

Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake

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Abstract: Using 12 years of data, we evaluated the mechanisms controlling largemouth bass, *Micropterus salmoides*, recruitment in a lake near the northern extent of the largemouth bass range. We found that complex interactions among adult demographics, size-selective predation, and overwinter mortality regulate the number of largemouth bass surviving the first year of life. The largest recruitment events required at least a moderate number of adults, but a large number of adults was not sufficient to produce a large cohort of largemouth bass. Predation was controlled by the number of both adult and juvenile bass and was not strongly correlated with reproductive output. Overwinter mortality was size dependent, strongly affecting bass entering the winter at <50–60 mm in length, and likely the result of starvation. Predation and overwinter mortality interacted with spawning date and growth rate to produce variable but predictable patterns of first year survival. At high adult and juvenile densities, predation regulates first year survival. At low adult and juvenile densities, first year survival was regulated by adult demographics and interactions among spawning date, growth rates, and overwinter mortality. Although we can forecast coarse patterns of cohort survival, the survival of individual fish was more difficult to predict because length and age were not highly correlated.

Résumé : À partir de données s'étalant sur 12 ans, nous avons évalué les mécanismes régissant le recrutement de l'achigan à grande bouche, *Micropterus salmoides*, dans un lac situé près de la partie septentrionale de l'aire de répartition de ce poisson. Nous avons observé que des interactions complexes entre les paramètres démographiques des adultes, la prédation selon la taille et la mortalité hivernale déterminent le nombre d'achigans qui survivent plus d'un an. Les recrutements les plus importants étaient obtenus quand il y avait au moins un nombre modéré d'adultes, mais la présence d'un grand nombre d'adultes n'était pas suffisant pour produire une cohorte importante d'achigans. La prédation était régie par le nombre d'adultes et de juvéniles et n'était pas fortement corrélée avec la production génésique. La mortalité hivernale était fonction de la taille et touchait fortement les achigans dont la longueur au début de l'hiver était de moins de 50 à 60 mm; elle était probablement attribuable à l'inanition. La prédation et la mortalité hivernale étaient reliées à la date de fraye et au taux de croissance, d'où des profils de survie durant la première année variables mais prévisibles. Quand les densités des adultes et des juvéniles étaient élevées, la prédation déterminait la survie durant la première année. Quand ces densités étaient basses, la survie durant la première année était déterminée par les caractéristiques démographiques des adultes et les interactions entre la date de fraye, les taux de croissance et la mortalité hivernale. Bien que nous ayons pu prévoir les caractéristiques générales de la survie des cohortes, la survie des individus était plus difficile à prévoir parce que la longueur et l'âge n'étaient pas fortement corrélés.

[Traduit par la Rédaction]

Introduction

Fish recruitment is problematic for fish ecologists and fisheries managers because it is inherently variable and diffi-

cult to quantify (e.g., Fogarty et al. 1991). Despite these difficulties, the emerging paradigm is that recruitment is regulated by the interaction of density-dependent and density-independent mortality involving size-dependent processes at early life history stages (e.g., Sissenwine 1984; Houde 1987). For this reason, mechanistic studies focusing on survival of fish in their first days, weeks, and months of life are critical to understanding recruitment variability (Crowder et al. 1992). A holistic approach has been called for (Sissenwine 1984), but few studies have assessed the constraints on recruitment for more than a short period of life and most have evaluated only one or a few of the potential mechanisms (however, see Elliott 1984).

This study focuses on largemouth bass, *Micropterus salmoides*, a geographically widespread fish species that supports recreational fisheries throughout its range. Recruitment of largemouth bass is highly variable (Summerfelt 1975).

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Largemouth bass are well studied and provide an ideal subject for studying how the interaction of density-dependent and density-independent mechanisms influence fish recruitment. Most individual mechanisms have been documented, but no study has yet integrated observations on multiple mechanisms in a single system.

Multiple mechanisms are likely to interact hierarchically to regulate recruitment. Adult demography strongly influences the number of eggs spawned and is the ultimate constraint on recruitment potential. The number of largemouth bass that survive the first year of life, however, seldom correlates strongly with the number of young spawned. Predation during summer months and overwinter mortality are considered common sources of mortality and likely constrain recruitment through the first year of life. These sources of mortality are size selective and therefore interact with spawning date and growth rates, two factors that govern size at age (e.g., Miller and Storck 1984). In general, rapid growth and large size reduce the risk of predation (e.g., Miller et al. 1988; Luecke et al. 1990) and lower the probability of overwinter mortality resulting from starvation (e.g., Oliver et al. 1979; Miranda and Hubbard 1994a). However, these constraints do not operate independently. Modeling efforts suggest that predation may interact strongly with growth rates through a density-dependent growth response and therefore influence overwinter survival (DeAngelis et al. 1991). Model results suggest that increased predation could increase growth, which would increase the probability of overwinter survival. While strongly suggestive, these results remain untested.

Here we evaluate the mechanisms influencing recruitment of largemouth bass in a lake near the northern extent of the largemouth bass range. We show that the number of bass surviving the first year of life results from complex interactions among adult demography, spawning date, young-of-the-year growth rates, predation, and overwinter mortality. We estimate the major sources of mortality and test the theory that size-selective mortality differentially affects the survival of fish of different ages. Our results are placed in the context of both individual and cohort survival. Finally, we discuss the effects of largemouth bass recruitment on long-term population dynamics, fish community dynamics, and food web structure.

Methods

Study site

Paul Lake is a small (1.7 ha, maximum depth 15.0 m), oligotrophic lake located at the University of Notre Dame Environmental Research Center, Gogebic County, Michigan, U.S.A. Paul Lake is located near the northern extent of the largemouth bass range and largemouth bass dominate the fish community (>95% of the fish biomass). This population of largemouth bass has been unmanipulated and unexploited since it was established in 1976 (Leavitt et al. 1989). Paul Lake and its history are fully described in Leavitt et al. (1989) and Carpenter and Kitchell (1993).

Fish population estimates

All bass ≥ 150 mm in total length (TL) were marked with individually numbered Floy tags. Fish ≥ 300 mm TL (4–5 years of age) were considered reproductively mature adults (Scott and Crossman 1973). Individuals < 300 mm TL and at least 1 year old were con-

sidered juveniles. All bass in the first year of life were considered young-of-the-year (YOY). Population estimates of juvenile and adult bass were conducted in mid-May and mid-August of each year using Petersen or Schnabel mark–recapture methods (Krebs 1989). Schnabel mark–recapture estimates were used when multiple recapture events were possible. To minimize recapture bias, marks and recaptures were conducted using a combination of angling and electroshocking. The mark for fish ≥ 150 mm was their individually numbered Floy tag and the mark for fish < 150 mm was a clipped caudal fin. Annual population densities for juveniles and adults were calculated as the average of May and August population estimates.

Mark–recapture population estimates for YOY largemouth bass were made in mid-August. Because angling was not possible for YOY bass, all marks and recaptures were made by electroshocking. The mark for YOY bass was a caudal fin clip. Standard error estimates for YOY populations were estimated according to Krebs (1989). When mark–recapture population estimates were not available, the abundance of YOY largemouth bass was estimated from the relationship between catch per unit effort and mark–recapture estimates from other years (population estimate = $8.3 \cdot \text{number caught} - 156.7$; $N = 7$; $R^2 = 0.94$). We used the standard error estimate for predicted values around the fitted regression for the standard error of these population estimates (Draper and Smith 1981). The entire shoreline was sampled when electroshocking for population estimates. Effort was the number of times that the entire lake was shocked.

The number of YOY largemouth bass at swim-up was estimated using two techniques: direct nest counts and estimates reconstructed indirectly from predation estimates (Forney 1977). Nest count estimates were derived from the number of successful nests and an estimate of the average number of fry per nest (3000, range 2000–7000; Scott and Crossman 1973). Nest surveys were conducted by underwater observation (snorkeling). Nest surveys were conducted in 1993–1995 from late May until all eggs had hatched and nest schools of fry were dispersed. The entire lake was surveyed once every 2–3 days. All nests were counted and the stage of YOY largemouth bass development was recorded. The hatching dates of nests with eggs that hatched between observations were corrected by 1–2 days based on developmental stage of fry. We defined a successful nest as a nest that produced swim-up fry and a nest school.

We sampled YOY largemouth bass throughout the summers of 1993–1995 using dip nets and electroshocking. Samples were collected by dip netting while nest schools persisted. After the schools dispersed, YOY largemouth bass were sampled by electroshocking. YOY largemouth bass between 15 and 25 mm TL were generally not vulnerable to the combination of dip netting and electroshocking. Fish longer than 25 mm were vulnerable to electroshocking and were sampled accordingly. All YOY largemouth bass were measured to the nearest 1 mm.

Forney (1977) demonstrated that, when accurate predation estimates can be made, the number of YOY fish hatched can be closely estimated by the cumulative number of YOY fish eaten plus the number of YOY alive at that time. In Paul Lake, adult and juvenile bass are the only important predators of YOY bass. Our predation estimates derive from whole-lake, mark–recapture population estimates for adult and juvenile bass, regular sampling to collect diet information, and a well-corroborated bioenergetics model (Rice and Cochran 1998; Whitley and Hayward 1997). Our cumulative predation estimates plus August mark–recapture estimates are a good estimate of the number of YOY bass hatched in each year. There is a strong correlation ($r = 0.98$) between estimates of the number of YOY hatched (as derived from nest counts) and from predation estimates in 1993–1995. There is uncertainty around this relationship because we have assumed an average number of fry per nest and because there is error associated with our

adult and juvenile population estimates. However, the range of possible nest-count-based estimates and cumulative-predation estimates overlap almost completely (see Table 2).

Diet information

In 1984–1995, we collected diet data from adult and juvenile largemouth bass to estimate predation on YOY bass. Diet data were collected by angling and electroshocking. Samples were taken each year between mid-May and late August at intervals of 2–3 weeks. Samples were collected between 0800 and 1130 h, and 1600 and 2000 h. The mean sample size was 26 (SE = 1.2). Diets were generally similar between morning and evening samples. Statistical analysis of sample size and intra- and inter-sample diet variance are presented elsewhere (Hodgson and Cochran 1988; Hodgson et al. 1989). Stomach contents were flushed from the stomach with water, collected in a 0.28 mm mesh concentrator, and preserved in 95% ethyl alcohol. Diet collection techniques are fully described in Carpenter and Kitchell (1993). All diet items were identified to the lowest relevant taxonomic group and enumerated. Diets were analyzed as percent composition by wet mass using standardized weights for each prey item (Carpenter and Kitchell 1993).

Predation estimates

Predation by adults and juveniles on YOY largemouth bass was estimated using the bioenergetics approach of Kitchell et al. (1977), with largemouth bass parameters from Rice et al. (1983) and Trebitz (1991). Modeling was conducted with the generalized fish bioenergetics software developed by Hewett and Johnson (1992). Water temperatures for this model were from weekly temperature profiles taken each year from May through September. We assumed that largemouth bass experienced water temperatures comparable with those recorded at a depth of 1 m. Adult and juvenile energy densities were assumed to be 1000 cal·g wet mass⁻¹ (Hewett and Johnson 1992).

We quantified the relationship between adult and juvenile cannibalism and YOY largemouth bass abundance by comparing adult and juvenile diets with YOY abundance in August of each year. We used the asymptotic model

$$(1) \quad Y = a \cdot [1 - \exp^{(-b \cdot X)/a}]$$

where Y was the percent (by mass) of YOY largemouth bass in the diet of adults and juveniles, X was the abundance of YOY largemouth bass in Paul Lake, and a and b were free parameters describing the asymptote and slope of the curve, respectively. The asymptote, a , represents the maximum percent of YOY largemouth bass in the diets of adult and juvenile bass. Because this relationship contained errors in the predictors, we weighted each data point by the inverse of its variance and fit the model using negative log likelihood (Clutton-Brock 1967; Reilly and Patino-Leal 1981). Parameter standard errors were calculated by bootstrapping residuals (Efron and Tibshirani 1993).

To quantify the impact of cannibalism on recruitment, we compared our direct and indirect estimates of the number of YOY hatched to predation estimates and an estimate of the maximum potential predation. Predation estimates derive from bioenergetic calculations using the observed temperatures, growth rates, and diet composition of adult and juvenile bass in each year. They represent our best estimate of the total number of YOY bass eaten from hatching through late August. Our estimates of maximum potential predation represent the maximum number of YOY bass that could have been eaten in each summer. We calculated the maximum potential predation in each year using observed temperatures and growth rates but assumed that adult and juvenile diets contained the maximum percent of YOY largemouth bass possible (estimated by a from eq. 1) for the period from the first incidence of

YOY largemouth bass in adult and juvenile diets to late August. By holding everything except diet composition constant, maximum potential predation represents the number of YOY largemouth bass that could have been eaten in a summer had there been at least that many YOY hatched. Dividing the number of YOY eaten by the maximum potential predation provides a useful index of the intensity of predation. When this index is low, adult and juvenile bass could have eaten many more YOY than they did. When this index is high (approaching 100%), adults and juveniles were eating as many YOY as they could. Because of uncertainty of our population estimates and our estimate of a , we would not expect our estimates of predation and maximum potential predation to be equal.

We sampled in 1993 and 1994 to assess prey size selectivity by adult and juvenile bass. A length frequency distribution of YOY largemouth bass was collected from Paul Lake within a day of collecting adults and juveniles for diet analysis. We measured the TL or standard length (SL; length from snout to the end of the vertebral column) of all measurable fish found in adult and juvenile stomachs. Standard lengths were converted to total length using the relationship

$$TL = 1.19 \cdot SL - 0.37$$

($n = 34, R^2 = 0.99, P < 0.01$)

The total length of fish from diet samples preserved in 95% ethyl alcohol were corrected for shrinkage using the relationship

$$TL_F = 1.07 \cdot TL_P - 1.25$$

($n = 26, R^2 = 0.97, P < 0.01$)

where TL_F was the fresh (unpreserved) total length and TL_P was the preserved total length. We did not correct for variable storage time because all preserved fish were measured after they had been preserved for >1 year.

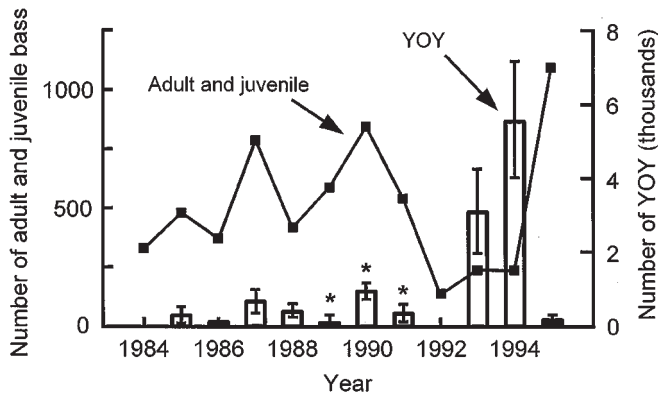
We used the Kolmogorov–Smirnov test (Sokal and Rohlf 1981) to test the null hypothesis that the length frequency distributions from diet samples were the same as length frequency distributions of YOY largemouth bass in the lake. A non-significant result indicates that adults and juveniles were selecting YOY largemouth bass at random, and a significant result indicates that predation was size selective. The in-lake length frequencies for 23 June, 30 June, and 7 July in 1994 are likely biased because of sampling limitations. The sample on 23 June does not include large, early-spawned fish from dispersed nest schools, and samples on 30 June and 7 July may underrepresent fish <25 mm because they are difficult to accurately sample with electroshocking techniques. These biases, however, do not change our interpretation of the results.

Growth rate estimates

Otolith microstructures were analyzed to evaluate age-specific growth rates and to estimate age-dependent summer survival. The daily rings of largemouth bass otoliths (sagittae) provide a reliable estimate of age for fish in their first summer of life (e.g., Miller and Storck 1982). We collected YOY largemouth bass for otolith analysis in late August of 1993 and 1994. Over 100 fish were haphazardly collected in each year. Otoliths were prepared according to the methods of Miller and Storck (1982) and Isley and Nobel (1987). The number of daily rings in each otolith was counted a minimum of three times. If the three counts were within one day, the mode was taken as the age. If the three counts were not within one day, the otolith was aged an additional 2–4 times and the mode was used as the age. For >90% of all otoliths, an age mode was evident after 3 to 5 counts. Based on our observations and previous studies (Miller and Storck 1982; Isley and Noble 1987), we believe that our otolith-based age estimates are accurate to ± 3 days.

The pattern of age-dependent mortality over the summer was estimated using the chi-squared test for goodness of fit (Sokal and

Fig. 1. Population dynamics of Paul Lake largemouth bass for 1984–1995. The population estimates for adults and juveniles are the summer average. The YOY largemouth bass estimates are from August only (± 1 SE). Estimates in some years (*) derive from the relationship between catch per unit effort and population estimates for young-of-the-year in the other years.



Rohlf 1981) to compare the age distribution of fish sampled in late August (from otolith analysis) to the hatching date distribution of successful nests. We assigned surviving fish and successful nests to early- and late-hatched categories. The division for early and late hatched was based on the median hatching date for each year. Only two categories were used to increase sample size and to minimize the effects of otolith aging errors.

Overwinter mortality

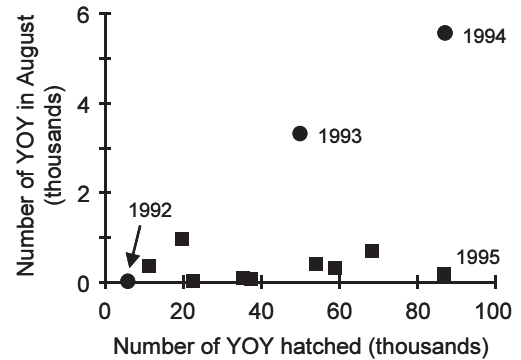
We assessed the pattern of overwinter mortality by sampling the 1993 and 1994 cohorts in early October after water temperatures were $<10^{\circ}\text{C}$ and in May just after temperatures reached $10\text{--}12^{\circ}\text{C}$. Largemouth bass growth is minimal at water temperatures $<10^{\circ}\text{C}$ (Johnson and Charlton 1960; Coutant 1975). We collected >150 fish on each sampling date when possible. All fish were measured to the nearest 1 mm TL and weighed to the nearest 0.01 g on an analytical balance. We used the Kolmogorov–Smirnov test to test the null hypothesis that spring and fall length frequency distribution were the same. We then used quantile–quantile plots to differentiate size-selective mortality from growth and to determine the pattern of size-selective mortality when detected (Post and Evans 1989). Data points used in quantile–quantile plots were taken at 1, 5, 10, 25, 50, 75, 90, 95, and 99% of the length distributions for each cohort in the fall and spring. Regressions through quantile–quantile data points were fit using least squares and were tested for significant deviations from a slope of one and an intercept of zero (Draper and Smith 1981).

To evaluate the prospect that overwinter mortality was caused by starvation, we tested for declines in condition factor from fall to spring for the 1993 and 1994 cohorts. We also compared spring length distributions with those predicted by the physiologically based overwinter mortality model of Shuter et al. (1980). For this model, we assumed winter duration of 150 days in 1993 and 145 days in 1994 (number of days with water temperature $<5^{\circ}\text{C}$). Winter duration was estimated from water temperature data taken by the North Temperate Lakes Long Term Ecological Research Project in lakes located about 30 miles south of Paul Lake.

We used data from both the 1993 and 1994 cohorts to estimate the general relationship between overwinter survival and total length in Paul Lake. We used the sigmoidal relationship:

$$\text{relative survival} = \frac{\text{length}^a}{\text{length}^a + b^a}$$

Fig. 2. Relationship between the number of YOY bass in August and the number of YOY bass hatched for the years 1984–1996. Years with low adult and juvenile abundance are shown with circles and years with high adult and juvenile abundance are shown with squares.



where relative survival was the percentage of fish surviving the winter and length was total length (mm) entering the winter. We grouped fish by 5 mm length categories and then calculated relative survival (number of fish in fall divided by the number of fish in spring) from fall to spring for each length group. Because the sample size of each length category varied, each data point was weighted by its sample size. The model was fit using the nonlinear module in SAS (SAS Institute 1985).

Results

Over the 12-year period, the abundance of adult and juvenile bass fluctuated between 131 and 1095 individuals (Fig. 1), with biomass roughly paralleling adult densities. Adult and juvenile abundance was high in 1984–1991, low in 1992–1994, and high again in 1995 (Fig. 1). Adult and juvenile bass were three times more numerous in high abundance years than low abundance years [604 ± 255 vs. 200 ± 60 individuals, respectively ($\bar{x} \pm \text{SD}$)]. The number of YOY largemouth bass surviving to late August of each year ranged from a few hundred individuals in 1984–1992 and in 1995 to several thousand in 1993 and 1994 (Fig. 1).

There was a strong correlation between the number of reproductively mature adult bass in spring of each year and both the number of nests ($n = 3$, $r = 0.99$, $P = 0.09$) and the number of YOY hatched ($n = 12$, $r = 0.70$, $P = 0.01$; estimated from predation estimates) but not with the number of YOY bass surviving to August ($n = 12$, $r = 0.07$, $P = 0.82$). There was no correlation between the number of YOY largemouth bass hatched and the number of YOY surviving to August ($n = 12$, $r = 0.46$, $P = 0.11$; Fig. 2). The number of YOY bass hatched was, therefore, strongly related to the number of reproductively mature adult bass, but the number of YOY bass hatched was not a strong predictor of survival through the summer.

Hatching dates and growth rates

In 1993–1995, successful hatching occurred over a range of 41 days beginning in mid-May and ending in early July (Fig. 3). Within a single year, the duration of successful hatching dates was 17 to 21 days. In 1994 and 1995, hatching was early, while in 1993, hatching occurred relatively late (Fig. 3). The temporal pattern of hatching across and

Fig. 3. Hatching date distributions for the 1993–1995 YOY bass cohorts (cross-hatched bars, 1993; open bars, 1994; solid bars, 1995). Each point represents the hatching date of one successfully hatched nest.

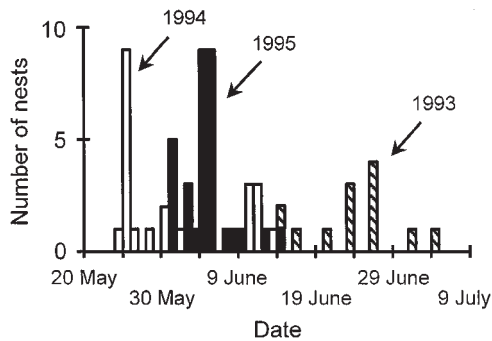
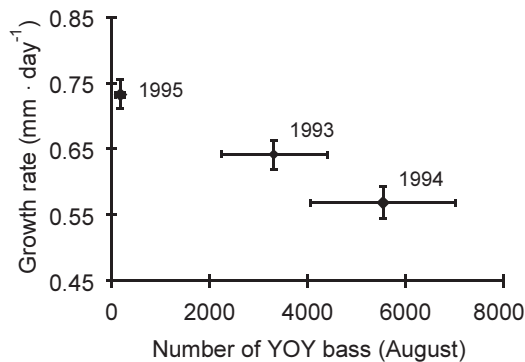


Fig. 4. Growth rates ($\pm 95\%$ CI) and late August densities (± 1 SE) of the 1993–1995 YOY bass cohorts.



within years was generally consistent with water temperature patterns. For example, the spring of 1993 was cold and hatching was postponed until late June and early July. In contrast, Paul Lake warmed rapidly in 1994 and 1995 and hatching dates were earlier. A cold snap during late May and early June of 1994 caused a bimodal hatching distribution.

Average summer growth rates (from hatching to late August) of YOY largemouth bass were inversely related to cohort density (Fig. 4). Growth rates were similar for fish <25 mm, but after reaching 25 mm growth trajectories diverged (Fig. 5). Across years, individual length increased with age (Fig. 6). Otolith analysis demonstrated that each additional day of growth (as a result of an earlier hatching date) added an average of 0.53 mm in length. However, age explained only 38% and 17% of the variability in length in 1993 and 1994, respectively, and the variability of length increased with age (Fig. 6). Although young fish tended to be of small to average size, older fish spanned the entire range of lengths from the smallest to largest (Fig. 6). Thus, the largest fish were all older individuals and small- to medium-sized fish ranged in age from the oldest to the youngest.

Patterns of summer mortality

We used otoliths from fish sampled in late August to infer patterns of summer mortality with respect to fish age. There were differences between the observed hatching date distribution and the back-calculated hatching date distribution in

Fig. 5. Growth trajectories of the 1993–1995 YOY bass cohorts (squares, 1993 cohort; diamonds, 1994 cohort; open circles, 1995 cohort). Error bars are ± 1 SD.

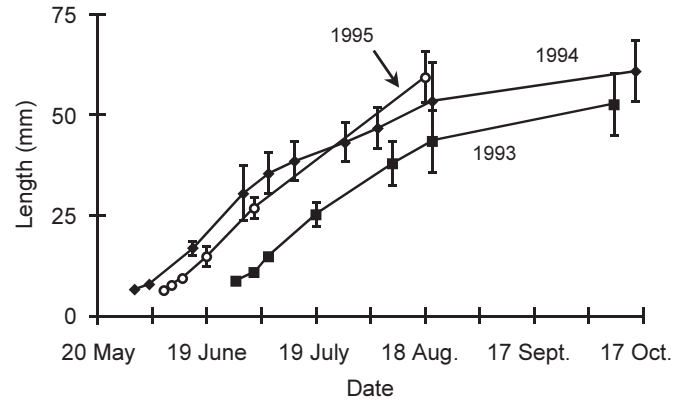


Fig. 6. Relationship between age and length for members of the 1993 and 1994 YOY bass cohorts (on 20 August). Age estimates are from otolith analysis. The dotted line is the approximate size required (in August) to survive the winter (~47 mm, assuming 8 mm of growth from late August to winter). See text for a further discussion.

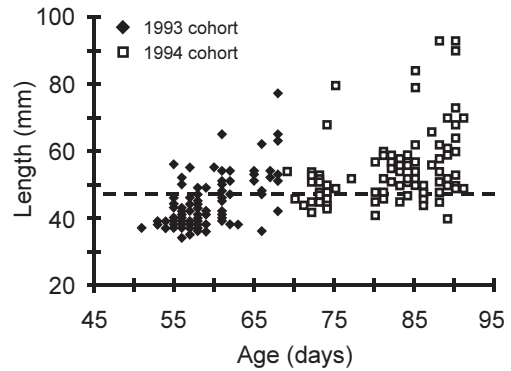


Table 1. Temporal distribution of hatching dates of successful nests and fish surviving the summer for 1993 and 1994.

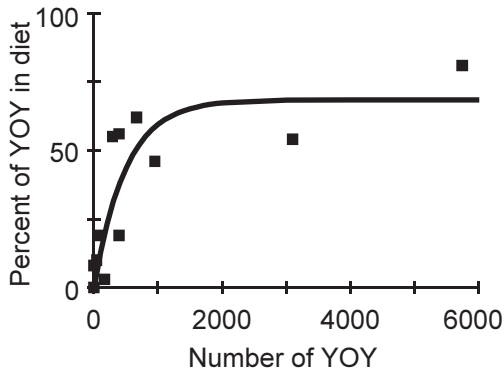
Year and hatching period	Nests, %	Fish, %
1993		
Early hatched (before 24 June, ≥ 57 days old)	46	74
Late hatched (after 24 June, <57 days old)	54	26
1994		
Early hatched (before 3 June, ≥ 80 days old)	68	75
Late hatched (after 3 June, <80 days old)	32	25

1993 (chi-square test for goodness of fit, $\chi^2 = 56.6$, $P < 0.05$) and 1994 ($\chi^2 = 6.4$, $P < 0.05$). In both years, late-spawned fish were underrepresented in late August samples (Table 1), indicating differentially high mortality among later-spawned individuals.

Cannibalism

YOY largemouth bass were an important component of the adult and juvenile diets when YOY were abundant in the lake (i.e., greater than a few hundred individuals, Fig. 7). At

Fig. 7. Relationship between the percentage of YOY in adult and juvenile bass diets (by mass) and YOY bass densities in August of 1984–1996.



densities above ~1000 YOY, cannibalism represented about 68% of adult and juvenile diets. The relationship was described by the function

$$Y = 68.2 \cdot [1 - \exp^{(-0.139 \cdot X)/68.2}] \quad (R^2 = 0.65)$$

where Y was the proportion of YOY in adult and juvenile diets, and X was the August density of YOY largemouth bass. The parameter estimates and standard errors were: $a = 68.2$ (11.2) and $b = 0.139$ (0.066).

Predation can account for all of the observed mortality in 1993–1995, years in which we have independent estimates of the number of YOY hatched and the number of YOY eaten, although there is some uncertainty associated with our estimates (Table 2). This confirms that adult and juvenile bass were the only important predators of YOY and that the number of YOY eaten plus the number of YOY alive in August is a good estimate of the number of YOY hatched.

Juvenile bass were the most important predators in Paul Lake. Around 90% of the cannibalism in each year was caused by juvenile bass (mean 92%, range 82–99%). In some years, for example, 1995, most of the cannibalism by juvenile bass was caused by bass in their second summer of life (age 1+).

In years of high adult and juvenile abundance (1984–1991 and 1995), predation on YOY largemouth bass was intense, and adult and juvenile bass could have eaten many more YOY than were hatched (Table 2). Predation rapidly eliminated most of the YOY cohort in these years. In 1995, for example, predation eliminated 98% of the YOY cohort in less than 4 weeks. The largest recruitment events occurred in years of low adult and juvenile abundance (Fig. 1). In 1993 and 1994, the number of YOY eaten and the maximum potential predation were similar, indicating that adult and juvenile bass diets were saturated with YOY (Table 2). It would have been difficult for adult and juvenile bass to eat more YOY bass than they did. The YOY that survived the summers of 1993 and 1994 were those that adult and juvenile bass were unable to eat by late August. The exception to this pattern was the summer of 1992. Although adult and juvenile abundance was low in 1992, the number of reproductively mature adults was extremely low and the number of YOY hatched was the lowest recorded (Fig. 2). There was

no measurable survival of YOY through the summer of 1992 (Fig. 1).

When the number of predators is high, the number of YOY surviving the summer is low. The predation potential in these years is much higher than the potential reproductive output. When the number of predators is low, the number of YOY surviving the summer can be high but is clearly mediated by the number of YOY hatched (Fig. 2). The number of YOY hatched was a good predictor of August YOY abundance in years with low adult and juvenile abundance ($R^2 = 0.998$, $n = 3$) but not in years with high adult and juvenile abundance ($R^2 = 0.002$, $n = 9$). Thus, large year-classes (estimated in August of their first year) occurred only when predation was low and reproductive output was relatively high (Fig. 2).

There is no absolute size refuge from cannibalism for YOY largemouth bass in Paul Lake. Based on an average adult and juvenile length of 235 ± 52.1 mm ($\bar{x} \pm$ SD, 1984–1995) and a predator–prey maximum size ratio for cannibalism of 2:1 (Lawrence 1958), bass must reach at least 118 mm in length before obtaining a size refuge from the average cannibalistic bass. In their first year of life, largemouth bass in Paul Lake reach 75 ± 10.7 mm in length (1984–1995).

Cannibalism by adult and juvenile bass was size selective (Fig. 8). Initially, adult and juvenile largemouth bass selected the largest individuals in the cohort. However, dispersed fish between 15–30 mm TL were not vulnerable to dip-net sampling and are not represented in the 23 June 1994 length frequency distribution. After all nest schools had dispersed, predators selected fish that were smaller than the average size, although larger fish were taken on occasion (Fig. 8).

Overwinter mortality

We detected strong size-selective overwinter mortality in the 1993 cohort (Fig. 9a). The 1993 cohort entered the winter of 1993–1994 with median and modal lengths of 50 and 48 mm, respectively. However, few individuals <55 mm survived the winter. The fall and spring distributions were significantly different (Kolmogorov–Smirnov test, $P < 0.05$, $D = 0.727$, $D_{\alpha=0.05} = 0.263$), and quantile–quantile plots indicated size-selective mortality on smaller individuals over the winter (H_0 : slope = 1, $n = 9$, $t = -2.8$, $P < 0.05$). The result of this size-selective overwinter mortality was the virtual elimination of the 1993 cohort. Only 74 (31–215, 95% CI) of 3303 (1789–6167) bass from the 1993 cohort survived the period from late August to May. This corresponds to an overwinter survival rate of only 2.2%.

Members of the 1994 cohort entered the winter at a much larger size and did not suffer significant size-selective overwinter mortality (Fig. 9b). The fall and spring length distributions were similar (Kolmogorov–Smirnov test, $P = 0.19$, $D = 0.116$, $D_{\alpha=0.05} = 0.145$), and quantile–quantile plots indicated no size-selective mortality and little growth over the winter (H_0 : slope = 1, $n = 9$, $t = -1.9$, $P = 0.1$; H_0 : intercept = 0, $n = 9$, $t = 2.5$, $P = 0.04$). As a result, the 1994 cohort had much higher survival over winter than the 1993 cohort. An estimated 1465 (942–3296) of 5551 (3587–9757) bass from the 1994 cohort survived the period from late August to May (26.4% survival).

Table 2. Estimates of the number of YOY bass hatched and eaten and the maximum potential number of YOY bass eaten.

Year	Young-of-the-year bass (in thousands)			Maximum potential number eaten (range) ^d	Number eaten as percent of maximum potential
	Number hatched (range) ^a	Number hatched (range) ^b	Number eaten (range) ^c		
1984		22	22	243	9
1985		59	58	281	21
1986		37	37	173	21
1987		68	67	321	21
1988		53	53	270	20
1989		35	35	198	18
1990		19	18	127	14
1991		11	10	178	6
1992		5	5	51	10
1993	45 (30–105)	57 (35–104)	54 (33–98)	64 (40–117)	84
1994	66 (40–154)	68 (42–152)	62 (38–142)	78 (52–173)	80
1995	99 (66–231)	94 (52–191)	94 (52–190)	333 (203–700)	28

Note: For 1993–1995, we present a range of possible estimates. The number of YOY bass eaten as a percent of the maximum potential number of YOY bass eaten is an index of how saturated adult and juvenile bass diets were by YOY bass. A low percentage indicates that adult and juvenile bass could have easily eaten all of the YOY hatched in that year and probably did so rapidly. A high percentage indicates that adult and juvenile bass were feeding on YOY bass near their maximum possible rate.

^aEstimated from nest counts and assuming 3000 fry per nest (range 2000–7000).

^bThe number of YOY eaten by late August plus the number of YOY alive at that time is an index of the number of largemouth bass hatched in that year. Note the strong correlation ($r = 0.99$) and nearly one-to-one relationship between our two estimates of the number of YOY hatched in 1993–1995. The range was estimated using 95% CI around our adult and juvenile population estimates and the 95% CI around our YOY population estimates for late August.

^cCumulative number of YOY bass eaten by adult and juvenile largemouth bass by late August of each year. We estimated the range using 95% CI around our adult and juvenile population estimates.

^dWe estimated the range using the 95% CI around our adult and juvenile population estimates.

We detected significant declines in condition factor from fall to spring for both the 1993 (ANCOVA, $P < 0.05$) and 1994 cohorts ($P < 0.05$). Length-standardized mass of the 1993 and 1994 cohorts declined over winter by 0.12 and 0.06 g, respectively. The winter of 1993–1994 was longer than the winter of 1994–1995, which may help explain the greater mass loss for the 1993 cohort. The pattern of overwinter survival closely matched predictions derived from the Shuter et al. (1980) physiologically based, overwinter mortality model (Fig. 10).

The general relationship between overwinter survival and total length for Paul Lake bass was estimated using data from both the 1993 and 1994 cohorts (Fig. 11). The resulting sigmoidal relationship was

$$\text{relative survival} = \frac{\text{length}^{15}}{\text{length}^{15} + 54.5^{15}}$$

where relative survival was the percentage of fish surviving the winter and length was total length (mm) entering the winter. The parameter estimates and standard errors were $a = 15$ (3.9) and $b = 54.5$ (1.0). The standard error of estimates for this model was 0.97. This model indicates that the relative overwinter survival of 50 mm bass was 20%, while the relative survival of 60 mm bass was 80%.

Discussion

Our results indicate that adult demography, predation, and size-selective overwinter mortality act in series to regulate

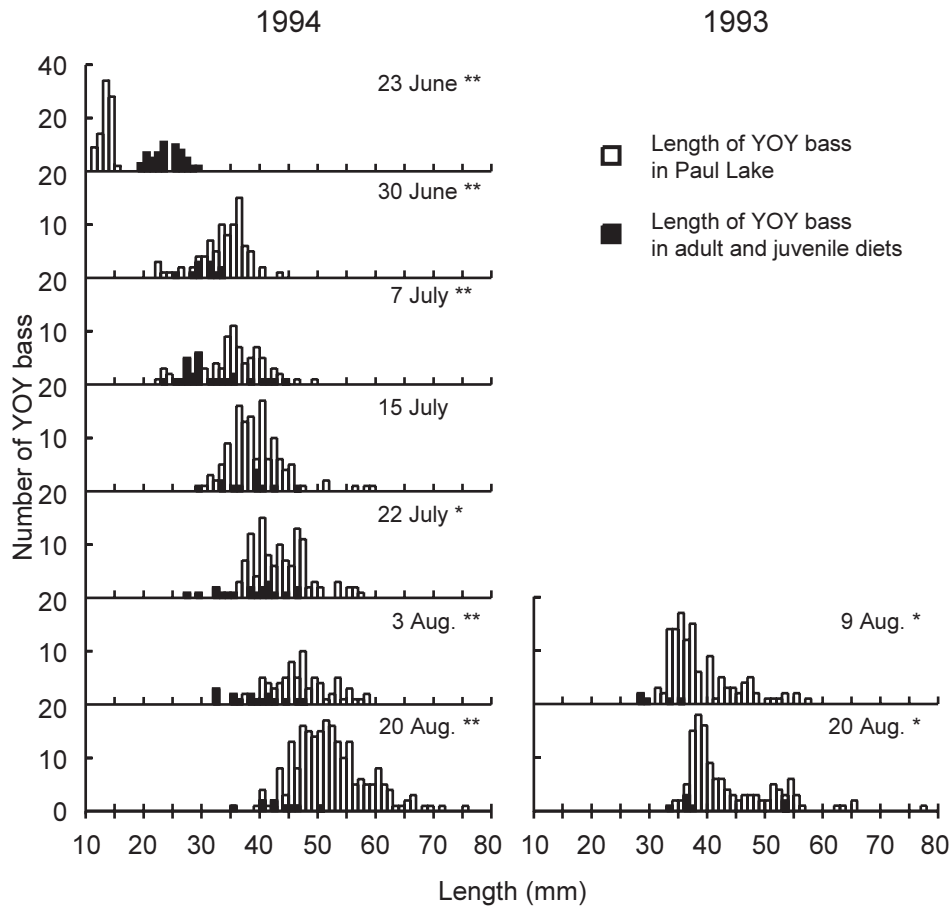
recruitment in Paul Lake. Furthermore, hatching date, predation, and growth rate interact to influence overwinter mortality. It is the complex hierarchical interaction of these processes that governs recruitment of largemouth bass in Paul Lake.

There is strong correlation between the spring density of reproductively mature adults and the number of YOY hatched but not between the number of YOY hatched and August YOY densities. This is consistent with previous studies (e.g., Elliott 1984; Sissenwine 1984) that report a positive correlation between the number of adults and the number of eggs spawned but no correlation between the number of eggs spawned and cohort abundance later in life. Thus, adult density and the number of eggs spawned are generally poor predictors of eventual year class size. In Paul Lake, the number of eggs spawned (and fish hatched) provides the backdrop for recruitment but by itself is not a good predictor of year-class strength.

Impact of inter-cohort cannibalism

The pattern of summer survival for a YOY cohort depends on the intensity of inter-cohort predation. In years of high adult and juvenile abundance, most YOY bass are eaten. In these years, adult and juvenile bass could have eaten many more YOY bass than were available (Table 2) and cannibalism was so intense that YOY bass would appear in adult and juvenile diets for only a few weeks of the summer. Thus, predation was limited by the number of YOY hatched. The few YOY bass that survive the summer are likely a conse-

Fig. 8. Evidence for size-selective predation by adult and juvenile largemouth bass in 1993 and 1994. Significant differences in the YOY size distributions from the lake and from adult and juvenile bass diets are indicated by * ($P < 0.05$) and ** ($P < 0.01$).



quence of the adult and juvenile diet response. As the abundance of a YOY largemouth bass cohort declines below a few hundred individuals, cannibalism by adults and juveniles declines. Reduced predation likely results from low encounter rates and (or) effective refuging behavior by YOY bass. In years of low adult and juvenile abundance, there are fewer predators, and although they prey on YOY throughout the summer, their impact on a cohort is less. In these years, more YOY bass survive the summer.

Although there is no absolute refuge in larger size for YOY bass in Paul Lake, cannibalism was strongly focused on the smaller members of each YOY cohort. In years with relatively low predation, the interaction of size-selective predation and relative spawning date were important for the survival of individual YOY bass. In 1994, YOY were subject to intense predation immediately after nest school dispersal. This corresponded with the cessation of nest school guarding behavior of adult male largemouth bass. YOY bass are guarded in nest schools by adult males until they reach about 15–20 mm in length (Brown 1985; personal observation), and male guarding limits predation during this period (Bain and Helfrich 1983). Early-spawned fish that survived the first few weeks after nest school dispersal and remained larger than average had a higher survival probability. However, many early-spawned fish did not maintain high growth rates and were, therefore, subject to cannibalism throughout the summer. In contrast, late-spawned individuals remained

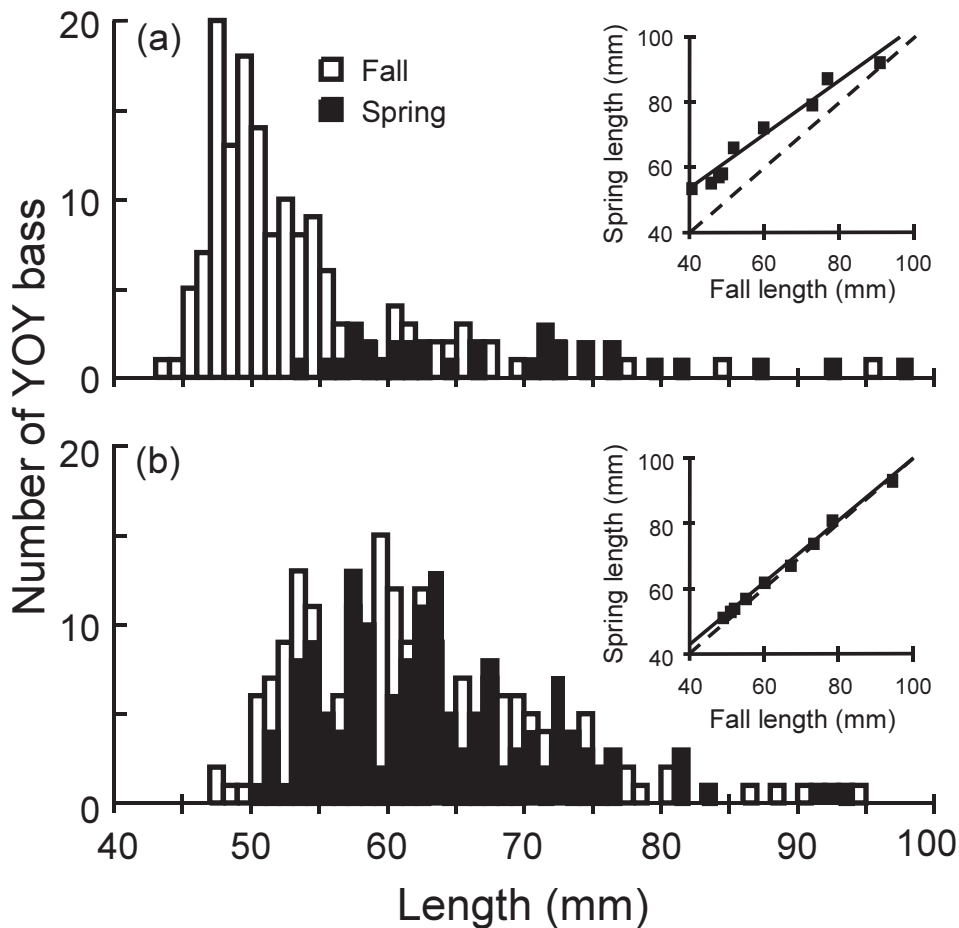
smaller than average and were vulnerable to predation throughout the entire summer. These patterns of size-selective predation should result in disproportionately high mortality rates for late-spawned fish. This pattern of mortality was confirmed by otolith analysis; late-spawned fish were underrepresented in the August sample (Table 1). We do not know which fish survive summers with high predation rates because the intense predation limits sample size. It is likely, however, that there is little or no age or size selection in these years because predation is intense and survival may be largely stochastic.

YOY largemouth bass in lakes with more complex fish communities may be subject to relatively low cannibalism because of the availability of alternative fish prey. Other studies have reported low occurrence of cannibalism in lakes with more complex fish communities (Timmons et al. 1980; Keast 1985). However, predation by other littoral predators (e.g., smallmouth bass, black crappie, bullheads, etc.; Keast 1985) may compensate for reduced cannibalism.

Growth rates and density

Density-dependent growth is widely reported among fish species (e.g., Peterman 1984; Bromley 1989) and can strongly impact fish survival and ultimate recruitment (e.g., Houde 1989). In Paul Lake, adult largemouth bass body condition was negatively correlated with adult densities (Schindler et al. 1997), indicating density-dependent growth.

Fig. 9. Length frequency distributions of the (a) 1993 and (b) 1994 YOY bass cohorts in late fall (October) and early spring (early May). Insets show quantile–quantile plots for the 1993 and 1994 cohorts. The broken line is the 1:1 relationship and the solid line is the least squares regression for each cohort. Points represent 1, 5, 10, 25, 50, 75, 90, 95, and 99% of the fall and spring length distributions.



Although our sample size is small, the pattern of decreasing growth rates with increasing density is striking (Fig. 4) and is consistent with patterns of density-dependent growth of YOY bass shown experimentally in YOY bass (Olson et al. 1995) and many other species of fish. Furthermore, although temperature is an important factor governing growth (Kitchell et al. 1977; Rice et al. 1983), the observed pattern of growth rates was not consistent with interannual temperature patterns. Growth rates in 1993, a cold summer, were higher than growth rates in 1994, a relatively warm summer. Although not conclusive, our results suggest density-dependent growth of YOY largemouth bass in Paul Lake. The best fit relationship between density and growth rate (growth rate = $0.739 - 0.00005 \cdot \text{August density}$; $R^2 = 0.99$) indicates that for every 1000 fish·ha⁻¹ increase in August densities, there should be a 7% decline in growth rates.

Overwinter mortality

Our results demonstrate that fish <50–60 mm do not survive the winter in Paul Lake. The length-dependent patterns of mortality, changes in condition factor overwinter, and predictions derived from the Shuter et al. (1980) overwinter mortality model are all similar to those from laboratory experiments on a variety of fishes (e.g., Oliver et al. 1979;

Fig. 10. Observed and predicted cumulative frequency curves for the (a) 1993 and (b) 1994 YOY bass cohorts. The predicted curve was generated from the physiologically based overwinter mortality model of Shuter et al. (1980) assuming a winter duration of 150 days in 1993 and 145 days in 1994.

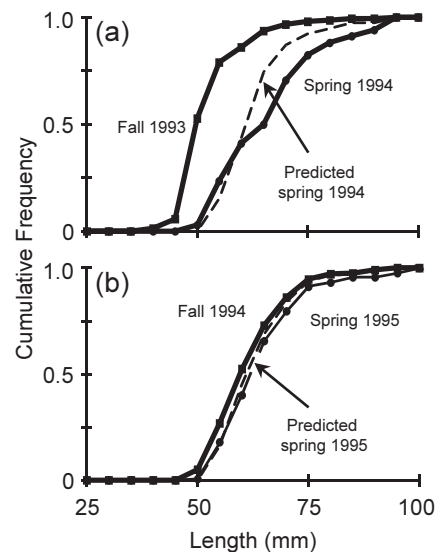
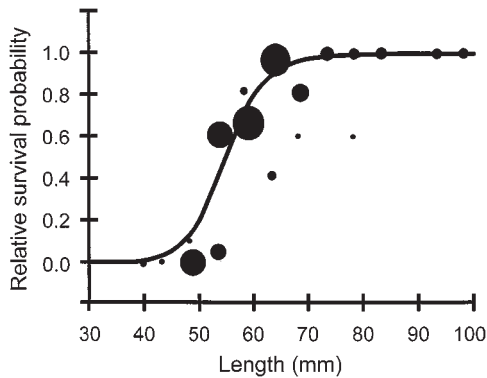


Fig. 11. The relationship between relative overwinter survival probability and length entering the winter for the 1993 and 1994 largemouth bass cohorts. The size of each data point is proportional to its sample size and was used to weight the fitted relationship.

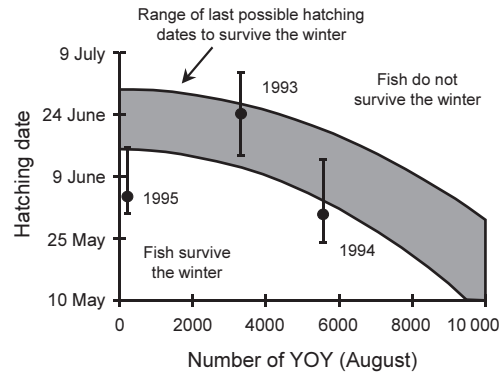


Post and Evans 1989) and strongly suggest that overwinter mortality was ultimately caused by starvation. This is consistent with the observation that overwinter mortality can strongly regulate recruitment in fish population near the northern limit of their range (Shuter and Post 1990).

Our result differs markedly from those of more southerly lakes and reservoirs where largemouth bass ≤ 90 – 100 mm are considered most susceptible to overwinter mortality (e.g., Toney and Coble 1979; Miranda and Hubbard 1994a). These studies were all located at sites well south of the northern extent of the largemouth bass range, and all of them studied fish ≥ 60 mm in length. Latitudinal differences in overwinter mortality patterns may result from different proximate causes of mortality. Miranda and Hubbard (1994b) demonstrated that predation was the proximate source of size-dependent overwinter mortality in southern largemouth bass populations. Smaller fish suffered higher overwinter mortality in ponds with predators present than in ponds with no predators. In the absence of predators, Miranda and Hubbard (1994b) observed little size-dependent overwinter mortality. Their results, however, did not discount the possibility that starvation may increase susceptibility to predation. In lakes located at or near the northern extent of the largemouth bass range, starvation is probably most important. Largemouth bass of any size generally feed little at water temperatures $< 10^{\circ}\text{C}$ (Johnson and Charlton 1960; Coutant 1975). Our fall and spring sampling occurred after temperatures had fallen below 10°C and just after temperatures had reached 10 – 12°C . Thus, the high overwinter mortality that we observed was not likely the result of predation. We can not, however, rule out the possibility that starvation increased the vulnerability of smaller YOY to predation and that predation was the proximate cause of death.

Spawning date, growth rate, and winter duration interact strongly to determine overwinter mortality. Although hatching date and winter duration are density independent, growth rate is inversely related to density. Furthermore, the intensity of cannibalism regulates August densities. Thus, the average length for members of a cohort entering the winter is indirectly affected by the intensity of cannibalism. We calculated a range of last possible hatching dates (LPHD) required to survive the winter across a range of YOY large-

Fig. 12. Range of last possible hatching dates to survive the winter. Predicted conditions are from the observed patterns of density-dependent growth and assuming 100% mortality for fish < 50 – 60 mm when entering the winter. The mean and range of hatching dates for the 1993–1995 cohorts are plotted against their respective August densities.



mouth bass densities based on the observed pattern of growth (Fig. 4). We assumed that fish must reach 50 to 60 mm in length to survive the winter, that growth from hatching until late August was inversely related to density, and that individuals grow 8 mm from late August until winter (average growth rate from late August until winter for the 1993 and 1994 cohorts). As YOY largemouth bass density increases, the LPHD becomes progressively earlier (Fig. 12). Over the range of observed August abundance (from 0 to about 6000), the LPHD recedes by nearly 20 days.

Winter duration varies from year to year and affects the LPHD by changing the minimum size required to survive the winter (Shuter et al. 1980). For example, as winter duration increases, the minimum size required to survive the winter increases. This shifts the LPHD isocline down, requiring earlier spawning or faster growth for overwinter survival. In contrast, a decrease in winter duration might permit a longer spawning season and the survival of later-spawned and slower-growing fish. A decrease in winter duration would also minimize the effects of density-dependent growth. Even at high densities (and slow growth), the longer growing season and shorter winter would allow better overwinter survival.

These observations are similar to those generated for smallmouth bass by DeAngelis et al. (1991) using an individual-based model. Overwinter mortality is not independent of summer mortality because of the density-dependent growth response. Thus, increased predation can increase growth rates, which may, depending on the hatching date, increase the probability of overwinter survival.

Although we can predict the general patterns of cohort survival, individual survival is harder to predict. If size and age were strongly correlated, then LPHD would predict which individuals survive the winter based on hatching date alone. However, in Paul Lake, age accounts for $\leq 40\%$ of the observed variability in size. Late-spawned individuals were generally smaller than early-spawned individuals and were, therefore, more vulnerable to overwinter mortality. However, the growth rates of early-spawned individuals were variable, and many early-hatched fish enter the winter < 55 mm

(equivalent to <47 mm in late August, assuming 8 mm of growth between late August and winter; Fig. 6). Although overwinter mortality was generally highest for late-spawned individuals, it was also a substantial source of mortality for early-hatched, slow-growing individuals.

Hierarchical process of recruitment

Our observations allow us to make qualitative predictions about the patterns of recruitment for largemouth bass in Paul Lake. The number of adults provides the ultimate constraint on recruitment. When the number of adults is low, recruitment will be low regardless of other processes. Furthermore, if the number of predators (adult and juvenile bass, but predominately juveniles) is high, recruitment will be low regardless of adult densities and overwinter mortality. If the number of adults is moderate to high and predation is low, then recruitment through the first year of life depends on the number of adults and the interaction of overwinter mortality, hatching date, and summer growth rates. If the hatching date is early, the growing season is long enough to allow high overwinter survival, except at exceptionally high YOY densities, and the number of YOY surviving the first year of life depends on the number of mature adults. When hatching date is late, however, overwinter mortality becomes more important.

Of the multiple pathways possible, only one allows high recruitment through the first year of life. There must be a relatively large number of adults, low density of predators, and early spawning to allow good overwinter survival. A large number of adults with a low density of predators only occurs when there are few juvenile bass present. All other scenarios result in low recruitment. From 1992 through 1995, we observed four of the possible scenarios. In 1992, the number of adults was very low and recruitment was negligible. In 1993 and 1994, there were a moderate to high number of adult bass and predation was low, but the 1993 cohort was hatched late and therefore suffered high overwinter mortality. The 1994 cohort was hatched early, despite slow growth rates, and had relatively low overwinter mortality, and first year survival was high. In 1995, there were a lot of adult bass and the cohort hatched early, but the density of predators was very high (because of the large 1994 cohort) and summer survival was poor.

Population dynamics and food web structure

YOY largemouth bass are the only important vertebrate zooplanktivore in Paul Lake and can have a large impact on the pelagic food web when abundant (Post et al. 1997). Thus, pelagic food web dynamics are closely linked to largemouth bass population dynamics through recruitment.

The intense cannibalism produces two alternate population states in Paul Lake: high or low adult and juvenile densities. The high density state may be initiated by a large recruitment event such as the 1994 cohort. A large cohort increases predation pressure and maintains high reproductive potential over its effective life span. The high predation potential will suppress subsequent strong recruitment events. If predation eliminates entire cohorts, then predation pressure will decrease as the cohort ages and irruptive recruitment events will occur at a periodicity near that of the life span of a cohort (Carpenter 1988). However, because a few YOY

bass survive each year in Paul Lake, high predation pressure will be maintained past the effective cohort life span. The length of the high density period is a function of the ratio of recruitment and adult mortality (R/M). If $R/M = 1$, the population will remain stable until externally perturbed. As R/M approaches 0, the length of high density periods approaches the effective cohort life span. Factors that would move Paul Lake from high to low adult and juvenile densities include a series of reproductive failures (like those observed in acidified lakes), partial winter-kill events, increased fishing pressure, and cohort senescence.

The alternative state in Paul Lake, low adult and juvenile densities, is transient. At low densities, irruptive recruitment events (like we observed in 1994) move the population back to the high density state. Although low density states may persist for >1 year as a result of density-independent reproductive failure (e.g., no spawning, nest abandonment, or high overwinter mortality), consecutive large recruitment events should be rare. A large cohort that survives both the summer and winter will re-establish the high juvenile density in its second summer. That is what occurred in 1995 when the 1994 cohort recruited into the juvenile population and, through cannibalism, helped suppress the 1995 cohort. By the fall of 1996, the large 1994 cohort represented over 80% of the adult and juvenile largemouth bass population.

At high adult and juvenile densities, Paul Lake is a piscivore-dominated system. There are few small planktivorous fishes (Carpenter and Kitchell 1993) and benthic invertebrates serve as alternative prey, which maintains high adult and juvenile biomass (Carpenter and Kitchell 1993; Schindler et al. 1997). However, small fish (including YOY largemouth bass) are the preferred and optimal prey for largemouth bass (Hodgson and Kitchell 1987). The high potential for piscivory (maintained by benthic foraging) and preference for small fishes buffers Paul Lake from invasions by planktivorous fishes (including YOY largemouth bass) and maintains piscivore dominance. Any breakdown in piscivore dominance will be transient. The pulse of planktivory caused by a large cohort of YOY largemouth bass will usually be short lived (Post et al. 1997). As the cohort matures and switches from zooplanktivory to benthivory and piscivory, its role in the food web reverses and piscivore dominance is re-established (Post et al. 1997). Because largemouth bass dominate the Paul Lake fish community, largemouth bass population dynamics, fish community structure, and pelagic food web structure are all tightly coupled.

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