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## COMPLETE ESTIMATES OF REPRODUCTIVE SUCCESS IN A CLOSED POPULATION OF SMALLMOUTH BASS (*MICROPTERUS DOLOMIEUI*)<sup>1</sup>

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**Abstract.** We conducted a 4-yr study of 154 parental male smallmouth bass (*Micropterus dolomieu*) and 982 nests in a closed natural population (a temperate seepage lake in Wisconsin). Our goal was to test common assumptions and hypotheses about reproduction in natural populations. Mark-recapture techniques were used to measure changes in the demography, age-specific sex ratios, and mortality rates of the whole population. An area-density method was used to estimate the number of eggs spawned in each sampled male's nest, and we volumetrically estimated the number of larvae produced by sampled males. The lake is closed to migration, allowing us to accurately estimate total population size and individual variance in reproductive success (RS) for each year without having to assume a demographically stable population. We found that a large proportion of non-breeding adults of both sexes were present in each year. We compared estimates of variance in RS among subsets of males and females in the population to examine the effect on variance when mature non-breeding individuals are included in the analysis. Excluding non-breeders resulted in the true variation in RS being underestimated and the mean RS overestimated, both by a factor of  $\approx 3$  for males and 2 for females. Most male bass spawned only once in their lifetimes, and size at age 3 yr appeared to determine whether a male spawned or postponed reproduction. Males that bred at age 3 yr were among the largest of their cohorts, and males that bred at age 5 yr were among the slowest growing. There may be greater selection on adults for opportunity to breed than there is selection in RS among breeding adults in this population.

**Key words:** *age-specific sex ratios; demography; evolution; field experiment; mating systems; Micropterus dolomieu; parental care; population dynamics; recruitment; sexual selection; smallmouth bass; Wisconsin.*

### INTRODUCTION

Theories of the effects of natural and sexual selection stress the importance of measuring the variance of individual reproductive success in natural populations (Fisher 1930, Trivers 1972, Wade and Arnold 1980, Arnold 1983). Many researchers have attempted to estimate the total variance in reproductive success in natural populations of vertebrates (Howard 1979, Payne 1979, Downhower and Brown 1980, Clutton-Brock et al. 1982). To estimate potential sources of natural and sexual selection, the individual variance in reproductive success must be estimated for the whole population, in addition to the breeding sample (Wade and Arnold 1980). If more than one breeding-age cohort is present, one must calculate the mean and variance in individual reproductive success for each age cohort, summed from seasonal values for each surviving member, to arrive at measures that correctly reflect the potential for selection. Most animal populations are

“open” and have unknown rates of immigration, emigration, and mortality, making accurate estimates of absolute abundance difficult or impossible. Often adult animals cannot be accurately assigned to an age cohort, so a simplifying (but often false) assumption of a stable age distribution is made to arrive at a mean and variance (Taylor 1979).

Typical studies base estimates only on a sample of the sexually mature individuals that attempt to breed. Rarely is that sample a known proportion of the surviving adult population. Indeed, many studies of birds, mammals, and fishes have demonstrated the existence of a surplus population of non-breeders whose absolute magnitude is unknown (Brown 1975). An ideal population would have the following key properties: (1) the population would be closed, so that future individuals are the direct products of individuals now alive in the population; (2) the population should be easily counted by a method that is nondestructive and yields a count independent of breeding status; and (3) the individuals should be easily aged, so that breeding and non-breeding individuals can be reliably ascribed to age cohorts.

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We report data on such an "ideal" population. We have estimated the proportion of breeding smallmouth bass (*Micropterus dolomieu*) in a closed population where changes in the demography, age-specific sex ratios, and mortality rates were measured directly. We compare estimates of variance in reproductive success to demonstrate how the variance changes when mature but non-breeding individuals are included or excluded in the analysis. Sampled breeding males are compared to the adult male population with respect to age and to their cohorts with respect to size and mortality.

The smallmouth bass normally lives and breeds in small, temperate, freshwater lakes. Such lakes are closed populations to the resident freshwater fishes if no streams enter or leave them. Closed populations of fishes are normal for a large number of lakes throughout the world. Because smallmouth bass spawn in conspicuous nests in shallow water, and territorial males provide extended parental care, the number of breeding males can be easily counted, and the number of eggs they fertilize and the number of larvae successfully raised to independence can be counted directly. Mark-recapture using electroshock sampling and fyke-netting (live-trapping) can estimate total population size. Individuals can be accurately aged by examining scale annuli. We show that commonly used simplifying assumptions lead to large errors in estimating the mean and variance in individual reproductive success.

## MATERIALS AND METHODS

### *Study site*

Nebish Lake, a 40-ha, clear, seepage lake in the Northern Highland State Forest of north-central Wisconsin, is managed and intensively studied by the Wisconsin Department of Natural Resources (WDNR). In addition to smallmouth bass, the lake contains yellow perch (*Perca flavescens*) and bluntnose minnows (*Pimephales notatus*).

The WDNR has continuously monitored the population of smallmouth bass since 1967 when the lake was poisoned with rotenone and restocked (Kempinger and Christenson 1978, Serns 1979–1981, 1982–1985, 1984c, Christenson et al. 1982, Kempinger et al. 1982). Prior to and during the present study the adult bass population was sampled annually by fyke net and electroshock sampling. All fish collected were weighed, measured, and aged by scale annuli. Aging smallmouth bass from temperate lakes by means of scale annuli is particularly reliable (Carlander 1982); the technique was verified in Nebish Lake by the WDNR at the beginning of their population study by resampling tagged individuals in later years. A mean of 45% of the population >20.2 cm total length (TL) were permanently marked with uniquely numbered Floy FD-67C anchor tags each year of this study. The number of young-of-the-year bass was estimated in the fall (Schnabel method; Ricker 1975). Annual population data include the

number of individuals in each year-class (Peterson and Schnabel estimates; Ricker 1975), size by age, growth, mortality, and exploitation rates. Serns (1984a, b) studied smallmouth bass fecundity and survival from egg to fall young-of-the-year for the period 1979–1981. Fishing is permitted only on a special permit basis, and a mandatory creel census is in effect for the lake year around. All fish checked in by fishermen are examined and recorded as in the spring census.

### *Total adult population*

Petersen population estimates by age group (Ricker 1975) were obtained for Nebish Lake from the WDNR data (Serns 1982–1985). Size at maturity and the sex ratio of each cohort were calculated using age-length frequency distributions (males mature at a smaller size and younger age than females). The distributions were constructed from fyke-net data, age-specific sex ratios of the annual creel census, a length-fecundity regression equation calculated for mature eggs from data collected in Nebish Lake by Serns (1984b), and length data collected from captured, tagged, parental male fish.

Sex ratios for each age group were estimated from the creel census because fish sampled during fyke-netting could not be sexed during the years of this study. The smallest parental males captured during the course of this study were 20.0-cm TL (total length), and this size was arbitrarily used to estimate minimum male size at sexual maturity. The length-fecundity regression indicated that females were 22.0-cm TL when they could be predicted to have mature eggs (Fecundity =  $-12\,251.5 + 593.9(\text{Length})$ ;  $r^2 = 0.39$ ; 73 df;  $P < .01$ ; range: 1181–28 570 eggs). Length, rather than mass, was the size measure used, as fecundity is not independent of mass and mass is not a measure with high repeatability (Pitcher and MacDonald 1973). The formulae used in these calculations are presented in the Appendix (section A1).

### *Estimated breeding population*

The number of males breeding each year (those males procuring eggs) was assumed to be the same as the number of nests containing eggs (spawned nests). We located nests by snorkeling, SCUBA diving, and observation from boats. This simultaneous combination ensured that all nests constructed in the lake were found. Every excavated nest was mapped and checked for eggs and larvae at least twice during the breeding season so that the proportion of constructed nests actually used could be determined. Re-nesting by some males could have inflated the number of breeding males, but re-nesting was assumed to be minor due to the synchronous breeding characteristic of smallmouth bass in this lake (the breeding season lasts 3–4 wk) and the observed low rate of early nest desertion.

Unlike males, the total number of breeding females could not be counted because female smallmouth bass

leave the nest immediately after spawning. We calculated and compared three estimates of the number of breeding females each year (see Appendix: A3). The first (Method I) was calculated by dividing the overall estimate of egg deposition for a year by the estimated average fecundity of all the mature females in the population (4106 in 1982, 2592 in 1983, 2807 in 1984, and 3223 in 1985). This method, commonly used to estimate the abundance of marine species (see Saville 1964, Gjosaeter and Saetre 1974, Pitcher and Hart 1982), assumes that total egg deposition can be accurately estimated from subsamples collected in the open ocean or along stretches of beach, and that all females contribute equally to the total egg deposition when, in reality, older, larger females have more eggs than females in younger cohorts (Bagenal 1973). We were able to make a more accurate estimate (Method II) because we knew with certainty the number of "batches" of eggs spawned in the lake, and we could calculate the fecundity of each cohort. In Method III, we assumed that the number of spawned nests equaled the number of breeding females.

We determined the total annual egg deposition in Nebish Lake by estimating in situ the number of eggs spawned in each of a sample of nests and multiplying the mean number of eggs per sample nest by the total number of nests spawned in that year (see Appendix: A2). We estimated the number of eggs spawned in a nest by covering the clutch with a sheet of clear acrylic and tracing the perimeter of the egg mass with a grease pencil. The number of eggs per square centimetre was counted in three locations along a radius line through the mass (the center, midpoint, and edge). The area of the egg mass and the average number of eggs per square centimetre were calculated, and the estimated number of eggs per nest determined from the product of these measures. We validated this method of estimating eggs by taking close-up photographs of five nests, counting the eggs projected onto a screen, and comparing the estimates with the in situ counts ( $r^2 = 0.61$ ;  $\bar{X}_{\text{diver}} = 6205$  eggs/nest,  $\bar{X}_{\text{photo}} = 6203$  eggs/nest).

The mean fecundity of each cohort was calculated each year from the population estimates, age-specific sex ratios, age-length frequency distributions, and the length-fecundity regression equation. The population fecundity and each age group's proportional contribution were calculated to estimate the number of individual females contributing to the total observed egg deposition. This estimate of the number of adult females actually spawning assumes that every adult female, regardless of age, has an equal probability of spawning, and that every spawning female deposits all, or nearly all, of her egg potential. However, since larger, older females produce disproportionately more eggs, and are probably more likely to breed in a given season than younger females, the first assumption would tend to overestimate the number of breeding females. Because spent female smallmouth bass are known to re-

tain some residual mature eggs, the number of breeding females may be underestimated by the second assumption (Vogele 1981).

#### *Estimate of larvae numbers*

Larvae were counted shortly before they were ready to disperse from their nests. In 1982 and 1983 larvae were collected with a kitchen baster. In 1984 and 1985 we used a more efficient air-lift suction device connected to the low-pressure port of a SCUBA first-stage regulator (Raffetto 1987). All larvae collected were poured into a graduated cylinder and their total volume measured. The number in a 1.0-mL subsample was then counted. The number of larvae in each nest was calculated by multiplying the total volume of larvae (in millilitres) by the number of larvae in the 1-mL sample. All larvae were then replaced in the nest. We validated this method by counting the total number of larvae collected from five nests and comparing the counts with our estimates ( $r^2 = 0.96$ ;  $\bar{X}_{\text{estimate}} = 1351$  larvae/nest,  $\bar{X}_{\text{count}} = 1291$  larvae/nest).

#### *Age, growth, and mortality of breeding males*

Individual breeding males were captured by hand-netting them off their nests; they were then weighed, measured, and had their tag numbers read in a nearby boat before they were released. Age and growth histories were determined by examining scales collected during spring fyke-netting and electroshocking. For each sampled male, the previous years' growth was back-calculated by measuring the growth zones between year marks on the scales (Ricker 1975). Annual mortalities of sampled breeding males were determined from creel census records, fyke net, and electroshocking data in years following breeding. Tagged breeding males that were not caught by fishermen, did not appear in later sampling, or were not found alive by us, were assumed to have died due to natural causes.

The ages, sizes, and mortality estimates of breeding males were compared with their male cohorts (Raffetto 1987). The annual mortality rate of each male cohort was determined from the population estimates of age groups in successive years. We searched for our sampled males in years subsequent to their breeding to determine the lifetime reproductive success of individual breeding males. Fish tagged in previous years were recognizable at a distance by a coating of algae on their tags. All male breeders with algae-coated tags were potential re-breeders and, as target males, special attempts were made to find and recapture them.

## RESULTS

### *Total adult population*

The age-size composition of age-3 yr and older fish in the WDNR's annual fyke-net samples changed substantially through the years of this study. The age distributions were not stable ( $\chi^2 = 590.11$ , 9 df,  $P < .001$ ),

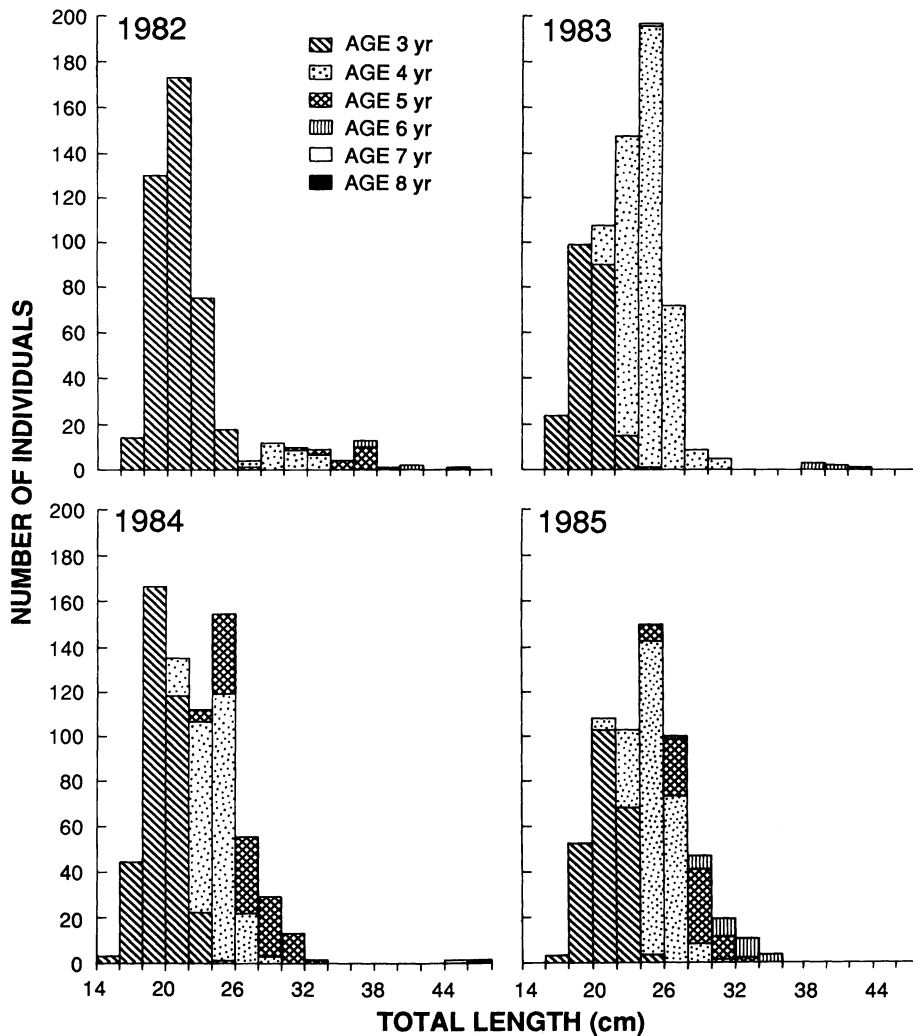


FIG. 1. Total lengths of age-3 through age-8 fish captured by the Wisconsin Department of Natural Resources during spring fyke-netting in 1982–1985. Ages are given in years.

and hence our data are based on separate calculations for each year class (Fig. 1). These data represent a marked sample equal to an average of 45% of the total adult population of the lake per year, and are assumed to reflect the age-size structure of the population accurately. They were used in this study for calculating annual size at maturity and cohort fecundities. These distributions are assumed to have no sex biases because no sex differences in length were found within age groups 3–5 in the May–June creel censuses. Too few age-6 males appeared in the censuses to determine annual sex-length estimates for this age group.

Data used for estimating the number of mature males and females available in each breeding season are given in Table 1. The estimated population of mature males available to breed varied from 503 to 755 during the

study period. The male proportion for each age class in the creel census varied from 0% to 68%. The overall proportion of males was 33% in 1982, 53% in 1983, 45% in 1984, and 44% in 1985.

The estimated population of females large enough to breed ranged from 351 to 562. The proportion of females for each age class in the creel census varied from 32% to 91%. In 1982 and 1985, all age-4 and older females were estimated to be mature. In 1983 and 1984, respectively, 4% and 7% of the age-4 females were estimated to be too small to have eggs.

#### *Estimated breeding population*

We located 658 breeding males during the 4 yr of this study, ranging from a low of 56 in 1982 to a high of 252 in 1983. The number and proportion of males

TABLE 1. Estimated numbers of mature males and females age 3 yr and older; 95% confidence intervals are given in parentheses. TL = total length. See Appendix A1 for calculations.

Age (yr)	Total number of adults*	Males			Females		
		% in creel	% >20.0 cm TL	Estimated total mature	% in creel	% >20.0 cm TL	Estimated total mature
1982							
3	1889 (804-6288)	40	65	491 (209-1635)	60	23	261 (111-868)
4	68 (41-122)	41	100	28 (17-50)	59	100	40 (24-72)
5	45 (23-105)	13	100	6 (3-14)	87	100	39 (20-91)
6	15 (4-150)	0	100	0	100	100	15 (4-150)
Total	2017 (872-6665)			525 (229-1699)			355 (159-1181)
1983							
3	679 (444-875)	33	46	103 (67-133)	67	07	32 (21-41)
4	1164 (552-1602)	56	100	652 (309-897)	44	96	492 (233-677)
5	0	0	0	0	0	0	0
6	20 (6-200)	0	100	0	100	100	20 (6-200)
Total	1863 (1002-2677)			755 (376-1030)			544 (293-782)
1984							
3	892 (735-1283)	68	40	243 (200-349)	32	6	17 (14-25)
4	404 (353-472)	44	100	178 (155-208)	56	93	210 (184-246)
5	206 (164-267)	40	100	82 (66-107)	60	100	124 (98-160)
6	0	0	0	0	0	0	0
Total	1502 (1252-2022)			503 (421-664)			351 (296-431)
1985							
3	861 (630-1145)	47	76	308 (225-409)	53	31	141 (104-188)
4	528 (444-632)	49	100	259 (218-310)	51	98	264 (222-316)
5	157 (119-215)	37	100	58 (44-80)	63	100	99 (75-135)
6	44 (26-82)	9	100	4 (2-7)	91	100	40 (24-75)
Total	1590 (1219-2074)			629 (489-806)			544 (429-720)

\* Data from Wisconsin Department of Natural Resources, based on mark-recapture of, on average, 45% of the population each year.

breeding each year are shown in Table 2. Except for 1982, one-third of the adult male population was estimated to breed each year.

Three estimates of the breeding female population were made (Table 2). Estimates from Method I range from 49 females in 1982 to 424 females in 1983. Method II, shown in Table 3, represents the number of females of each age that would contribute to the total egg deposition for that year, assuming each age group contributes a proportion of the egg potential (fecundity) to the total. In this analysis, the number of breeding females required to produce the total egg deposition each year ranged from 64 in 1982 to 415 in 1983. Both

of these methods overestimate the number of breeding females, especially if larger, more fecund females are more likely to breed than smaller females. Method III simply assumes that each nest contains the eggs of only one female (monogamy). With only one exception (the Method III estimate in 1984), the Method I and Method III estimates fall within the 95% confidence intervals of Method II.

All estimates of breeding females indicate that some mature females do not breed. Because the Method I and II estimates of breeding females surpass the number of spawned nests, it appears that males may spawn with more than one female. However, other evidence,

TABLE 2. Estimated numbers and proportions of breeding males and females. Three different methods were used to estimate numbers of female breeders.

Year	Sex	Estimated number mature	Method*	Estimated number breeding	% breeding
1982	M	525	I	56	11
	F		II	49	14
			III	64	18
1983	M	755	I	56	16
	F		II	252	33
			III	424	75
1984	M	503	I	415	74
	F		II	252	45
			III	157	31
1985	M	629	I	226	64
	F		II	238	68
			III	157	45
			I	193	31
			II	277	50
			III	304	55
				193	54

\* For Method I the estimated total egg deposition each year was divided by the average fecundity of mature females based on values obtained from Serns (1984b). Method II adjusts for demography, fecundity, and age (see Table 3). Method III assumes each nest contains the eggs of only one female (monogamy).

including the number of eggs actually deposited in each nest sampled, suggests that this is not the case (Raffetto 1987). This is a discrepancy that can only be resolved by a radio-tagging study that follows individual female movements and visits to nests.

*Reproductive success*

We calculated various estimates of male reproductive success (RS) using our estimates of the number of adult males in the population, the number of nests constructed, the number of males with eggs, and the observed number of eggs ( $n = 212$  nests) and fry ( $n = 128$  nests) in sampled nests. If our definition of RS is the number of eggs males procure, that success will be the result of the decision tree depicted in Fig. 2A. Depending on how the categories at the bottom of the tree are combined, different measures of RS will result (Table 4). We used the proportion of nests sampled to determine the number of non-breeding males to include in the calculations for "total nests" and "total males" (Appendix: A4). For example, in 1982 we sampled 25 of 56 nests with eggs (45%). To estimate  $RS_{eggs}$  of all the nests constructed ("total nests"), we added 14 nests without eggs (45% of the 31 nests not sampled). To estimate  $RS_{eggs}$  of all the adult males ("total males") we added 197 non-breeding males (45% of 437), giving a total of 236 males (45% of the 525 mature males estimated to be in the lake in 1982). Adding an equal proportion of "zero class" males at each higher level allowed us to calculate a sample variance and coeffi-

cient of variation without making assumptions about the distribution of unsampled nests. As the sample size of males considered in the analysis is increased to include an increasing proportion of non-breeders, the mean number of eggs per male decreases, and the overall variance also decreases because  $n$  is increased and males with no eggs are all added to the "zero" category. However, the coefficient of variation ( $cv = [\text{standard deviation/mean}] \times 100$ ) increases at each step, indi-

TABLE 3. Estimated number of breeding females by age, Method II. 95% confidence intervals are given in parentheses. See Appendix A3 for calculations.

Age (yr)	Mean cohort fecundity	Age-group fecundity	Number of breeding females
1982			
3	1513	394 893	47 (20-156)
4	5592	223 680	7 (4-13)
5	8808	343 512	7 (4-16)
6	10 567	158 505	3 (1-30)
Totals		1 120 590	64 (29-213)
Total egg deposition* = 200 000			
1983			
3	1336	42 752	24 (16-31)
4	2370	1 166 040	376 (178-517)
5	0	0	0
6	11 556	231 120	15 (5-150)
Totals		1 439 912	415 (224-597)
Total egg deposition = 1 100 000			
1984			
3	1314	22 338	12 (10-18)
4	2153	452 130	142 (124-166)
5	3743	464 132	84 (66-108)
6	0	0	0
Totals		928 600	238 (202-291)
Total egg deposition = 635 000			
1985			
3	1312	184 992	79 (58-105)
4	2716	717 024	148 (124-177)
5	4429	438 471	55 (42-75)
6	6287	251 480	22 (13-41)
Totals		1 591 967	304 (164-437)
Total egg deposition = 893 000			

\* Total number of eggs spawned in a reproductive season by the whole population. See Appendix: A2 for calculations.

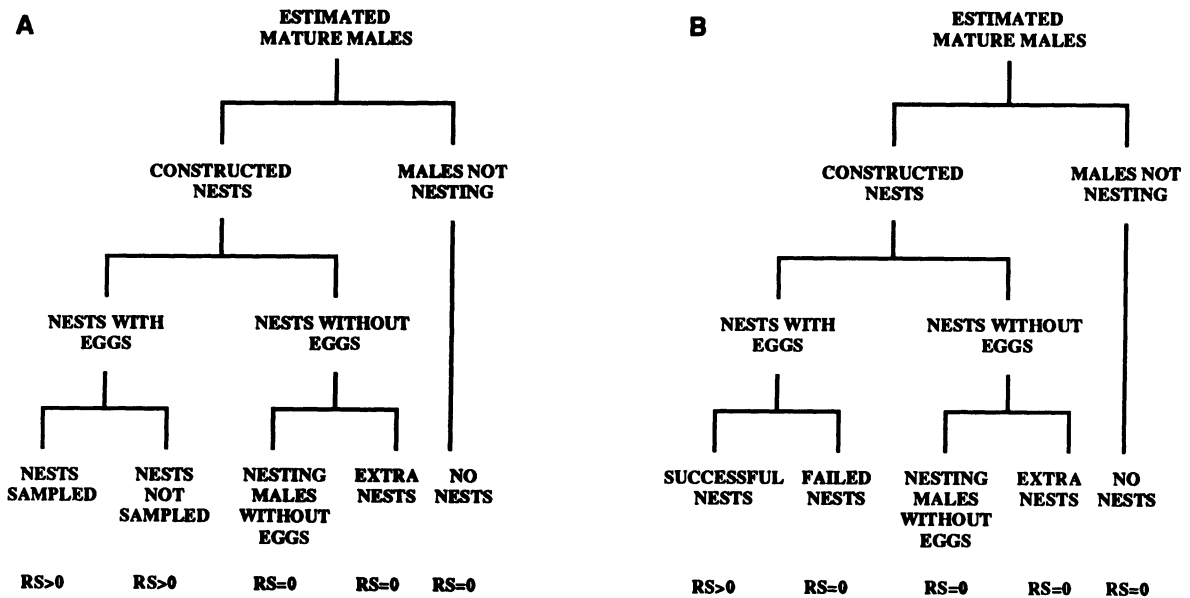


FIG. 2. Decision trees used to determine the categories of breeding fish to combine when calculating the different estimates of reproductive success (RS) shown in Tables 4 and 5. RS can be defined as (A) the number of eggs deposited in a male's nest or (B) the number of larvae a male produces.

ating that as more and more non-breeders are included, the variance expressed in terms of the mean is actually increasing (Sokal and Rohlf 1969). This is also reflected in  $I_F$ , the variance in fitness divided by the square of the mean fitness, which measures the opportunity for selection on fertility as a fitness component (Crow 1958, Wade and Arnold 1980). Thus, if non-breeders are not included as "zero" producers in estimates of RS, the true variation in the system will be underestimated and the mean RS overestimated, both in this case by a factor of  $\approx 3$ .

The same results are obtained when the measure of RS is the number of larvae a male produces. Fig. 2B is an extension of the decision tree under this definition. "Successful" nests are those producing larvae, "failed" nests are those that received eggs but did not produce larvae. Again, different measures of RS can be calculated depending on the extent to which the "zero" producers are included (Table 4). While the means and variances are substantially lower than when RS is estimated from egg production, the cv and  $I_F$  values are similar across the two measures.

Measuring the reproductive success of females in this population is complicated by the fact that we cannot count the number of females actually breeding (the equivalent of "total nests" for males). We believe most females spawn their whole clutches in one nest each, based on evidence from time-lapse films and comparisons of the distributions of female fecundities in the population each year with the mean number of eggs per nest (Raffetto 1987). If we assume monogamy in this population, we can say that the RS of females is

the same as for males with respect to "sampled nests" and "total nests." The RS for "total females" can be calculated, based on the estimates of total mature females in the lake each year (Table 5). The mean numbers of eggs per female, larvae per female, and the variances are greater than for males, primarily due to the fact that there are fewer mature age-3-yr females than males. As with males, the mean number of eggs and the overall variance decreases when "zero class" females are added but the cv and  $I_F$  both increase.

#### *Age, growth, and mortality of breeding males*

We captured 153 breeding males during this study. Of these, 137 were tagged and their growth in previous years was back-calculated.

Differential growth early in life appears to have had an effect on breeding age (Fig. 3). Males that spawned at age 3 yr had a larger mean size during their early years than males who spawned at ages 4 and 5, and males that spawned at age 4 yr had a more rapid growth rate than those that spawned at age 5. Males that spawned at ages 4 and 5 yr were  $<20.0$ -cm TL on average at age 3, and were most likely sexually immature at that age.

When the observed age structure of sampled males was compared to the expected age structure based on the population of mature males, we found that there were usually fewer age-3-yr males breeding and more age-4-yr males breeding than expected based on their proportion of the adult population, but these differences were only significant for 1984 ( $\chi^2 = 29.31$ , 2 df,  $P < .01$ ).



TABLE 4. Comparison of reproductive success (RS) measured as both eggs and larvae per male, and calculated with increasing proportions of non-breeding males in the population.\*

	RS sampled nests		RS total nests		RS total males	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
	1982					
$\bar{X}$	3477	482	2173	304	368	51
$s^2$	8 133 904	141 376	7 912 423	143 378	1 980 740	36 588
$N$	25	24	39	38	236	226
cv	82	78	129	125	382	375
$I_F$	0.67	0.61	1.66	1.56	14.59	14.06
	1983					
$\bar{X}$	3996	397	2482	244	1355	134
$s^2$	11 621 281	177 241	10 969 561	146 069	7 496 212	94 527
$N$	59	56	95	91	174	166
cv	85	106	133	157	202	229
$I_F$	0.72	1.12	1.77	2.46	4.08	5.24
	1984					
$\bar{X}$	4046	1242	3342	1021	1271	383
$s^2$	7 273 809	1 340 964	8 382 718	1 327 375	5 797 716	737 309
$N$	38	37	46	46	121	121
cv	67	93	87	113	189	224
$I_F$	0.45	0.86	0.76	1.28	3.57	5.02
	1985					
$\bar{X}$	4627	1699	3110	1133	1437	521
$s^2$	6 478 315	2 762 244	9 114 497	2 478 953	6 596 516	1 454 450
$N$	41	58	61	87	132	189
cv	55	98	97	139	178	231
$I_F$	0.30	0.96	0.94	1.93	3.17	5.34

\* "Sampled nests" are those from which data were collected; "total nests" are the total numbers of nests built that year; "total males" includes all breeding and non-breeding adult males. "Zero class" males were added into RS of "total nests" and "total males" in the same proportion as the ratio of sampled males to total nests receiving eggs. cv = coefficient of variation ( $[s/\bar{X}] \times 100$ ; Sokal and Rolf 1969);  $I_F$  = opportunity for selection on fertility ( $[cv/100]^2$ ; Crow 1958).

While the nests are very conspicuous and the males seemingly vulnerable to capture, angling accounted for only half of the nest failures, in spite of anglers often intensively fishing the nests. Table 6 shows the fate of the tagged breeding males we captured that failed to produce larvae. About half of the nest failures were due to capture of the guarding male, but the total pro-

portion of failed nests was very small. One reason for this low overall angling mortality was that over half of the nesting males were of sublegal size (83% in 1982, 67% in 1983, 85% in 1984, and 57% in 1985) and were thus protected by the size limit. Few nest failures were attributed to environmental causes other than cold water temperatures. The small size of the lake and protected

TABLE 5. Reproductive success (RS) measured as both eggs and larvae per female, calculated for breeding and non-breeding adult females.\* See Table 4 for definitions of cv and  $I_F$ .

	Year			
	1982	1983	1984	1985
	RS <sub>eggs</sub> total females†			
$\bar{X}$	543	1828	1830	1649
$s^2$	2 832 489	9 259 849	7 344 100	7 225 344
$N$	160	129	84	115
cv	310	166	148	163
$I_F$	9.61	2.76	2.19	2.65
	RS <sub>larvae</sub> total females			
$\bar{X}$	76	179	547	597
$s^2$	52 441	118 336	966 289	1 620 529
$N$	153	124	84	165
cv	301	192	180	213
$I_F$	9.06	3.69	3.24	4.54

\* These calculations assume that each breeding female spawns her whole clutch in one nest, and that the male guarding that nest spawns only with her. Given this assumption, the RS<sub>eggs</sub> of "sampled nests" and "total nests" are the same as those presented for males in Table 4.

† RS<sub>eggs</sub> total females is calculated with "zero class" females added in the same proportion as the ratio of sampled nests to total nests receiving eggs.

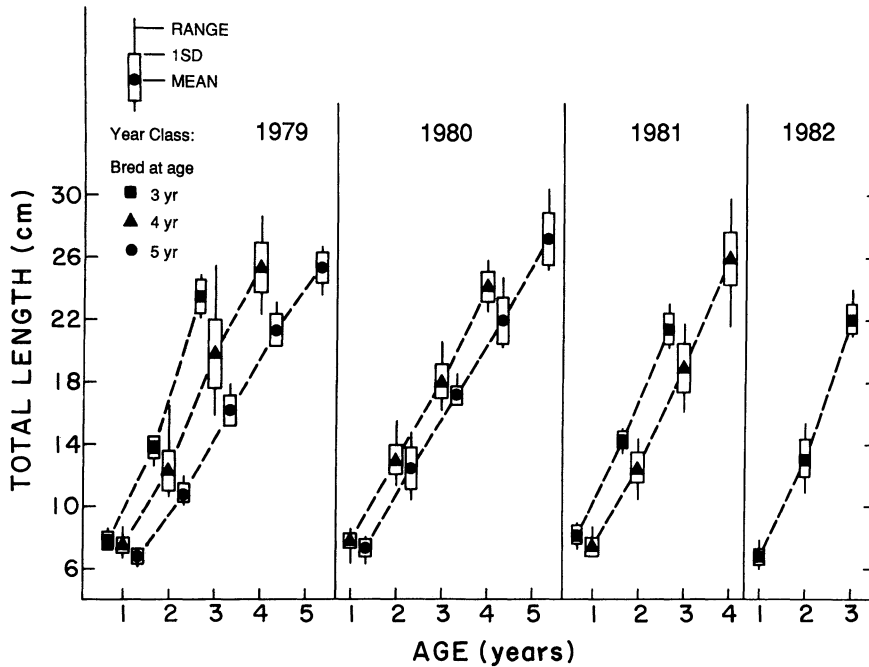


FIG. 3. Back-calculated total lengths of the breeding sample of males organized to illustrate the differences in growth among fish that bred at different ages within their year classes. Males in the 1979 year class were found in our samples in 1982, 1983, and 1984; no males in the 1980 year class were found in 1983. Because this study ended in 1985 there are no age-5 fish shown in the 1981 year class column and no age-4 and -5 fish in the 1982 year class column.

shorelines buffered the nests from such stochastic events as flooding, as is frequently found in streams (Wine-miller and Taylor 1982), or wind fetch, as is frequently found in large lakes and bays (Goff 1986).

Overall, 35% of our sampled breeding males were lost to anglers during the year they bred, 5% were seen the following year (three attempted to breed the following year, two of which were successful; five were captured in fyke nets or by anglers) and 60% were never seen again following the breeding season. That so few males bred more than once in their lifetimes was an unexpected result. Only 23 breeding males with algae-coated tags were seen, and of these 13 were captured and identified. We failed to catch 13 target males (2 in 1983, 6 in 1984, 2 in 1985 and 3 in 1986). In 1986 all but three tagged males nesting in the lake ( $n = 79$ ) were captured, and only one was a male sampled the previous year. Thus, while a few target males may have escaped our detection and reproduced a second or third year, the vast majority of males in this population bred only once in their lifetimes. It is possible that some age-4 and 5 breeding males tagged in the spring could have spawned in former years and been undetected by us.

DISCUSSION

We have estimated RS in a closed population in an attempt to examine the sources of variance in RS in a

system with a minimum of assumptions. We found a substantial proportion of the adult population of both sexes failed to breed in each of the 4 yr of the study, and this normally hidden “zero class” was the largest contributor to an index of the opportunity for selection ( $I_F$ ). Although there is much debate over the utility of measuring variance in RS (Wade and Arnold 1980, Sutherland 1985, Downhower et al. 1987a, b), we believe the exercise is useful when the results are not misapplied. We have used it here to detect the largest potential source of variance in RS in the adult population that could respond to selection. The largest source was not variance in RS among the breeders, but rather variance contributed by non-breeders. In this system

TABLE 6. The number of sampled nests that received eggs but failed to produce larvae. The last three columns indicate the fate of the guarding male.

Year	Total sampled nests	Number nests failing	Male angled on nest	Abandoned, male later angled	Abandoned, male fate unknown
1982	6	0	0	0	0
1983	45	3	1	2	0
1984	47	6	4	1	1
1985	49	2	1	1	0

there is greater potential for selection acting on who gets to breed than among those who do breed. Opportunity to breed may be a more important source of selection than variation in such traits as body size, coloration, etc., within the breeding segment of the population. This is shown in Table 4, where the large zero class of non-breeding males clearly has the largest potential contribution to variation in RS relative to the mean RS, and hence the greatest  $I_F$  value contribution. In this case variance in RS "told" us to look for those characteristics within a cohort that most affected the opportunity to breed. For males, that character was growth rate. Faster growing individuals within a cohort were more likely to show up as breeders than slow-growing individuals, and small size early in life delayed maturity. A correlation between size early in life and age at first reproduction has also been noted in amphibians (Smith 1987, Semlitsch et al. 1988).

By counting the offspring we have directly measured the female fecundity component of male reproductive success. We have avoided the usual simplifying assumption of merely counting the number of matings or assigning the mean clutch size to every mating, as is usually done (Wade and Arnold 1980, Fincke 1982, Downhower et al. 1987a, b, Koenig and Albano 1987; but see Bateman 1948, Clarke 1970, 1971, Howard 1979). An advantage of working on a mating system with external fertilization and paternal care is that male RS is easily measured, and the female fecundity component is accounted for. In smallmouth bass this is especially important, as female fecundity varies over a 20-fold range of values, and the female with the highest fecundity may produce seven times the mean clutch size (Raffetto 1987). The potential for male sexual selection resulting from female choice is large, even though the species is essentially monogamous, because a high-quality female may produce as many eggs as several "average" females.

The possibility that not all sexually mature individuals in a population breed has ramifications for both theory and empirical studies of the effect of variance in reproductive success on the potential for natural and sexual selection. Most theoretical models and empirical studies of natural and sexual selection contain the implicit assumption, revealed by the numbers used to calculate measures of RS, that all or most members of the adult population breed or attempt to breed (see Baylis [1981] for an exception). In models or theories one commonly assumes that female fecundity limits the reproductive potential of the population. Thus empirical studies are directed towards studying mating aggregations or breeding sites, rather than towards a comprehensive census of the adult population at large. While acknowledging the existence of a population of non-breeders or "floaters," most authors proceed to calculate measures of RS without a complete assessment of the non-breeding population. This carries the implicit assumption that the breeding census is rep-

resentative of the entire adult population. If a large component of the adult population does not breed in a given year, then this may account for much of the observed difficulty of predicting future year-class strength from present adult population sizes (Pitcher and Hart 1982). One may be accurately assessing the size of the adult population, but if only a small proportion of the adult population actually breeds, then egg production will be grossly overestimated by assuming all females breed. Thus, the standard life table assumption that zygote production will be determined by the number of females alive in the preceding interval can be very misleading. Similarly, variation in reproductive success will be underestimated or overestimated if it is calculated from breeding individuals only, when a cryptic population of non-breeding, sexually mature individuals is present. If the population of non-breeders is a substantial proportion of the adults, as in this study, the underestimate of variance relative to the mean in reproductive success could lead to an underestimate of the potential for selection and a misunderstanding of the potential sources of selection.

Ideally, we should have calculated RS separately for each year-class and summed them from year-to-year until the entire year-class had died. However, the present study has not lasted long enough to perform the calculations in that manner. We do not believe that our conclusions would be materially altered in any case: given the observed mortality schedules, the proportion of non-breeders will be large within any given year class. However, we suspect that females are commonly iteroparous in this population, unlike the males. Year-class by year-class calculations would potentially reveal a greater mean RS for females than for males, if our suspicion is correct.

In populations with a large proportion of non-breeders, individuals that do not breed may contribute more to the total variation in reproductive success than do the breeders. This fact has implications for management and conservation as well as for evolutionary studies. The practice of stocking populations to increase the number of breeders, or the enhancement of breeding sites, may have no effect in increasing the overall reproductive success of the population, and may actually decrease the mean reproductive success if the number of breeders is limited by social or environmental factors to a small subset of the total original population. Under such circumstances, augmentation of the adult population would only increase the size of the zero class.

Our finding that the zero class is a significant contributor to variance in RS is not unique in the literature. There exist at least two other field studies in which the zero class has been estimated, because the studies were long term and the populations were effectively closed. Woolfenden and Fitzpatrick (1984) have followed a population of Florida scrub jays for more than a decade, and found that relatively few of these birds breed

as adults. Because of strong year-round territoriality by the birds and an aggressive banding program by these workers, immigration and births can be separated, and hence recruitment and eventual breeding success can be measured. A high proportion of potential recruits fail to ever breed. Because the males tend to remain resident as "helpers" on the natal territory, this is often viewed as an "atypical" breeding system peculiar to a social species, with non-breeding helpers being viewed as the avian equivalent of insect sterile workers—an interpretation that is avoided by Woolfenden and Fitzpatrick. Here we have enough information to detect a zero class that we suspect is present in many animal populations; in this case, those adults that fail to acquire the resources necessary to successfully breed in a given year remain on the natal territory and are accessible to census.

Clutton-Brock et al.'s (1982) now classic study of red deer is the second example of a population exhibiting closure. The red deer of Rhum are "culled"; like the bass of Nebish Lake, the top predator is man, and hence the chief source of predation can be accounted for. Here again an adult zero class can be detected, although it is relatively small. Both of these long-term studies contain some surprises, including an effective population size smaller than one would expect; most of the scrub jays on Woolfenden's study plot could be traced to a single ancestral pair. Both of the above studies are, however, based on organisms of low fecundity. Here we have provided evidence that a large zero class also occurs in a high-fecundity organism, and that most of the zero class cannot be detected by examining breeding or nesting sites. Other researchers have counted smallmouth bass nests and noted an excess population of adults (Cleary 1956, Winemiller and Taylor 1982, Goff 1984), but they did not quantify the size of the zero class.

The present study shows the power of examining a closed system to test assumptions and hypotheses about reproduction in natural populations. We suspect the presence of a large proportion of adults who fail to breed in a given year is not peculiar to the bass in Nebish Lake, but may be characteristic of a great many animal populations. Such populations offer the added advantage that when one conducts a longitudinal study, the animals alive in subsequent generations are the direct result of the mating system and reproduction observed in previous generations. Closed populations are by no means artificial or uncommon; small seepage lakes are one of the commonest and widespread of temperate freshwater habitats, and historically were inhabited by a variety of fish species, the smallmouth bass included (Ruttner 1966, Wetzell 1975, Becker 1982). To the best of our knowledge, this is the first study of this kind on an organism of high fecundity in a completely closed population outside of a laboratory (e.g., Bateman 1948). It suggests that the assumption that all or most adult animals in a population breed is

not justified in the case of smallmouth bass, and should be viewed with skepticism for any population.

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## APPENDIX

For definitions of all symbols used in the Appendix, see A5, below.

### A1. NUMBER OF MATURE *MICROPTERUS DOLOMIEUI*

For each year, the number of mature males (*A*) and females (*B*) in the population was estimated by

$$A = \sum_{i=1}^6 N_i \times p_i \times M_i$$

and

$$B = \sum_{i=1}^6 N_i \times q_i \times G_i,$$

respectively.

### A2. NUMBER OF EGGS SPAWNED

The total number of eggs spawned (*C*) in a reproductive season by the whole population is estimated by

$$C = \frac{\sum_{n=1}^S E_n}{S} J.$$

**A3. NUMBER OF BREEDING FEMALES**

We estimated the number of breeding females (Method II) (D) each year by

$$D = \sum_{i=3}^6 \frac{F_i}{T} \times C$$

where

$$\bar{F}_i = \sum_{x=22}^{\max TL} \frac{L_x \times F_x}{N_i \times G_i} q_i,$$

$$F_i = G_i \times N_i \times q_i \times \bar{F}_i,$$

and

$$T = \sum_{i=3}^6 F_i.$$

**A4. REPRODUCTIVE SUCCESS**

Following is the calculation of yearly sample estimate of male reproductive success. Female reproductive success is calculated in the same manner, but substituting *B* for *A*.

*Eggs.*

$$\overline{RS}_{eggs} = \frac{\sum_{n=1}^W E_n}{W},$$

and

$$s^2_{eggs} = \frac{\sum_{n=1}^W (E_n - \overline{RS})^2}{W},$$

where

$$E_n = 0 \text{ for } n = S + 1 \text{ to } W,$$

$$K = [(S/J) \times (A - J)],$$

and

$$W = K + S.$$

*Larvae.*

$$\overline{RS}_{larvae} = \frac{\sum_{n=1}^R V_n}{R}$$

and

$$s^2_{larvae} = \frac{\sum_{n=1}^R (V_n - \overline{RS})^2}{R},$$

where

$$V_n = 0 \text{ for } n = H + 1 \text{ to } R,$$

$$Y = [(H/U) \times (A - U)],$$

and

$$R = Y + H.$$

**A5. DEFINITION OF VARIABLES**

Sym- bol	Definition
<i>A</i>	Number of mature males
<i>B</i>	Number of mature females
<i>C</i>	Total egg deposition
<i>D</i>	Number of breeding females, Method II
<i>E<sub>n</sub></i>	Estimated number of eggs in nest <i>n</i>
$\bar{F}_i$	Mean fecundity of cohort <i>i</i>
<i>F<sub>i</sub></i>	Total fecundity of cohort <i>i</i>
<i>F<sub>x</sub></i>	Estimated individual fecundity of females of <i>x</i> cm TL
<i>G<sub>i</sub></i>	Proportion of age <i>i</i> fish >22.0 cm TL in the fyke-net census
<i>H</i>	Number of nests sampled for counts of larvae
<i>J</i>	Total number of nests receiving eggs
<i>K</i>	Proportion of the total non-breeding adult males that corresponds to the ratio of nests sampled for egg counts to the total number of nests receiving eggs
<i>L<sub>x</sub></i>	Fyke-net estimate of the number of age <i>i</i> fish of <i>x</i> cm TL
<i>M<sub>i</sub></i>	Proportion of age <i>i</i> fish >20.0 cm TL in the fyke-net census
<i>N<sub>i</sub></i>	Estimated total number of fish age <i>i</i> from fyke-net census
<i>p<sub>i</sub></i>	Proportion of males age <i>i</i> in the creel census
<i>q<sub>i</sub></i>	Proportion of females age <i>i</i> in the creel census
<i>R</i>	Number of males sampled for larvae, and the appropriate number of adult males who failed to produce larvae
$\overline{RS}$	Mean reproductive success
<i>S</i>	Total number of nests sampled
<i>s<sup>2</sup></i>	Variance in reproductive success
<i>T</i>	Estimated population fecundity
TL	Total length (in centimetres)
<i>U</i>	Total number of nests producing larvae
<i>V<sub>n</sub></i>	Estimated number of larvae in the <i>n</i> th nest
<i>W</i>	Number of male breeders and non-breeders sampled
<i>Y</i>	Number of adult males that failed to produce larvae; this is the product of the fraction of breeding nests sampled and the number of unsuccessful males