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Population dynamics of bloaters *Coregonus hoyi* in Lake Huron, 1980–1998*

Jeffrey S. Schaeffer

USGS Great Lakes Science Center, 1451 Green Rd., Ann Arbor, MI 48105, USA

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I investigated population dynamics of bloaters *Coregonus hoyi* in Lake Huron using data collected during 1980–1998 from fixed-site trawl surveys. Bloaters were uncommon in 1980, but abundance increased during 1980–1992 through a series of strong year classes. High adult abundance appeared to suppress recruitment after 1992, and the population subsequently declined. Growth was similar between sexes up to age-5, thereafter females grew faster than males. Both sexes lived to age-9, but females tended to live longer than males. A Ricker least-squares stock–recruitment relationship defined the relationship between adults and age-3 recruits, and may have been due to egg predation by adult bloaters. Higher female survival and shift in age structure toward older ages after 1990 led to female predominance in the population during 1995–1998. Female predominance appeared to be a consequence and not a cause of the observed population cycle.

Introduction

The bloater *Coregonus hoyi* is the smallest and only remaining species from a species flock of seven deepwater coregonines formerly occurring in Lakes Michigan or Huron (Koelz 1929, Smith 1964). Known collectively as deepwater ciscoes, other members of the flock were extirpated through a combination of overfishing and interactions with invasive marine fishes (Smith 1968, Crowder 1980, Brown *et al*. 1985, Brown *et al*. 1987). Although the only extant deepwater cisco within Lake Huron, bloaters are numerically abundant in offshore habitats between 30 and 100 m, have high commercial value, and they serve occasionally as prey for lake trout *Salvelinius namaycush* and burbot *Lota lota* (Fratt *et al*. 1997, Madenjian *et al*. 1998).

Historically, bloaters were a minor component of the deepwater cisco fishery because they had low market value due to their small size and thin abdominal wall (Jobes 1942). However, their commercial importance increased during the 1950s after sea lampreys decimated native lake trout and other cisco fisheries collapsed (Baldwin & Saalfield 1962, Brown *et al*. 1987). Bloater yields increased after 1950 and reached historic highs during 1955–1965, but the population collapsed during 1965–1970, and had not recovered by 1980 despite restrictions on most Lake Huron commercial fisheries in 1971 (Brown *et al*. 1987).

Although overfishing and interactions with exotic species were thought to underlie stock collapse, extreme female predominance may have exacerbated the decline. Brown (1970)

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Fig. 1. Locations of fixed site trawl collections for bloaters, Lake Huron, 1980–1998.

and Brown *et al.* (1987) found extreme female dominance in Lakes Michigan and Huron during 1965–1970, and believed that reproductive inefficiency resulting from female dominance reduced stock resilience during periods of overfishing. Reasons for skewed sex ratios are not known, but several mechanisms have been proposed. Female predominance has been observed in most Great Lakes coregonids and has been attributed simply to seasonal differences in male and female distributions (Dryer & Beil 1968), but alternative hypotheses include differential mortality between sexes (Hile 1936, Jobes 1946, Deason & Hile 1944), endocrine response to changes in population size (George 1977), and possibly interactions with alewife (Brown *et al.* 1987). However, recent data from Lake Michigan suggest that female predominance was a consequence of shift in age structure toward older fish combined with higher male mortality (Tewinkel *et al.* 2002).

In Lake Huron bloaters again became abundant during the late 1980s, but declined during the 1990s even though fishing mortality was apparently low. This study uses results of long-term monitoring to examine bloater population trends in Lake Huron from 1980 to 1998, and evaluates possible mechanisms underlying bloater recovery and subsequent decline during this period. I also corroborate the mechanism proposed by Tewinkel *et al.* (2002) for female predominance in Lake Michigan.

Methods

Each year, trawling was conducted near five ports in U.S. waters: De Tour, Hammond Bay, Alpena, Au Sable Point, and Harbor Beach (Fig. 1). At each port, four bottom tows were made using a 21-m wing trawl towed on-contour for 10 minutes at the four depths contours where bloaters were generally most abundant: 46 m, 55 m, 64 m, and 73 m.

After 1991, the bloater survey was expanded by adding on-contour tows at shallower and deeper depths. I used a subset of tows from the expanded survey to make the data comparable with the bloater survey. This allowed analysis of population characteristics from 1980 through 1998. The bloater survey was usually initiated and completed during September, while the expanded survey was usually carried out during October or November. I assumed that there were no differences in bloater abundance or distribution between September and October. Annual abundance was calculated for age-0 and adult bloaters as mean catch per 10-minute tow (catch-per-unit-effort, CPUE).

All trawl catches were sorted to species, counted, and weighed in aggregate. Catches greater than 20 kg were subsampled. Bloaters less than 120 mm TL were designated as age-0 based on results of historic age and growth data (USGS Great Lakes Science Center, unpublished data). Bloater longer than 120 mm were assigned ages based on scale samples. A random sample of adult bloaters were measured (mm) from each tow for length frequency.

From each port, a randomly stratified subsample of 5 individuals per 5 mm length group

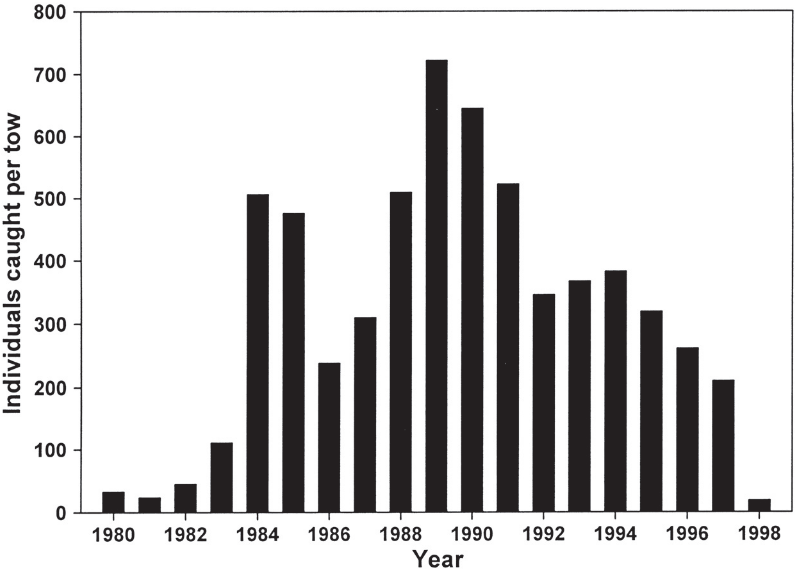

Fig. 2. Abundance (mean CPUE) of adult bloaters at fixed trawl sites in Lake Huron, 1980–1998.

was measured (mm) weighed (g), sexed, and a scale sample was taken for ageing. Scale samples collected from bloaters were pressed into acetate slides and read by GLSC personnel.

Sex ratio by age was pooled among years. Relationships among sex ratio, age structure, and relative abundance were examined using linear regression. Recruitment was modeled using a Ricker stock–recruitment model in a manner similar to Brown and Eck (1992) and Tewinkel *et al.* (2002) where,

$$R = aSe^{-bS} \tag{1}$$

where R is relative number of recruits, S is relative number of number of eggs spawned, a is a constant, and b is a parameter with the dimensions $1/S$ (Eq. 1). Relative number of eggs spawned (S) was based on CPUE of mature females collected the previous fall, percent mature at age, and weight-specific fecundity, presented as

$$F = 560.60 + 58.80W \tag{2}$$

where F = estimated number of eggs per individual female, and W is mean weight (g) of females of a given age in a given year (Eq. 2). Coefficients for this relationship were taken from Lake Michigan bloaters (Emery & Brown 1978) and assumed to be identical for the Lake Huron population. Relative abundance of spawned eggs was estimated annually by multiplying female age-specific CPUE by age-specific fecundity, then summing totals across age classes. Because age-0 through 2 bloaters are generally pelagic and not susceptible to bottom trawls (Wells & Beeton 1963, Wells 1968, Crowder & Crawford 1984), I used CPUE of age-3 recruits as an index of year class strength (R).

Results

Adult bloaters were rare at the beginning of the study, but abundance increased sharply during 1982–1985 (Fig. 2). Peak abundance occurred during 1988–1995, but was followed by rapid decline during 1996–1998 when the population declined to levels observed during 1980 (Fig. 2).

Abundance of age-0 bloater was highly variable. Age-0 bloaters are pelagic and generally not vulnerable to bottom trawls (Crowder & Crawford 1984), but high CPUE of age-0 fish were observed during 1983, 1985, 1988, and 1989 (Fig. 3). Year class strength based on age-0 CPUE was consistent with time lagged CPUE of age-3 fish for 1985, 1988, and 1992, but the two indices were inconsistent during 1982, 1983, and 1989 (Fig. 3).

Male and female bloater lived up to age-9, but females lived longer than males and domi-

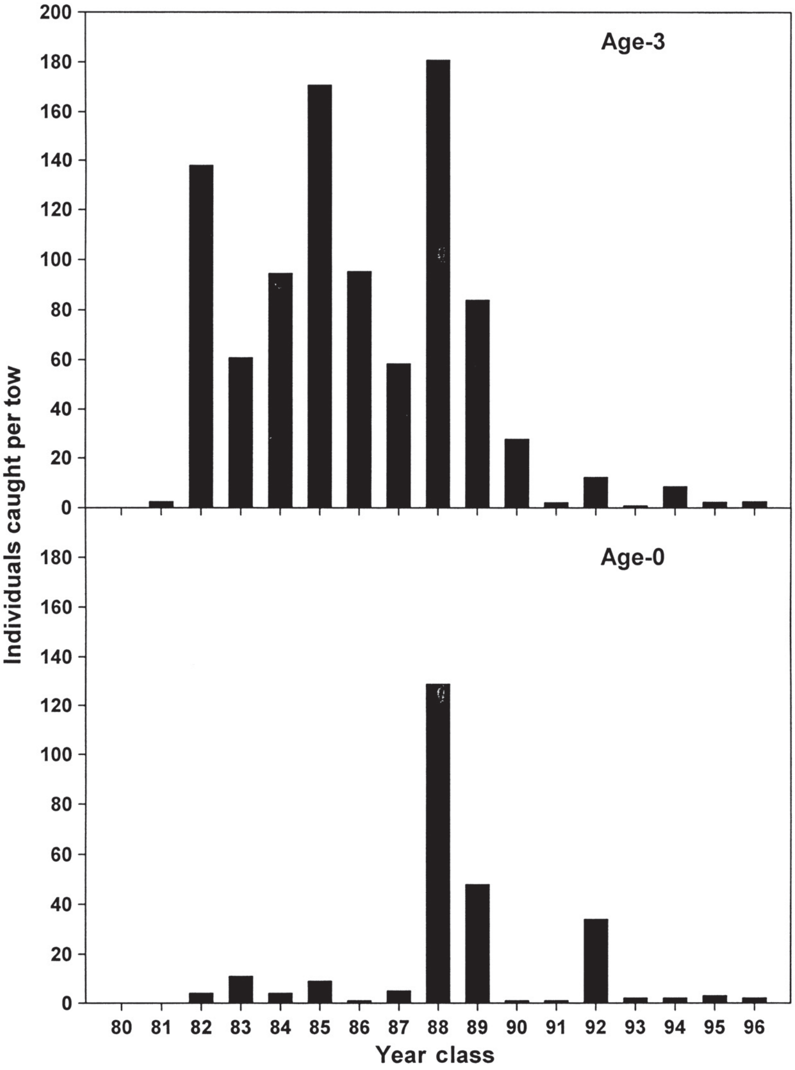

Fig. 3. Bloater recruitment tends based on bottom trawl CPUE of age-0 and age-3 fish, Lake Huron, 1980–1998.

nated older age classes (Fig. 4). Mean length at age was similar between sexes up to age-6, thereafter females were significantly larger than males (ANOVA: $P < 0.05$, 9 tests) (Fig. 5). Mean length at age of age-3 and older bloaters decreased as population size increased during 1980–1991 (Fig. 6). Mean length at age was negatively correlated with total abundance index for age-3 through age-8 fish ($P < 0.05$, 6 of 6 comparisons significant). Correlation coefficients ranged from –0.42 to –0.79, and increased with age, suggesting that intraspecific effects were more severe for older fish. After 1991, mean length at age increased for most age classes as abundance declined (Fig. 6).

A Ricker least-squares stock–recruitment model suggested that 65% of the variability in recruitment from 1981–1996 could be explained by relative estimates of egg deposition (Fig. 7). Model results suggested that strong year classes were produced during the 1980s, but that little or no reproduction occurred after 1990 despite higher potential egg deposition compared with the 1980s (Fig. 7).

From 1980 through 1998, the percentage females in the population increased linearly (Percent female = 37.301 + (0.272 × Percent > age 4), $P < 0.05$, $r^2 = 0.46$) (Fig. 8). Lack of reproduction after 1992 combined with a tendency of females to outlive males caused a shift in age

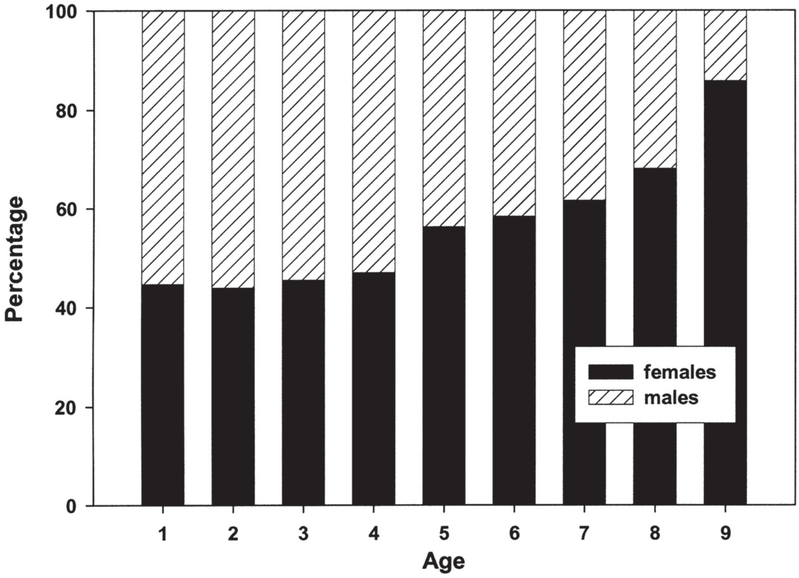

Fig. 4. Change in sex ratio with age for bloaters collected from Lake Huron. Data from 1980–1998 were pooled.

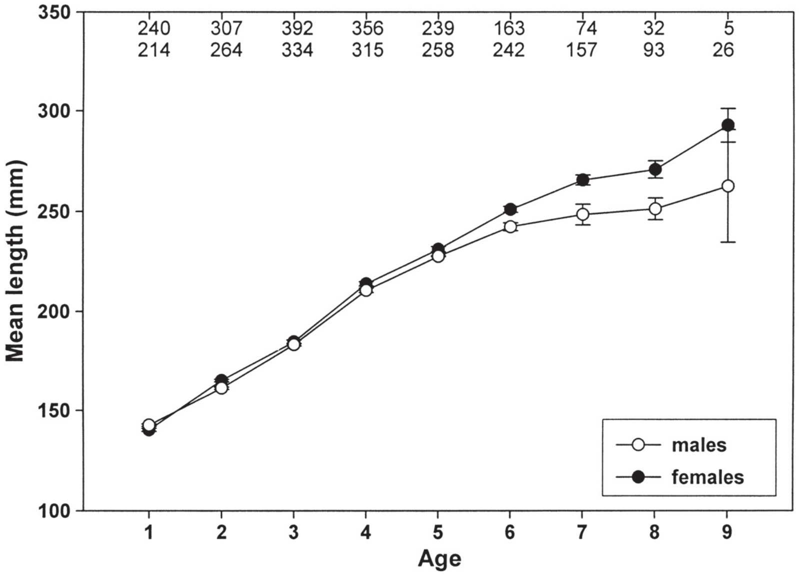

Fig. 5. Mean length at age and confidence intervals for male and female bloaters from Lake Huron. Data from 1980–1998 were pooled. Sample sizes of aged fish are listed above point estimates, and confidence intervals smaller than symbols are not visible.

structure toward older fish, but high female predominance occurred only during the final years of the study (Fig. 8).

Discussion

In Lake Huron, bloaters exhibited a population increase beginning about 1980. Population levels increased throughout the 1980s, remained stable at lower abundance during the early 1990s, and declined during 1994–1999. Mean length at age declined for most age classes as population size increased, but then increased as abundance declined through the 1990s. Population decline appeared to be caused by lack of recruitment after 1992. After recruitment ceased, the age structure shifted toward older fish. A combination of higher female survival and shift in age structure led to female predominance in the population during 1996–1998.

My results were almost identical to population charactistics observed in Lake Michigan bloaters during 1973–1998. There, bloater abun-

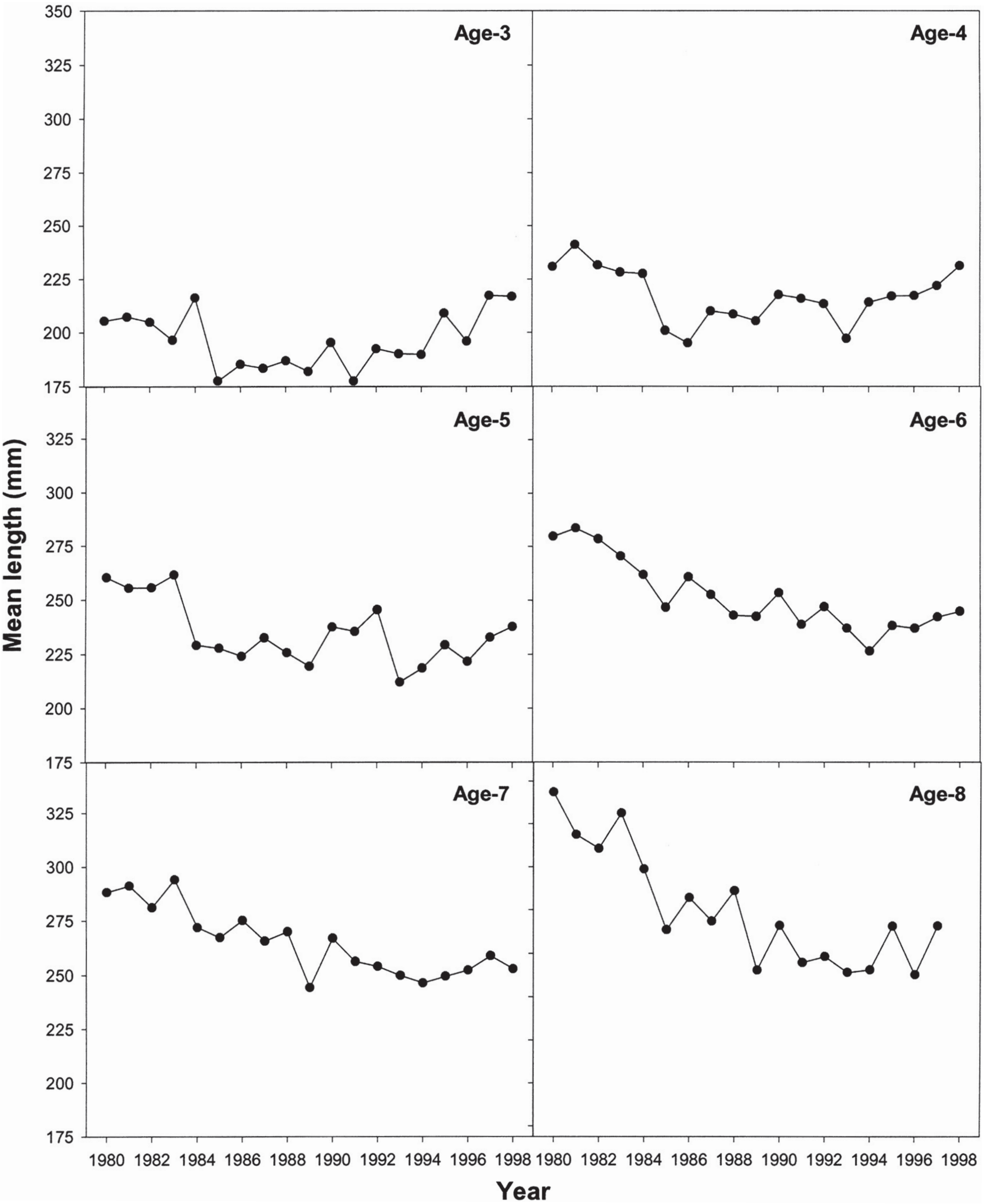

Fig. 6. Change in mean length through time for age-3 through age-7 bloater collected from Lake Huron, 1980–1998. Sexes were pooled.

dance increased during 1979–1984 (Brown *et al.* 1987), reached a plateau during 1984–1989, and then declined steadily through 1998 (Tewinkel *et al.* 2002). Population increase during the 1980s was followed by density dependent growth reduction, reduced recruitment, and a shift in age structure toward older fish. Greater longevity of females under those conditions led to female predominance (Tewinkel *et al.* 2002).

My results were inconsistent with obser-

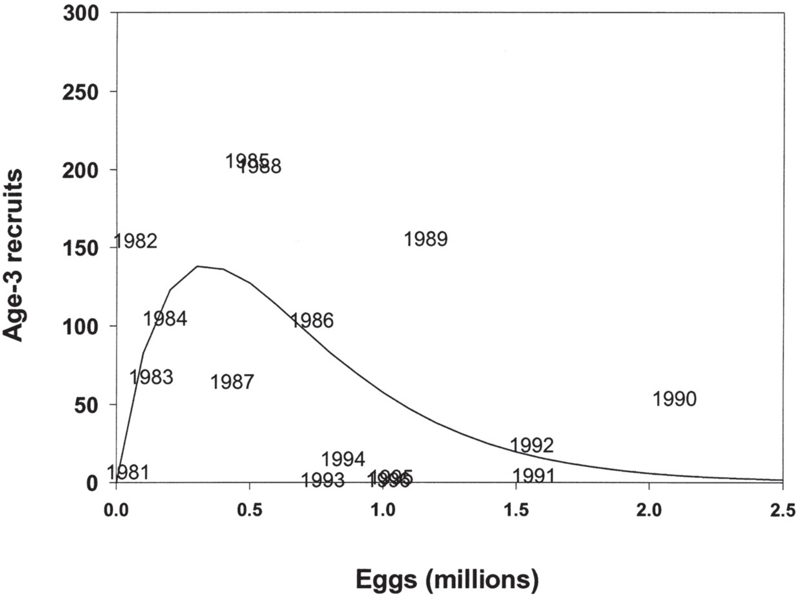

Fig. 7. Ricker least-squares stock–recruit relationship for bloaters, Lake Huron, 1981–1996. Stock size was calculated as relative number of eggs spawned, and recruits represent relative abundance of age-3 fish.

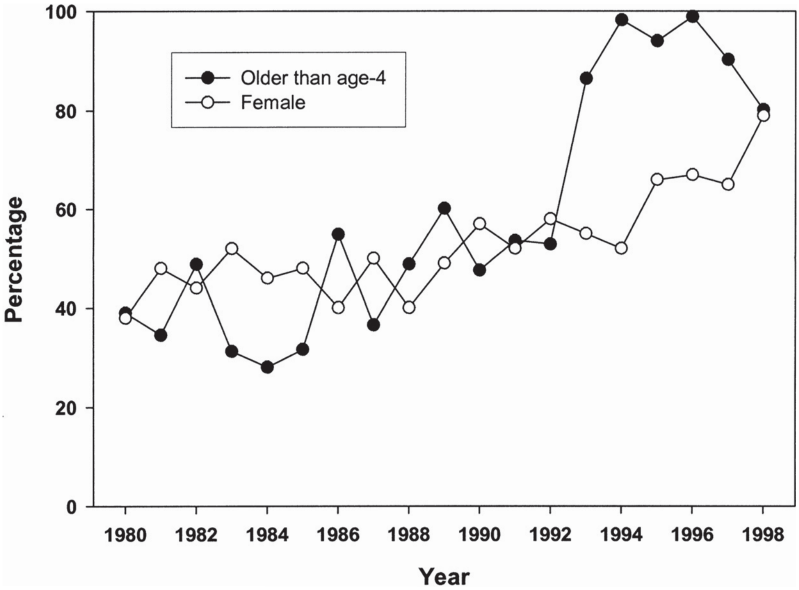

Fig. 8. Temporal trends in age structure and female predominance for bloater, Lake Huron, 1980–1998.

vations on bloater dynamics of Lake Michigan during the 1960s. Brown (1970) found chronic, extreme female predominance during 1960–1970, and found four consecutive year classes (1960–1964) in which sex ratios were established by age-3. I found a shorter period of female predominance, and sex ratios did not become skewed until the proportion of age-4 and older fish exceeded 80%. Higher differential mortality in the Lake Michigan population during 1960–1970 could have caused female predominance at a younger age.

Reasons underlying higher male mortality are not known, but Tewinkel *et al.* (2002) suggested that male bloaters may have higher energetic costs or that females survive better under adverse environmental conditions. Alternatively, Bowen *et al.* (1991) suggested that female predominance in lake herring (and possibly other coregonids) was more likely due to change in age of maturity. This was probably not the case for bloater in Lake Huron because there was no detectable relationship between maturation schedule and abundance.

I assumed that all age classes had similar spatial distributions that were consistent through time. This assumption was probably violated. Juvenile bloaters are pelagic, and undergo a habitat shift to the benthos at age-3 (Crowder & Crawford 1984). It is likely that fast-growing individuals made the transition sooner and became more vulnerable to the trawl. This would have overestimated mean length at age for age-1 through 3 fish in all years, and especially in years of high abundance. This could have obscured mid-cycle decreases in growth for those age classes. Since growth declines of age-3 bloater were observed, the bias was not severe enough to obscure the trend, but density-dependent effects may have been even more severe than estimated by growth declines.

As growth declined, bloaters may have required longer to transition to the benthic habitat, and at times of slower growth age-3 bloater may have remained in pelagic habitat longer. Consequently, abundance of age-3 bloaters may have been underestimated during times of peak abundance. This would have not biased conclusions regarding population increase and subsequent decline, but it could have altered the stock recruitment curve by underestimating egg deposition rates and recruit abundance during the middle years of the population cycle. This would not have affected the central conclusion that a Ricker model was appropriate because the contribution of age-3 fish to total egg deposition was nearly always small as compared with other age classes, and age-3 fish dominated total CPUE during only 2 of the 16 years used in the analysis.

Bloaters were arbitrarily assigned as age-0 based on length. This may have biased age-0 abundance estimates during 1983 and 1989 because slower growing age-1 bloaters from the putatively strong year classes of 1982 and 1988 may not have exceeded 120 mm the following year, and would have been incorrectly classified as age-0 fish. This undoubtedly occurred during 1983 and 1989 because year class strength estimates based on CPUE of age-3 fish were lower than those obtained from age-0 fish.

The mechanism underlying the stock–recruitment relationship is unknown. Ricker models can often be fit in situations where there is cannibalism, disease transmission, reproductive interference among adults, or a combination of density-dependent growth coupled with size-dependent predation (Hillborn & Walters 1992). None of these mechanisms seem applicable to bloater. Cannibalism is unlikely because adults and juveniles are segregated spatially, and adult bloaters are rarely piscivorous (Wells & Beeton 1963). During this study, no large scale epizootics were reported and spawning interference seems unlikely because bloaters are probably broadcast spawners. Bloaters exhibited density dependent growth, but adults are not considered to be a common prey of introduced salmonids, lake trout, or burbot (Diana 1987, Fratt *et al.* 1997, Madenjian *et al.* 1998). Thus, size selective predation seems unlikely. However, one possible mechanism might be egg predation.

Although Lake Michigan bloaters generally consumed zooplankton, fish eggs were eaten commonly, with the highest egg consumption occurring during spring at depths of 78–110 m (Wells & Beeton 1963). Wells and Beeton (1963) believed that consumed eggs were those of bloater, and thought that winter sampling would have revealed high levels of egg predation. Cannibalism through egg predation by adult bloaters would be consistent with the observed stock–recruitment pattern.

Brown *et al.* (1987) hypothesized that female predominance might be population regulation mechanism for bloaters, and predicted that female predominance should occur during the late 1980s. My results would refute that hypothesis because female predominance did not appear until the mid-1990s, and recruitment failure began when population abundance was high and female predominance absent. Sex ratios shifted only after five consecutive years of low recruitment, differential mortality, and population decline. Female predominance appeared to be a consequence rather than a cause of decreased abundance, thus reproductive inefficiency seems unlikely.

Bloaters experienced a population cycle that occurred over 18 years in the absence of extrinsic factors commonly thought to regulate their abundance such as overfishing (Brown *et al*. 1987) or interactions with non-native marine fishes (Brown & Eck 1992). The increase and decline during 1980–1998 occurred in the absence of any significant commercial fisheries in U.S. waters, and during a time period when invasive species were less common as compared with the 1960s and 1970s (USGS unpubl. data). Intrinsic stock–recruitment relationships may regulate bloater abundance. If true, bloater abundance should increase again during 2000–2005, with an age structure skewed toward younger age classes and even sex ratios. This hypothesis can be tested because annual assessment of bloaters will continue. Although the mechanism underlying the stock–recruitment relationship is unknown, bloater abundance may be predictable, which would benefit commercial fishers and fisheries managers.

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