



The Relative Influence of Body Size and Territorial Behaviour on Nesting Asynchrony in Male Smallmouth Bass, *Micropterus dolomieu* (Pisces: Centrarchidae)

M.S. Ridgway; B.J. Shuter; E.E. Post

The Journal of Animal Ecology, Vol. 60, No. 2 (Jun., 1991), 665-681.

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THE RELATIVE INFLUENCE OF BODY SIZE AND
TERRITORIAL BEHAVIOUR ON NESTING
ASYNCHRONY IN MALE SMALLMOUTH BASS,
MICROPTERUS DOLOMIEUI
(PISCES: CENTRARCHIDAE)

BY M.S. RIDGWAY,* B.J. SHUTER* AND E.E. POST†

* *Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, P.O. Box 5000, Maple, Ontario, L6A 1S9, Canada; and* † *Department of Zoology, University of Toronto, Toronto, Ontario, M5S 1A1, Canada*

SUMMARY

(1) Nesting asynchrony among male smallmouth bass, *Micropterus dolomieu* Lacépède, varied significantly from year to year (1980–85). Much of the observed variation in timing of nesting was explained by a consistent relationship between the size of individual males and their thermal history (number of degree-days above 10 °C) immediately prior to nesting: larger males accumulated fewer degree-days prior to nesting than smaller males. Larger females also appeared to spawn earlier than smaller females.

(2) Environmental effects were stronger than phenotypic effects in explaining the seasonal timing of reproduction in males that renested in subsequent years. A significant proportion of adult males did not nest, and the magnitude of that proportion was negatively density-dependent. Nesting habitat was not limiting the number of nesters.

(3) Removal experiments showed that the territorial behaviour of nesting males did not affect the seasonal timing of nesting among males of different sizes nor did it limit the total number of nesting males. These experiments did show that removal of experienced spawners from nesting areas in one year was followed by increased recruitment of inexperienced males to the nesting areas in subsequent years. However, this was not accompanied by a significant increase in the total number of nesters.

(4) Two bioenergetic hypotheses can account for why male body size acts as a constraint on the timing of reproduction: (i) large males emerge from winter with a lower energy deficit and are therefore capable of breeding before smaller males; (ii) large males allocate energy to reproduction rather than growth earlier in a season than small males. Both of these hypotheses could also account for our observation of size dependence in female reproductive behaviour.

INTRODUCTION

Many studies support the general hypothesis that food limitation and differences among adults in energy reserves are important sources of annual variation in the seasonal timing of reproduction (Martin 1987). An implicit assumption in this work is that variation in adult size is not a systematic constraint on reproductive synchrony

in populations of birds and mammals, largely because breeding adults vary little in size. This assumption does not apply to fish species in which there is large variation in body size among breeding adults. In fish, there are allometric relationships between body size and metabolic rate (negatively allometric) and between body size and energy reserves (positively allometric) (Brett & Groves 1979; Weatherley & Gill 1987; Shuter & Post 1990). Thus, body size could represent a systematic constraint on the seasonal timing of reproduction in fish, particularly in northern populations where adults rely on stored reserves to survive through winter (Keast 1968).

The smallmouth bass, *Micropterus dolomieu*, is a centrarchid fish with male parental care (Ridgway 1988). In northern populations, adults do not forage during winter and presumably rely on accumulated energy reserves to survive to the following spring (Keast 1970). Two field observations of breeding adult bass are relevant to this study: (i) length of breeding males and females in a population can vary by as much as 100%, and (ii), large adults of both sexes tend to spawn earlier in a season than small adults (Turner & MacCrimmon 1970; Robbins & MacCrimmon 1977; Hubert & Mitchell 1979). Two general hypotheses can account for why the timing of spawning varies systematically with size. First, such size-dependent differences in timing could stem directly from size-dependent differences in energy reserves and metabolic rate. Second, such differences could simply reflect the superior ability of large males to establish and retain breeding territories.

If allometric differences in energetics constrain the timing of nesting, then large males should consistently initiate nesting prior to small males. Similar allometric constraints on females should lead to large females spawning prior to small females within each season. In order to test this prediction, we examined the influence of male body size and water temperature (degree-days) on the seasonal timing of reproduction in a northern population of smallmouth bass.

We evaluated the alternative behavioural hypothesis using Watson & Moss' (1970) four conditions for demonstrating territorial limitation of breeding density: (i) part of the adult population does not breed; (ii) other resources, e.g. nest sites, do not limit the number of breeders; (iii) there is negative density dependence between the number of breeding males and the total number of adult males; (iv) adults replace any territorial adults removed from the breeding population.

STUDY SPECIES

Male smallmouth bass move into the littoral zone of lakes and rivers in spring, sweep out a nest in the substrate with their caudal fin, court females, spawn, and provide sole parental care of the offspring (Ridgway 1988; Ridgway, Goff & Keenleyside 1989). Spawning begins when water temperature reaches 15 °C and parental care can last 4 weeks or longer. Males are considered solitary nesters (Vogele 1981).

Stochastic environmental variation (i.e. water temperature, winter severity) can greatly affect survival of young-of-year smallmouth bass (Shuter *et al.* 1980). These fish do not feed during their first winter (Keast 1968), and rely on accumulated energy reserves for survival to the following spring. As autumn size and energy content of young-of-year are both highly correlated with length of growing season, variation in the timing of spawning by adults may be an important source of variation in winter survival of young-of-year.

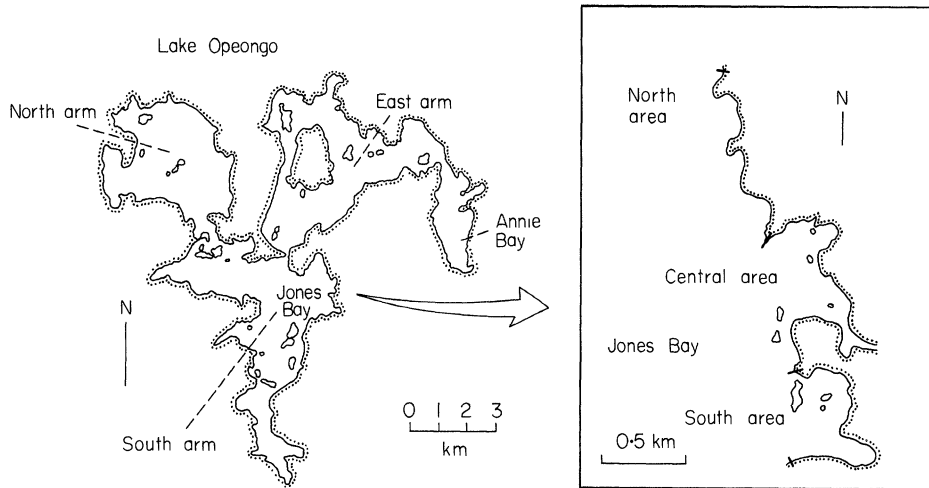


FIG. 1. Map of Lake Opeongo with an enlarged map of Jones Bay.

MATERIALS AND METHODS

Data were collected from nesting males in Jones Bay, Lake Opeongo (Fig. 1; 45°42'N; 78°22'W), Ontario, during the breeding seasons of 1980–85 and 1988. Lake Opeongo is a large oligotrophic lake with good visibility (area = 58.6 km²; secchi disc readings of 6 m). Smallmouth bass were introduced into Lake Opeongo in the early 1920s to supplement the sport fishery for native salmonines. The Lake Opeongo population has been extensively studied for over 50 years, primarily through an annual survey of anglers. The angling fishery is closed for most of the parental care period (late May to early July). The fishery opens in late June and continues into early September. The angling survey operates daily and covers the entire fishing season. It was begun in 1936 and has operated continuously through 1990. Fish sampled during the survey are measured, weighed, aged by the scale method and examined for sex and maturity. A complete description of the survey methodology, a recent summary of population statistics, and further information on Lake Opeongo is provided in McMurtry & Shuter (1985), Shuter, Matuszek & Regier (1987), and Martin & Fry (1972), respectively.

A continuous recording thermograph was used to measure water temperatures from May through October 1970–86, at the southern end of Lake Opeongo at a depth of 1 m in the littoral zone (a typical depth for smallmouth bass nests). Temperatures in Jones Bay were highly correlated ($r = 0.98$) with temperatures recorded at the thermograph site.

In 1981, a special trap net survey monitored differences in the activity of small and large adults during the pre-spawning period. Six nets were set in the littoral zone of the South Arm (Fig. 1) and lifted daily from ice-out in early spring to the start of nesting. Temporal shifts in the size distribution of adults taken in this survey should reflect shifts in the relative activity of small and large adults.

Locations of individual nests and times of spawning were determined by underwater surveys. In each year (1980–85, 1988), we swam (with mask and snorkel) the 6-km

shoreline of Jones Bay once every 3 days from the last week of May until mid-July. The pre-spawning thermal history of each nesting male was expressed as the number of degree-days greater than 10 °C that the fish had accumulated by its spawning date. Spawning date was our estimate of the date on which eggs were deposited in the nest.

Nesting males were captured by angling and tagged with small, numbered plastic tags for individual identification. Survey, tagging and handling procedures are outlined in Ridgway (1988, 1989). Each nesting male from Jones Bay was aged from a scale sample and measured for fork length. As nests with eggs appeared, their positions were marked with numbered bricks and mapped. Guarding males were always returned to their nests within 1.5 min of first capture.

Because we could not be certain of the date of egg-laying for individual females, we used the peak in the ratio of gonad weight to body weight ($\times 100$) as an index of when females were ready to spawn. This peak is concurrent with the stage in ova development when diameter and yolk content are maximal (Hubert & Mitchell 1979; Post 1982; Orendorff 1983). Females were collected from mid-May to mid-June in 1980 and 1981 to determine when this peak occurred for the following fork length classes: (i) 20.0–24.9 cm; (ii) 25.0–29.9 cm; (iii) 30.0–34.9 cm; and (iv) 35.0+ cm.

Abundance estimates

Annual, age-specific abundance estimates for the population were determined by Shuter, Matuszek & Regier (1987) for the years 1936–83 using separable virtual population analysis (Pope & Shepherd 1982) of the total catch-at-age data from the angling fishery. These estimates were independently verified in some years by mark-recapture experiments. We extended this series of abundance estimates through 1988 using the same methodology.

Annual abundance estimates for individual age groups of nesting males were obtained for 1959, 1961–64, 1977–85 and 1988. In late June of each year, from 1980 through 1984, a preliminary estimate of the total number of nesting males in the lake was obtained by conducting a single underwater survey of the entire shoreline (approx. 110 km), using a team of swimmers equipped with mask and snorkel. We used the total count of active nests (i.e. nests containing viable young) as our preliminary estimate of the total number of nesting males in the lake. This preliminary estimate suffered from two sources of underestimation bias: some nests were abandoned prior to the day of the whole lake survey and, therefore, could not be counted; some active nests were undetectable on the day of the survey because their larvae were transparent and sedentary. From 1980 through 1984, the percentage of nests in each of these categories was estimated for the control section (South area, Fig. 1) of our intensive study site (Jones Bay). We used these estimates to adjust our preliminary lake counts upward, to obtain our final estimates of the abundance of nesting males in the years 1980–84.

For the years 1959–79, 1985 and 1988, accurate nest counts for the control area of Jones Bay were available, but nest survey counts for the entire lake were not. For these years, we estimated the abundance of nesting males in the lake by dividing our control area count by the average proportion ($\bar{X} = 0.06$, S.D. = 0.006, $n = 5$) of the nesting male population that used the control area of Jones Bay in the years 1980–84.

Estimates for the age and fork length distributions of nesting males were based on

the intensive Jones Bay surveys. Age–frequency data from undisturbed areas of Jones Bay were used to partition the total count of nesters into individual age groups. These age-specific estimates of the total number of nesting males were then combined with age-specific estimates of total male abundance to provide annual estimates (1980–84) of the percentage of males of different ages nesting in Lake Opeongo. Our age-specific estimates of total male abundance were derived from our SVPA estimates of total abundance at age, assuming a 1:1 sex ratio.

Removal experiments

We conducted a removal experiment in Jones Bay to determine if established nesting males limit the recruitment of new males to the nesting population. Data were collected over 7 years: 1980–85 and 1988 (Table 1). In 1980, we divided part of Jones Bay into two sections (Fig. 1) of approximately equal size: one control area (the South area) and one removal area (the Central area). At least 90% of the nesters in our control and removal areas were given numbered tags. The number, size, age and spawning time of nesting male in the removal area were compared with those in the control area. Spawning time for each male was expressed as the number of degree-days (above a baseline of 10 °C) that had accumulated at the nest site on the day of egg deposition.

Different treatments were tried in the removal area: block removal (1980) and continuous removal (1981–83). For the block removal, active nests were monitored but left untouched for the first 2 weeks of the spawning season. Then, over 2 days, all guarding males were removed and prevented from returning to their nests. All males that spawned after this 2-day period were monitored but were permitted to continue guarding their broods. For the continuous removals, males were removed from their nests as soon as possible (1–2 days) after spawning and prevented from returning. These removals were continued until spawning had ceased for the year.

Under the territorial limitation hypothesis, block removal should cause an immediate increase in the recruitment of small nesting males to the removal area. Continuous removals should cause earlier spawning among smaller nesters, increases in the relative number of smaller nesters and increases in the total number of nests in the removal area.

All removed males were released in Annie Bay (Fig. 1), and none returned to re-nest in the same season. Of all the nesting males taken from the removal area, only

TABLE 1. Treatments applied in each area, 1980–88, and the number of nests recorded in each area in each year. Only nests that received eggs are counted

Year	Area			
	Control (south)	<i>n</i>	Removal (central)	<i>n</i>
1980	Monitor	77	Block removal	52
1981	Monitor	40	Continuous removal	38
1982	Monitor	39	Continuous removal	40
1983	Monitor	36	Continuous removal	30
1984	Monitor	32	Monitor	45
1985	Monitor	42	Monitor	36
1988	Monitor	64	Monitor	66

one was ever observed to spawn again.

The treatments carried out in each area in each year are summarized in Table 1. In most years, both areas were systematically searched by at least two swimmers every other day from late May to early July. All active nests were checked and the status (presence and developmental stage of young) of each was noted. They were not disturbed on subsequent visits to those nests. Similar procedures were followed in the removal area in those years when we were monitoring its recovery from the removal treatments (1984–85 and 1988).

RESULTS

Male body size and the timing of spawning

Larger males and females initiated spring activity prior to smaller males and females. In our pre-spawning trap net survey, the largest males and females were captured early, immediately after ice-out (\bar{x} male fork length = 36.5 cm; \bar{x} female fork length = 34.8 cm). Smaller adults were captured later, just prior to the start of spawning (\bar{x} male fork length = 28.0 cm; \bar{x} female fork length = 29.0 cm).

There was a similar tendency for larger males to spawn prior to smaller males. Within each of the years from 1980 through 1985, a linear relation with negative slope linked male body size (\log_e transformed) to degree-days accumulated prior to spawning (Fig. 2). We used analysis of covariance to compare these relations across years. Slope estimates were not significantly different from each other ($F = 1.75$; d.f. = 5; N.S.); however, there were significant differences among the intercepts (Table 2). Given these results, we derived a common slope estimate for all years (Pedhazur 1982; $b_c = -0.355$; 1 S.E. = ± 0.023 ; $t_{324} = -15.52$; $P < 0.001$) and used it, plus the appropriate year-specific intercept estimates, to characterize the relation between male body size and degree days for the period 1980–85 (Fig. 2). We carried out a similar analysis of the relation between male age and degree-days accumulated prior to spawning. Again slopes were similar across years ($F = 1.13$; d.f. = 5; N.S.), the common slope was negative ($b_c = -3.135$; 1 S.E. = ± 0.27 ; $t_{316} = -11.6$; $P < 0.001$) and intercepts were significantly ($P < 0.01$) different. Thus, larger older males began nesting earlier in the season than smaller, younger males. The similar slopes demonstrate some consistency in this relationship across years.

These results do not reflect size-dependent variation in the delay time between building a nest and fertilizing a clutch of eggs (e.g. Skutchbury & Robertson 1987). The correlation between date of nest-digging and date of receiving eggs was significant ($N = 18$; $r = 0.984$; $P < 0.01$) when the two dates were distinguishable (mean delay = 1.9 days); usually, these dates were not distinguishable.

Twenty-seven males nested in two consecutive years in the South Area of Jones Bay (Fig. 1). We used the two spawning dates for each repeat spawner to estimate year-to-year repeatability in degree-days accumulated prior to spawning (Falconer 1981; Lessells & Boag 1987). The following procedure was used to correct successive spawning times for the growth of the male between spawnings: for each year, cumulative degree-days were regressed on male fork length using data on all males observed in that year; the standardized residual of the observed degree-days for each repeat male in that year was calculated from the equation for that year, using the length of the repeat male as measured in that year. These standardized residuals

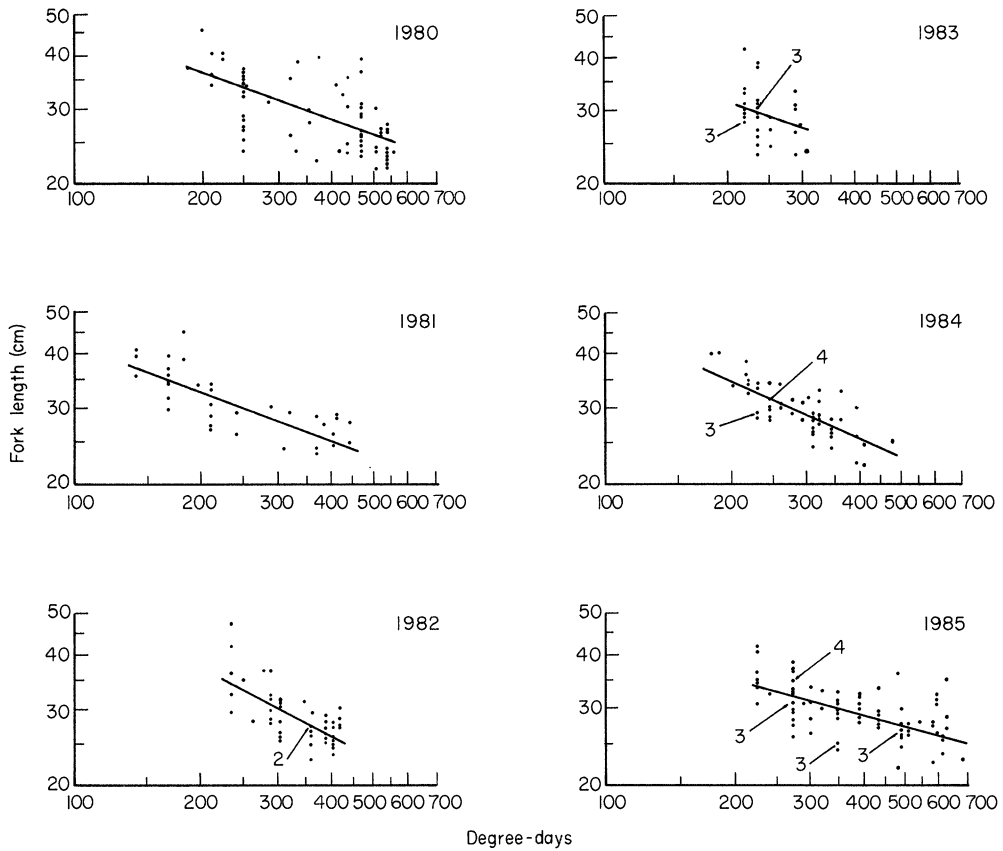


FIG. 2. Relation between male body size and degree-days accumulated prior to spawning for each year from 1980 through 1985; sample sizes are 66, 32, 52, 36, 58 and 82, respectively; correlation coefficients for log-log transformed data are -0.63 , -0.77 , -0.69 , -0.32 , -0.75 , and -0.66 respectively. Each correlation is statistically significant ($P < 0.01$), except that for 1983 ($P > 0.05$). The lines are from a covariance analysis of the entire data set and follow the form $\log_e(\text{degree days}) = a_i - 0.355 \cdot \log_e(\text{fork length})$, where a_i values for 1980-85 are 5.453, 5.431, 6.415, 5.327, 5.964, and 5.072, respectively.

TABLE 2. Tests (P -values) of adjusted means from ANCOVA of male fork lengths on cumulative degree-days prior to initiating parental care

Year	1980	1981	1982	1983	1984	1985
1980		0.0001*	0.0110	0.0001*	0.0001*	0.8845
1981			0.0490	0.1696	0.4954	0.0001*
1982				0.0005*	0.1060	0.0115
1983					0.0240	0.0001*
1984						0.0001*
1985						

* P -values are significant; based on Bonferroni's inequality, acceptable level of significance is $P < 0.003$.

were pooled across years and used in the repeatability calculations. The results demonstrate a low ($r_{\text{intra class}} = 0.153$) and non-significant repeatability among nesting males in the number of degree-days they accumulate prior to spawning ($F = 1.36$; d.f. = 51; N.S.). Environmental effects are much stronger (84.7% of variance) than phenotypic effects (15.3% of variance) in explaining the timing of reproduction in males that re-nest in subsequent years.

Female body size and the timing of reproduction

In 1980 and 1981, large females (35.0+ cm) reached their peak gonad weight/body weight ratio prior to small females (20.0–24.9 cm; 25.0–29.9 cm; 30.0–34.9 cm) (Fig. 3). This result suggests that the spawning period for large females begins earlier in a season than for small females. Large females (35.0+ cm) also had a greater percentage of their body weight allocated to gonads than females in the smaller size-classes.

Male abundance, available habitat and number of spawning males

As age increases, the percentage of males with mature gonads increases more rapidly than the percentage of males that nest (Fig. 4a). Thus, a significant part of the population is sexually mature but does not breed.

The number of nesting males in the control area fluctuated widely from year to year (Fig. 4b). Thus, significant numbers of suitable nest sites must have gone unused in some years. This indicates that the amount of nesting habitat did not, by itself, set an effective limit on the number of breeders. A second, independent test (Maynard Smith 1974) of habitat limitation among territorial breeders requires examination of the relation between number of nesters and degree of asynchrony in breeding times: if habitat is limiting, sequential settlement on breeding territories should lead to fewer territory holders than simultaneous settlement. Low variance in spawning time implies simultaneous settlement and high variance implies sequential

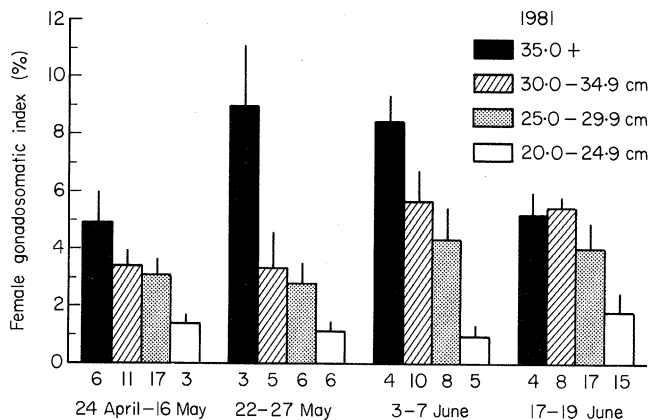


FIG. 3. Mean value (± 1 S.E.) for gonad weight as a percentage of body weight for different length categories of females prior to and during the nesting season. Sample sizes are below the abscissa.

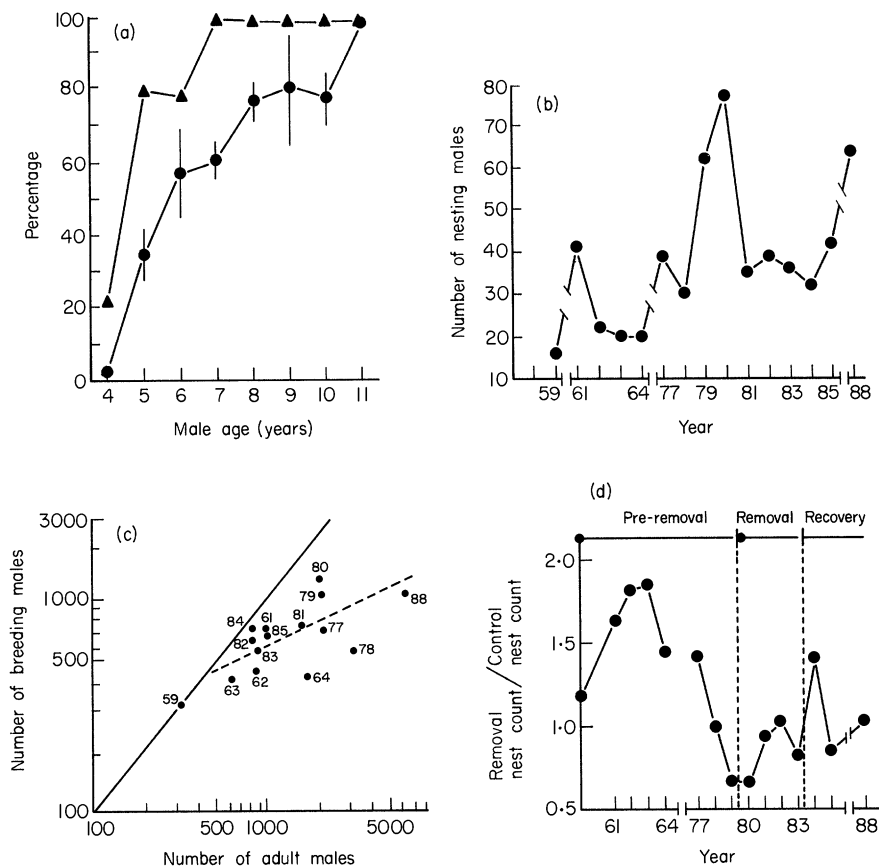


FIG. 4. (a) Age dependence of the percentage of males that are sexually mature at different ages (▲; 1976–82) and the percentage of males that establish nests and acquire a brood (●; 1980–84; ± 1 S.E.). (b) Number of nests with eggs in the Control area of Jones Bay, 1959–88. (c) Number of breeding males in the Control area of Jones Bay versus number of adult males (aged ≥ 5 years and sexually mature) in Lake Opeongo. The solid line gives the predicted relation in the absence of density dependence while the dotted line is derived from regression analysis of observed data ($\log_e[\text{breeder numbers}] = 3.76 + 0.38 \cdot \log_e[\text{adult numbers}]$). (d) Year-to-year variation in the ratio of number of nests in the Removal area to number of nests in Control area.

settlement. Thus, we would expect to find a negative relation between number of nesters and variance in spawning time if nesting habitat were limiting the number of nesters. The actual relationship is positive and non-significant ($P > 0.05$). Thus, our data indicate that spawning habitat is not limiting the number of breeders.

Next, we examined the relation between number of breeding males and number of adult males (Fig. 4c) across years. As almost all nesting males were at least 5 years old (Fig. 4a), we used the abundance of sexually mature males aged 5 years and over as our estimate of adult male abundance. The slope estimate (0.38; S.E. = 0.13) from a log–log regression of number of nesting males on number of adult males was significantly ($P < 0.02$) greater than 0.0. Thus, the number of active nest sites did increase with increases in the number of potential breeders, as expected

given our previous finding that nesting habitat was not limiting. However, the slope estimate was also significantly ($P < 0.01$) less than 1.0, indicating that increases in the number of nesting males did not keep pace with increases in the number of potential nesters. Thus, there was negative density dependence between the number of breeding males and the total male population.

Immediate response of nesters to removal experiments

Two predictions follow from the territorial limitation hypothesis. First, removal of early nesters will cause the number of new nesters in the removal area to increase, relative to the number of new nesters in the control area. Second, the removal area should have more nesters (relative to the control area) in those years (1980–83) when removals took place. With respect to the first prediction, the distribution of new nesters between removal and control areas was not changed by the 1980 block removal (pre-removal new nests 1980: control area = 37 and removal area = 23; post-removal new nests 1980: control area = 40 and removal area = 29; 2×2 contingency table; $\chi^2 = 0.18$; d.f. = 1; $P > 0.05$, one-tailed). With respect to the second prediction, the relative number of nesters observed in the removal area in the removal years (1980–83: control area = 192 nests; removal area = 160 nests) was not significantly different from the relative numbers observed in the years immediately preceding (1977–79: control area = 131 nests; removal area = 127 nests; 2×2 contingency table; $\chi^2 = 0.85$; d.f. = 1; $P < 0.05$, one-tailed) and immediately following (1984–85, 1988: control area = 138 nests; removal area = 147 nests; 2×2 contingency table; $\chi^2 = 2.4$; d.f. = 1; $P > 0.05$, one-tailed) the removal years.

Interpretation of the latter result is complicated by the fact that the relative number of nests in the removal area declined from 1977 through 1979 (Fig. 4d). Thus, it is possible that the effects of the removal were obscured by a progressive deterioration in removal area nesting habitat, beginning prior to 1979 and continuing throughout the removal years. However, this hypothesis cannot account for the fact that there was no within-year response to the block removal in 1980, nor can it account for the fact that the relative number of removal area nests observed during the recovery years was essentially identical to the number observed during the removal years (Fig. 4d).

When all of our observations are taken together, we find no evidence that non-breeding adults respond immediately to the removal of breeders by replacing them on the nesting grounds.

Long-term response of nesters to removal experiments

Beginning in 1981, significant differences ($P < 0.05$) between removal and control areas were noted in both the size distribution of nesting males and the timing of nesting. For the removal area, annual values for each summary statistic (mean, maximum value, coefficient of variation) were divided by the comparable control area values and this ratio was then plotted against year (Fig. 5). With respect to size, nesters in the first year after removal tended to be smaller and less variable in size than nesters in the control area (ratio < 1.0 , Fig. 5a). With respect to timing of spawning, nesters in the first year after removal tended to spawn later and over a

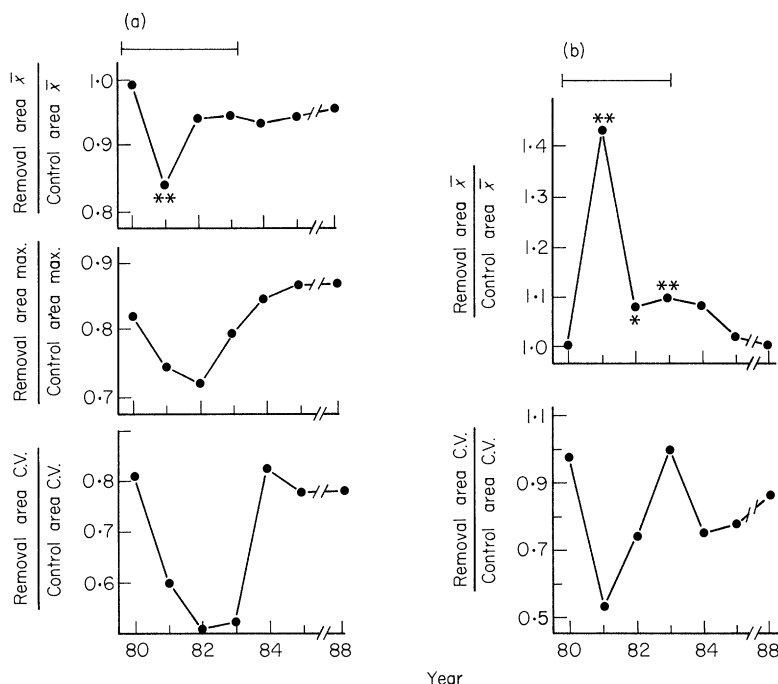


FIG. 5. (a) Comparison of the size of fish in the removal area, relative to the Control area (1980–88). The removal years are identified by a horizontal bar at the top; C.V. = coefficient of variation. (b) Comparison of the spawning time (degree-days) of fish in the removal area, relative to the Control area (1980–88). The removal years are identified by a horizontal bar at the top. C.V. = coefficient of variation. Significant differences between frequency distributions from Removal and Control areas (Kolmogorov–Smirnov two-sample test) are identified as follows: * $P < 0.1$; ** $P < 0.05$.

narrower time-span than nesters in the control area (ratio >1.0 , Fig. 5b). These effects were strongest in the first year after removals were begun (1981), and were detectable through the removal years of 1982–83 and into the recovery years of 1984–85. By 1988, removal and control areas were essentially identical, as they had been in 1980.

The territorial limitation hypothesis predicts that removals will cause an increase in the relative number of small nesters using the removal area, and that those small nesters will nest earlier than their counterparts in the control area. The mean size of nesters in the removal area did decrease (Fig. 5a). However, the coefficient of variation for size also decreased substantially (Fig. 5a), indicating that much of the drop in mean size could be attributed to the complete absence of large experienced nesters rather than to an influx of small inexperienced nesters. Also, removal area nesters did not spawn earlier than control area nesters of similar size. Pooling the spawning time data from the three continuous removal years (1981–83) showed that removal area nesters tended to spawn somewhat *later* than control area nesters of similar size (Fig. 6). We used a relative time-scale, based on the last spawning date of each year, to pool spawning time data across years. For each year, the spawning time for each male was divided by the latest spawning time observed in that year. This yielded a time-scale with a maximum value of 1.0 denoting the end of the

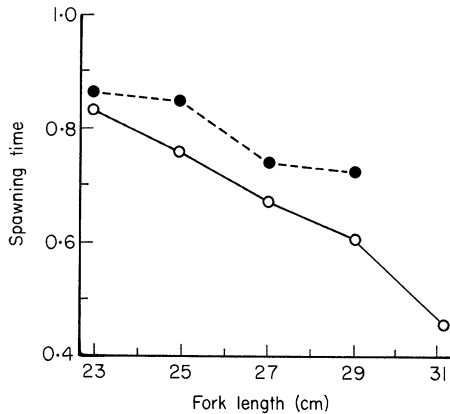


FIG. 6. The timing of spawning in Removal (●) and Control (○) areas among similar sized fish in continuous removal years (1981–83) only.

spawning season (Fig. 6).

A coherent explanation of our results must account for the following: first, there was no detectable effect of removals on the total number of nesting males, either immediately or in subsequent years; second, there were strong effects on both the size of nesters and the timing of nesting and these effects lagged behind the experimental treatments by one spawning season. To develop such an explanation, we must take a broader look at the factors controlling recruitment of inexperienced males to nesting areas.

Recruitment of inexperienced males to nesting areas

The seasonal pattern of space use by adult males can be split into two distinct phases. The first phase (the 'lake' phase) involves the use of space during the non-reproductive season; with many *Micropterus* sp. populations this consists of selecting and defending a well-defined home range (Hubert & Lackey 1980; Fish & Savitz 1983). The second phase (the 'nest' phase) involves selecting a nest site, defending the territory immediately surrounding the site and defending the brood within it (Ridgway 1988, 1989). Energy accumulated during the lake phase supports much of the activity of the nest phase (Adams, McLean & Parrotta 1982).

In 1980, our removal of nesting males affected the nest phase alone. The preceding lake phase was undisturbed. In the next 4 years (1981–84), our experimental design disturbed both lake and nest phases. Each of our nest phase removals (1980–83) prevented experienced adults from re-establishing their traditional patterns of space-use during the subsequent lake phase. In addition, because experienced males exhibit strong nest site fidelity from year to year (Ridgway 1986), each nest phase removal eliminated the influence of experienced nesters from all aspects of nesting activity in the removal area in the following year. Thus, the 1981–83 nest phases were affected by prior removals of experienced males, as well as current removals of new nesting males. The 1984 nest phase was affected only by prior removals of experienced males. In the recovery years of 1985 and 1988, both lake and nest phases were undisturbed.

None of our comparisons clearly addresses the question of how removals affect the recruitment of new, inexperienced males to a spawning area. To do this, we must separate inexperienced from experienced nesters in both removal and control areas. In the years 1981–84, we assumed that all untagged, nesting males found in the removal area were inexperienced, first-time nesters. This inference is based on the following facts: year-to-year nest site fidelity is strong among experienced males (Ridgway 1986); the influence of experienced males previously associated with the removal area was eliminated by removal treatments in prior years; experienced males from other nesting areas in Jones Bay were tagged and therefore could be identified if they strayed into the removal area. In the control area, all experienced males were tagged. Therefore, we could assume that all untagged, nesting males in the control area were inexperienced nesters.

The age distributions of inexperienced nesters in the removal and control areas were similar (Table 3). Thus, the age distribution of inexperienced males recruiting to a nesting area is not strongly influenced by the presence of older experienced males prior to nesting, or during nest site selection. This suggests that the lagged size structure shifts noted earlier (Fig. 5a) result simply from the elimination of the older and larger experienced males from the removal area.

Does the absence of the experienced males usually associated with a spawning area permit a greater *number* of inexperienced males to recruit to that area? In the years when experienced males were absent (1981–84), the proportion of inexperienced nesters found in the removal area was significantly greater than in those years (1980, 1985) when experienced males were present (1981–84: number inexperienced nesters in removal area = 118, number in control area = 99; 1980, 1985: number inexperienced nesters in removal area = 50, number in control area = 68; 2×2 contingency table: $\chi^2 = 4.41$, 1 d.f. $P < 0.02$, one-tailed). Thus, when the influence of experienced males is eliminated from both lake and nest phases of the annual behavioural cycle, the number of inexperienced males recruiting to a spawning area does increase.

DISCUSSION

Although a large proportion of younger adult males do not nest, our removal experiments failed to show that substantial numbers of younger adults were excluded from nesting areas by early nesting, older adults. Thus, our results do not meet the criteria of Watson & Moss (1970) and we must conclude that the establishment of nest territories and the defence of broods does not limit the number of nesting males in Lake Opeongo. Our removal experiments also failed to advance the timing of

TABLE 3. Average age distributions (%) of inexperienced males, obtained by pooling all data for the years 1981–84

Age	Control area ($n = 99$)	Removal area ($n = 114$)
5	10.5	20.2
6	39.4	42.1
7	19.2	28.9
8	16.2	15.0
9	3.0	3.5
10	2.0	0.0

nesting among younger, smaller males. Thus, the territorial limitation hypothesis of Watson & Moss (1970) cannot account for the fact that older, larger males tend to nest earlier than younger, smaller males.

Our observation of a consistent, inverse relation between male body size and the timing of nesting in males can be explained by our energetics hypothesis. A similar bioenergetic explanation can account for our observation of an inverse relation between female body size and the timing of gonadal development in females. The latter observation does raise the possibility that the timing and location of male nest selection may be driven by the distribution of ripe females in Lake Opeongo. However, if this were the case, early nesting of small males should have occurred in the removal area in 1981–83, when large mature females were available and there were no large experienced males to mate with them. Premature nesting of small males was not observed in 1981–83.

There are two energetic hypotheses which can account for the general relationship between male size and cumulative degree-days until the start of parental care. First, the nesting pattern may derive from the allometric differences among males in their metabolism and energy reserves after winter. During winter, smallmouth bass in northern populations are inactive (Webster 1954), do not forage (Webster 1954; Keast 1968, 1970), and appear to rely on accumulated energy reserves until the following spring (Keast 1970). Metabolic rate, measured as a fraction of body weight, is inversely proportional to size in poikilotherms (Robinson, Peters & Zimmerman 1983). This implies that the energy deficit of males coming out of the inactive winter period should be negatively correlated with body size (Shuter *et al.* 1980; Shuter & Post 1990). Larger males should require a shorter post-winter foraging period prior to nesting in order to recoup energy losses incurred during winter. Also, parental care in fish should require some minimum level of energy reserves prior to initiating nesting as parental care can be energetically costly (Chellappa *et al.* 1989). If this is the case in smallmouth bass, then large males will meet this requirement before small males.

Second, the nesting pattern may reflect allometric differences among males in their strategies of energy allocation prior to reproduction. The inverse relationship between growth rate and size in adult fish marks a shift from a strategy of allocating energy to maintenance and growth to a strategy of allocating energy largely to maintenance and reproduction (Brett & Groves 1979; Weatherley & Gill 1987). If large males allocate energy to reproduction early in a season, whereas small males allocate a greater proportion of energy to growth rather than reproduction, then large males may be ready to nest earlier in a season than small males.

There are two implications for mating systems in *Micropterus* spp. fishes based on the observation that larger individuals in both sexes appear to be active earlier in a season, prior to nesting, than smaller individuals. First, the allometric hypotheses we have outlined for the timing of male nesting may also apply to females. Second, mate choice in both sexes may be limited to a more narrow size range than that observed over the entire season.

Our results stand in clear contrast to a large body of research on spacing behaviour in fish which tends to demonstrate the generality of competition for suitable spawning sites. Space or spawning sites are a common limiting resource for breeding adults (e.g. Downhower & Brown 1979). In some cases, available space may be completely

occupied (e.g. Clayton & Vaughan 1986). In contrast, suitable nesting habitat does not appear to be a limiting resource for parental males in some populations of gasterosteid (Whoriskey & FitzGerald 1985) and centrarchid fishes (Bietz 1981; Noltie & Keenleyside 1987; this study).

Removal of experienced nesters from the lake phase of the annual behavioural cycle results in more inexperienced nesters in the following nest phase. This observation suggests that the negative density dependence between nesting males and the total male population (Fig. 4d) derives from mechanism(s) operating during the lake phase of the adult life cycle. One mechanism may be exploitative competition, in which more adult males living at times of low density are able to acquire food resources sufficient for nesting. Another, more likely mechanism may be non-exploitative competition, primarily based on spacing behaviour, in which large males are able to maintain home ranges in areas of good food resources relative to small males. In other fish, interference competition of this sort can modify individual growth rates, body size and social behaviour (Rubenstein 1981a, b). Both these mechanisms assume that food limitation is an important determinant of the negative effect density has on the fraction of mature males that nest. Thus, both provide a bioenergetic account of nest acquisition that fits naturally into our bioenergetic explanation of the effects of male body size on the timing of spawning.

Studies of the seasonal movements of centrarchid fishes, particularly of the genus *Micropterus* have repeatedly demonstrated the presence of well-defined home ranges during the lake phase of the annual behavioural cycle (e.g. Warden & Lorio 1975; Winter 1977; Hubert & Lackey 1980; Fish & Savitz 1983; Pflug & Pauley 1983). Unfortunately, little is known about the mechanisms determining space use among smallmouth bass during this phase. Home-range size of the closely related congener, the largemouth bass (*Micropterus salmoides* Lacépède), can be reduced by supplemental feeding (Savitz, Fish & Weszely 1983), and the location of a home range can persist for more than one season (Lewis & Flickinger 1967). In smallmouth bass, restricted space use by adults is largely limited to summer and winter months, with wider ranging movements occurring during spring and fall (Hubert & Lackey 1980). Individual variation in the tenure and size of home ranges in bass may be based on individual differences in foraging profitability. Thus, the behavioural mechanisms which allocate space among adult smallmouth bass during the non-reproductive part of each year in Lake Opeongo may play an important role in determining why such a low percentage of young males nest in most years (Fig. 4a). The importance of spacing behaviour in the ecology of Opeongo smallmouth bass during the lake phase is the focus of our current field research.

ACKNOWLEDGMENTS

We thank Jim MacLean for his many contributions to this work. We thank Leon Carl, Bryan Henderson, Nigel Lester and Cheryl Lewis for constructive comments on the manuscript, and Audrey Chui for drafting the figures. We also wish to thank numerous summer students for their strong effort and assistance over the years of this study. This is contribution number 89-06 from the Fisheries Research Section, Ontario Ministry of Natural Resources.

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(Received 18 June 1990; revision received 3 December 1990)