Ecology of Freshwater Fish 2002: 11: 190–195
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ECOLOGY OF
FRESHWATER FISH
ISSN 0906-6691

The influence of stunted body size on the reproductive ecology of bluegill *Lepomis macrochirus*

Aday DD, Kush CM, Wahl DH, Philipp DP. The influence of stunted body size on the reproductive ecology of bluegill *Lepomis macrochirus*. Ecology of Freshwater Fish 2002: 11: 190–195. © Blackwell Munksgaard, 2002

Abstract – Although stunting is a common phenomenon in fish populations, the consequences of stunted body size on the reproductive ecology of individuals has received little attention. The present study compares the reproductive ecology of bluegill in established stunted and non-stunted populations. Three ponds (two non-stunted and one stunted) were monitored for spawning activity throughout the summer. Parental male bluegill from both non-stunted populations were older, larger, and had greater mating success (number of eggs or fry within nests) than parental males in the stunted population. Stunted bluegill also experienced a shortened reproductive season owing to the delay in onset of spawning. The present study demonstrates that individual size and population size structure can have a marked influence on the reproductive ecology of bluegill.

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Key words: bluegill; mating success; spawning activity; stunted

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Accepted for publication March 26, 2002

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Stunting is a common phenomenon in fish populations, and can be the result of a variety of mechanisms (e.g., Swingle & Smith 1941; Burrough & Kennedy 1979; Diana 1987). In particular, it has been postulated that stunted body size can result from a decision to mature early relative to the 'normal' age and size for the species (Burrough & Kennedy 1979; L'Abée-Lund et al. 1990; Jansen 1996). For example, an extensive study of bluegill (*Lepomis macrochirus*) populations throughout Illinois revealed a significant difference in age-at-maturation between populations containing stunted and non-stunted individuals, with stunted males maturing at younger ages and smaller sizes (J.E. Claussen, unpublished data). Although attention has been given to growth and maturation rates of individuals in stunted populations, as with other species, little is known about the reproductive ecology of stunted bluegill and differences that might exist between stunted and non-stunted individuals.

Bluegill are important components of freshwater communities and are numerically dominant in many freshwater lakes throughout North America (Werner et al. 1978). The reproductive behaviour of male bluegill is elaborate and quite variable compared to many other fish species. Bluegill are social fishes that nest and spawn in colonies that range from a few individuals to several hundred abutting nests (Gross 1982). Parental males construct bowl-shaped nests in water between 0.1 and 1.5 m deep. Following nest construction, these males exhibit territorial defence behaviours (e.g., display, thrust, swipe, chase or nip) and courtship behaviours (e.g., rim circling) above and slightly beyond the nest boundary (Avila 1976). Parental care of offspring is left entirely to the male bluegill, which fan and guard the eggs and fry (Gross 1982). A brood-guarding period of up to 10 days typically passes between egg deposition and fry departure, after which parental male bluegill abandon their nests (Gross 1982). Because of the energetic demands of this reproductive activity, physiological trade-offs in available energy often result in decreased (or cessation of) growth of mature fish (Roff 1983; 1984). Further, fecundity is often directly related to body size (e.g., females, Wootton 1979; both sexes, Roff 1983). Therefore, the reproductive success of individuals within a population could be directly related to the size and the age at which they mature.

Relative size within a population is an important factor for determining maturation schedules of parental male bluegill; the presence of large, mature parental males has been shown to influence the reproductive investment decisions of smaller males (Jennings et al. 1997). However, among populations, questions remain regarding differences in reproductive ecology of individual parental males as a function of population size structure. In the present study, we assess the influence of population size structure on bluegill reproductive ecology by examining variables such as length of spawning season, colony variables (e.g., colony size and success), and mating success of parental male bluegill in stunted (all parental males <160 mm, total length) and non-stunted (all parental males >180 mm, total length) populations.

Study sites

Several small (<2 ha) ponds in Champaign County, Illinois, were surveyed by snorkeling and angling during fall 1998 and spring 1999 to determine the species composition and size structure of fish populations in each pond. Categorization of bluegill populations (stunted or non-stunted) was done in accordance with a priori classifications of bluegill populations throughout Illinois (Aday et al. 2000; Hoxmeier et al. 2001). Three ponds were chosen for further study; two ponds (Big Pond and Hedge Pond) contained large, non-stunted bluegill, and one (Jill Pond) contained an historically stunted bluegill population. All ponds were located less than 100 m apart, and other than size structure of the bluegill populations the ponds were quite similar; surface areas were approximately 1 ha with similar shape and depth profiles, and each was a closed system that received no fishing pressure. The fish communities were also similar, dominated by bluegill and largemouth bass (*Micropterus salmoides*), although Hedge Pond also contained some readear sunfish (*Lepomis microlophus*).

Materials and methods

Field and laboratory

Beginning in May 1999, each pond was monitored for spawning activity by visual inspection from a boat and by snorkeling. The date of formation and location of colonies were recorded on a map of each pond. Further, a more detailed map of each colony was constructed, showing the number of individual nests it contained and their spatial arrangement. Snorkelers attempted to examine the nests in each colony for eggs; however, owing to heavy volume of spawning activity and rapid egg development, some colonies were not located until fry were present. A numbered tag was placed next to each nest that contained eggs or fry in a colony, and the tag number was recorded on the colony map; untagged nests (i.e., nests without eggs or fry) were simply counted. A brood score for each tagged nest was calculated by scoring the number of eggs or fry on a relative scale of 1 (few) to 5 (many) as per Claussen (1991). Eggs and fry were scored in the same manner. We did not attempt to quantify the number of eggs or fry that corresponded with each score because we were interested in relative mating success; egg and fry scores can, however, be used to measure absolute mating success (Claussen 1991). All nests were scored by the same two investigators throughout the summer to ensure consistent, precise measurement.

A method was derived called the Colony Success Index (CSI) for calculating the mating success of male bluegill in each colony, which was determined as follows:

$$\mathrm{CSI} = \frac{\text{number o nests with brood} \times \text{ mean brood score}}{\text{number of nests built}}$$

This index was calculated for each bluegill colony in Big Pond and Jill Pond. The presence of congeners prevented the use of CSI in our comparisons with Hedge Pond because many bluegill colonies also contained some nesting redear.

Parental male bluegill exhibiting nest-guarding behaviour were angled from nests by a snorkeler carefully floating above the colony. Fishing line tied to a 2-ft section of a fishing pole was used to dangle a hook baited with an earthworm above the nest of a targeted fish. Caution was taken to avoid disturbing the substrate. Once the fish was hooked, the snorkeler handed the fish to a second researcher in a boat. Total length (mm) and weight (g) of each captured male was recorded and scales were removed for age analysis. In addition, the upper caudal fin of each captured fish was clipped to indicate that the fish had been collected and data recorded. A unique series of clips of anal and dorsal spines were given to represent the colony from which the fish was collected (e.g., the first dorsal spine was clipped on a fish from colony one, the first dorsal and first anal spines were clipped on a fish from colony 11, etc.). The fish were returned to their nests as soon as all data were collected, and the handling time was kept to a minimum. Because of potential for egg predation by other fish, the snorkeler remained in the water above the nest to protect the brood.

In Hedge pond, individuals were identified as a bluegill, redear, or hybrid based on visual assessment of colour patterns. This was done to ensure that only bluegill were used in the analysis. Bluegill are easily distinguished by large, elongated opercular tabs that are dark to the margin (Robinson & Buchanan 1992). Bluegill also have a distinctive dark spot near the posterior margin of the dorsal fin. Redear, conversely, have smaller opercular tabs with a red margin and no dorsal fin spot (Robinson & Buchanan 1992). To determine success of field identification, a small sample of bluegill, redear, and suspected hybrids were collected and taken to the laboratory for genetic analyses. For these analyses we used protein electrophoresis to examine several diagnostic protein loci (PGM-A*, MDH-B*, and PGDH-A*) that exhibit fixed allelic differences between the two species.

Laboratory

Scales taken from fish were pressed on acetate slides and read with a microfiche machine. The age of each fish was determined by counting the number of annuli on each scale (Regier 1962). To insure accuracy of age determination, the age of each fish was determined independently by at least two readers. We determined the condition of each individual based on total length and weight measurements taken in the field. The condition factor was determined according to the following equation:

$$K = \frac{W}{L^3} \times 10^5$$

where W is weight (g) and L the total length (mm).

Statistical analyses

Analysis of variance (ANOVA) was used to assess differences in length, weight, age, condition, and brood score among populations (PROC GLM, SAS Institute Inc. 1989). *Post hoc* comparisons were made with Tukey's multiple comparisons tests. Values were considered significantly different at $P < 0.05$. Treatment means and standard errors were determined with the PROC GLM (SAS Institute Inc. 1989) procedure.

Results

Bluegill characteristics

Field identification of bluegill was easily done in Hedge pond. Genetic analyses indicated that all bluegill and all hybrids were correctly identified, but two fish identified in the field as redear were actually hybrids. Parental male bluegill in both non-stunted populations were significantly larger (total length and weight; $P < 0.0001$) and older ($P < 0.0001$) than parental male bluegill in the stunted population (Table 1), validating our original assessment of population size structure. Parental male bluegill from Big Pond also exhibited significantly higher ($P < 0.0001$) condition factors than parental males in the stunted population (Table 1). Parental males from Hedge Pond, however, exhibited similar condition factors to the parental male bluegill in the stunted population (Table 1), suggesting that competition with congeners may decrease condition in parental male bluegill.

Nesting characteristics/mating success

Spawning seasons were quite different in all three populations. Parental male bluegill in Big Pond spawned early and for a total of 18 days (18

Table 1. Mean (±SE) total length, weight, condition, age, egg score, colony size, number of nests per colony with brood, and Colony Success Index (CSI) for non-stunted (Big Pond and Hedge Pond) and stunted (Jill Pond) parental male bluegill.

	Big Pond (non-stunted)		Hedge Pond (non-stunted)		Jill Pond (stunted)		
	Mean	N	Mean	N	Mean	N	P-value
Length (mm)	183.7^{a} (1.09)	32	198.1^{b} (0.71)	117	152.6^{c} (1.07)	36	0.0001
Weight (g)	139.5^{a} (3.49)	32	150.7^{b} (2.04)	105	70.3^{c} (1.80)	36	0.0001
Condition (K)	2.24^{a} (0.04)	32	1.92^{b} (0.02)	105	1.96^{b} (0.02)	35	0.0001
Age (years)	4.4^{a} (0.11)	30	3.5^{b} (0.07)	107	2.3^{c} (0.08)	35	0.0001
Brood score	3.2^{a} (7.90)	9	2.4^{b} (0.08)	223	0.79^{c} (0.07)	78	0.0001
Colony size	35.0 (7.90)	9	NA	32.1	(5.90)	11	0.77
Nests with brood/colony	11.3 (2.80)	9	NA	5.10	(1.58)	11	0.05
CSI	1.05 (0.18)	9	NA	0.13	(0.04)	11	0.0001

Owing to mixed colonies of bluegill, redear, and hybrids, we were unable to calculate mean colony size, nests with brood/colony, and CSI values for Hedge Pond. N indicates the number of individuals or colonies sampled for each metric. Different letters in superscript ($^{a, b, c}$) within a row indicate significant differences ($P < 0.05$); P-values were generated from analysis of variance (ANOVA).

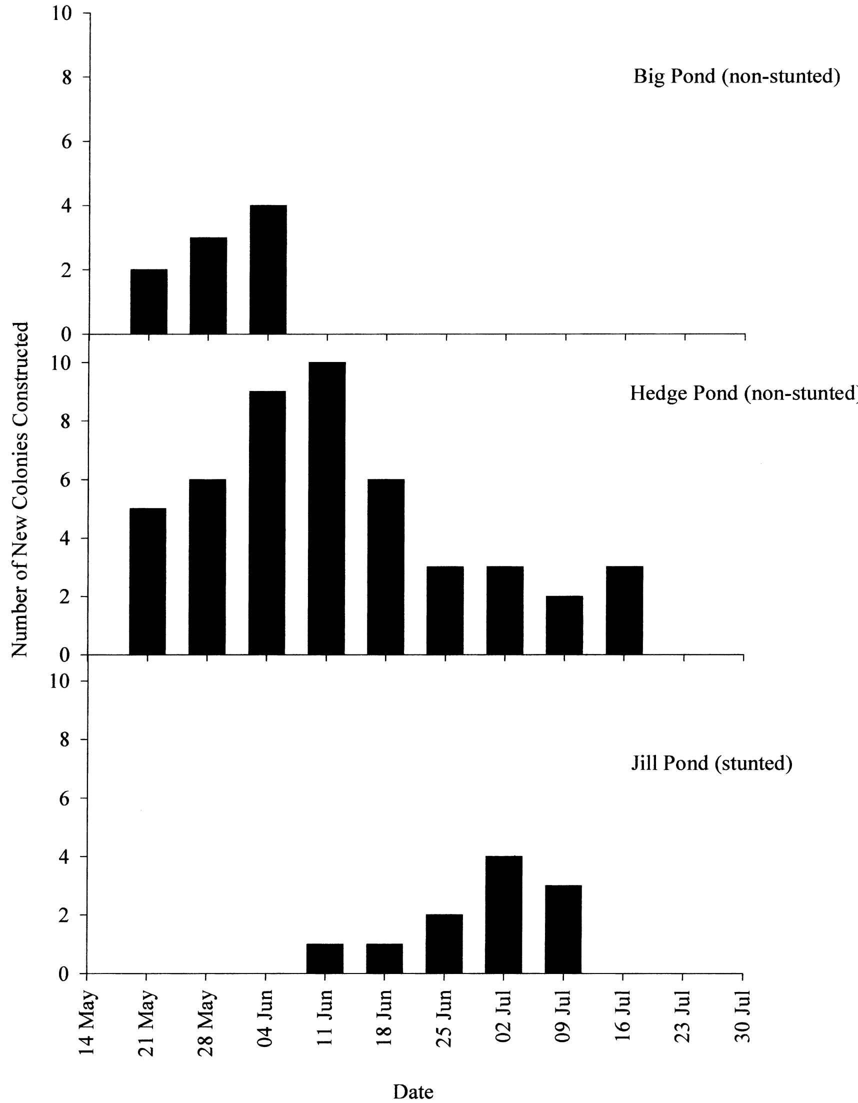

Fig. 1. Number of new colonies constructed during weekly intervals from May 14 to July 30 in Big and Hedge ponds (non-stunted bluegill) and Jill Pond (stunted bluegill).

May–4 June), whereas parental male bluegill in the stunted population initiated spawning much later and spawned over a longer period (33 days: 7 June–July 9; Fig. 1). The spawning season in the second non-stunted population, Hedge Pond, overlapped that of the other two populations and lasted 61 days (20 May–19 July; Fig. 1). Likely because of the longer spawning season, the number of colonies containing parental male bluegill in Hedge Pond (39) far exceeded the number of bluegill colonies formed in the other non-stunted population (9).

Overall, 9 colonies with 315 nests formed in Big Pond and 11 colonies with 353 nests formed in Jill Pond, so the average colony size was not significantly different between these two populations ($P = 0.77$; Table 1). However, the number of nests per colony that received brood was significantly higher ($P = 0.05$) in the non-stunted population than in the stunted population, resulting in a significantly higher mean CSI value in Big Pond (Table 1). Because Hedge Pond contained mixed colonies of bluegill, redear, and hybrids, the bluegill colony metrics (number of nests with brood per colony, colony size and CSI) could not be determined for this population. However, brood scores for parental male bluegill were different among all three populations ($P < 0.0001$; Table 1); brood scores were higher in both non-stunted populations than in the stunted population ($P < 0.05$).

Discussion

Previous investigations have measured reproductive investment of different-sized fishes within a population (L'Abée-Lund et al. 1990; Jansen 1996; Jennings et al. 1997). Usually, this has been done by quantifying gonadosomatic indices (ratio of gonad weight to body weight) of individuals to estimate reproductive investment. No studies, however, have examined directly the effects of population size structure on mating success among populations. Our results suggest that the size structure of bluegill populations can influence the reproductive ecology of individual males.

There were several apparent differences in reproductive ecology between bluegill in the stunted and non-stunted populations. Parental male bluegill in the stunted population had lower mating success than bluegill in both non-stunted populations. Consequently, CSI values were significantly lower in the stunted population. At least two potential factors may contribute to the low brood scores observed for parental males in the stunted population. The first and most likely explanation is that fecundity increases with age and size (Roff 1983). Females in the stunted population likely had fewer eggs to deposit than those in the non-stunted populations, which translated to decreased brood scores for parental males in the stunted population. Brood predation may also have contributed to low brood scores in the stunted population. Small bluegill represent significant sources of predation on eggs (Dominey 1981). However, egg predation is likely a source of brood loss in each of our populations, as egg predation by large bluegill and hybrid sunfish is also common (Gross & MacMillan 1981). Because we were unable to quantify brood predation in our populations, we cannot assess whether or not this mechanism may be responsible for differences in brood scores of our stunted and non-stunted populations. However, brood predation by conspecifics appeared to be consistent among populations.

The spawning season of bluegill in the stunted population started later than in both non-stunted populations. Within a population, smaller fish emerge from winter with lower lipid reserves, and therefore, less energy available for spawning than their larger counterparts (Justus & Fox 1994). The delay in onset of spawning in the stunted population could result from the necessity of acquiring adequate energy reserves for spawning activity. Late-starting, shortened breeding seasons have also been found in birds exhibiting early maturity (Stearns 1976). Also unusual was the abbreviated spawning season in non-stunted Big Pond. Extremely high growth of the macrophyte duckweed (*Lemna minor*), which completely covered Big Pond by the second week of June, may explain this result. The macrophyte cover was approximately 12-mm thick throughout the pond, resulting in no light penetration below the surface. Peak spawning in both non-stunted populations occurred during the second week (4–11) of June. In the absence of dense macrophyte cover, spawning likely would have continued in Big Pond in a similar manner to Hedge Pond, and similar to other non-stunted populations throughout Illinois (D. Aday, unpublished data).

Smaller size and decreased mating success of stunted individuals could be due to density-dependent mechanisms. Densities of mature individuals appeared similar in each population, but inaccessibility for boat electrofishing and large-scale seining made it impossible to determine total fish densities. Density-dependent slow growth has been implicated in studies of bluegill (e.g., Swingle & Smith 1941; Murnyak et al. 1985), and could be responsible for the smaller size of bluegill observed in the stunted population. It seems less likely, however, that differences in density would be responsible for variation in nesting success of males among populations. Mean colony size for the two populations in which only bluegill were present (Big Pond and Jill Pond) was similar (35 vs. 32 nests per colony), yet the non-stunted males were significantly more successful. Further, the mixed colonies in Hedge Pond were much larger (average colony size = 71 nests) than the other two populations. Despite this, parental male bluegill in Hedge Pond experienced higher mating success than those in the stunted population. These results provide some evidence that differences in densities were not responsible for differences in mating success of individual parental males in these two populations.

Bluegill exhibit complex social structures and tremendous variation in life-history characteristics such as growth rate, and age- and size-at-maturation. As the result of a variety of potential mechanisms, individual bluegill often exhibit stunted body size. Our results demonstrate that variation in the size of mature individuals can influence their reproductive ecology through changes in timing and duration of spawning season and mating success of individuals. As a consequence, we suggest that population size structure is an important variable that should be considered in conservation and management initiatives.

Resumen

1. Aunque el fenómeno de 'stunting' (o reducción del tamaño por crecimiento inhibido) es común en las poblaciones de peces, sus consecuencias sobre la ecología reproductiva de los individuos ha recibido poca atención. Este estudio compara la ecología reproductiva entre poblaciones stunted y no stunted de *Lepomis macrochirus*. Esta es una especie socialmente compleja que hace nidos coloniales donde interacciones con machos maduros pueden influenciar las estrategias biológicas de machos juveniles. El fin de este

estudio fue determinar el éxito reproductivo de los pequeños machos 'stunted' respecto de los machos 'no-stunted'. La actividad reproductiva fue monitorizada en tres lagunas (dos 'stunted' y una 'no-stunted') durante el verano.
2. Nidos de machos individuales fueron examinados en cada población y el éxito de nidaje de los machos individuales fue determinado cuantificando el número de huevos o juveniles en cada nido. Los machos parentales de ambas poblaciones 'no-stunted' fueron mayores en edad y tamaño y tuvieron mayor éxito cuantificado como el número de huevos o juveniles en el nido que los machos parentales de la población 'stunted'. Estos últimos tambien experimentaron una estación reproductiva mas corta debido a un retraso en el comienzo de la reproducción. Este estudio demuestra que el tamaño individual y la estructura de tamaños de la población puede tener una influencia marcada sobre la ecología reproductiva de *L. macrochirus*.

Acknowledgments

We appreciate the field assistance of Vicki Ursitti, Dondrae Coble, Julie Claussen, Cory Suski, Brock McCarty, and Todd Kassler. In addition, Todd Kassler provided valuable assistance with genetic analyses. This paper benefited from the comments of the Aquatic Ecology Discussion Group at the Kaskaskia Biological Station, John Hoxmeier, and two anonymous reviewers. S. Steuwe and L. Dunham helped coordinate activities with the Illinois Department of Natural Resources (IDNR). Funding for this investigation was provided in part by the Environmental Council at the University of Illinois and the Federal Aid in Sport Fish Restoration Act under Project F-128-R administered by the IDNR.

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