Influence of Spring Runoff and Water Temperature on Hatch Date and Growth of Age-0 Largemouth Bass in a Montana Reservoir

Abstract
Largemouth bass are a popular sport fish in Montana and the Northwest, however, maintaining quality angling is difficult. Montana is at the northern extent of the largemouth bass range and low water temperatures may limit recruitment by reducing the size fish attain entering the winter season. Little is known about how different flow and temperature regimes influence hatch date and growth of largemouth bass in a northern reservoir environment. Such information is important for predicting good year classes or planning population enhancement measures. Two years with disparate hydrographs and water temperature regimes were compared from a Montana reservoir. High flows and low water temperatures occurred in 1997 whereas the converse happened in 1998. Age-0 largemouth bass were sampled throughout the summer and fall of both years to estimate hatch date, growth rate, body condition, and length entering the winter season. The median hatch dates were in mid-July and 5 d earlier in 1998 than in 1997. Hatching began 12 d earlier in 1998. Spawning and hatching were controlled by spring runoff and were later than reported for lakes elsewhere in northwest Montana. Growth rate was higher in 1998 (0.76 mm/d) than in 1997 (0.46 mm/d) from the date mean lengths were ~50 mm to early October. Higher growth rates and longer lengths were achieved by hatching early in a year with high water temperature. Length entering into winter was greater in 1998, averaging 87 mm versus 64 mm in 1997. Body condition was similar between years. Growth of age-0 fish appeared to cease by early October of both years. Growth rate had a greater effect on length of largemouth bass entering into winter than length of growing season.

Introduction
Popularity of fishing for warm and coolwater fishes has increased in the Northwest (Bennett et al. 1991, McMahon and Bennett 1996). In northwest Montana, angling pressure on warm and coolwater species increased nearly 20% from 1991 to 1999 (McFarland and Hughes 1994, McFarland and Merideth 2000). The largemouth bass (Micropterus salmoides) is an introduced warmwater fish species that provides angling opportunity. Largemouth bass were introduced to the region sometime in the late 1880s (Lampman 1946). Since their introduction, however, habitats suitable for largemouth bass have increased with the building of 99 hydroelectric facilities throughout the Northwest (Bennett et al. 1991). In many cases, the increase in warmwater fish habitat corresponded to a decrease in coldwater habitats that supported highly valued trout and salmon fisheries. As a result, fishery managers have sought the enhancement of warmwater fish, such as largemouth bass, to provide recreational fishing that can be supported by existing habitat conditions. Yet, largemouth bass pose a difficult fishery to sustain from year-to-year in many Northwest waters (Bennett et al. 1991).

Variable year class strength is common in largemouth bass populations (Kramer and Smith 1962, Aggus and Elliot 1975, Bennett et al. 1991, Post et al. 1998). Much of the variability is the result of survival rates to age-1, making this period critical in determining recruitment to a fishery (Summerfelt 1975, Toney and Coble 1979, Post et al. 1998). A possible reason for infrequent strong year classes is that the Northwest United States is the northern extent of the largemouth bass distribution. Overwinter mortality may regulate recruitment for species at the northern limits of their range (Shuter and Post 1990, Fullerton et al. 2000). Low water temperatures at northern latitudes slow growth rates and shorten the growing season by delaying hatch and extending winter (Post et al. 1998). Consequently, low water temperatures in northern waters result in small size of age-0 largemouth bass entering into winter. Larger size provides more energy reserves to avoid starvation (Gutreuter and Anderson 1985, Miranda and Hubbard 1994a) or predation (Miranda and Hubbard 1994b) during winter, thus increasing survival to age-1. Higher temperatures during the growing season have been related to stronger year classes for smallmouth bass (M. dolomieu) (Fry and Watt 1955) and other freshwater fishes (Craig and Kipling 1983).
Longer largemouth bass become piscivorous sooner and maintain piscivory longer than smaller bass (Phillips et al. 1995), and greater piscivory has been related to greater growth (Aggus and Elliot 1975, Miller and Storck 1984). Other investigators have distinguished different growth rates between times of hatching (Miller and Storck 1984, Goodgame and Miranda 1993, Phillips et al. 1995). In these studies, early-hatched fish grew faster because of their greater ability to switch to a piscivorous diet. Coincident with this was the inability of age alone to account for much of the variation in length without considering time of hatch (e.g., early or late) largely because variation of length increased with increasing age. These studies found that increased variation in length with age was explained by time of hatch and that earlier hatched fish were longer at a particular age than later hatched fish. For example, at 50 d old a fish that hatched early tended to be longer than a fish hatched late.

Hatch date and growth rate interact to affect the length age-0 largemouth bass reach entering the winter season in several regions of the U.S., including a northern lake (Post et al. 1998), and midwestern (Miller and Storck 1984, Kohler et al. 1993) and southeastern reservoirs (Phillips et al. 1995). Information is lacking regarding the recruitment process in northwestern reservoirs. Such information could be useful in predicting year class strength and recruitment to a fishery and when assessing population enhancement measures (e.g., supplemental stocking or habitat enhancement). In this study, I obtained information on the recruitment process of largemouth bass in Noxon Rapids Reservoir, Montana by contrasting hatch date, growth, and length of fish entering into winter between two years with disparate flow and temperature regimes. I studied the population dynamics of age-0 largemouth bass with the following objectives: (1) evaluate the effect of water temperature, age, and hatch date on growth rate of age-0 largemouth bass within an annual cohort, (2) compare, between years, spring runoff (discharge) and water temperature and their influence on hatch date distribution, growth, and size entering winter, and (3) compare within-year population dynamics among-years.

Study Area

Noxon Rapids Reservoir is located on the Clark Fork River ~225 km northwest of Missoula. The reservoir is ~732 m above sea level, encompasses nearly 3,200 ha, and was created to provide hydroelectric power. Typical operations are a weekly 1.2 m draw with a maximum 3.1 m draw during late winter or early spring. Trophic status ranges from oligotrophic at high flows during spring snowmelt to mesotrophic at low flows (Washington Water Power 1996). Maximum surface water temperatures typically are 20-25°C. Water retention is about 2 wk during summer low flows. The reservoir rarely stratifies, and then partially and for a short time. The reservoir inundated a deep river canyon to a level above much of the canyon walls. As a result, there are several bays and extensive flats that provide suitable habitat for largemouth bass. Flow capacity of the dam is ~1.550 m³/s.

The fish community is dominated by Cyprinidae, including northern pikeminnow (Ptychocheilus oregonensis) and peamouth (Mylocheilus caurinus) (Washington Water Power 1995). Yellow perch (Perca flavescens) are abundant and stunted at ~200 mm. Largemouth bass and smallmouth bass are common. The few Salmonids are confined to coldwater refuges at tributary mouths and springs during summer. Species of Salmonidae include brown trout (Salmo trutta), rainbow trout (Oncorhynchus mykiss), westslope cutthroat trout (O. clarki lewisii), bull trout (Salvelinus confluentus), lake trout (Salvelinus namaycush), lake whitefish (Coregonus clupeaformis), and mountain whitefish (Prosopium williamsoni).

Methods

I used a 15.2 x 3.1 m bag seine with 10 mm mesh and a 1.2 x 1.2 m bag. Boat and backpack electrofishing were attempted to capture larger age-0 fish (Jackson and Noble 1995) but were ineffective due to growth of macrophytes in deep water. I sampled these deeper water habitats by deploying the seine into the macrophytes from a boat, then pulled it to shore. Sampling with only a bag seine may have underestimated the length of bass because seining tends to be biased toward smaller (<70 mm) fish (Jackson and Noble 1995).

Sampling was conducted throughout the summer and fall to capture the range of age-0 bass ages and lengths. This strategy insured sampling of similar aged fish during different times of the year and growing conditions. I sampled six times from 3 August to 11 October 1997, and five times from 3 August to 19 October 1998. No bass were
captured during the first two sampling occasions (3 and 11 August) in 1997. Sampling sites were intended to remain constant throughout the study, however, catch of largemouth bass varied spatially by season and year. Therefore, I sampled bass where desired sample sizes could be obtained while standardizing sites to the extent possible. Fish were collected from two to five sites on each sampling date. Length of fish (TL, mm) was recorded and specimens for otolith dissection and aging were taken to the laboratory. I sampled between 24 and 121 fish per sampling occasion.

Water Temperature and Flow

Mean daily water temperature was recorded during summer (defined as 1 July-30 September) with thermographs taking readings 10 times a day. Thermographs were placed at two bays typical of young largemouth bass habitat. The operators of the dam provided data on river discharge. Mean daily summer water temperature was compared between years using a t-test (P < 0.05).

Hatch Date

I counted daily rings on otoliths to estimate age and calculate hatch date following the methods of Taubert and Coble (1977) and Miller and Storck (1982). Because age-0 bass do not form a daily ring until they are about 5 d old, 5 d were added to the age determined by counting rings (Miller and Storck 1984). Hatch date was calculated by subtracting the age (d) from the sample date. Hatch date distributions were developed using otoliths from all samples in each year. Median and range of hatch dates were compared between years. Difference in median hatch dates was tested using a Mann-Whitney U-test (P ≤ 0.05).

Growth Rate

I compared growth rates between years by inspecting trajectory plots of mean length on sampling dates through summer and fall, and calculating mean daily growth rates (mm/d). Because growth rate is influenced by foraging capability (i.e., gape size that is length-dependent) (Lawrence 1958) and growing conditions (i.e., water temperature and forage availability), three aspects of daily growth rates were compared between years, (1) incremental and season-long (from first capture until maximum mean length), (2) from the dates when fish reached similar mean lengths until they reached the maximum mean length, and (3) across similar dates.

I investigated the influence of age, cumulative degrees (sum of mean daily water temperature from hatch to capture date), and hatch period (early or late) on growth rate of age-0 bass. Cumulative degrees described the combined effects of duration and intensity of temperature experienced. Hatch period was determined by dividing cohorts into early- and late-hatch fish. Early-hatch fish were hatched within the first one-third of the range of hatch dates and late-hatch fish were in the later two-thirds. This division allowed for sufficient separation of early-hatch fish whose contribution to recruitment may be significant, particularly in northern waters (e.g., Post et al. 1998), and avoided problems with small sample sizes. Pearson's product-moment correlation was used to test for significant relationships. Because cumulative degrees were a combined effect of age and temperature, I tested for differences in r between the age-length and cumulative degrees-length relationships for each year. Significant and greater r-values for the cumulative degrees-length relationship indicated greater variation explained (r², Zar 1999), and thus a significant influence of water temperature on growth rate. The effect of hatch period for each year was evaluated using analysis of covariance if slopes for age-length relationships were equal between hatch periods. Hatch period was the main effect with length the dependent variable and age the covariate. If slopes were unequal and significant, I visually inspected plots and compared slopes of regression lines to assess the rate of length gained with age. Non-linear data were transformed using (x²) and (log, x) to improve linearity. Statistical tests were considered significant at P < 0.05.

Body Condition and Length Entering Winter

Condition was estimated using transformed (log, x) length-weight correlations. To compare condition between years, I first tested for differences in the slopes of the length-weight relationship. If slopes were equal, I then tested for differences in the y-intercept to evaluate differences in weight at a given length. Length entering winter was estimated as the maximum mean length of age-0 largemouth bass during summer and fall sampling. A t-test was used to compare lengths.
of bass entering winter between years. All tests were considered significant at $P \leq 0.05$.

**Results**

**Water Temperature and Flow**

Mean daily summer water temperature was significantly higher in 1998 than in 1997 ($P < 0.001$). In 1997, summer water temperature averaged 19.5°C whereas in 1998 water temperatures averaged 22°C. Higher summer water temperature was associated with lower discharge (Figure 1). In 1997, spring runoff from snowmelt resulted in high flows (peak flow of 3520 m$^3$/s) lasting from mid-May to late June. In 1998, spring snowmelt resulted in little flow (peak flow of 1636 m$^3$/s) and lasted from late May to early June. Suitable temperatures for spawning (15°C) were reached in early July 1997 and in early May 1998. In 1998, however, spring runoff decreased water temperature below 15°C from mid-May until early June. Rains created a second pulse in the hydrograph in mid- to late June that corresponded with stabilizing temperatures above 15°C. Water temperatures at the end of the growing season dropped precipitously and became similar between years. From 1 October - 18 October, water temperatures dropped from 16.9°C to 13°C in 1997 and from 18.6°C to 13.5°C in 1998.

**Hatch Date and Periods**

The median hatch dates were significantly different between years ($P < 0.05$; Figure 1). Median hatch date was five days earlier in 1998 (13 July) than in 1997 (18 July). Hatching began 12 d earlier in 1998 than in 1997 but ended on the same date in both years. Hatch dates ranged from 3 July to 17 August in 1997 (46 d long) and 21 June to 17 August (58 d long) in 1998. Hatching started when temperatures reached about 15°C, and peak hatch occurred in the second week of July in both years. In 1998, hatching slowed from early to mid-July in response to stabilized water temperatures from mid- to late June. As a result, there was an earlier hatch mode in early July and later hatch mode in mid-July.

Hatch periods differed between years, corresponding to the different hatch date distributions. The early hatch period was 3-17 July (15 d) in 1997, and 21 June-9 July (19 d) in 1998 (Figure 1). Early-hatch fish in 1998 were generally hatched before early-hatch fish in 1997. The two-mode distribution in 1998 resulted in proportionally less of the hatch occurring in the early period than in 1997 when the distribution was skewed towards earlier dates. In 1998, 31% ($n = 67$) of the hatch occurred in the early period, and in 1997, 49% ($n = 143$) of the hatch was in the early period.

**Growth Rate, Body Condition, and Length Entering Winter**

Growth rate was greater in 1998 than in 1997 (Figure 2). Mean lengths of age-0 largemouth bass ranged from 48 mm (SE = 0.66) to 64 mm (SE = 1.3) in 1997 and from 39 mm (SE = 1.4) to 87 mm (SE = 1.6) in 1998. Precision of mean length estimates was high (mean SE = 1.5 mm), so estimates of growth rates should be similarly precise. In both years, growth rate was negative and the lowest from early to mid-October. Maximum mean lengths were recorded in early October, suggesting the end of the growing season was between early and mid-October. Mean growth rates from first capture to maximum mean length was 0.46 mm/d in 1997 and 0.83 mm/d in 1998. Growth rate was highest in 1997 from 19 September to 3 October when fish grew from a mean of 53 to 64 mm (0.69 mm/d). In 1998, the highest growth rate (1.15 mm/d) was recorded from 13 August to 1 September when fish grew from a mean of 49 to 70 mm. From dates when bass were similar in mean length (29 August 1997 and 13 August 1998) to maximum mean lengths in early October, growth rate was higher in 1998 (0.76 mm/d) than in 1997 (0.46 mm/d). This suggests that fish in 1998 grew faster despite having similar initial foraging capabilities as those in 1997. Similar dates of capture were the periods of 29 August to 3 October 1997 and 1 September to 1 October 1998. During this time, growth rate was higher in 1998 (0.57 mm/d) versus 1997 (0.46 mm/d) again suggesting better growing conditions in 1998. Growth trajectories differed. In 1997, the trajectory (growth rate) increased with time whereas in 1998 it decreased. The mean length estimates for fish on 1 September and 1 October 1998 are likely conservative because of the bias seine sampling has for fish <70mm, particularly for the October sample when fish were larger.
Figure 1. Relationship between flow, water temperature, and largemouth bass hatch date in Noxon Rapids Reservoir, Montana during A) 1997 (n = 294) and B) 1998 (n = 215). Dashed line at 15°C was added to illustrate when water temperature reached suitable temperatures for spawning. Hatch dates are grouped into 3 d periods.
Length entering into the winter season was significantly greater in 1998 than in 1997, whereas condition was similar. Largemouth bass entered into winter at a mean length of 64 mm (SE = 1.3) in 1997 and a mean length of 87 mm in 1998 (SE = 1.2), so fish averaged 23 mm larger in 1998 than in 1997 ($P < 0.001$, Figure 2). These mean lengths were recorded on 1 October in 1997 and 3 October in 1998. Condition of age-0 fish was similar between the two years. Correlations of length and weight [both transformed using (log$_{10}$)] were significant ($r = 0.99$, $P < 0.001$) for both years. Slopes and intercepts were not significantly different (slope = 2.94 and intercept = -4.75 in 1997, and slope = 2.97 and intercept = -4.80 in 1998).

Age-length correlations were significant ($P < 0.001$) for both years suggesting that older fish were longer (Figure 3). Age explained 55% of the variation ($r = 0.74$) in length in 1997 and 71% ($r = 0.84$) in 1998 using log$_{10}$ transformations of age and length. For the 1997 data, transformations of age ($x^3$ and log$_{10}$) and length (log$_{10}$) did not result in increased r-values ($r \leq 0.74$), so they were not used. The relationship between cumulative temperature and length resulted in significant correlations ($P < 0.001$) in both years and higher r-values ($r = 0.75$ in 1997 and 0.87 in 1998) than age-length relationships, but did not describe a significantly greater proportion of variance in either year. Mean temperatures experienced by individual bass ranged from 19.1 to 22.5°C in 1997 and 20.5 to 25.2°C in 1998.

Early hatching resulted in greater length in 1997 and 1998 (Figure 3). For 1997, hatch periods had significant correlations ($r = 0.74$ for early-hatch and 0.76 for late-hatch, $P < 0.001$ for both) and similar slopes (slopes = 0.53 for early-hatch and 0.60 for late-hatch). Adjusted means of length were significantly different using analysis of covariance ($P < 0.05$). Adjusted mean was 55.4 mm for early-hatch fish and 53.1 mm for late-hatch fish, indicating a 2.3 mm advantage for early-hatch fish at a given age. In 1998, correlations using log$_{10}$ transformations of age and length were significant for both hatch periods ($r = 0.92$ for early-hatch, $r = 0.83$ for late-hatch, and $P < 0.001$ for both periods), but slopes were not equal ($P < 0.001$).
Figure 3. Relationships between age and length by hatch period for age-0 largemouth bass in Noxon Rapids Reservoir during the summers of A) 1997 and B) 1998. Note difference in scales.
The slope for early-hatch fish was 1.18 versus 0.71 for late-hatch fish. The greater slope suggests that length was gained more rapidly with increasing age in 1998. Inspection of the scatterplot for 1998 (Figure 3B) indicated that early-hatch fish were slightly smaller than late-hatch fish from about 30 to 45 d then were larger at older ages. According to correlations, a 30 d old early-hatch fish averaged 30 mm versus 35 mm for late-hatch fish. At 75 d old, early-hatch fish were 88 mm and late-hatch fish 68 mm. The division of the overall age-length relationship in 1998 (n = 215) into hatch periods helped explain part of the variation in length at ages over 45 d old. This was indicated by the generally higher r-values for early- and late-hatch fish (r = 0.92 and 0.83, respectively) versus the overall age-length relationship (r = 0.84). The lower r-value for late-hatch versus early-hatch fish was largely due to remaining and higher variation of length at ages over 45 d.

**Discussion**

Largemouth bass in Noxon Rapids Reservoir hatched earlier in 1998 (median difference = 5 d, start 12 d earlier) when flows were lower and temperatures warmed more quickly. Spawning and hatching were largely controlled by snowmelt and spring runoff and, as a result, were later than reported for lakes in the same region of Montana. Within a year, earlier hatching resulted in faster growth, presumably because of increased piscivory. Only 1998 had a large enough difference in growth rate between early- and late-hatch to be of biological significance, however. Water temperatures experienced by individual fish did not result in different growth rates within an annual cohort. Highest growth rates were achieved by hatching early in the year with higher water temperatures (i.e., 1998). Among years, differences in length of age-0 largemouth bass entering winter between 1997 and 1998 was primarily due to differences in growth rate, whereas growing season was less important because of its low variability. Water temperature was probably the most influential factor for differences in growth rate between years. Body condition was similar between years. Age-0 largemouth bass in Noxon Rapids Reservoir achieved greater lengths entering winter more by growing faster than by having longer to grow.

Spring runoff affected the timing and duration of hatching for largemouth bass in Noxon Rapids Reservoir (Figure 1). Spring runoff mediates the effects of warming air temperatures in May and June by increasing the volume of cold water coming from snowmelt. Later hatching dates were likely the result of later spawning due to low water temperature. Water temperature in concert with photoperiod controls the onset of spawning. Bass spawn between 15 and 24°C (Kramer and Smith 1962). In northwest Montana lakes, largemouth bass spawning begins in mid-May to late June depending on water temperatures (Walker-Smith 1995), indicating that photoperiod would be suitable in May at Noxon Rapids Reservoir. However, at Noxon Rapids Reservoir, hatching began in late June in 1998 and early July in 1997 after high flow and when water temperatures were above 15°C and suitable for spawning. In 1998, spring rains slowed hatching in early July, even though water temperature exceeded 15°C. The lack of a rising trend in temperature appeared to reduce hatching and probably spawning. A similar response to temperature was reported in an Illinois reservoir where rising water temperatures above 15°C stimulated largemouth bass to spawn (Miller and Storck 1984).

My results suggested that growth of age-0 fish ceased when temperatures were still suitable for growth (Figure 2). The growing season ends when water temperatures fall below 10°C (Coutant 1975, Adams et al. 1982). However, water temperatures in Noxon Rapids Reservoir were at ~13°C in mid-October of both years, suggesting conditions were still favorable for growth. Immediately prior to the decrease in length of fish according to mid-October sampling was a cold front. Maximum air temperatures dropped from 28 to <15°C on 2-4 October 1997 and 3-5 October 1998 (U.S. Forest Service weather station near Noxon Rapids Reservoir, unpublished data, 1999). Movement by age-0 largemouth bass out of littoral areas to deeper water in response to cold fronts was observed in two Montana lakes (Walker-Smith 1995) and reported elsewhere (Coutant 1975). In Noxon Rapids Reservoir, smaller age-0 largemouth bass may use shallow water to avoid predators despite the potential for starvation because of low, fluctuating temperatures (Miranda and Hubbard 1994a, Garvey et al. 1998). Thus, the fish sampled on
the last sampling date in both years consisted of the smaller age-0 bass within their respective year classes, whereas larger individuals moved to deeper water and were not sampled.

Earlier hatching resulted in longer bass in both 1997 and 1998, but was more important in 1998. Being hatched earlier simply allowed fish more time to grow (get older) and reach longer lengths (Figures 2 and 3). In addition to having a longer growing season, early-hatch fish grew faster than late-hatch fish in both years. The benefit of early hatching in 1997 was small (an additional 2.3 mm in length), suggesting that this difference was not biologically important. However, in 1998, earlier hatching had a greater benefit (20 mm for a 75 d old fish). Conversely, bass that experienced higher water temperatures than fish of similar age were not longer. This suggests that, within an annual cohort, early-hatch fish grew faster and longer than late-hatch fish because of foraging opportunity rather than higher water temperatures. Information on diet was not collected in this study but past studies support this hypothesis. Growth rate of age-0 largemouth bass increases with the rate of piscivory (Aggus and Elliot 1975, Miller and Storck 1984) and is higher for earlier hatched fish (Maceina and Isely 1986, Goodgame and Miranda 1993). Furthermore, Phillips et al. (1995) linked hatch date and piscivory directly to growth rate of age-0 largemouth bass by finding that early-hatch fish were more piscivorous and grew faster than later-hatch fish in a North Carolina reservoir.

Water temperature among years is the most probable and influential reason for observed differences in largemouth bass annual growth rates and length entering winter. Mean daily summer water temperatures in 1997 (19.5°C) and 1998 (22.0°C) were below the optimum for growth (Figure 1). Optimal temperature for growth of largemouth bass is 27.5°C (Coutant 1975). Growth rate increases to the optimum. Therefore, higher temperatures, as long as they are below the optimum, should correspond to higher growth rates. This suggests that growth rates would be higher in 1998 than in 1997, as was seen in this study.

Growth rate had a greater influence on length of largemouth bass entering the winter season in Noxon Rapids Reservoir than length of growing season during this study. Using growth rates when foraging capabilities were initially equal, the increased growth rate estimated in 1998 (0.76 mm/d) versus 1997 (0.46 mm/d) added an additional 26 mm for a fish 85 d old fish. Generally, the growing season was from ~15 July to 10 Oct or 85 d in Noxon Rapids Reservoir. Furthermore, the difference of 26 mm corresponds well with the difference in estimates from sampling (23 mm) (Figure 2). Conversely, length of growing season was relatively similar between 1997 and 1998. The beginning of the growing season was 5-12 d earlier in 1998 (as indicated by the difference of median and range of hatch dates) (Figure 1) and both seasons ended at similar times according to growth trajectories and water temperature. Again, using the predicted growth rates, and a 5 to 12 d extension in the growing season, the additional time from earlier hatching in 1998 adds only 2 to 9 mm in length.

Further study is needed on the relationship of growth to number of fish, mortality rates through summer and winter, and recruitment to the population. Investigation of the relationship between length entering winter and survival to age-1 and the fishery is needed. Overwinter survival is size-dependent in some systems (Adams et al. 1982; Bowles 1985; Post et al. 1998; Miranda and Hubbard 1996a, 1996b) but not others (Hatch 1991, Kohler et al. 1993, Jackson and Noble 2000). Garvey et al. (1998) reported variable size-dependent survival across a range of northern and southern waters. Results of this study identify key environmental conditions and population factors that influence hatch timing and growth, two critical elements of the recruitment process.

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