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Temporal Shifts in Demography and Life History of an Anadromous Alewife Population in Connecticut

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Abstract.—Populations of anadromous alewives *Alosa pseudoharengus* are declining throughout much of the species' range, particularly in southern New England, where fishery moratoriums have recently been instituted in three states. The alewife run at Bride Brook, a coastal stream in East Lyme, Connecticut, was studied from 2003 to 2006 to assess shifts in demography and life history. Annual censuses of abundance and sampling for size, age, and spawning history structure were conducted. These data were compared with similar data from 1966 to 1967 at this site. Recent alewife runs at Bride Brook featured lower abundance and younger, smaller fish that were less likely to be repeat spawners. The 1966 spawning run was dominated by repeat spawners of ages 5–7, while runs in 2003–2006 were dominated by age-3 and age-4 first-spawn fish. Mean length declined by 10% between 1966 and 2006. Alewives are also recruiting to the spawning run at younger ages and smaller sizes, indicating a shift in life history. The first-spawn portion of the 1966 spawning run was dominated by age-5 fish, while recent first-time spawners were primarily age 3. The shifts in demography and life history observed at Bride Brook are consistent with exploitation or predation concentrated on older, larger individuals in the population. The results of this study suggest recent increases in predatory pressure or bycatch mortality as promising hypotheses that merit further investigation.

A prominent theme in recent reconsideration of fisheries management is recognition of the dynamic relationship between extrinsic mortality, population demography, and life history. Shifts in mortality schedules, resulting from either anthropogenic or natural factors, can profoundly change not only the abundance but also the demographic composition and life history traits of fish populations (Ricker 1981; Reznick and Endler 1982; Levin et al. 2005; Harvey et al. 2006). Furthermore, the direction of life history evolution is often diagnostic with respect to the ontogenetic stage experiencing elevated mortality (Rodd and Reznick 1997; Conover et al. 2005; Reznick and Ghalambor 2005). Assessment of changes in demography and life history within declining populations can therefore greatly inform the formulation of hypotheses concerning causative factors. Some life history shifts may also alter the intrinsic growth rate of populations and therefore hamper recovery (De Roos et al. 2006; Walsh et al. 2006). Shifts in demography and life history must therefore be considered when formulating management plans for declining populations and setting benchmarks by which to measure restoration progress.

This case study examines temporal shifts in demography and life history within a population of anadromous alewives *Alosa pseudoharengus*. Anadromous alewives, often referred to collectively with the sympatric blueback herring *A. aestivalis* as “river herring,” are distributed along the Atlantic coast of North America from Labrador to South Carolina (Loesch 1987). Anadromous alewives (hereafter referred to as simply alewives, but not to include the derived landlocked populations) inhabit continental shelf waters until sexual maturity is reached (Neves 1981). Sexually mature individuals make spawning migrations or “runs” into freshwater systems during spring months (Loesch 1987). Migrants typically return to natal streams, yet straying does occur (Messiah 1977; Jessop 1994). The degree of iteroparity within alewife populations is positively correlated with latitude, and mortality during the freshwater spawning period can be highly variable (Mullen et al. 1986). Juvenile alewives typically spend 1 to 3 months in freshwater nursery areas prior to a gradual migration to estuarine and then marine habitats (Loesch 1987).

River herring are of ecological significance as they transport marine-derived nutrients to freshwater environments (Durbin et al. 1979; Garman 1992; MacAvoy et al. 2000). They are also important forage species, particularly for many economically significant marine and freshwater finfish (Yako et al. 2000; Walter et al. 2003). River herring historically supported significant coastal and ocean-intercept commercial fisheries along the Atlantic coast of the United States, but recent

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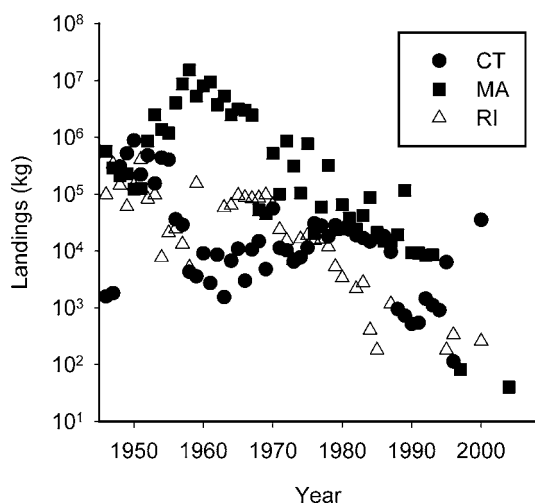


FIGURE 1.—Commercial landings of alewives in the states of Connecticut (CT), Massachusetts (MA), and Rhode Island (RI) from 1946 to 2004. Note the logarithmic scale on the y-axis.

landings have been small relative to peak landings recorded in the 1940–1960s (Atlantic States Marine Fishery Council 2007). Recreational anglers also commonly collect river herring for personal consumption and for use as bait (Atlantic States Marine Fishery Council 2007). These fisheries primarily occur in-river during spawning runs, but harvest, while potentially significant, is poorly documented (Schmidt et al. 2003). River herring are also taken as bycatch in some oceanic fisheries (Atlantic States Marine Fishery Council 2007; Kritzer and Black 2007; Cieri et al. 2008).

A precipitous decline in river herring populations has recently been observed in southern New England (Gephard et al. 2004; National Oceanic and Atmospheric Administration 2008; U.S. Fish and Wildlife Service 2008a, 2008b). Commercial landings of alewives in all three southern New England states (Connecticut, Massachusetts, and Rhode Island) have declined to a small fraction of peak landings recorded in the 1950–1960s (Figure 1). Blueback herring run size has declined four orders of magnitude at the Holyoke Dam fish elevator on the Connecticut River, and similar abrupt declines in abundance have been noted at other index sites in Massachusetts and Rhode Island (Figure 2). While comparable time series are not available in Connecticut, observations by Connecticut Department of Environmental Protection (CDEP) personnel indicate there have been significant declines in run size at a majority of sites (Gephard et al. 2004). In response to population declines, CDEP instituted an

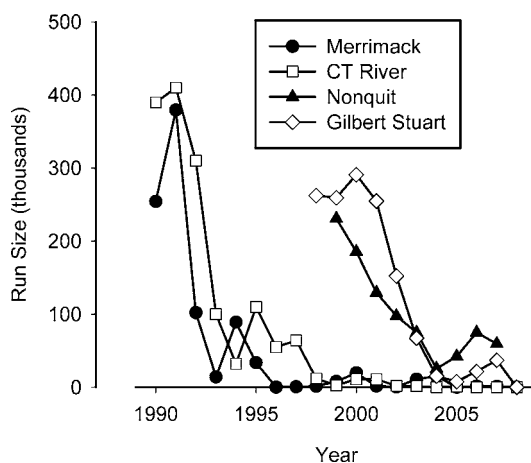


FIGURE 2.—Annual river herring (alewife and blueback herring) run size at index sites in Massachusetts (Essex Dam fishlift on the Merrimack River, Holyoke Dam fishlift on the Connecticut [CT] River) and Rhode Island (Nonquit River fishway, Gilbert Stuart Brook fishway). All counts represent both species in aggregate, with the exception of Holyoke Dam (blueback herring only).

emergency closure of the state's river herring fishery in 2002. Similar closures were instituted in the neighboring states of Massachusetts and Rhode Island in 2005. The closures apply to both coastal and ocean-intercept fisheries and therefore constitute a moratorium on directed fisheries for river herring in southern New England.

The recent declines in river herring populations represent an urgent challenge for fisheries managers in southern New England. Fishery closures were a pragmatic response, but it is not clear that exploitation contributed significantly to population declines. It is also not known whether current management practices have provided an opportunity for population recovery. If recovery has begun, then population responses should include increases in run size and greater proportions of older fish in the population. The alewife population at Bride Brook, a coastal stream in Connecticut, is an appropriate test case for postclosure population recovery. Bride Brook alewives were presumably subject to harvest in the mixed-stock ocean intercept fishery, and also supported a substantial in-river fishery (S. Gephard, CDEP, personal communication). Bride Brook is also the only site in Connecticut for which detailed historical demographic data are available. This case study represents the first detailed study of a southern New England river herring population following the fishery moratorium and will inform assessments of current management and testing of hypotheses concerning causative factors.

The results of this study also have relevance for river herring management outside of southern New England as the regional declines described here reflect a coastwide pattern (Rulifson 1994; Schmidt et al. 2003; Atlantic States Marine Fishery Council 2007). Partial or complete fishery closures have now been implemented in five states, and the federal government has listed river herring as Species of Concern (Atlantic States Marine Fishery Council 2007; National Oceanic and Atmospheric Administration 2007). There are several potential factors in river herring declines, but the primary cause has not been determined (National Oceanic and Atmospheric Administration 2007). In addition, recent rangewide review of available data has been limited to large rivers (Schmidt et al. 2003). Published records of detailed demographic data from relatively small systems such as Bride Brook are rare and will be useful in assessing the generality of the patterns evident in large river systems. Insights gained through study of the alewife population at Bride Brook will also inform prioritization of future research efforts.

The specific objectives of this study were to (a) compile a 4-year time series of abundance and demographic data for an alewife population; (b) compare contemporary data with historic data to characterize shifts in demography (size, age, and spawning history structure) and life history (age and size at first spawn); and (c) assess whether the population evinced signs of recovery after the recent fishery closure.

Methods

Study site and field sampling.—Our study site was Bride Brook, a coastal stream located in East Lyme, Connecticut (41°19'30.7164"N, 72°14'26.7792"W). Bride Brook originates from an 18-ha pond named Bride Lake and flows 3 km to Long Island Sound. This site was selected because it supports a sizeable alewife run, because its physical configuration is conducive to trap construction, and because it is the only site in Connecticut for which historic demographic data exist. Kissil (1969) reported run sizes and size structure at Bride Brook for 1966–1967. Marcy (1969) reported age structure, spawning history structure, and mean length at age for alewives collected at Bride Brook in 1966. These historic data were used as a basis for analysis of temporal variation on a decadal time scale.

Annual censuses of the spawning run were performed at Bride Brook in 2003–2008. Weir traps were constructed at the entrance to Bride Lake in spring (March–June) to capture all upstream migrants. In 2003–2004, we hand-counted all captured alewives each day. In 2005–2008, an electronic fish counter was installed at the trap entrance. In these years, the counter

served as the primary means of enumeration, but hand-counts of captured fish were still made weekly to ensure counter accuracy. Trapping operations were discontinued in late spring (late May–early June) after upstream migration ceased (>7 d without capture). Downstream passage was provided for spent adults in all years, generally beginning in late May.

We conducted weekly demographic sampling. Samples were collected systematically on the same day of the week. To estimate size structure, we randomly selected and measured up to 100 fish (total length [mm]) captured on a single day or on two subsequent days if the catch on the first day was low (<30 fish). We subsampled up to five fish per 5-mm size-class to determine species, sex, age, and spawning history. All subsampled alewives were immediately placed on ice and frozen within 6 h. These fish were later thawed and dissected to determine sex and species.

Age and spawning history estimates.—We removed scales from the area of the body anterior to the dorsal fin and above the lateral line (Hattala 1999). Six nonregenerated scales from each fish were cleaned and mounted between glass microscope slides. Scale samples were analyzed by viewing projections of the samples on a microfiche reader. Age was estimated in accordance with the methods for alosine scale aging reported by Cating (1953) and Marcy (1969). A check mark in close proximity to the baseline of the scale was considered a freshwater mark, and all subsequent check marks extending in a smooth and continuous manner through the anterior field of the scale were counted as annuli. The relative thickness and proportional spacing of check marks were used as criteria for distinguishing false annuli. The edge of the scale was considered the final annulus. Erosion and re-absorption of the scale margin during the spawning run cause formation of jagged, asymmetric check marks, known as spawning marks, on the scale. These marks obscure annuli formed during the spawning year; therefore, spawning marks were counted as annual marks. We estimated spawning history by counting spawning marks, and we estimated age by adding the number of annuli and spawning marks. Each scale sample was independently read “blind” (no prior knowledge of length or sex) by three readers.

After scale readings were completed, the samples were first screened for sufficient levels of inter-reader agreement on age. Acceptable levels of inter-reader agreement were defined as unanimous agreement on age or two-way agreement on age with the dissenting estimate differing by ± 1 year. In the case of the latter agreement condition, the majority age estimate was assigned to that sample. Samples failing to produce

sufficient levels of agreement were removed prior to further analysis. After screening for age agreement was complete, samples were re-screened for agreement on spawning history in an identical fashion. The samples remaining after this second screening were used to estimate age and spawning history structure.

Precision of age estimates was quantified by calculating the mean coefficient of variation (V) of replicate age estimates (Chang 1982). We also quantified within-reader agreement in a randomly-selected set of scale samples ($n = 50$). Validation of the accuracy of our scale aging techniques (i.e., testing age and spawning history estimation in a sample of known fish) was not possible for this study. To provide a measure of corroboration, we aged sagittae from a subsample ($n = 293$) of alewives used in the scale aging analysis. Otoliths were cleared in immersion oil and examined by means of a dissecting scope at 12 \times magnification. Three readers independently examined each pair of otoliths and estimated age in accordance with the methods outlined by Libby (1985). Age was assigned in a manner identical to that for scale aging. An age bias plot was constructed to examine bias of otolith age estimates relative to those derived from scales (Campana et al. 1995). To provide another measure of corroboration, scale samples ($n = 30$) were sent to Canadian Department of Fisheries and Oceans (CDFO) biologists with extensive experience in river herring scale aging. These outside experts provided estimates of age and spawning history for each scale sample. Age bias plots were constructed to examine bias of our scale age estimates relative to CDFO estimates (Campana et al. 1995).

Comparison of present and historical age structure is valid only if our approach to age estimation was consistent with that used previously. To address this issue, we aged scales from alewife specimens ($n = 8$) that were collected for the study reported by Marcy (1969). Inter-study age determination was then assessed indirectly by comparing the length at age of the specimens we examined with the length at age reported by Marcy (1969).

Age and spawning history structure.—We used age-length keys to estimate age structures for each year (Devries and Frie 1996). We used a separate key for each sex because of previously demonstrated differences in growth and age at first spawn (Loesch 1987). Sex and age composition of each 5-mm size-class for each year were determined from dissection and scale analysis. These sex-specific age keys were then used to estimate the sex and age composition of the size structure sample for each year:

$$F_{i(a,b)} = F_i \times P_{i(a,b)}, \quad (1)$$

where $F_{i(a,b)}$ = estimated number of fish of sex a and age b in size-class i ; F_i = number of fish measured in size-class i ; and $P_{i(a,b)}$ = proportion of fish of sex a and age b in size-class i (from dissection and scale analysis). The total estimated number of fish of each sex and age within the size structure sample was then calculated as

$$F_{(a,b)} = \sum_i F_{i(a,b)}. \quad (2)$$

A spawning history/age key was developed for each sex. These keys were then applied to the estimated age structures for each sex to estimate the frequency of each spawning class within each age-class:

$$F_{a,b(r)} = F_{(a,b)} \times P_{a,b(r)}, \quad (3)$$

where $F_{a,b(r)}$ = estimated number of fish of sex a and age b in spawning history class r ; $F_{(a,b)}$ = estimated number of fish of sex a and age b (obtained via equation 2); and $P_{a,b(r)}$ = proportion of fish of sex a and age b in spawning history class r (from scale analysis). The estimated number of fish of each sex in each spawning history class was then calculated as

$$F_{a(r)} = \sum_b F_{a,b(r)}. \quad (4)$$

We also estimated mean length at age for each year by pooling all aged fish within each year.

Interannual differences in population structure.—Annual means and standard deviations of Bride Brook alewife length in 1966–1967 were derived from summary statistics reported by Kissil (1969). Analysis of variance was used to test for year effects on size, followed by Tukey's honestly significant difference tests to test the significance among years. Year effects on age structure, spawning history structure, and the age structure of first-spawn fish were tested by means of χ^2 tests (Statistical Analysis System [SAS] version 9.1; SAS Institute, Cary, North Carolina). Because of low cell counts for repeat-spawning classes, spawning history was reduced to a two-level variable (first-time spawner versus repeat spawner) for analyses of year effects on spawning history structure. Age was also reduced to a two-level variable (age ≤ 3 , age ≥ 4) for analyses of year effects on age structure of first-spawn fish. Analysis of covariance (ANCOVA) was used to test for year effects on length at age and heterogeneity of slopes of age-length relationships across years in the contemporary sample (SAS version 9.1, SAS Institute). Only ages 3–5 were used for this analysis because few fish of age 2 or age 6 were collected. A full model including year, age, and the year \times age interaction was used for the initial ANCOVA; in cases where the

TABLE 1.—Alewife run size at Bride Brook (East Lyme, Connecticut), in 1966–1967 (Kissil 1969) and 2003–2008. Run size represents the total number of pre-spawn alewives entering Bride Lake during the spring spawning run. Counts in 1966–1967 and 2003–2004 represent hand-counts of trapped fish. Counts in 2005–2008 were made using an electronic fish counter (data provided by Connecticut Department of Environmental Protection).

Year	N
1966	184,151
1967	140,203
2003	117,158
2004	81,350
2005	68,757
2006	129,114
2007	66,975
2008	76,108

interaction term was nonsignificant, we evaluated reduced models that retained only the two main effects.

Results

Run size at Bride Brook in 2003–2006 ranged from 68,757 to 129,114 fish (Table 1). Immediate mortality from trapping and handling in 2003–2004 was low (<2.0%). All recent run sizes were 20–58% lower than the mean run size for 1966–1967 (mean = 162,177).

Agreement of Age and Spawning History Estimates

The initial sample size for the scale aging analysis was 1,400 individuals. Ten samples were discarded because all recovered scales were regenerated. Another 167 samples were discarded due to insufficient levels of inter-reader agreement. The remaining 1,223 samples were re-screened for agreement on spawning history estimation. Of these, agreement among independent evaluations of spawning history was unsuitably low (see Methods) in 18 samples. Therefore, 1,205 samples were used to estimate age and spawning history structures.

Random error in age estimation was relatively limited ($V = 8.5\%$). Mean within-reader agreement was 73% (minimum = 63%, maximum = 84%) and 95% (minimum = 88%, maximum = 100%) for age and spawning history, respectively. Replicate age and spawning history estimates produced by individual readers differed by more than 1 year or previous spawn in only two instances. Age-bias plots of mean University of Connecticut (UConn) age estimates against CDFO age estimates suggest that UConn aging was biased high for young fish (age 3) but otherwise suggest good concordance between CDFO and UConn readers (Figure 3). There was unanimous agreement on spawning history for 90% of samples. All age and spawning history estimates derived from the eight

historic scale samples produced acceptable levels of inter-reader agreements. For seven of the eight historic samples, the estimated length at age fell within one standard deviation of historic mean lengths at age reported by Marcy (1969).

Age determinations derived from otoliths were concordant with scale determinations. Sufficient levels of inter-reader agreement were reached for 272 of the 293 otoliths aged. A total of 251 alewives yielded age estimates from both scales and otoliths. For 249 of these individuals, scale and otolith age estimates agreed or differed by 1 year. An age-bias plot of mean otolith age against scale age indicates that otoliths tended to produce older age estimates for younger fish (Figure 4).

Interannual Differences in Population Structure

Age structure at Bride Brook differed significantly ($\alpha = 0.05$) across years (females: $\chi^2 = 1,418$, $df = 8$, $P < 0.0001$; males $\chi^2 = 1,278$, $df = 8$, $P < 0.0001$). Four age-classes (ages 4–7) were represented in the 1966 run (Figure 5). In contrast, the age-classes in 2003–2006 were younger and fewer (primarily ages 3 and 4). Recent runs contained age-2 and age-3 fish, while no individuals less than age 4 were reported in the 1966 run. Reduction in mean age of spawners was evident both on a decadal time scale and across the 4-year time period of this study (Table 2).

The spawning history structure of the run at Bride Brook also differed significantly across years (females: $\chi^2 = 759$, $df = 4$, $P < 0.0001$; males $\chi^2 = 855$, $df = 4$, $P < 0.0001$). The 1966 run was composed primarily of individuals that had spawned at least once or twice and as much as three times previously (Figure 6). In contrast, the contemporary runs were dominated by first-spawn fish and the representation of repeat spawners decreased steadily from 2003 to 2006 (Table 2). The age structure of first-time spawners was also significantly different across years (females: $\chi^2 = 288$, $df = 4$, $P < 0.0001$; males $\chi^2 = 193$, $df = 4$, $P < 0.0001$). First-spawn fish in 1966 were primarily age 5, while recent first-time spawners were primarily age 3 (Figure 7).

Year had a significant effect on size distribution at Bride Brook ($F = 1,176$; $df = 5$, 7,472; $P < 0.05$), and mean length was significantly different between all years except for 2005 and 2006 (Figure 8). Mean lengths of alewives at Bride Brook in 2003–2006 were 5.0–10.0% lower than those reported for the 1966–1967 runs. Mean length further declined by 4.0% from 2003 to 2006.

Mean length at age declined for both sexes from 2003 to 2006 and was intermediate to historic values (Figure 9). The slope of the length–age relationship differed significantly across years in female alewives

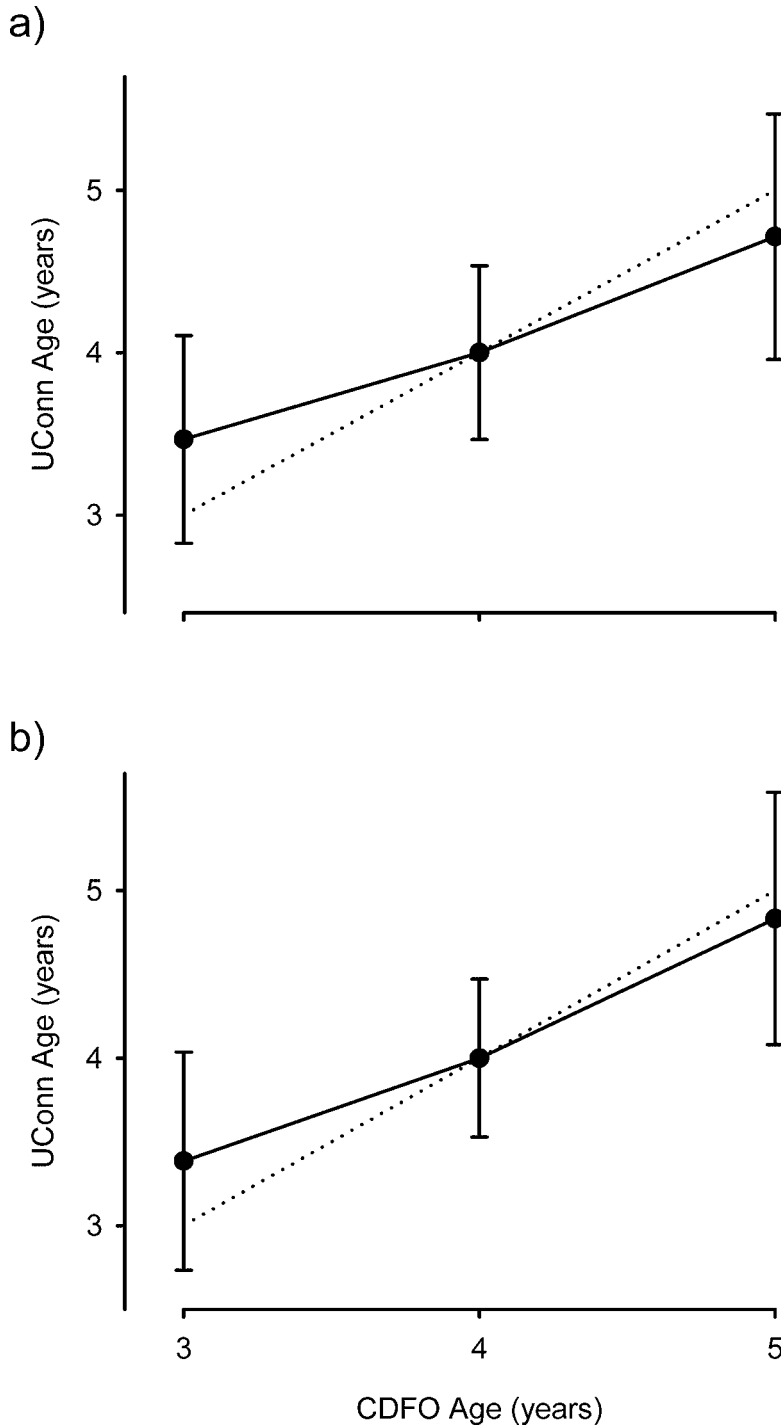


FIGURE 3.—Age-bias plots of mean University of Connecticut (UConn) age estimate (\pm standard deviation) versus Canadian Department of Fisheries and Oceans (CDFO) age estimate for alewife scale samples ($n = 30$) collected at Bride Brook (East Lyme, Connecticut): (a) UConn versus CDFO reader 1 and (b) UConn versus CDFO reader 2. Dashed line is the zero bias reference line.

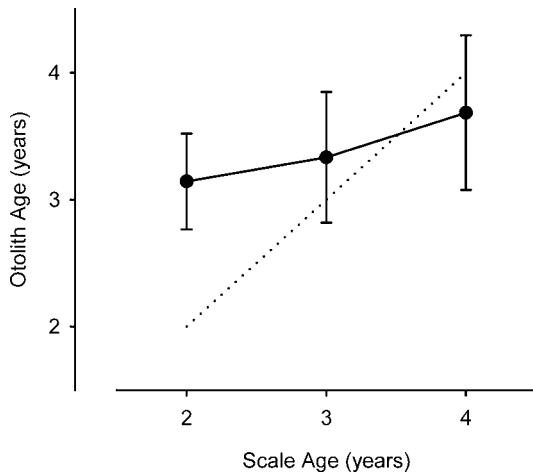


FIGURE 4.—Age-bias plot of mean otolith age estimate (\pm standard deviation) versus scale age estimate for alewives ($n = 251$) collected at Bride Brook (East Lyme, Connecticut). Dashed line is the zero-bias reference line.

(year \times age interaction: $F = 4.2$; $df = 3, 585$; $P = 0.006$) but not in male alewives ($F = 0.3$; $df = 3, 572$; $P = 0.86$). Length varied with age ($F = 108$; $df = 1, 585$; $P < 0.0001$) but not year ($F = 2.1$; $df = 3, 585$; $P = 0.10$) among females. Length varied with both age ($F = 176$; $df = 1, 575$; $P < 0.0001$) and year ($F = 38$; $df = 3, 575$; $P < 0.0001$) among males.

Discussion

We provide evidence of changes in abundance, demography, and life history traits of an alewife population on an inter-annual and decadal time scale. Mean length, proportion of older, repeat-spawning individuals, and mean length at age declined throughout the 4-year period of this study. Comparison with historical samples indicated an even greater shift in population structure: contemporary alewife runs at Bride Brook contain a higher proportion of younger, smaller individuals and are composed of fewer age-classes than in the 1960s. Furthermore, alewives of both sexes are currently recruiting to the spawning run at smaller sizes and younger ages, indicating temporal shifts in age and size at first spawn. Inter-annual variation in demographic composition of alewife runs is common due to variable recruitment, environmental variation, and demographic stochasticity (Jessop 1990). However, the consistent and substantial difference between historic and contemporary data suggests directional shifts in demography and life history rather than simple inter-annual variation.

We did not study blueback herring, but the rationale for this study (widespread declines, fishery closures)

applies to both river herring species. While there are some important differences between the species, such as extent of geographical range and spawning habitat selection (Loesch 1987), we believe that our study has relevance for management of both species. Factors affecting alewife populations also have a high probability of affecting blueback herring populations due to the high degree of spatial and temporal overlap in their habitats. In addition, regional fishery management councils and many coastal states manage the two species in aggregate. Therefore, any management actions taken to address declines in alewife stocks are likely to apply to blueback herring as well.

The data collected by Marcy (1969) and Kissil (1969) at Bride Brook represent the only available historic baseline for alewife demography and life history in Connecticut. While there is a paucity of quantitative data on river herring runs in southern New England prior to the 1980s, available information suggests that river herring runs in the region were robust during the 1960s (Kissil 1969; Loesch 1969; Gephard and McMenemy 2004; Marcy 2004). The large commercial landings recorded during the 1960s support this assertion. Therefore, although the 1966–1967 runs at Bride Brook do not represent an unexploited condition, they offer an appropriate baseline to elucidate changes that are relevant to recent river herring population declines.

Our conclusions rely on the reliability of scale aging. Scales have been widely used to determine age and spawning history in numerous biological studies of river herring and other alosines (Cating 1953; Marcy 1969; Messieh 1977; Leggett and Carscadden 1978; Crecco and Savoy 1984; Jessop 1993; Limburg et al. 2003; Harris et al. 2007). However, the validity of this approach has recently been called into question (McBride et al. 2005). Unfortunately, as is the case for many fish species (Campana 2001; Maceina et al. 2007), a validated age determination method for alewives does not currently exist. In lieu of validation, we have instead focused on the agreement of age estimates among studies, among readers, within reader and between structures. The precision of our scale age estimates ($V = 8.5\%$) was close to the median ($V = 7.6\%$) obtained from a summary of 117 published aging studies (Campana 2001), and the overwhelming majority of our scale readings produced age estimates that were precise within 1 year. Both the length-at-age profile derived for historic scale samples and the similarity of our length-at-age estimates to historic length-at-age data suggest good inter-study consistency in scale aging. While we recognize that precision does not imply accuracy, the high degree of inter-reader and inter-study precision described here precludes obser-

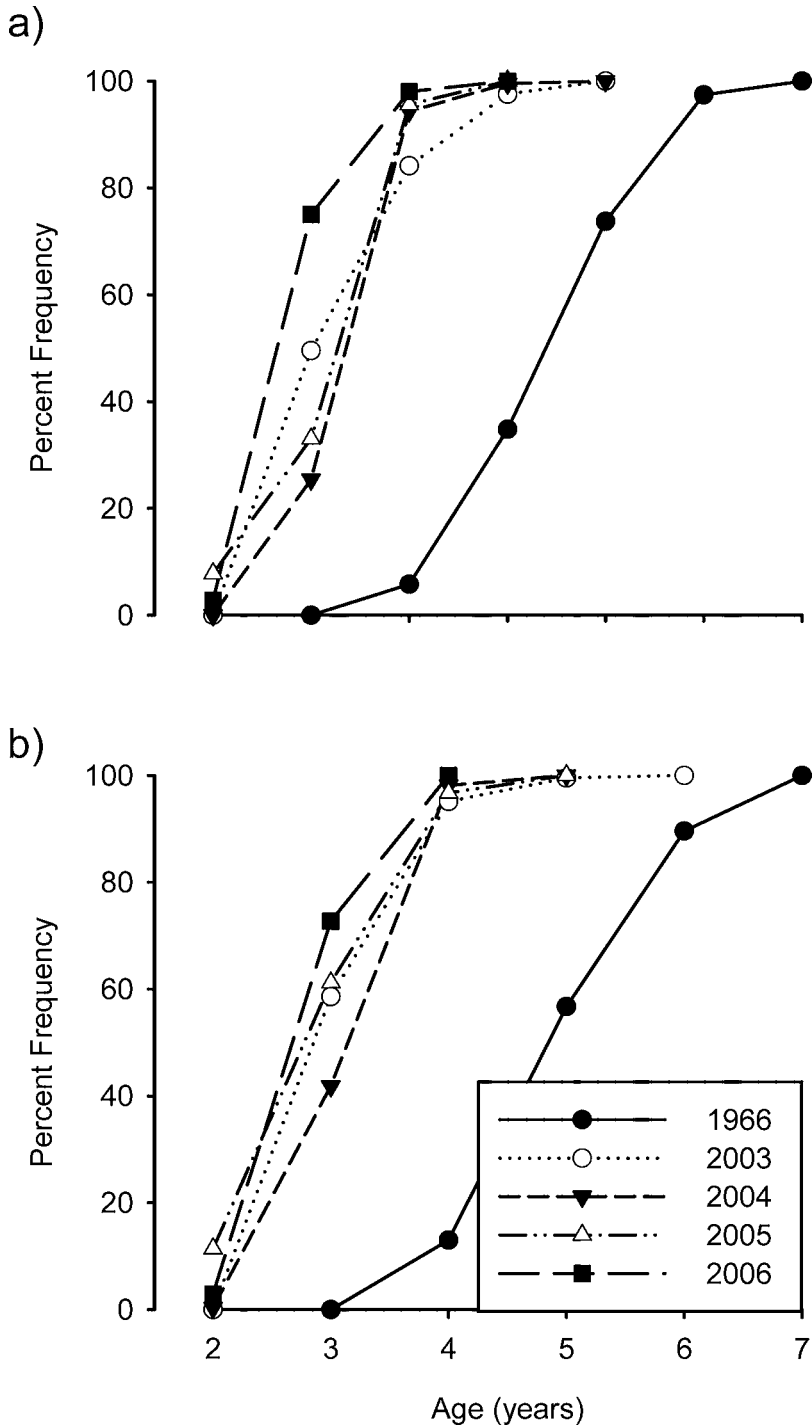


FIGURE 5.—Cumulative age frequency of alewives at Bride Brook (East Lyme, Connecticut), in 1966 and 2003–2006: (a) females and (b) males.

TABLE 2.—Mean age (years) and percentage of repeat spawners for alewives at Bride Brook (East Lyme, Connecticut), in 1966 (Marcy 1969) and 2003–2006. Standard error of mean age is shown in parentheses. Percentage of repeat spawners reflects the estimated percentage of fish in the spawning run that had spawned at least once previously.

Year	Female		Male	
	Mean age	% repeat spawn	Mean age	% repeat spawn
1966	5.9 (0.4)	78	5.4 (0.4)	76
2003	3.7 (0.3)	20	3.5 (0.3)	11
2004	3.8 (0.2)	6	3.6 (0.2)	4
2005	3.6 (0.3)	3	3.3 (0.3)	4
2006	3.2 (0.2)	5	3.2 (0.2)	0

variation error (error arising from inconsistent or incorrect interpretation of aging structures) as an explanation for the apparent decadal shifts in age structure. Analysis of inter-structure agreement indicates that scale ages may be biased low relative to otolith ages for young fish. However, this directional bias was only pronounced for nominal age-2 fish, and the overwhelming majority of scale and otolith age estimates were precise within 1 year. Finally, our conclusions pertaining to shifts in age structure are also corroborated by decadal shifts in size structure.

Our results suggest that population viability, defined as probability of persistence over a time frame relevant to current management (Morris and Doak 2003), has decreased in recent decades. While we did not perform quantitative analyses of population viability, there are numerous reasons to believe that the Bride Brook alewife population is currently at risk. Decreases in population size afford reduced resistance to stochastic environmental factors that negatively impact annual recruitment and survival (Holsinger 1995). Furthermore, the homogeneous age structure and lack of repeat spawners in contemporary runs at Bride Brook suggest reduced population stability (Leggett and Carscadden 1978; Leggett et al. 2004). The reproductive potential of the study population may also be reduced due to the prevalence of younger, smaller spawners (LaPlante and Schultz 2007). Fecundity is strongly correlated to length in river herring (Jessop 1993), and survival of larvae produced by younger fish may be relatively poor (Monteleone and Houde 1990; Berkeley et al. 2004). Finally, shifts to younger age at maturity such as those documented here (assuming that recruitment to the spawning run is a reasonable proxy for the onset of maturity) have been a precursor to collapse in some fisheries (Olsen et al. 2004). Identification and mitigation of the factors driving these deleterious changes in the study population are critical steps in managing for long-term persistence.

Our results suggest causative agents responsible for regional river herring declines. Size-selective mortality can have significant effects on demography and life history within fish populations (Ricker 1981; Reznick and Endler 1982). Our results are consistent with expected responses to increased levels of extrinsic mortality on older, larger individuals. Predation and fishing mortality are two likely sources of this mortality. Top-down control by predators often plays an important role in regulating prey population structure (Estes et al. 2004; Frank et al. 2005; Gotelli and Ellison 2006), and predation on larger, older individuals within a population can favor the rapid evolution of earlier maturation at smaller sizes (Reznick and Endler 1982). Similarly, fisheries that selectively harvest older, larger fish have the capacity to shift the demographic composition of the exploited population towards younger, smaller individuals (Beard and Essington 2000; Levin et al. 2005). Such selective fishing pressure may also favor rapid evolution of earlier-maturing phenotypes (Olsen et al. 2004; Conover et al. 2005; De Roos et al. 2006). Shifts in demography and life history, such as those noted at Bride Brook, have been demonstrated in heavily fished populations of river herring and American shad *A. sapidissima* (Maki et al. 2002; Jessop 2003).

Correlative evidence supports hypotheses centered on predation. The striped bass *Morone saxatilis*, a highly predatory marine finfish that is sympatric with river herring, has recently risen to historic levels of abundance (Hartman and Margraf 2003). While river herring do not appear to be a significant diet item for striped bass during the majority of the year in southern New England (Nelson et al. 2003), striped bass are known to feed heavily on adult river herring in the spring (Savoy and Crecco 2004). In particular, striped bass are capable of pursuing river herring well above the salt wedge in large river systems and are probably a significant source of spawning mortality for these populations (Savoy and Crecco 2004). Resurgent populations of the double-crested cormorant *Phalacrocorax auritus*, a piscivorous bird now common to the inshore waters of southern New England, may also be exerting predatory pressure on river herring populations (Dalton et al. 2009). Cormorant predation may be particularly significant for river herring runs in systems like Bride Brook that are located in close proximity to double-crested cormorant breeding colonies (Dalton et al. 2009). Given the recent proliferation of sympatric predators, the predation hypothesis presents a persuasive explanation for recent river herring declines (Savoy and Crecco 2004). However, conspicuous predator-prey interactions do not always prove to be significant mechanisms for top-down control (Davis et

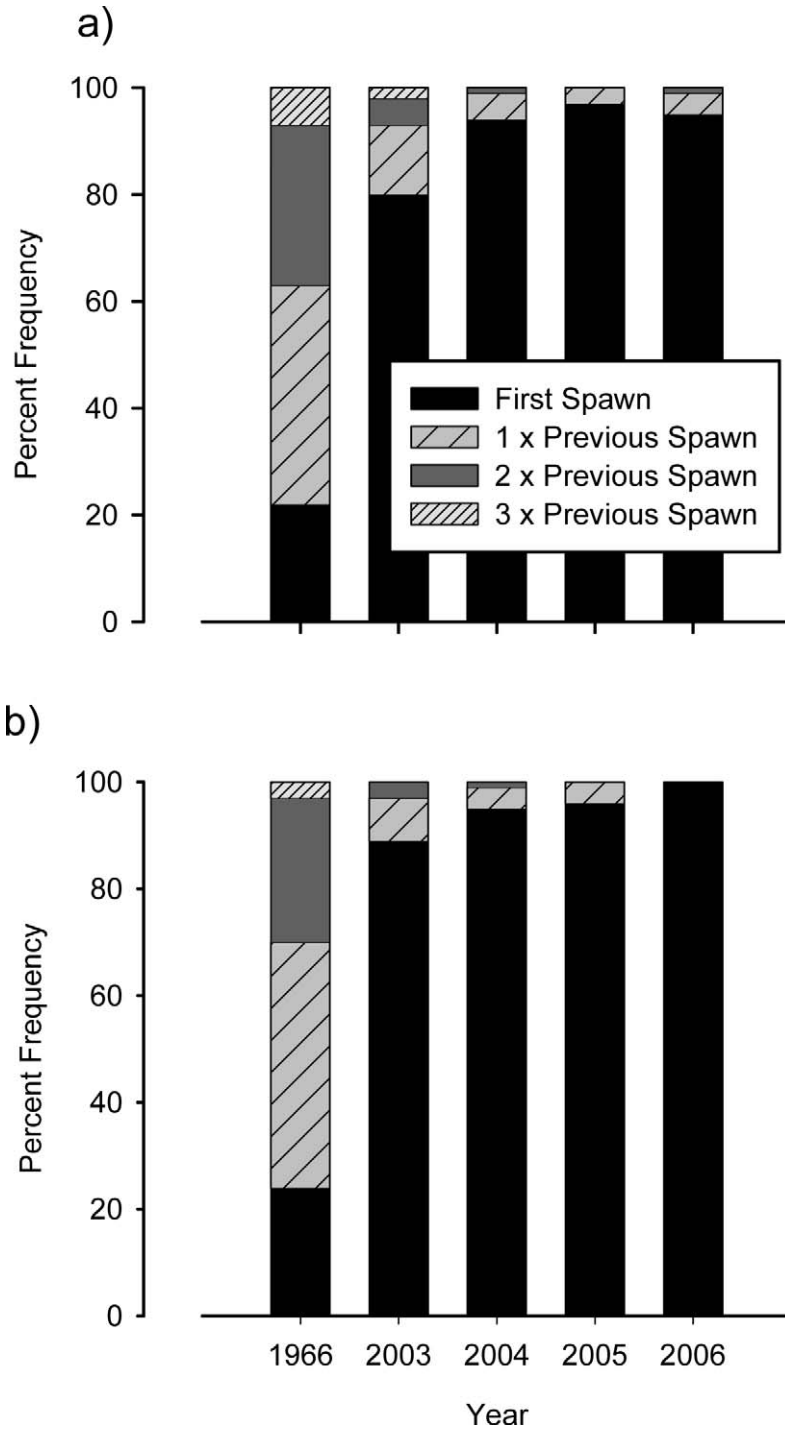


FIGURE 6.—Spawning history structure of alewives at Bride Brook (East Lyme, Connecticut), in 1966 and 2003–2006: (a) females and (b) males.

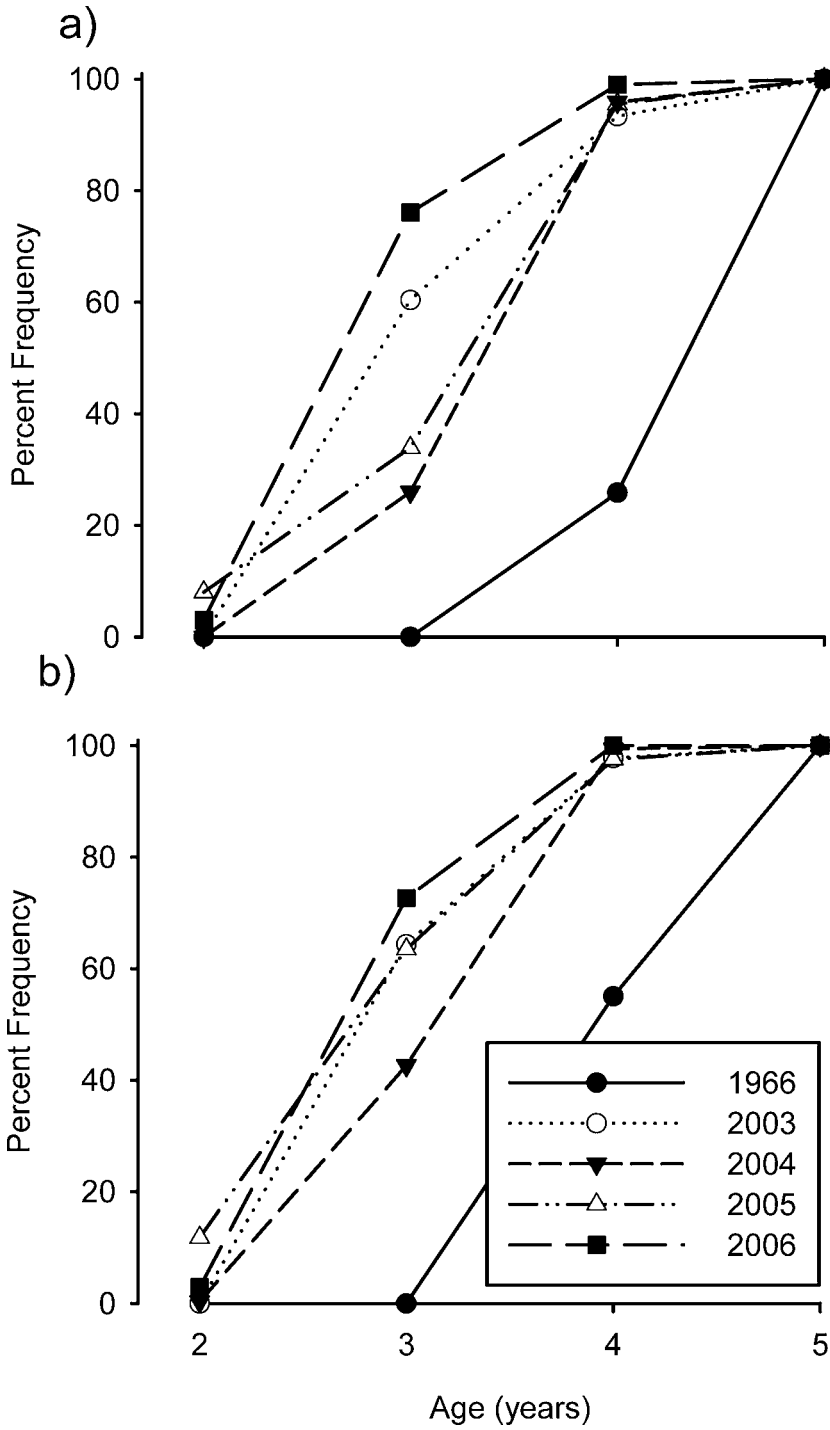


FIGURE 7.—Cumulative age frequency of first-spawn alewives at Bride Brook (East Lyme, Connecticut), in 1966 and 2003–2006: (a) females and (b) males.

al. 2004). The demographic and life history shifts detailed here are also consistent with heavy exploitation, and therefore overfishing must also be considered as a contributing factor. While the lack of postmortality recovery may appear to discount the overfishing hypothesis, fishery closures are often unsuccessful at producing effective recovery of heavily exploited species (Dempson et al. 2004; Hutchings and Reynolds 2004). This is particularly true for instances in which recovery of a population at low abundance is hampered by heavy predation or deleterious life history shifts (Bundy and Fanning 2005; Hutchings 2005; De Roos et al. 2006; Walsh et al. 2006). It is therefore premature to dismiss the possibility that prolonged exploitation over the last 40 years contributed to shifts in abundance, demography, and life history at Bride Brook. Furthermore, the moratorium on directed harvest has not completely eliminated fishing mortality. River herring are taken as bycatch in some oceanic commercial fisheries, particularly the paired midwater trawl fishery for Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus* (Atlantic States Marine Fishery Council 2007; Kritzer and Black 2007; Cieri et al. 2008). This fishery experienced considerable growth in the 1990s (New England Fisheries Management Council 2005; Mid-Atlantic Fishery Management Council 2007), roughly coincident with regional river herring declines. While available observer data do not support river herring bycatch of the magnitude necessary to explain recent declines (Savoy and Crecco 2004; Crecco and Benway 2008), observer coverage on midwater trawl vessels has been well below levels needed to produce robust estimates of river herring bycatch (Babcock et al. 2003; Kritzer and Black 2007). Recent analyses suggest that bycatch mortality may be as significant as mortality previously produced by directed fisheries, particularly in southern New England (Cieri et al. 2008). Future studies should test the plausibility and relative contribution of predation and bycatch mortality as mechanisms for river herring declines.

There is no evidence that the alewife run at Bride Brook is recovering under the current management regime. Indicators of population recovery relevant to the time frame of this study should include small but detectable increases in abundance and proportions of larger, older fish in the population (Schram et al. 1995; Olney et al. 2003; Mills et al. 2005; Phelan et al. 2008). Our study provides no evidence of such a recovery; on the contrary, all indications are that stressors sufficient to hamper recovery are still in effect. Fisheries managers must therefore seek to move beyond the initial pragmatic step of closing river herring fisheries and develop a more comprehensive plan for river

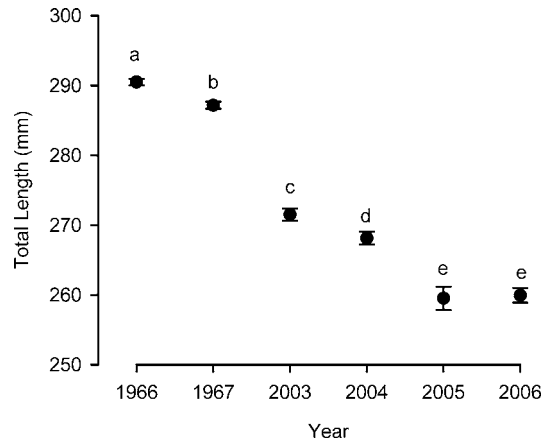


FIGURE 8.—Mean total length (± 2 standard errors) of alewives sampled at Bride Brook (East Lyme, Connecticut), in 1966–1967 and 2003–2006. Means with the same letters are not significantly different ($\alpha = 0.05$, Tukey's honestly significant difference tests).

herring recovery. Research efforts should focus on quantitative tests of hypotheses concerning likely causative factors, such as predation and bycatch mortality. The results of these studies will inform the development of new management strategies to ameliorate river herring declines. Expanded monitoring across a broader spatial scale will also be necessary to assess the generality of the demographic and life history shifts described here. Monitoring over a prolonged time period will be required to assess population recovery. While river herring populations have high resilience due to short generation time and high fecundity (Gotelli 2001), complete recovery to historic abundance and population structure will likely not occur within a decade even upon complete mitigation of population stressors. Recovery will be hampered by deleterious changes in life history traits, which will likely be much slower to recover to a historic condition (De Roos et al. 2006; Walsh et al. 2006). Given these considerations, monitoring efforts will have to occur over multiple decades to adequately assess population recovery. Finally, studies of river herring populations have largely focused on adults during the spawning run. The characteristics of other ontogenetic stages, particularly the marine residence period, are relatively understudied. Studies that provide greater understanding of the critical factors regulating river herring populations throughout their life cycle may provide fresh insight into recent declines.

Our results demonstrate the utility of demographic and life history assessment in addressing population declines. The types of directional shifts described in

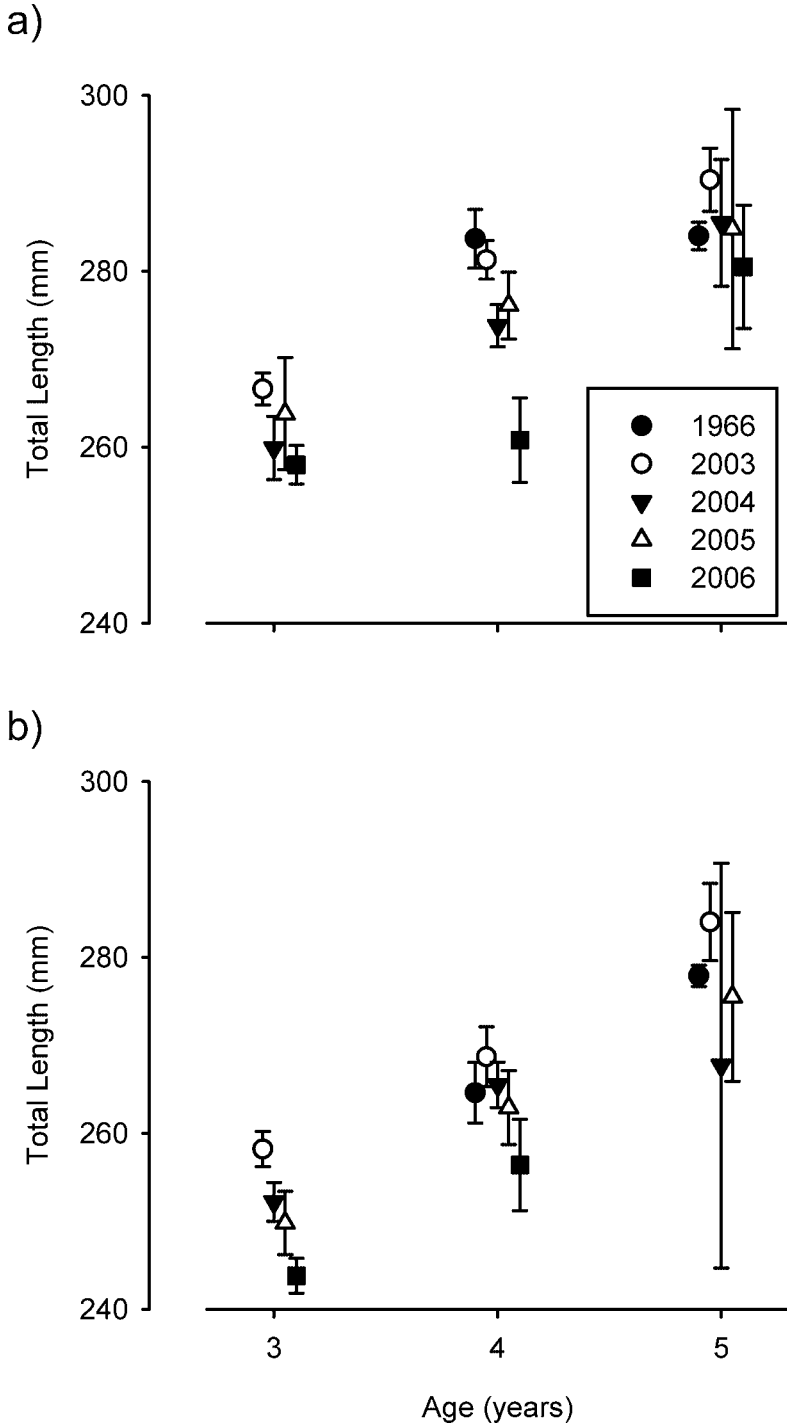


FIGURE 9.—Mean total length at age (± 2 standard errors) of alewives at Bride Brook (East Lyme, Connecticut), in 1966 and 2003–2006: (a) females and (b) males. Data points are offset for clarity.

this study greatly inform development of testable hypotheses concerning the agents of decline and also identify important information gaps that will need to be addressed to test these hypotheses. The informative nature of these types of studies also underscores the importance of accumulating baseline data on demography and life history so that in the event of unanticipated population declines, there is a comparative basis for assessment of temporal shifts.

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