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THE RELATION OF MALE BLUEGILL REPRODUCTIVE STRATEGIES TO EXPLOITATION AND POPULATION SIZE STRUCTURE IN TWELVE MINNESOTA LAKES[1]

Cynthia M. Tomcko and Rodney B. Pierce

Minnesota Department of Natural Resources
Section of Fisheries
500 Lafayette Road
St. Paul, MN 55155-4012

Abstract.--No conclusive relationship between the proportion of parental male bluegill and rate of exploitation was established in this study. High proportions of cuckolder males were sampled from two lakes with high fishing pressure (> 200 angler-hours/hectare). In contrast, relatively low proportion of cuckolders were sampled in the lake with the highest fishing pressure. Low proportions of cuckolder males were also sampled from lakes with < 200 angler-hours/hectare fishing pressure. A valuable result of this study was the development of techniques for studying male bluegill reproductive strategies and insights into the difficulties of doing a study of this type.

Introduction

Many Minnesota lakes, particularly those subjected to high fishing pressure, have bluegill *Lepomis machrochirous* populations with poor size structure. It is unclear, however, to what extent exploitation might affect the development or maintenance of poor size structure in bluegill populations.

Exploitation can negatively affect bluegill population size structure both directly and indirectly. One direct effect is the physical removal of considerable numbers of bluegill (Coble 1988). The subsequent recruitment response could lead to overly dense bluegill populations as bluegill are capable of early maturation and are less cannibalistic than esocids (Werner 1977; Mittelbach and Chesson 1987). Increased recruitment could shift the size structure to smaller individuals. The selective harvest of larger bluegill could also reduce average sizes in the population (Coble 1988). Furthermore, removal of large bluegill could stimulate recruitment because large, territorial bluegill may limit spawning and recruitment. Indirectly, harvest of predators that control bluegill densi-

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ties could enhance bluegill recruitment (Swingle and Smith 1942).

Male bluegill exhibit two distinct reproductive strategies - a parental nesting strategy or a cuckolder strategy (Gross 1982). The strategies are partially heritable (D. Philipp, Illinois Natural History Survey, personal communication).

Parental males mature in 7-8 years, attain large body size, build nests, and care for their brood (Gross 1982). The parental strategy incurs high metabolic costs because of pre- and post-spawning behavior such as aggressive competition for nest sites, nest construction, fighting and displays, repelling predators, and lack of feeding (Dominey 1981). The largest parental males are most likely to win prime nest sites through aggressive defense and thus most likely to attract females. However, nesting parental males are more vulnerable to anglers and their selective harvest may contribute to poor bluegill population size structure.

The metabolic cost of cuckoldry may be less than for the parental strategy (Dominey 1981), yet cuckolders gain the reproductive benefits of fertilizing eggs. Cuckolders mature in 2-3 years at a smaller size than parental males, and die in about 5 years or 1-2 years before parental males reach maturity (Gross 1982). Cuckolders do not build nests, but steal fertilizations from parental males by sneaking (small cuckolders) among breeding pairs and by female mimicry (large cuckolders). Mimics release copious amounts of sperm compared to parental males, and their sperm fertilizes eggs as readily as that of parental males (Dominey 1980).

The ratio of cuckolders to parental males may change with fishing pressure because of the size-selective nature of angling and the vulnerability of nesting males. Gross (1982) theorized that the ratio of cuckolders to parental males tended to stabilize at an intermediate equilibrium value. In populations where parental males are selectively harvested, the proportion of cuckolders might increase. With the cessation of fishing, the population would tend to return to its equilibrium frequency. But if fishing pressure was consistently high, a high percentage of cuckolders may persist.

The purpose of this study was to determine if there was any relationship between exploitation and the relative abundance, age, and growth rates of male bluegill with different reproductive strategies.

Methods

Lake selection

Study lakes were selected based on fishing pressure estimates. Lakes near high population centers or other high use situations, such as location in a popular state park, were selected to represent heavily exploited bluegill populations. Calhoun, Hyland, Orchard, and Lake of the Isles, located in or near the Twin Cities, were considered to receive high fishing pressure (Table 1). Two lakes, Coon-Sandwick in Itasca County and Minnewawa in Aitkin County, received moderate pressure (91-107 angler-hours/hectare). French, Sissabagamah, and Wilkins lakes in Aitkin County, North Twin Lake in Beltrami County, Sand Lake in Cass County, and Long Lake in Itasca County were considered to receive low fishing pressure (50-73 angler-hours/hectare). These lakes fall into 11 different lake classes (Schupp 1992), and have different physical characteristics, water chemistry, and bluegill abundance (Table 1).

Estimates of fishing pressure were available from all lakes except Sand Lake, where it was assumed to be low based on personal observation, and from Long Lake. At Long Lake, a volunteer following our creel design, recorded the total numbers of anglers fishing the main basin of the lake. These observations were considered a stratified random sample and used to estimate fishing pressure on Long Lake.

Fish Sampling

Bluegill were usually sampled with 19 mm mesh trap nets (bar measure) set overnight, but some fish included in the study were collected by electroshocking (pulsed-DC), seining (15 m bag seine with 6 mm mesh (bar measure)), or in 13 mm mesh trap nets (bar measure).

Table 1. Physical and chemical characteristics, fishing pressure (angler-hours/hectare), lake classification (Schupp 1992), bluegill catch-per-unit-effort (CPUE) in trap nets, and survey year for 12 Minnesota lakes, 1990-1992.

Lake	County	Surface area (ha)	Max. depth (m)	Total alkalinity (ppm)	Summer fishing pressure	Lake class	Bluegill CPUE Median for lake class	Bluegill CPUE Mean from survey	Year
Calhoun	Hennepin	162	25	98	158	24	30	101	1987
Coon-Sandwick	Itasca	254	12	40	91	35	12	9	1990
French	Aitkin	55	11	80	65	20	20	9	1989
Hyland	Hennepin	34	4	79	497	43	3	404	1991
Isles	Hennepin	44	10	100	662	38	22	40	1990
Long	Itasca	49	24	100	52	25	22	22	1977
Minnewawa	Aitkin	1017	6	34	107	35	12	11	1987
North Twin	Beltrami	127	18	90	54	31	31	14	1988
Orchard	Dakota	101	10	140	203	33	18	137	1986
Sand	Cass	54	17	37	low	20	20	12	1984
Sissabagamah	Aitkin	148	11	60	73	29	24	10	1989
Wilkins	Aitkin	150	12	35	50	31	31	37	1989

Sampling schedules varied among lakes and years. During 1990 and 1991, we attempted to sample all bluegill ages and reproductive strategies. Sampling was done in spring or early summer to assure maximum gonad weight. Bluegill were sampled during July 1990 and during May and June 1991. Reproductive type was determined based on length at age and Gonadosomatic Index (GSI) (Gross 1982).

During 1992, bluegill were subsampled from length ranges corresponding to lengths of age 3 fish taken in 1990-91 to remove the subjectivity of determining reproductive types. Sampling was done from July to September. Gonads of age 3 males were sufficiently developed to distinguish cuckolders from immature parental males as late as September (M. Gross, University of Toronto, Ontario, Canada, personal communication) permitting sampling outside the spawning season. Also by targeting one age class of bluegill, we attempted to avoid bias caused by differential mortality among age classes (M. Gross, University of Toronto, Ontario, Canada, personal communication). However, the percentage of cuckolders could not be calculated based solely on age 3 bluegill because of small sample sizes. Thus the percentage was calculated based on fish ages 2, 3, and 4.

Bluegill preserved in alcohol or formaldehyde were difficult to sex so fish were either processed immediately or frozen. Total length (mm), body weight (g), and gonadal weight (g) were measured, sex was determined, and scales were removed for aging. About one-half the fish from Coon-Sandwick, Orchard, and Sand lakes were processed fresh and one-half were frozen. Samples from all other lakes were frozen. Fresh and thawed gonads were analyzed separately to evaluate differences in gonad weight by treatment. Rank sum tests were performed to compare fresh and thawed gonad weights for ages 2, 3, and 4 bluegill and differences were not significant.

In addition to netting, bluegill reproductive behavior was observed. Colonies were located in Coon-Sandwick, Long, and Orchard lakes. Spawning events were witnessed in Coon-Sandwick and Long lakes. Post-spawning behavior was observed in Long and Orchard lakes. During the spawning event on Coon-Sandwick Lake 26 June 1991, the numbers of dips made by a female and the number of successful and unsuccessful intrusions by cuckolders were recorded for 5 minutes per spawning act for comparison with Canadian data (Gross 1982). Eggs were extruded by females on each dip and were fertilized by attending males.

Length at annulus was back-calculated from scale measurements using DisBcal (Frie 1982). A standard intercept of 15.2 mm was used for back-calculation. Age and year effects on growth were estimated by ANOVA using a linear growth model (Weisberg and Frie 1987).

Growth rates between reproductive types and sexes were compared using F tests of the variance of age and year effects (Weisberg 1993).

Results

Cuckoldry varied among lakes. Percentages of age 2 to 4 cuckolder males ranged from 0% to 94% (Table 2). The percentages of cuckolders in two lakes, Hyland and Orchard were estimated to be > 75%. Fishing pressure was high at both lakes (Table 1). The percentages of cuckolders in three lakes, Calhoun, Lake of the Isles, and Long, ranged from 12% to 14%. Fishing pressure at Lake of the Isles was the highest estimated for lakes in this study while pressure at Long Lake was among the lowest. Cuckolders were estimated to be 4% or less in the remaining 7 lakes.

The proportion of cuckolders sampled varied between gear and dates within the same lake. In a sample of 16 males caught by electrofishing at Long Lake, 12 (75%) were cuckolders (Table 3). In a sample of 57 males caught by trap netting two weeks later, only one could be identified as a cuckolder.

The absence of cuckolders in samples from Coon-Sandwick Lake (Tables 2 and 3) was supported by direct observations of low intrusion frequencies by cuckolders during spawning bouts. No successful cuckoldry was recorded during two hours of spawning colony observation in Coon-Sandwick Lake. Intrusion by cuckolders was observed in only 4% of the total dips by female bluegill. In contrast, Gross (1982) found an intrusion frequency of 60%, and successful intrusion frequency of 17% for colonies in Lake Opinicon, Ontario, Canada, where cuckoldry was more prominent.

The GSI of male bluegill varied seasonally. GSI of cuckolders caught from four lakes during early to mid-summer ranged from 3.2 to 7.2 (Table 4). The mean GSI of 83 cuckolder males sampled from 6 lakes during mid-summer to fall 1992 was 1.1. GSI of parental males and cuckolders caught during early to mid-summer 1990-91 (Table 4) were similar to those reported by Gross (1982).

The ratio of males to females for ages 2, 3, and 4 was highest in the two lakes with the highest percentage of cuckolders (Table 2). The ratio was 4.3 (1992) in Hyland Lake and 4.0 (1991) in Orchard Lake. North Twin Lake had the next highest ratio, 3.8 (1992), but had little cuckoldery. The mean ratio was 2.0 (all years). No consistent relationship between sex ratio and percentage of cuckolders could be detected.

Differences in growth between parental males and cuckolders could not be analyzed statistically because of small sample sizes for at least one reproductive strategy in any particular lake. Inspection of Tables 4 and 5 suggest that parental males grow faster than cuckolders. Maximum mean lengths of cuckolders did not reach 150 mm in the 8 sampled lakes. On the other hand, maximum mean lengths of mature parental males exceeded 150 mm in 5 lakes. The oldest cuckolders were age 6, while the oldest sampled parental males ranged from age 7 to 9.

There were growth differences between female bluegill and males of either breeding strategy. Parental males grew faster than females in Coon-Sandwick (F=6.41, P < 0.01)

Table 2. Percentage of cuckolder bluegill males (95% confidence interval in parentheses) based on age 2, 3, and 4 fish and male:female sex ratios (ages 2, 3, and 4 bluegill) in 12 Minnesota lakes, 1990-1992.

Lake	Number	Percent cuckolders (%)	M:F ratio
	1990		
Long	56	2 (0-11)	3.2
	1991		
Coon-Sandwick	15	0 (0-75)	3.0
Long	21	14 (4-37)	2.1
Orchard	28	75 (55-89)	4.0
Sand	65	2 (1- 9)	1.1
	1992		
Calhoun	16	12 (2-40)	2.0
French	7	0 (0-44)	0.7
Hyland	55	94 (84-99)	4.3
Lake of the Isles	14	14 (6-28)	1.5
Minnewawa	25	0 (0-16)	1.8
North Twin	44	4 (1-19)	3.8
Sissabagamah	70	1 (0- 9)	1.1
Wilkins	62	3 (0-12)	1.1

Table 3. Sampling dates, gear, and number of bluegill sampled by sex and reproductive strategy in 12 Minnesota lakes, 1990-92.

Lake	Date sampled	Gear	Male	Cuck-older	Par-ental	Unas-signed	Female	Total
Long	7/ 2/90	electrofish	16	12	2	2	1	17
Long	7/17/90	19 mm trap	57	1	4	52	36	93
Coon-Sandwick	6/ 7/91	19 mm trap	148	0	67	81	78	226
Long	5/31/91	19 mm trap	53	3	14	36	41	94
Orchard	5/24/91	19 mm trap	165	36	3	126	40	205
Sand	5/22/91	19 mm trap	102	1	13	88	110	212
						Immature parental		
Calhoun	8/18-19/92	seine	49	5		44	58	107
French	9/23/92	seine	13	0		13	19	32
Hyland	8/18/92	seine	79	62		17	24	103
Isles	8/19/92	seine	153	6		147	161	314
Minnewawa	7/24/92	19 mm trap	25	0		25	14	39
North Twin	9/16/92	seine	65	5		60	23	88
Sissabagamah	7/22,8/5-6/92	13 mm trap	70	1		69	67	137
Wilkins	7/23,8/6/92	13 mm trap	82	4		78	70	152

Table 4. Mean physical characteristics of parental and cuckolder male bluegill from four Minnesota lakes, early to mid-summer 1990-91. Gonadosomatic index (GSI) was estimated as gonad weight/total body weight x 100. Standard deviation is in parentheses.

Lake	Year	Number	Age (year)	Total length (mm)	Body weight (g)	Gonad weight (g)	GSI
				Cuckolders			
Long	1990	13	2.7(1.4)	84(26)	14.3(18.0)	0.4(0.4)	3.7(1.5)
Long	1991	3	3.0(0.0)	80(5)	9.3(1.5)	0.7(0.1)	7.2(0.4)
Coon-Sandwick	1991	0	-	-	-	-	-
Orchard	1991	36[a]	4.2(0.8)	119(18)	33.2(15.1)	0.9(0.4)	3.2(1.1)
Sand	1991	1	4.0	106	22.2	1.3	5.9
				Parental Males			
Long	1990	6	6.0(0.0)	188(12)	138.3(22.3)	1.2(0.8)	0.9(0.5)
Long	1991	14	7.2(0.9)	189(13)	151.4(30.7)	3.4(1.8)	2.1(0.9)
Coon-Sandwick	1991	67[a]	7.5(0.6)	177(5)	112.8(11.4)	1.3(0.4)	1.2(0.3)
Orchard	1991	3[a]	7.0(0.0)	173(4)	91.8(6.1)	1.4(0.4)	1.5(0.5)
Sand	1991	13	5.6(0.8)	187(16)	156.8(49.4)	2.5(1.7)	1.4(0.6)

[a] Three cuckolders and one parental male from Orchard Lake and one parental male from Coon-Sandwick Lake could not be aged.

Table 5. Mean annual growth increments (mm), L∞ (mm), and k from Walford plots of parental males, cuckolder males, and female bluegill from Long, Coon-Sandwick, Orchard, and Hyland lakes.

	Long		Coon-Sandwick		Orchard		Hyland	
	Parental		Parental		Cuckolder		Cuckolder	
Age	♂	♀	♂	♀	♂	♀	♂	♀
1	32.7	33.8	29.2	30.1	44.6	40.8	43.5	45.6
2	21.9	21.0	22.0	22.8	29.6	32.7	34.5	40.7
3	25.8	25.4	26.0	23.7	22.5	26.1	23.0	28.9
4	27.8	31.9	23.4	23.4	16.1	21.2	17.4	
5	28.7	26.2	24.4	23.1	14.0	17.5	10.9	
6	24.4	19.9	20.4	18.6	6.4	6.4		
7	22.1	16.7	18.2	12.5	6.2			
8	14.8	13.9	15.4	9.4	3.9			
9	5.9	6.2	8.2					
L∞	248[a]	223[b]	215[c]	207[c]	157[d]	179[d]	155[e]	
k	0.1682	0.2759	0.2818	0.2186	0.3104	0.2820	0.3685	

[a] From Walford plot using ages 5-8
[b] From Walford plot using ages 4-9
[c] From Walford plot using ages 3-9
[d] From Walford plot using ages 1-6
[e] From Walford plot using ages 1-5

and Long lakes ($F=5.27$, $P < 0.01$) (Figure 1). Females grew faster than cuckolders in Orchard Lake ($F=23.2$, $P < 0.01$). No significant difference could be detected between females and cuckolders from Hyland Lake, but a plot of available data suggested that females grew faster than cuckolders (Figure 1).

Growth of parental males and females from Long and Coon-Sandwick lakes was similar through age 5 (Figure 1). Annual growth increments of females declined rapidly after age 5 in both lakes (Table 5). Growth increments of parental males from Long Lake did not decline sharply until age 7 while growth increments of parental males from Coon-Sandwick Lake declined sharply after age 8. Growth of cuckolder males and females from Orchard Lake was similar through age 2, but females grew faster thereafter. Growth of Orchard Lake females, like growth of females from Long and Coon-Sandwick lakes, declined rapidly after age 5.

Walford plots indicated that parental males reach larger sizes than females, and that females reach larger sizes than cuckolders (Table 5). L∞ of parental males from Long Lake was 248 mm compared to 223 mm for females. L∞ of parental males from Coon-Sandwick Lake was 215 mm compared to 207 mm for females. L∞ of females from Orchard Lake was 179 mm compared to 157 mm for cuckolders. L∞ of cuckolder males from Hyland Lake was 155 mm.

Bluegill growth rates were faster in heavily fished Orchard and Hyland lakes through age 3 for both sexes than in the moderately fished Long and Coon-Sandwick lakes (Table 5). Growth rates after age 4 were faster in the more northerly lakes. By age 6, mean lengths of bluegill from Long and Coon-Sandwick lakes equaled or exceeded those from Orchard Lake, and differences continued to increase through age 8 and older.

Discussion

No conclusive relationship between the proportion of parental male bluegill and rate of exploitation was established in this study. The high percentages of bluegill cuckolders in two of the lakes with the highest fishing pressure - Hyland and Orchard lakes - provided some support for the hypothesis that high rates of exploitation were associated with increased cuckoldry. On the other hand, the relatively low

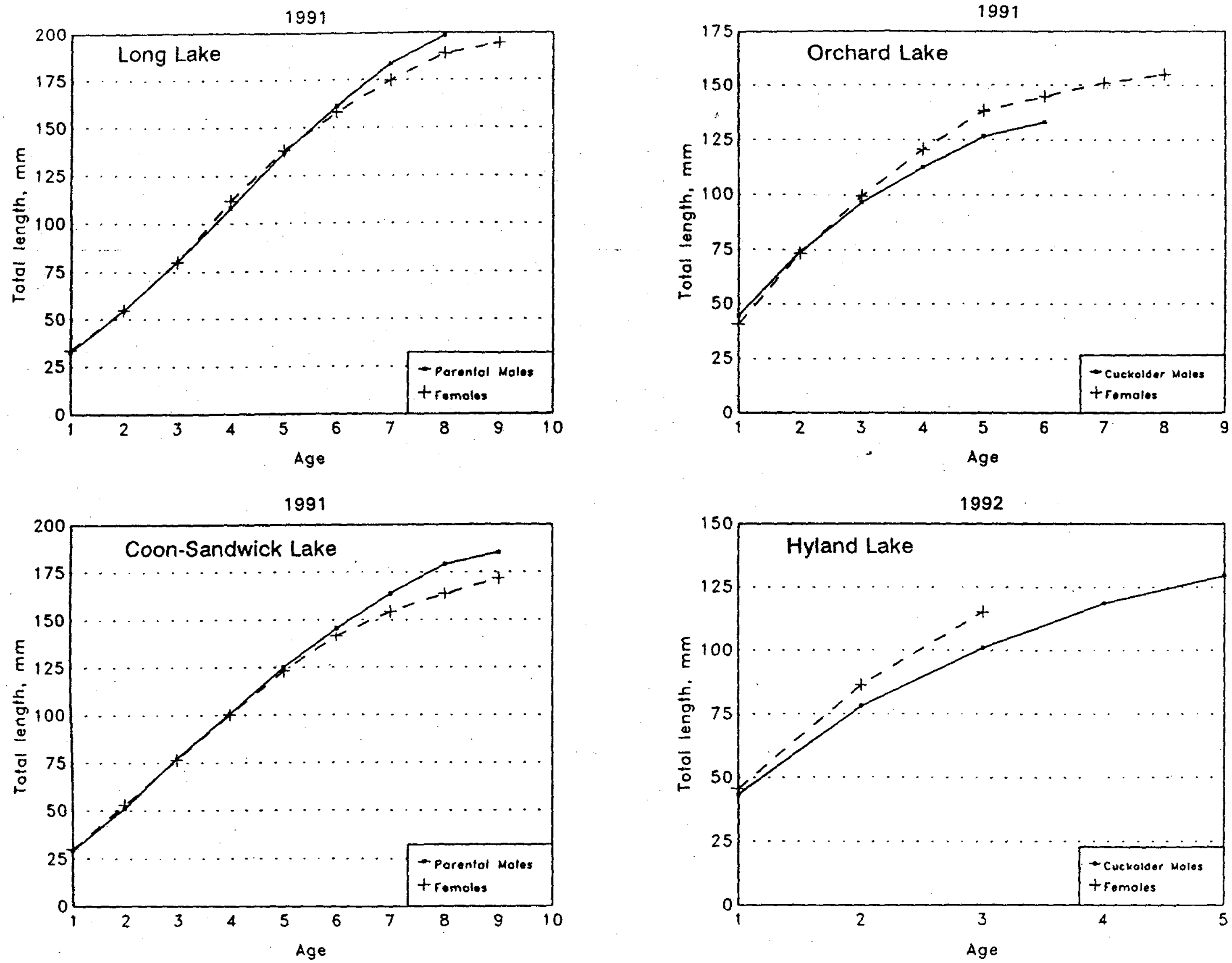

Figure 1. Backcalculated length at age for four lakes and selected sex or reproductive strategy.

proportion of cuckolders sampled in Lake of the Isles (which had the highest fishing pressure) was not explained. Faster growth and larger $L\infty$ of parental males underscores their importance in maintaining a population size structure desirable to anglers.

No relationship between cuckoldry and exploitation in the 12 lakes was detected possibly due to difficulties measuring both variables. Colonies of spawning bluegill were difficult to locate in Orchard, Coon-Sandwick, and Long lakes and were not the size that Gross (1982) described for Lake Opinicon. Furthermore, bluegill spawning occurs as several relatively short events of a few hours duration within a spawning season. Consequently, direct counts of intrusion frequencies by cuckolders are not practical if the study includes several lakes. In addition, estimating the proportion of cuckolders in several lakes from samples taken by traditional gears during spawning also is dependent on being at the right place at the right time and on the selectivity of the gear type.

The relative frequency of parental males and cuckolders on spawning colonies also may vary among lakes due to intrinsic factors. Factors which may cause the equilibrium relative frequency of cuckolders and parental males within lakes to vary include depth of colonies, degree of population instability (founding or declining populations), extrinsic mortality rates (Gross 1982), predator density, vegetation density, lake size, percent littoral area, and the physical-chemical attributes of the waters. All of these factors can confound the detection of the relationship between cuckoldry and exploitation. For example, the percentage of cuckolders should decrease as average depth of spawning colonies increases because of lack of hiding structure and increased predation (Gross 1982). Hyland Lake may be an example of an unstable population since the lake periodically winter kills.

Total hours of fishing pressure may be a weak measure of the effects of exploitation since not all fishing is directed at bluegill. Fishing pressure at Lake of the Isles was the highest in this study, but cuckoldry was moderate. Personal observations, however, suggested that little of the fishing effort was directed at bluegill.

Sampling times and gears to acquire a representative measure of the proportion of males of the two reproductive strategies within a lake need more research. The suggestion by M. Gross (University of Toronto, Ontario, Canada, personal communication) to sample during late summer and fall, and examine gonads of one age group has merit. It avoids the problem of sampling during a relatively short spawning season, and should reduce some of the potential biases identified in this study. However, cuckolders experience high mortality during spawning, therefore, the proportion of cuckolders in the fall could be significantly lower than it was at the beginning of the spawning season. The same is true for nesting parentals which experience high fishing mortality. Appropriate sampling gear and timing need to be identified. In this study, trap netting with nets of two different mesh sizes, seining, and electrofishing were used. Samples taken by trap netting and electrofishing on Long Lake during 1990 resulted in widely disparate estimates of cuckolder percentages. Electrofishing was, however, done 15 days earlier than trap netting.

If growth rates of parental male bluegill and cuckolders differ significantly in many Minnesota lakes as in Lake Opinicon, Ontario (Gross 1982), then only comparisons of female and male growth rates separated by strategy are valid. In this study, parental males grew significantly faster than females after age 5 in Long and Coon-Sandwick lakes, while females grew significantly faster than cuckolder males in Orchard Lake and appeared to grow faster in Hyland Lake. This suggests that the findings by Gross (1982) are probably applicable for Minnesota bluegill populations.

No conclusive relationship was detected between fishing pressure and growth in northern and southern Minnesota lakes. Bluegill growth to age 3 was better in the high pressure, southern Minnesota lakes compared to bluegill growth in low pressure, northern lakes. Young bluegill in southern Minnesota lakes may have been responding to the high angling pressure with an increased growth rate, or their growth may have been a response to the warmer temperature regimes and longer growing season in southern Minnesota. After age 3, bluegill growth rates in southern Minnesota lakes slowed, and growth rates of bluegill in some northern Minnesota lakes surpassed them. The cause of this reverse is unknown.

Management Implications

These results in two lakes tends to indicate that fishing pressure in certain circumstances could reduce the proportion of parental males in a bluegill population. If parental males have a significant influence on the size structure of bluegill populations, regulating fishing to reduce or eliminate harvest of parental males may be necessary to develop or maintain bluegill populations with a more acceptable size structure. Stocking may not be an alternative to harvest reduction due to unknown effects on current population structure, and the genetic considerations associated with stocking fish from another system into an established population. (Allendorf 1991; Wingate 1991).

In the development of techniques to study bluegill reproductive strategies, we found freezing was the best gonad preservation technique. The use of different sample gear and sample times was useful in targeting certain bluegill age classes.

Information on size-specific bluegill harvest and hooking mortality could provide more accurate estimates of how many parental bluegill are removed or lost to mortality. This would give a better estimate of the influence of angling on the proportions of the two reproductive strategies in a lake. Lakes with high and low angling pressure directed at bluegill as well as lakes with the same classification are needed to standardize factors other than fishing pressure.

References

Allendorf, F.W. 1991. Ecological and genetic effects of fish introductions: synthesis and recommendations. Canadian Journal of Fisheries and Aquatic Sciences. 48 (Supplement 1):178-181.

Coble, D.W. 1988. Effects of angling on bluegill populations: management implications. North American Journal of Fisheries Management. 8:277-283.

Dominey, W.J. 1980. Female mimicry in male bluegill sunfish - a genetic polymorphism? Nature. 284:546-548.

Dominey, W.J. 1981. Maintenance of female mimicry as a reproductive strategy in bluegill sunfish (Lepomis macrochirus). Environmental Biology of Fishes. 6:59-64.

Frie, R.V. 1982. Measurement of fish scales and back-calculations of body lengths using a digitizing pad and microcomputer. Fisheries 7(6):5-8.

Gross, M.R. 1982. Sneakers, satellites, and parentals: polymorphic strategies in North American sunfishes. Zeitscrift fur Tierpsychologie. 60:1-26.

Mittelbach, G.G., and P.L. Chesson. 1987. Predation risk: indirect effects on fish populations. Pages 315-332 in W.C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Schupp, D.H. 1992. An ecological classification of Minnesota lakes with associated fish communities. Minnesota Department of Natural Resources, Fisheries Investigational Report Number 417, St. Paul.

Swingle, H.S., and E.V. Smith. 1942. The management of ponds with stunted fish populations. Transactions of the American Fisheries Society. 71:102-105.

Weisberg, S. 1993. Using hard-part increment data to estimate age and environmental effects. Canadian Journal of Fisheries and Aquatic Sciences. 50:1229-1237.

Weisberg, S., and R.V. Frie. 1987. Linear models for the growth of fish. Pages 127-143 in R.C. Summerfelt and G.E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. American Naturalist 111:553-78.

Wingate, P.J. 1991. U.S. State's view and regulations on fish introductions. Canadian Journal of Fisheries and Aquatic Sciences 48 (Supplement 1):167-170.

Edited by:
P.J. Wingate, Fisheries Research Manager
D.H. Schupp, Fisheries Research Supervisor