aday et al. 2002). This phenomenon, referred to as sexual stunting, is a byproduct of male bluegills maturing early and devoting energy to somatic growth instead of body size growth. Early maturation may occur when large parental males are absent and thus little sexual competition exists. To evaluate this concept Drake et al. (1997) compared maturation schedules and ratios of male reproductive strategies between lakes with high fishing effort and low fishing effort. Drake et al. (1997) found that parental bluegills in lakes with high fishing pressure matured at younger ages and smaller size and had reduced growth potentials.

Managing Bluegill Growth

Although the link between physical and water quality variables associated with lakes and bluegill growth may be weak, these variables are easily measured and can be included in growth models. They can be used to initially screen lakes for bluegill regulations and to predict which lakes may support bluegill populations acceptable to anglers (Tomcko and Pierce 2001).

Porath and Hurley (2005) found that bluegill growth rates differed by waterbody type in a study in Nebraska. Supplemental feeding was correlated with increased growth increments in some waterbody types but not in others, and the presence of gizzard shad affected bluegill growth rates negatively in some waters. Harvest regulations had a mixed effect for some of the waterbody types. It is therefore important to incorporate waterbody type into an evaluation of bluegill growth.

Supplemental feeding has been suggested as an effective tool for managing slow-growing, stunted bluegill (Berger 1982). Growth and body condition were evaluated after bluegills were fed commercial food in a 30.4 hectare lake in Kansas. The supplemental feeding provided more harvestable-sized fish for anglers. This might not have been a direct effect of supplemental feeding and may have also been related to an increase in harvest and resulting change in population structure (Berger 1982). Woodard et al. (2013) documented increases in

growth rate, gonadosomatic index, and resulting larval production in pond stocked bluegill given supplemental feed compared to fish in control ponds with no feed. Despite the suggested gains in growth from supplemental feeding, the logistical and financial constraints to scale such a program up to be effective in Wisconsin lakes are plentiful.

Fishing effort can also have an effect on bluegill growth, particularly through sexual stunting (Drake et al. 1997; Beard and Essington 2000). Fishing regulations that reduce exploitation could alleviate this reduction of growth potential. In particular, regulations designed to retain large males in the population, thereby encouraging growth of younger or smaller males, offer the greatest positive impact on bluegill growth.

Adult Bluegill Mortality and Exploitation

Biotic Factors Affecting Adult Bluegill Mortality

The bacterial disease commonly known as Columnaris is a frequent, and potentially significant, source of adult bluegill mortality in North America (Post 1987) with Wisconsin being no exception. Columnaris is characterized as lesions on the body of the fish which can enter the blood stream and cause systemic infection. Treatments are available (Wandelaar et al. 2013), but are not likely to be feasible at a statewide level. Managers should be aware of the diagnostic signs of columnaris and be prepared to explain resulting fish kills to the public.

Mortality rate and longevity in male bluegills is influenced substantially by life history. Gross (1982) reported that sexually mature cuckolders grew 30% more slowly and had only 15% of the survivorship of future parental males. Most cuckolders died by age 5, whereas some parental males lived up to age 11.

Adult Bluegill Exploitation

Anglers tend to harvest the largest available bluegills and exploitation of large parental males can lead to serious consequences in population size structure and growth (see growth section for more; Drake et al. 1997). Similar findings were reported by Belk and Hales (1993) for 2,640-acre Par Pond, South Carolina, where a unique, unexploited population of bluegills matured approximately two years later and at lengths more than 2 inches longer than bluegills in angler-exploited reservoir fisheries of the southeastern United States. Tomcko and Pierce (1993) studied bluegill populations in 12 Minnesota lakes to examine the effect of fishing pressure on ratios of male bluegills exhibiting different life history strategies. They could establish no conclusive relationship between total hours of fishing pressure (all species) and highly variable ratios of male life-history variants (0-94% cuckolders) captured by various gears; but actual bluegill exploitation rates were not measured.

Estimates of bluegill fishing mortality rate (u) in several early studies reviewed by Coble (1988) ranged between 12 and 45%, but some may have been underestimates because they did not include a full year of exploitation, or their stock density estimates included fish smaller than anglers would likely harvest. Exploitation rates were significantly and positively related to angling effort and were never less than 18% at efforts exceeding 80 hours/acre/year. Exploitation rates generally exceeded 40% at efforts exceeding 250 hours/acre/year (Coble 1988).

Under a 20-daily bag limit in 1,680-acre Pelican Lake, Utah, anglers harvested an estimated 22,907 bluegills averaging 8.3 inches long during the 1977 season, which comprised an estimated 19% of August standing crop (Burdick and Wydoski 1989).

In a summary of trends documented in a 58-year fishing contest in Minnesota's northwestern lake region (~120 fishing lakes totaling 62,000 acres), Olson and Cunningham (1989) reported mean weights of 10,534 bluegills voluntarily entered into the contest by anglers had declined from ~1.3 pounds prior to 1953 to ~0.8 pounds by 1987; and "trophy-size" fish (defined as bluegills ≥ 1.25 pounds in this study) had all but disappeared by the late 1980s. Rapid declines in mean weight and trophy-size entries since the mid 1970s were thought to be indicative of overexploitation, supporting Coble's (1988) call for reexamination of the long-held belief that angling rarely results in overfishing of bluegill populations.

Beard and Kampa (1999) examined symptoms of quality overfishing in Wisconsin bluegill populations by summarizing length data for bluegills captured during 493 early-spring fykenetting surveys conducted between 1967 and 1991 (primarily targeting walleyes or muskellunge) and 205 angler creel surveys conducted between 1979 and 1991 on lakes throughout the State. Mean length of bluegills captured in early-spring fykenetting surveys declined almost 0.5 inch between 1967 and 1991. Mean RSD-P decreased significantly ($P < 0.05$) from 15% in 1967 to 7% in 1991. Mean catch rate (1.4/hour) and harvest rate (0.7/hour) among anglers targeting panfish did not change much over time. However, the regression of mean RSD-P in the angler harvest over time decreased significantly ($r = -0.60$, $P < 0.05$) from

28% in 1980 to 12% in 1991, confirming the 50%-plus decline in RSD-P indicated by early-spring fykenetting surveys.

Conservative estimates of annual exploitation based on angler tag returns from 5.0-inch and larger bluegills – uncorrected for tag loss and non-reporting – averaged 21% (range 10-36%) during 1990-1992 in four small Missouri impoundments (Kruse 1997). The lowest three-year average tag return rate (10%) was from a 36-acre private lake, and the highest annual tag return rate (60%) was from an 11-acre public pond. There was a strong positive linear relationship ($r = 0.71$) between total length at tagging and angler tag return rate. Only 6-12% of bluegills tagged at < 6 inches were returned by anglers, but $\geq 20\%$ of all bluegills tagged at ≥ 8 inches were returned during the three-year study.

Parsons and Reed (1998) examined rates of mortality and exploitation of bluegills ≥ 6 inches at four lakes (420 to 1,744 acres) of the Alexandria Chain in west central Minnesota. Average total annual mortality rate of quality-size bluegills was 75%. Based on voluntary angler tag returns conservatively corrected for non-reporting but not for tagging mortality, estimates of annual exploitation rate of quality-size bluegills on individual lakes varied between 8 and 32% and was statistically similar for all inch-groups ≥ 6.0 inches. Exploitation was not higher during the spawning period than at other times, possibly because the late spring season was dominated by anglers seeking walleye. Even at the low to moderate rates estimated in this study, exploitation seemed to negatively affect bluegill population size structure. Years of high angler harvest were also years of high exploitation rate; and this relationship was significantly more pronounced on two lakes with low-density bluegill populations than on two lakes with high-density populations. Among bluegill anglers who harvested at least one fish, at least 20% on each lake kept more than 10 bluegills per completed trip. A daily bag limit of 10 would have reduced annual harvest by up to 35% on three of the four study lakes (Parsons and Reed 1998).

At 293-acre Escanaba Lake in extreme northern Wisconsin, average estimated density of 4-inch and larger bluegills during the 24-year period from 1946 through 1969 was very low (1-8/acre), probably due to heavy predation by abundant (15-36/acre) age-2-and-older walleye

(Kempinger et al. 1975). At this extremely low density, exploitation rate of bluegill in the absence of harvest restrictions was very high (30-64% annually).

Snow (1978) performed a long-term study of 180-acre Murphy Flowage in north central Wisconsin – a shallow, clear, weedy impoundment with no closed seasons, bag limits, or size limits from 1955 through 1969. Annual population estimates and a compulsory creel census enabled calculation of all components of bluegill mortality for 15 consecutive years. Total fishing pressure averaged 74 hours/acre/year. Annual bluegill harvest averaged 116 fish/acre and 18 pounds/acre, and the average length of bluegill harvested was only 6.0 inches (range 5.8-6.3 inches). Fishing mortality (u) was a relatively minor component of total mortality of all bluegill ≥ 4 inches during the study (Table 1), but low estimates of exploitation were partially an artifact of including 4- to 5-inch bluegills (too small for most anglers to keep) in the population estimates.

Table 1. Mortality of bluegill ≥ 4 inches in Murphy Flowage, Wisconsin, 1955-1969.

Mortality Component	Mean (%)	Range (%)
Total Mortality (A)	61	49-74
Natural Mortality (v)	46	32-59
Fishing Mortality (u)	12	4-24

After only three years of harvest promotion and monitoring, anglers severely depleted the proportion of preferred-size bluegills 8 inches and longer in Murphy Flowage. The estimated density of preferred-size bluegills in the population declined 90% from 1955 (29/acre) to 1958 (2.8/acre) as anglers harvested 27% (range 16-34%) of the available preferred-size bluegills annually during the first three years of the study. The decline in population size structure was attributed, in part, to increased density of stock- to quality-size bluegills, which rarely recruited to preferred size later in the study due to reduced growth rate, despite angler willingness to harvest relatively small fish (6.0 inches on average). Reduced density and size structure of largemouth bass associated with a mean annual exploitation rate of 26% (of which 57% were <12 inches long) and total mortality rate of 48% may have facilitated excessive recruitment of bluegills to stock size. Snow (1982) later modeled the effects of various bag limits for bluegills

at Murphy Flowage and predicted that a 25-daily bag limit would have reduced harvest by only 12% in summer and 30% in winter. A 10-daily bag limit would have reduced harvest by 35% in summer and 60% in winter. A 5-daily bag limit would have reduced harvest by 60% in summer and 80% in winter. Predictions were not made on a length-specific basis, so there is no way to estimate the effects of these bag limits on the availability of preferred-size bluegills.

Goedde and Coble (1981) confirmed that angler harvest is probably the greatest cause of mortality of preferred-size bluegills in exploited populations. They studied fish community changes in 12-acre Mid Lake in east central Wisconsin after it was opened to fishing under liberal harvest regulations (50 panfish daily, no size limits) in May of 1976. For three years prior to exploitation, the bluegill population in this shallow, clear, weedy lake was characterized by a high proportion of fish ≥ 8 inches and 5 to 8 years old, with recruitment to stock sizes controlled by a high-density population of largemouth bass predominately 12 to 15 inches long. The harvest of bluegills in Mid Lake in May of 1976 was 37 fish per acre, representing a monthly exploitation (35%) that exceeded total annual mortality (30%) prior to 1976. For three years after the onset of exploitation, the bluegill population was characterized by overabundant fish in the 3- to 6-inch range, with virtually no fish greater than 7 inches long or older than age 4 – similar to a nearby control lake that had been open to angling continuously. This study demonstrated just how quickly a bluegill population with good size structure can be overexploited in a small lake under liberal harvest regulations. Long term, the standing stock of bluegills ≥ 6 inches declined 65% between 1976 and 1979, from 104 to 37 fish per acre (Goedde and Coble 1981).

Bluegill harvest fluctuates seasonally. Angler catch rates for sunfish (mostly bluegills) peaked in June during the early 1950s in 765-acre Linwood Lake in southeastern Minnesota (Lux and Smith, Jr. 1960). On four small impoundments in central Missouri, Kruse (1997) found that 60% of angler tag returns came from bluegills harvested during the peak spawning period in May and June. But winter harvest can be significant in the Upper Midwest. During his 15-year study of Murphy Flowage, Snow (1978) found that 27% of all bluegill harvest occurred in winter. Angler harvest rate peaked at 6 fish/hour in January compared with 1.5-2.0 fish/hour during open-water periods. A creel survey conducted during the winter of 1976-77 at Lake Onalaska,

Wisconsin revealed a harvest of 233,061 bluegills averaging 7.0 inches long, caught at a rate of 2.4 per hour (Rach and Meyer 1982). Bluegill catch rates were highest during the early ice period in late fall. In Lake Le Homme Dieu in west central Minnesota, 42% of total bluegill harvest and almost one-half of all angler returns of tagged, quality-size bluegills occurred during winter in the mid 1990s, and much of that harvest occurred just prior to ice-out in early spring (Parsons and Reed 1998).

Managing Bluegill Exploitation

Several studies have clearly demonstrated that angling exploitation has reduced the overall number and proportion of preferred-size bluegills in publicly accessible lakes of the upper Midwest. The question is what can be done from a regulatory standpoint to control angling exploitation and sustain quality fishing for “keeper size” bluegills in suitable waters? And what would anglers have to sacrifice in order to experience consistently higher bluegill fishing quality in such waters? Evaluations of strategies to manage bluegill exploitation can be divided into empirical field studies and modeling/simulation exercises.

Empirical Studies

One of the earliest documented attempts to experimentally reduce overharvest of bluegill and other fish combined a spatial refuge (no boats, and shore fishing along only 50% of shoreline) with a 10-bag daily limit on sunfish in a 25-acre impoundment at Auburn, Alabama (Hill and Shell 1975). Bluegills averaging 7.4 inches long and other tagged fish moved freely from sanctuary to non-sanctuary areas. Total annual harvest of all species (bluegills not reported separately) in 1967 was similar to harvest in a 22-acre control lake (1957 data) with no sanctuary. The only sanctuary effect seemed to be an approximate two-week lag in cumulative harvest in the study lake relative to the non-simultaneous “control” lake. Estimates of total annual fishing mortality for bluegill were 44% in previous work (1965) in the study lake (Elrod 1971) and 59% in the control lake used by Hill and Shell (1975).

In eight small Minnesota lakes, Jacobson (2005) found that reducing the daily bag limit for sunfish (bluegill and pumpkinseed) from 30 to 10 reduced bluegill harvest sufficiently to increase male size at maturity and significantly improve population size structure in treatment lakes compared with control lakes over time ($P = 0.10$). Jacobson (2005) concluded that regulations designed to significantly reduce angling harvest (by 39% annually with a 10-bag limit on sunfish in this case) have potential to improve bluegill population size structure. The treatment lake with the largest human population nearby (58,000 people 5 miles away in St. Cloud, Minnesota) exhibited the least improvement in bluegill size structure, suggesting that even a daily bag limit of 10 may not improve the quality of bluegill fishing if angling pressure increases or non-compliance occurs beyond some yet-to-be-defined thresholds. Jacobson (2005) cautioned that special regulations like bag limit reductions may have to be implemented across a high proportion of available lakes in order to minimize the risk of redistribution of effort to other waters, placing them at greater risk of overexploitation.

Rypel (2015) evaluated the effects of a 10 panfish daily reduced bag limit (from 25) on seven lakes in Wisconsin with paired control lakes. Mean lengths of bluegill were significantly higher in the treatment lakes by an average margin of 0.8 inches, though results varied considerably by lake and some showed a difference of up to 2.0 inches. Lakes that experienced larger gains in mean length typically had lower Secchi depth, indicating higher productivity, and had been managed under the reduced bag limit for a longer period of time. These results suggest that regulations should be applied carefully, but once applied, managers and anglers need to be patient to see positive results.

Simulation Studies

Beard et al. (1997) used a model to simulate restrictions on harvest of large male bluegills under various conditions of growth rate, angler effort, and vulnerability to angling. Simulations involving high growth rates and low angling efforts naturally led to notable increases in predicted mean fish length. But simulated regulations (including a 5-daily bag limit) had little effect on predicted size structure. The absence of predicted effect may have been related to the underlying assumption that fishing mortality would comprise only a minor component of total

mortality using the estimates reported by Snow (1978) for Murphy Flowage which found natural mortality to make up a large portion of total mortality while angling mortality was lower than levels reported in many other studies.

Beard and Essington (2000) developed an individual-based model that simulated growth and survival of male bluegills from age-4 to age-8. They were interested mainly in evaluating the relative effect of life history processes (defined as inhibition of early maturation of small male bluegills by larger parental males) and the direct effects of angling on bluegill population size structure. Assuming the number of mature parental bluegills in each year was fixed (no increase in response to overharvest of larger, older males, as some theorize) their simulations revealed that the direct effect of harvest on bluegill size structure was substantially greater than the effect induced by life history processes. However, life history processes had strong effects on the simulated recovery time for size structures in exploited populations, suggesting it could take 6-8 years to restore desirable size structures to overexploited populations under more restrictive harvest regulations.

Paukert et al. (2002b) used the dynamic pool model in FAST (Slipke and Maceina 2000) to simulate the response of bluegill populations to a potential 8-inch minimum length limit in 18 Nebraska Sandhill lakes (14-820 acres) where largemouth bass was an abundant predator. Based on empirical creel survey data from two of the lakes, simulated angling exploitation of bluegill was assumed to be less than 10%, probably because these lakes had limited access and were often too shallow (mean depths = 4-9 feet) and weedy (average coverage = 48%) to fish effectively in mid summer. Even under a liberal daily bag limit of 30 panfish in the aggregate and no length limit, estimated bluegill RSD-P in modified fyke nets during May and June exceeded 5% in most lakes and 20% in a third of them. Under a simulated 8-inch minimum length limit and various empirically-based growth rate scenarios (4.3-8.3 years to reach 8 inches), Paukert et al. (2002a) predicted that RSD-P would increase by an average of only 2.2 units in all 18 lakes with a 10% exploitation rate. Yield would decline by an average of 39% because growth rates were not fast enough to compensate for conditional natural mortality rates of 15-53% under the length limit. Exploitation would have had to exceed 30% in order for an 8-inch minimum length limit (relative to no length limit) to increase both size structure and yield,

and then only in populations with the lowest natural mortality. Paukert et al. (2002b) concluded that an 8-inch minimum length limit may not provide substantial benefits in lakes with moderate bluegill growth rates and low bluegill angling exploitation; but size limits may be useful in waters with fast bluegill growth rates and considerably higher angling exploitation.

Sammons et al. (2006) collected population metrics from sunfish populations in three eutrophic southeastern reservoirs and applied an updated FAST model (Slipke and Maceina 2001) to simulate the effects of increased harvest restrictions on bluegill and redear sunfish (*Lepomis microlophus*). Simulations predicted that reducing the daily bag limit for bluegills from 50 to 15 in the absence of any length limit would produce moderate benefits to bluegill size structure (70-156% increase in the number of preferred-size fish) with only modest decreases in the number harvested (34-35%) and yield (25-31%). But simulated minimum length limits of 6, 7, or 8 inches failed to produce improvements to bluegill size structure that were deemed worthy of the sacrifice in harvest. A 7-inch minimum length limit would have created a two- to four-fold increase in the number of preferred-length fish in these southeastern reservoirs at the high cost of 50-70% reductions in number harvested and yield. In this study, redear sunfish responded much more positively than bluegill to simulated application of minimum length limits, leading the authors to caution that the common practice of managing sunfish (or panfish in the case of Wisconsin) as a homogenous group may not be appropriate.

Mortality Associated with Catch-and-Release

With the advent of restrictive harvest regulations for panfish, the fate of bluegills that have been caught and released has become an important management concern. Post-release mortality is influenced by many factors, and the potential benefits of reduced harvest can go unrealized if mortality of released bluegills is high (Hoxmeier and Wahl 2009).

Siewart and Cave (1990) reported post-release mortalities of 88% for bluegills caught on worms and 28-32% for those caught on flies and lures; but post-release fish in that study were confined for 10 days in a non-natural setting. Muoneke (1992) reported 25% mortality within 72 hours for 75 bluegills (mean length 6.5 inches) caught on #4 hooks baited with crickets in Texas

reservoirs at summer temperatures of 86°F. Under a 20-daily bag limit in 1,680-acre Pelican Lake, Utah – where 58% of anglers used live bait – an estimated 11% of 5,158 released bluegills died from hooking mortality (usually within 24 hours), but those fish comprised only 2.5% of the estimated 22,907 bluegills harvested (mean length 8.3 inches) during 1977 (Burdick and Wydoski 1989).

At 168-acre Wakeley Lake, Michigan, Schneider (2001) demonstrated that density and size distribution of quality-size and larger bluegills could be improved after a decade of catch-and-release fishing by anglers with walk-in access. Anglers were allowed to fish with only artificial lures or flies during a short summer fishing season (June 15 through August 31). Improved bluegill size structure suggested that summertime hooking mortality was negligible. A notable decline in bluegill growth rate was offset by increased longevity, such that capture rates and proportions of 8.0- to 9.9-inch bluegills caught by anglers and fyke nets increased during the decade between 1986 (first year of public ownership and catch-and-release fishing) and 1997.

Recent studies confirm that post-release mortality of bluegills can be relatively low, depending on various factors. Mortality within 72 hours of release was negligible for bluegills caught at water temperatures of 64 and 72F, and only 3% of fish caught at 79F died after being caught on four conventional hook types in Lake Opinicon, Ontario (Cooke et al. 2003). Gingerich et al. (2007) evaluated the interactive effects of water temperature and duration of air exposure on 48-hour post-release mortality of bluegills caught in Lake Opinicon, Ontario. Negligible mortality (< 3%) occurred within 48 hours at water temperatures associated with pre-spawn (65F) and spawning (73F) seasons, irrespective of air exposures up to 16 minutes in duration. However, at a mid-summer water temperature of 81F, mortality was 20-27% for bluegills exposed to air for 30 to 120 seconds, and mortality increased significantly as fish were held out of water longer than two minutes. Mortality tended to occur several hours after the angling event, so anglers would not necessarily be aware of their impact on released fish. However, angled fish that were released immediately at all temperatures experienced no mortality – less than control fish captured by seine.

Barthel et al. (2003) experimentally angled bluegills averaging 5 inches in length at Lake Opinicon, Ontario and found that those hooked in the lip or the roof of the mouth experienced no mortality and lower injury rates than those landed by net. Mortality rates of fish landed and retained for 30 seconds in a net at a water temperature of 79F ranged between 4 and 14 percent; and most mortality occurred 2-4 days after release. Nets with knotted mesh caused higher mortality (10-14%) than nets with rubber and knotless mesh (4 and 6%, respectively).

Cooke et al. (2005) used circle hooks of various sizes (1/0, 2, 6, 10, and 14) and artificial bait to catch bluegills (100 per hook size) in the spring (water temperatures 59-72F) using a standard angling protocol in Lake Opinicon, Ontario. Large hooks (#1/0 and #2) were more likely to hook fish in the eye, and small hooks (#10 and #14) were slightly more likely to be swallowed, making the intermediate-size circle hook (#6) the least likely to hook fish in a debilitating or potentially fatal location. Cooke et al. (2005) suggested that intermediate-size hooks might provide a reasonable tradeoff between injury and capture efficiency.

Hoxmeier and Wahl (2009) examined the impact of public fishing on bluegill hooking mortality by season, bait type, retention time, retention gear, and fish size under restrictive and non-restrictive harvest regulations at 14-acre Ridge Lake, Illinois. Post-release mortality averaged only 4.4% and was low regardless of when or how bluegills were caught and retained. Despite a 22F difference in water temperature, bluegills caught in May at 70F exhibited no higher post-release mortality than those caught in July at 92F. Mortality of bluegills caught on live bait (6.6%) was significantly higher ($P < 0.001$) than mortality of lure-caught bluegills (0%). Bluegills held in live wells for 3-5 hours experienced significantly higher mortality (8-9%) than those held for only 1 hour (0%). Bluegills held in wire fish baskets exhibited the highest short-term, post-release mortality of any treatment (34%). The probability of dying from catch-and-release decreased significantly with fish length for bluegills caught with live bait. Under restrictive harvest regulations, bluegills lost from catch and release represented only 27% of the total kill (harvest and hooking mortality combined). Results did not support the hypothesis that catch-and-release angling has immediate adverse effects on bluegills (Hoxmeier and Wahl 2009).

Angler Opinion and Acceptance of Restrictive Harvest Regulations for Bluegill

In the first published account of angler attitudes toward bluegill harvest regulation, Reed and Parsons (1999) received 71 completed mail surveys from 100 anglers previously interviewed on the water in 1994 at four west-central Minnesota lakes. More than half thought the existing daily bag limit of 30 was about right, and there was little support at that time for daily bag limits lower than 20. Only 4% would have supported a daily bag limit of 10; and 56% opposed any minimum length limit for bluegills. Lack of support for increased harvest restrictions was attributed to the widespread belief among anglers that overabundance and slow growth rate were the main problems and that harvesting or removing more bluegills would be necessary to improve population size structure. Reed and Parsons (1999) emphasized that fishery managers need to make a concerted effort to dispel the long-standing myth that anglers cannot harvest enough bluegills to do any harm. Posing hypothetical questions to 194 anglers during on-water interviews, they predicted that improvements in bluegill size structure by even one inch at the four lakes in their study may have increased the number of trips and the annual harvest at those lakes by 21-38%, making it important to consider the application of appropriate harvest restrictions on a scale large enough to minimize overexploitation of isolated waters being managed under special regulations.

Support for a catch-and-release-only fishery allowing only artificial lures for all species (including a large number of preferred-size bluegills) at Wakeley Lake, Michigan increased from 86% in 1987 (second year of public ownership) to 96% in 1997 (after a decade of catch-and-release fishing by public anglers with walk-in access in a wilderness setting); and 89% of anglers interviewed at the lake in 1997 said they would support similar catch-and-release opportunities for sport fish (including bluegill) at more lakes (Schneider 2001).

Paukert et al. (2002b) found that the minimum length of bluegills anglers were willing to harvest at two Sandhill lakes in Nebraska was ~6 inches. All anglers (N = 39) interviewed at Pelican Lake hypothetically favored an 8" minimum length limit for bluegills if it would increase the number of bluegills > 10" despite the fact that 67% preferred to harvest fish to eat and only 33% preferred to target trophy bluegill.

Edison et al. (2006) surveyed 567 anglers at six shallow, eutrophic Illinois lakes (14-138 acres) during 1998-1999 to gauge attitudes toward hypothetically increased restrictions on bluegill harvest. Three of the study lakes had populations of “stunted” bluegills (few fish longer than 6 inches), and the other three had “quality” populations with abundant fish ≥ 7 inches. Responses indicated a majority of anglers would support catch-and-release-only during a presumed 5/1-7/15 bluegill spawning season, a 6-inch minimum length limit, and a 10-fish daily bag limit. Higher minimum length limits received significantly less support, and anglers were essentially neutral in their opinion of a 25-daily bag limit (as opposed to no bag limit). There was moderate opposition to year-long catch-and-release fishing and strong opposition to refuges involving $\frac{1}{4}$ to $\frac{1}{2}$ of the lake. In general, anglers from towns with more than 100,000 people ($P < 0.01$) and those who earned $> \$75,000$ annually ($P = 0.02$) showed the most support for increased harvest restrictions; and those who fished primarily for food or had driven the greatest distance to go fishing were significantly less supportive. This study produced two somewhat surprising and potentially important results. First, anglers in the low-experience group (0-19 days fished annually) showed significantly greater support for increased harvest restrictions than anglers who fished with moderate (20-50 days/year) or high (≥ 51 days/year) frequency (ANOVA: $P < 0.01$). Also, anglers fishing in lakes with stunted populations of bluegill were significantly more willing to support increased harvest restrictions than anglers fishing the “quality” lakes, despite the overabundance of sub-quality fish. Anglers harvested more than 10 bluegills per trip in only 7% of their trips on three of the lakes, and not at all on three others.

Implications for Managing Exploitation by Regulation in Wisconsin

There is ample support within the literature that size-selective harvest by anglers can cause declines in bluegill population size structure and fishing quality in all but the most lightly exploited fisheries. Yet, the traditional belief that we must “fish ‘em hard” in order to “thin ‘em out” still exists among many anglers, requiring fishery managers to better inform anglers about the real factors affecting bluegill fishing quality.

In order for bluegill populations to produce satisfactory numbers of “keeper-size” (≥ 7) and preferred-size (≥ 8) fish, the “thinning out” process must occur via consumption by carefully managed predators at early life stages on size classes of bluegills most anglers are unwilling to keep. (See section on Managing Bluegill Recruitment in this literature review). Therefore, effectively managing predators is a critical first consideration if managing for large bluegills. If relatively low exploitation rates (25-35%) (Goedde and Coble 1981) can diminish size structure, maintenance of satisfactory proportions of preferred-size fish will require more restrictive regulations in all but the most lightly exploited or highly productive waters. Under liberal daily bag limits, anglers have not demonstrated a willingness to harvest enough 4- to 6-inch bluegills (Paukert et al. 2002b) to prevent the intense intraspecific competition, slow growth, and high natural mortality that characterizes “stunting” in high-recruitment waters. But liberal bag limits have led to deterioration and sustained suppression of bluegill population size structure in Minnesota (Olson and Cunningham 1989) and Wisconsin (Beard and Kampa 1999). Observations reported by Kempinger et al. (1975) for Escanaba Lake, Wisconsin were confirmed by Parsons and Reed (1998), who found that low-density bluegill populations characterized by fast growth rates and desirable size structures in Minnesota lakes were more vulnerable to size-selective overexploitation than lakes with more abundant bluegills. They felt that any daily bag limit higher than 10 exposed such bluegill populations to high risk of quality overfishing.

More restrictive harvest regulations can sustain or improve bluegill population size structure and fishing quality, yet various factors may complicate success. Growth and survival should be high enough to make losses to natural mortality worth the gains in average size of fish caught and harvested. The scale at which regulations are set need to be considered as angler behavior (shifting effort differentially between alternatively regulation lakes) responds to both perceived implications of regulations as well as changes in fishing quality. A conservative daily bag limit for bluegills would probably improve many fisheries with little adverse impact to others if applied on a large enough scale and maintained for a meaningful length of time. According to modeling studies, size limits would have to be applied more carefully and locally than reduced daily bag limits in order for benefits to outweigh costs. Furthermore, a majority of anglers interviewed about their bluegill fishing did not favor minimum length limits of any kind at four Minnesota lakes (Reed and Parsons 1999) or length limits greater than 6 inches at six

Illinois lakes (Edison et al. 2006). But case histories reveal that special, high-quality fisheries can be created and sustained by applying minimum length limits to individual waters that meet specific criteria and experimentation with high minimum length limits (8 or 10 inches) for bluegill on a few individual waters might be reasonable (Paukert et al. 2002b). Because bluegills move among lakes in a connected chain (Parsons and Reed 2005), application of experimental bluegill fishing regulations should focus on either isolated lakes or entire chains of lakes, not individual lakes within chains.

Angler acceptance of reduced daily bag limits for panfish may vary geographically and be increasing over time. In a 1994 survey of anglers at four Minnesota lakes, Reed and Parsons (1999) documented little support for panfish daily bag limits lower than 20, and only 4% of respondents would have supported a daily bag limit of 10 at that place and time. But in a more recent survey (1998-1999) of anglers at six Illinois lakes, Edison et al. (2006) found that anglers supported a 10-daily bag limit by a 2:1 margin while remaining neutral toward the 25-daily statewide bag limit in effect at the time. In the Illinois study, anglers who fished infrequently (0-19 days/year) showed significantly greater support for increased harvest restrictions than those who fished with moderate (20-50 days/year) or high (≥ 51 days/year) frequency, calling into question the notion that increased harvest restrictions may chase casual anglers away from fishing.

Increased harvest restrictions for bluegill will require angler understanding and support. Hypothetical spatial refuges that would restrict fishing along $\frac{1}{4}$ to $\frac{1}{2}$ of a lake's shoreline were strongly opposed by Illinois anglers (Edison et al. 2006) and were demonstrably ineffective in reducing over-exploitation of bluegill in a 25-acre Alabama impoundment (Hill and Shell 1975). Support for a hypothetical catch-and-release-only season for bluegills during May 1 to July 15 was surprisingly high (56% supported, 17% opposed) among the 567 Illinois anglers interviewed by Edison et al. (2006). And wilderness walk-in anglers strongly supported season-long catch-and-release fishing for bluegills and other species at Wakeley Lake, Michigan (Schneider 2001). These studies suggest that anglers may support special catch-and-release fisheries during all or part of the season if experimentally applied to a few select waters with unique fishery potential.

Several recent studies suggest that mortality associated with catching and releasing bluegills is relatively low (generally < 5%) under typical angling circumstances, even when live bait is used (Cooke et al. 2003; Gingerich et al. 2007; Hoxmeier and Wahl 2009). Therefore, it should be possible to impose greater harvest restrictions on bluegill without losing significant portions of potential yield to post-release mortality. Several voluntary angling practices can further minimize post-release mortality of bluegills, including the use of artificial lures (Siewart and Cave 1990; Schneider 2001; Hoxmeier and Wahl 2009), releasing fish quickly (< 30 seconds air exposure) when water temperature is warm (> 80°F; Gingerich et al. 2007), landing fish by hand or in knotless or rubber mesh nets (Barthel et al. 2003), resisting the urge to hold fish in a livewell and cull them later (Hoxmeier and Wahl 2009), and using intermediate-size (#6) hooks, which are least likely to catch fish in a debilitating or potentially fatal location and provide a reasonable tradeoff between injury and capture efficiency (Cooke et al. 2005).

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