

Long-term trends of bloater (*Coregonus hoyi*) recruitment in Lake Michigan: evidence for the effect of sex ratio

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Abstract: Long-term population trends are generally explained by factors extrinsic (e.g., climate, predation) rather than intrinsic (e.g., genetics, maternal effects) to the population. We sought to understand the long-term population dynamics of an important native Lake Michigan prey fish, the bloater *Coregonus hoyi*. Over a 38-year time series, three 10- to 15-year phases occurred (poor, excellent, and then poor recruitment) without high interannual variability within a particular phase. We used dynamic linear models to determine whether extrinsic (winter and spring temperature, alewife predator densities) or intrinsic factors (population egg production, adult condition, adult sex ratio) explained variation in recruitment. Models that included population egg production, sex ratio, winter and spring temperature, and adult bloater condition explained the most variation. Of these variables, sex ratio, which ranged from 47% to 97% female across the time series, consistently had the greatest effect: recruitment declined with female predominance. Including biomass of adult alewife predators in the models did not explain additional variation. Overall our results indicated that bloater recruitment is linked to its sex ratio, but understanding the underlying mechanisms will require additional efforts.

Résumé : Les tendances démographiques à long terme s'expliquent généralement par des facteurs extrinsèques à la population, tels que le climat ou la prédation, plutôt que par des facteurs intrinsèques, comme la génétique ou les effets maternels. Nous avons tenté de comprendre la dynamique de population à long terme d'un poisson proie indigène d'importance au lac Michigan, le cisco de fumage, *Coregonus hoyi*. Dans une série chronologique de 38 ans, il s'est produit trois phases de 10–15 ans, de recrutement faible, excellent et de nouveau faible, sans grande variation entre les années durant une phase donnée. Des modèles dynamiques linéaires nous ont servi à déterminer si la variation du recrutement s'explique par des facteurs extrinsèques (températures de l'hiver et du printemps, densité des prédateurs) ou intrinsèques (production d'oeufs de la population, condition des adultes, sex-ratio des adultes). Les modèles qui incluent la production d'oeufs de la population, le sex-ratio, les températures d'hiver et de printemps et la condition des ciscos adultes expliquent le maximum de variation. De ces variables, le sex-ratio, qui va de 47 à 97 % dans la série chronologique, a régulièrement l'effet le plus prononcé : le recrutement diminue lorsque les femelles prédominent. L'addition de la biomasse des prédateurs, les gaspareaux adultes, dans le modèle n'explique pas de variation supplémentaire. Dans leur ensemble, nos résultats indiquent que le recrutement du cisco de fumage est relié au sex-ratio, mais il faudra faire des travaux additionnels pour comprendre les mécanismes sous-jacents.

[Traduit par la Rédaction]

Introduction

Ecologists have long sought to understand the dynamics of populations within a time series. Some dynamics are more short term, with stochastic fluctuations from year to year. Others are more long term, and some can even be characterized by predictable oscillations or cycles. To explain both types of trends, ecologists have focused on the role of factors both extrinsic (e.g., abiotic factors, predation, interspecific competition, disease) and intrinsic (e.g., cannibalism, genet-

ics, maternal effects) to the population. Extrinsic factors, however, have generally received greater attention when trying to explain long-term changes in population abundance. For example, decadal fluctuations in porcupine abundance relate to 11- and 22-year cycles in solar activity (Klvanan et al. 2004), and the well-known 10-year cycles of snowshoe hares appear to be regulated by both the abundance of their prey and the densities of their predator, the lynx (Krebs et al. 2001). Evidence for factors intrinsic to the population influencing long-term trends has generally been limited to ma-

Received 1 June 2005. Accepted 9 November 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 4 March 2006.
J18716

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ternal effects on reproductive output (e.g., Boonstra 1994; Ginzberg and Taneyhill 1994) or cannibalism or intraspecific competition among cohorts (Bjørnstad et al. 1999; Sander-son et al. 1999).

Ecologists studying fish populations have generally focused on year-to-year fluctuations in abundance rather than on long-term patterns and cycles in abundance. This bias is not a result of fish populations failing to exhibit long-term or cyclical trends. In fact, a meta-analysis of animal populations revealed mammals and marine and anadromous fishes to be the most common taxa to cycle (Kendall et al. 1998). Rather, focus on interannual fluctuations is more likely a result of fish populations commonly producing highly variable and unpredictable numbers of recruits. Because these fluctuations can have a considerable impact on commercial fisheries or on the dynamics within an ecosystem, understanding the mechanisms underlying interannual variation in recruitment has been a primary goal in fisheries (Houde 1987). Recently, however, attention is turning toward longer-term and cyclic trends in the recruitment and population dynamics of exploited anadromous and marine fishes. For example, researchers have found that regional climate patterns (i.e., Pacific Decadal Oscillation, Aleutian Low Pressure index) appear to influence the decadal and multidecadal population trends in Pacific salmon (Beamish and Bouillon 1993), Pacific halibut (Clark and Hare 2002), and Japanese sardine (Wada and Jacobson 1998). Long-term trends of Atlantic cod (*Gadus morhua*) populations off the Norwegian coast, conversely, appear to be influenced by cannibalism and competition among cohorts (Bjørnstad et al. 1999), factors intrinsic to the population.

In this paper, we seek to add to the understanding of long-term population trends of fishes by focusing on a freshwater taxon, the bloater (*Coregonus hoyi*), which exhibits a rather unusual recruitment (i.e., number surviving to age 3) and population trend. Over a 38-year time series in Lake Michigan, bloaters have gone from a phase of low recruitment (1964 to 1976) and low population size to a phase of increased recruitment (1977 to 1994) and population size, and then back to a phase of low recruitment (1995 to 2001) and reduced population size (Madenjian et al. 2002; TeWinkel et al. 2002). Thus, unlike other fishes that typically show strong interannual variability in recruitment over a 10- to 15-year period (e.g., Bjørnstad et al. 1999), bloaters appear to go through regular 10- to 15-year phases of either low or high recruitment (or subsequently low or high population size) without high interannual variation within a phase. Because of the regularity of these phases over 38 years of data, bloater populations have been hypothesized to undergo cycles in abundance (Madenjian et al. 2002), although additional data are needed to verify this hypothesis.

Factors both extrinsic and intrinsic to the population have been hypothesized to influence bloater recruitment in Lake Michigan. Exotic adult alewives (*Alosa pseudoharengus*) have been hypothesized to reduce bloater recruitment by preying on bloater larvae or reducing prey for zooplanktivorous bloater larvae (Wells and McLain 1973; Eck and Wells 1987). Similarly, cold temperatures during winter and spring have been hypothesized to reduce bloater recruitment by lengthening the period of egg development and reducing the growth rates of bloater larvae, which in turn increases sus-

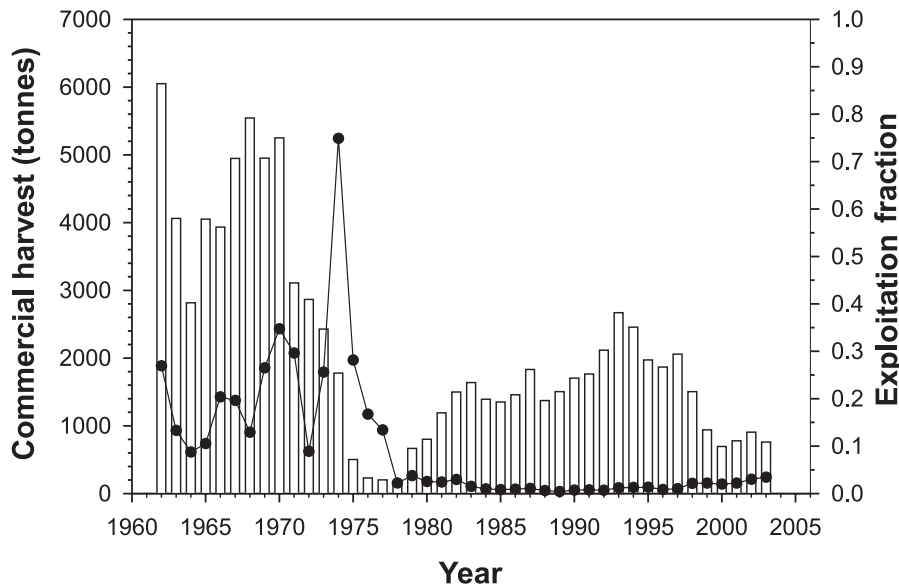
ceptibility to predators (Rice et al. 1987). With regard to intrinsic factors, female predominance among adults has been hypothesized to limit recruitment and regulate bloater population size (Brown et al. 1987). For other species such as Atlantic cod, recent studies have found maternal condition to influence the fecundity (Kjesbu et al. 1991), egg quality (Ouellet et al. 2001), and even recruitment to age 3 (Marshall et al. 1999). Because bloaters have exhibited density-dependent growth rates and one of their primary adult prey items, *Diporeia*, has precipitously declined in Lake Michigan (Nalepa et al. 1998), we may expect that changes in bloater condition could influence bloater recruitment. Finally, an underlying theory of fisheries biology is that recruitment is related to some measure of its stock size, such as population egg production (Hilborn and Walters 1992). Using a Bayesian approach to time series analysis, we investigated whether variation in bloater recruitment in Lake Michigan could be explained by these factors extrinsic (adult alewife biomass, winter and spring temperatures) or intrinsic (population egg production, adult sex ratio, adult condition) to the population.

Materials and methods

Bloater commercial fishing and life history in Lake Michigan

Bloaters are the smallest of the seven deepwater cisco species that were once found in the Laurentian Great Lakes (Smith 1964). The larger cisco species were largely extirpated from the lake by the mid-1960s, owing primarily to high rates of commercial harvest (Wells and McLain 1973). By default of the loss of the other ciscoes, bloaters became the target of the commercial fishery by the early 1960s. To estimate the impact of commercial fishing on bloater population dynamics, we calculated exploitation fraction (i.e., biomass of commercial harvest / biomass of population) from 1962 through 2004. Commercial harvest data were made available through the Great Lakes Commercial Catch Database (S.R. Nelson, US Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA, personal communication). We extrapolated depth-specific mean densities from our bottom trawl survey (details below) to the area of Lake Michigan between 5 m and 114 m to estimate adult bloater biomass (Madenjian et al. 2005a); this is a very conservative population biomass estimate because it assumes an unrealistic catchability coefficient of 1.0 and does not include bloater biomass that occurs in depths 115 m and greater. From 1962 through 1977, these putatively high exploitation fractions averaged 0.23, with an unusually high value of 0.75 in 1974 (Fig. 1). By 1964, commercial fisheries were dominated by gillnets, rather than bottom trawls, and the gillnets used large meshes (>6.4 cm) that targeted larger, older individuals, with age-4 and older bloaters comprising 92%–95% of the catch by number (Brown et al. 1985). Owing to declining bloater population sizes, a commercial fishery closure was enacted in 1976 (Brown et al. 1985). It is unclear when the closure was lifted, but the commercial harvest increased to more than nominal levels (i.e., >600 tonnes) by 1979. Since 1979, however, exploitation fractions have been less than 0.02, on average (Fig. 1). During the early 1970s, however, it is likely

Fig. 1. Time series of commercial harvest (open bars) and exploitation fraction (line graph) of bloaters (*Coregonus hoyi*) in Lake Michigan.



that the commercial fishery was reducing the bloater spawning stock biomass and resultant egg production. However, we did not include exploitation fraction as a potential explanatory extrinsic variable in our analyses to explain recruitment for two reasons. First, the commercial fishery was not harvesting age-3 bloaters, which was our index of bloater recruitment. Second, the effects of exploitation fraction were already reflected in population egg production, which was included in our analyses.

In Lake Michigan, bloaters spawn between January and March on bottom substrate in 40 m to more than 110 m of water (Wells 1966; Emery and Brown 1978; Rice et al. 1987). Newly hatched larvae (i.e., still containing yolk sacs) have been collected in this same habitat during mid-April through mid-August, with the peak densities observed during May and June (Rice et al. 1987). During June through September, larger, older larvae begin migrating to shallower waters and have been sampled near the surface during the day at the same depth contours (Crowder and Crawford 1984; Rice et al. 1987). Age-0 bloaters are zooplanktivorous and appear to be daytime feeders (Crowder and Crawford 1984). Bloaters continue to occupy the epilimnion and metalimnion through age 1 or even age 2 (Crowder and Crawford 1984). As bloaters age (>age 2) and grow to larger sizes (i.e., >150 mm total length, TL), they become benthic and occupy the hypolimnion for the remainder of their life (Crowder and Crawford 1984; TeWinkel and Fleischer 1999). They are concentrated at depths greater than 70 m and remain on the bottom during the day and vertically migrate about halfway through the hypolimnion at night (TeWinkel and Fleischer 1999). Bloaters primarily consume amphipods (i.e., *Diporeia* spp.) and opossum shrimp (*Mysis relicta*) but will also consume zooplankton (Crowder and Crawford 1984; TeWinkel and Fleischer 1999). The natural predators of bloaters, lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), also underwent a marked decline by the 1950s as a result of sea lamprey parasitism. Since then, Pacific salmonids have been

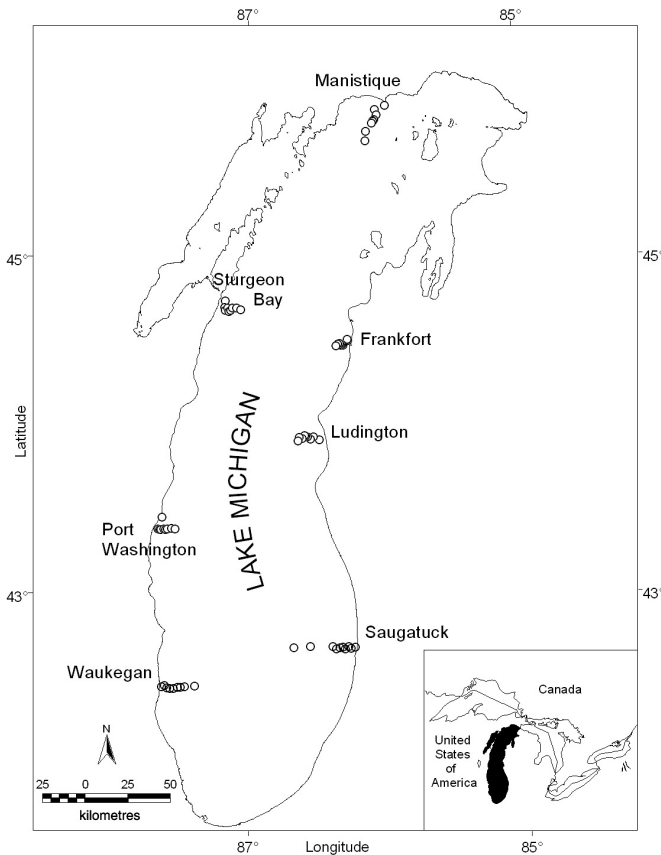
introduced and lake trout are sustained only through stocking, but these potential predators have generally made bloaters only a minor proportion of their diet (Jude et al. 1987; Madenjian et al. 1998).

Field sampling

Since 1962, the Great Lakes Science Center (GLSC) has conducted an annual bottom-trawl survey for preyfish on Lake Michigan (Madenjian et al. 2005b). Beginning in 1991, the survey was initiated about 3 weeks earlier than previously so that a GLSC lake trout spawning survey could be completed during late October and early November. The average duration of the survey has been 26 days. Minor changes in the ports and depths that are sampled have occurred over the years. In this paper, we use data from seven ports (Frankfort, Ludington, Manistique, Port Washington, Saugatuck, Sturgeon Bay, and Waukegan) that have been sampled with near consistency since 1973 (Fig. 2). Exceptions include Port Washington in 1976 and 2000, Manistique in 1995, 2000, 2001, and 2002, Saugatuck in 2000, and Waukegan in 2000. In 1998, all ports were sampled but we do not use density data from that year because the trawl was towed at an unusually fast speed ($4.7 \text{ km}\cdot\text{h}^{-1}$), which affected the catchability. Only one of these ports, Saugatuck, was sampled annually between 1962 and 1972. At each port, a transect of on-contour (i.e., constant depth) fixed sites was fished at up to 11 different depth strata, ranging between 9 m and 110 m with approximately 9-m increments. Because of bottom topography, not all depths could be sampled at all ports. In addition, some depths in some years were skipped for a variety of reasons (i.e., weather, daylight, boat functionality).

Since 1962, GLSC has fished a $\frac{3}{4}$ Yankee Standard No. 35 bottom trawl (12-m headrope, 15.5-m footrope, and a 13-mm mesh in the cod end) and most tows are generally 10 min in duration. Towing speed averages around $3.4 \text{ km}\cdot\text{h}^{-1}$. When the entire catch was less than about 20 kg, fish were sorted

Fig. 2. Map of ports sampled during the US Geological Survey Great Lakes Science Center annual bottom-trawl prey fish survey on Lake Michigan (the inset shows the location within the Great Lakes region). Each circle identifies a fixed depth station that is sampled within a particular port.



by species and counted, and an aggregate species weight was measured. In larger catches, a random sample of 10–15 kg was selected for species sorting and counting and aggregate weighing. The remainder of the catch was then weighed for later extrapolation of the sorted sample. The TL of up to 100 randomly encountered bloater from the sorted sample were measured to the nearest millimetre.

Bloaters captured from four ports (Frankfort, Manistique, Saugatuck, and Waukegan) were stored on ice for no more than 24 h so that subsequent processing would provide length, weight (nearest gram), sex, and maturity information, as well as scale collections. Through 1982, these fish were randomly selected at each port. After 1982, however, the first 10 fish encountered from each 10-mm length class at each port were selected. Visual inspection of the gonads revealed the sex and whether bloaters were mature or immature. In the laboratory, ages were determined by counting the number of annuli on a projected scale image. Bloater ages ranged from 0 to 13 years.

Generating time series estimates

Abundance of age-3 recruits

Bloaters do not fully recruit to our bottom trawl until age 3, which corresponds to the age at which bloaters are be-

lieved to have fully transitioned to the benthic habitat from the pelagic. For each trawl, we calculated the number of bloaters in each age class for each sex by constructing age-length and sex-length keys. To do this, we applied the keys to the length distribution of the catch and then expanded the resultant age and sex distributions to the total catch density of the trawl. Before 1998, bloaters were categorized into two stages, roughly age 0 and age 1 and older, and catch densities and length frequencies were recorded for each stage in each trawl. For 139 of 3227 combinations of year, port, depth, and stage (i.e., 4% of combinations), length frequencies were not available. When this occurred, we first sought to substitute with the average length frequency from the same stage, depth, and year of the other ports. We looked to similar depths because depth (age 0, $F_{[10,9601]} = 89.4$; age 1 and older, $F_{[10,55524]} = 932.1$) explained more of the variation in bloater size for a particular stage than port (age 0, $F_{[6,9601]} = 72.0$; age 1 and older, $F_{[6,55524]} = 372.6$) or year (age 0, $F_{[6,9601]} = 58.1$; age 1 and older, $F_{[29,55524]} = 449.8$) in a general linear model. Where similar depths from the same stage and year were unavailable, we used the average length frequency from adjacent depths at the same port of that year as a second option or from adjacent depths of other ports of that year as a third option. As a last option, we used the average length distribution from the same depth of all ports in adjacent years.

We constructed year-specific sex-length keys by pooling all bloaters of known sex and then calculating the proportion by sex for each 10-mm length class. However, we had insufficient sample sizes (i.e., ≤ 5 fish) to calculate the proportion of sexes for smaller (i.e., <180 mm TL) and larger (>290 mm TL) fishes. For example, in the 140-mm length bin, we had sufficient sample sizes for only 20 of the years between 1962 and 2004. In the year and length bin combination for which we had sufficient sample sizes, however, χ^2 tests rarely found proportions different from 1:1 (1 of 15 years in 120-mm bin; 0 of 17 years in 130-mm bin; 2 of 20 years in 140-mm bin; 1 of 24 years in 150-mm bin; 5 of 25 years in 160-mm bin; 2 of 30 in 170-mm bin). Hence, we assumed equal sex proportions in all length bins less than 180. When sample sizes were insufficient to calculate proportions by sex in length bins 290 mm and larger (occurred in only 13 out of 495 year and length-class combinations), we substituted the proportions from adjacent years.

Age-length keys also were constructed for each year by pooling all aged fish. Previous analysis of GLSC data by Krause (1999), however, suggested that one age-length key per year should be constructed for all southern ports and another for all northern ports because of differences in size at age between the ports in 1973–1993. We conducted a similar analysis with all 39 years of available aging data: we used a general linear model with age as the response variable and fish size, port, year, and interactions between fish size and port and fish size and year as explanatory variables. All explanatory variables except port exhibited a strongly significant effect on age (i.e., $P < 0.01$). The effect of port, however, was only marginally significant (i.e., $P = 0.06$). Bonferroni multiple comparisons of least-squares mean age at various bloater sizes revealed no latitudinal pattern in port groupings, as Krause (1999) had found. Manistique and

Saugatuck, which occur at northern and southern ends of the lake, respectively, generally exhibited small sizes at age. Sturgeon Bay and Port Washington, which are more centrally located on the western shore, generally exhibited large sizes at age. The remainder of the ports grouped with either the smaller or larger sizes at age, depending on the size at which the least-squares mean was calculated. Hence, without clear groupings of ports emerging across the lake, we decided to pool all age data to make one age-length key per year.

Even with only one age-length key per year, we still had to fill in age proportions when aging data were unavailable for some length bins. This occurred in only 3.5% of the year and bloater 10-mm length bin combinations and was limited to bins less than 180 mm and greater than 280 mm. To substitute missing values, we averaged the age proportions in the same 10-mm length bin of adjacent years. During the 1960s, however, bloaters were not aged in 1962–1964 and 1966. For all these years, we used the same age-length key, which was the average of all available annual age-length keys between 1965 and 1977, when bloaters were at a relatively low abundance (and density-dependent effects on size at age should have been minimized).

After applying the keys to the length distribution, we then used the catch density (number-ha⁻¹) to estimate the density of bloaters by age class and sex. The area swept was corrected for trawl width (in metres, = 9.693 – (43.93/depth)) and time on bottom (in minutes, = tow time – 3.875 + depth^{0.412}) as a function of depth (m), based on trawl mensuration results. Because we were interested in the abundance of age-3 recruits, we calculated the average density of age-3 recruits at each of the 11 depth strata and then multiplied the mean density by the area of the lake represented by its depth strata. We then summed the density of recruits across the 11 depth strata to represent the abundance of age-3 recruits. We note that our abundance estimate is not truly lake-wide because our summation includes only depths between 5 m and 114 m, which represent about 67% of the entire lake.

To estimate age-3 bloater abundance between 1962 and 1972, we have data for only one port, Saugatuck, and only seven depth strata were consistently measured over that time period. To make these data more comparable with years 1973 and later, when all seven ports and all 11 depth strata were available, we calculated a conversion factor (sensu Madenjian et al. 2005b). Using data from 1973–2004, we divided the lake-wide abundance estimates based on mean densities using all ports and depth strata by the lake-wide abundance estimate based on densities using only Saugatuck and its seven depth strata that were available before 1973. These annual ratios were lognormally distributed, ranging from 0.45 to 14.6. The mean of this lognormal distribution equaled 2.38. For the years 1962–1972, we then multiplied the Saugatuck lake-wide abundance estimate by the 2.38 conversion factor.

Population egg production

To calculate population egg production, we used the aforementioned length distributions, age-length and sex-length keys. In addition, we constructed an annual maturity key that was a function of bloater sex and size (10-mm length bin). As in the sex-length key, when proportional maturity data

were unavailable for a particular size in a given sex and year, data from adjacent years with the same size and sex of the bloater were substituted. With these keys, we could estimate the density of mature females in each 10-mm length bin in each depth and port and then calculate the mean density at each depth across ports. We then extrapolated the number of mature females in each 10-mm length bin in the 5- to 114-m depth strata (as with the abundance of age-3 recruits). Because bloater total fecundity is best predicted by bloater weight in grams (fecundity = 580.6 + 58.88(weight); Emery and Brown 1978), we then calculated an annual length-weight regression to convert each 10-mm length bin to a weight and then calculate the number of eggs that would be produced. We assumed that our autumn bottom trawl survey would provide an estimate of the population egg production for the following year. To calculate population egg production between 1962 and 1972, we used the same methods as with age-3 bloater abundance to calculate a conversion factor of 2.40.

Condition and sex ratio of adult bloaters

We used Fulton's condition index (K) as a measure of adult bloater condition. Our estimates of annual mean K are highly correlated ($r = 0.87$, $P < 0.0001$) with mean percent lipid content in 14 years for which lipid data are available (Hesselberg et al. 1990; Madenjian et al. 2000). For years 1967 and later, we calculated the annual mean K of all age-2 and older bloaters, where $K = (\text{weight-length}^{-3}) \times 100\,000$. For years prior to 1967, so few fish were aged that we included bloaters greater than 165 mm TL in our calculation of annual mean K . As with population egg production, we used the condition of bloaters in our fall survey to represent the condition of the adults that would produce the year class for the following year.

To represent adult sex ratio, we calculated the percentage of adults that were female. For the years 1966 through 2004, we considered adults to be those bloaters age 2 and older. On average, this percentage was calculated using 439 bloaters (range 97–1145). For the years before 1967 when few bloaters were aged, we considered adults to be larger than 165 mm TL. On average, this percentage was calculated using 250 bloaters (range 57–517).

Adult alewife biomass and winter-spring temperatures

For a time series of adult alewife biomass, we used the same time series from Madenjian et al. (2005b), which was based on the same GLSC data that we used. To construct a time series of winter and spring temperatures, we used a model of evaporation and thermodynamic fluxes developed for Lake Michigan by the Great Lakes Environmental Research Laboratory (Croley 1995). The model uses daily inputs of air temperature, wind speed, humidity, and cloud cover at six locations around the lake and was calibrated using surface water temperatures and ice cover concentrations during 1991–1995. The model generates a daily profile of water temperatures at 1-m depth increments from the surface to the bottom of the lake (282 m). We used habitat data of age-0 bloaters (see Bloater life history in Lake Michigan above) to select the 40- to 100-m depth strata for use as an index of winter-spring temperatures. We calculated a daily integrated temperature for that depth layer and subtracted 4

from each daily temperature value so that colder values were smaller (or more negative). The annual winter– spring temperature index equaled the sum of the daily values between 1 January and 30 June of each year.

Time series analysis

We used dynamic linear models (DLMs) to determine how the time series of bloater recruitment to age 3 related to the time series of population egg production, population sex ratio, adult condition, adult alewife biomass, and winter and spring temperatures. DLMs have been used successfully in many different ecological time series to detect trends and identify important explanatory variables (e.g., Lamon et al. 1998; Scheuerell et al. 2002; Schindler et al. 2005). Initially, however, we had attempted to fit our data to a Ricker stock–recruit model that included external variables (Hilborn and Walters 1992). A nonstationary pattern in the stock–recruit time series was apparent, however (Fig. 3). For a given level of population egg production, there was a much higher level of recruitment in the 1980s than in the early 2000s, making a “loop” in the time series (sensu Walters 1987). Using a DLM, we acknowledged that the sequence of the data was providing critical information in that the response in one year was strongly related to the response one year earlier.

DLMs are Bayesian time series models (for a full description, see Pole et al. (1994)). Because Lamon et al. (1998) and Scheuerell et al. (2002) provide detailed explanations for ecological applications of DLMs, we will only briefly describe our methods here. Each DLM uses two time-dependent (t) equations, referred to as observation and systems equations. In the observation equation, the response variables (Y_t) are sequentially fitted to a $1 \times m$ vector of predictor variables (X_t) with a $m \times 1$ vector of model parameters (θ_t) and a normally distributed error term (v_t):

$$(1) \quad Y_t = X_t \theta_t + v_t, \quad v_t \sim N[0, V_t]$$

In our models, the value of m equaled the number of explanatory regression variables that were included, plus the level and growth parameters associated with a dynamic linear trend. The observation errors had a time-dependent variance (V_t) that was estimated from prior data and used a “discounting” scheme that determines how many years of prior data are used (see below).

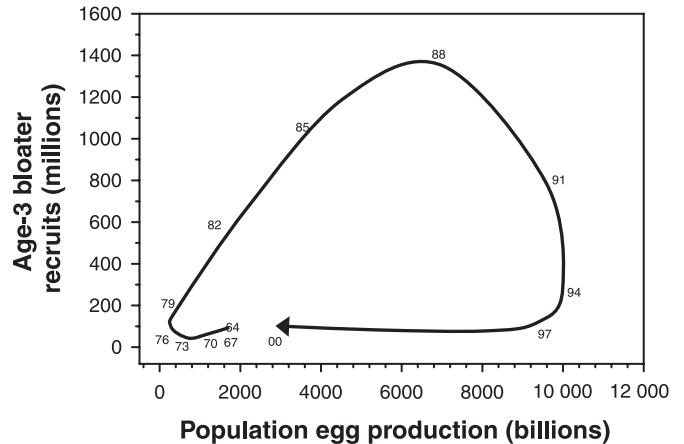
The systems equation uses prior information through Bayesian learning to allow the model parameters θ_t to change with each time step through a first-order Markov process:

$$(2) \quad \theta_t = G \theta_{t-1} + \omega_t, \quad \omega_t \sim N[0, W_t]$$

where G is the $m \times m$ system evolution matrix that determines how the model parameters change and ω_t is $m \times 1$ vector that describes the stochastic change in normally distributed parameters through time. The system covariance matrix W_t describes the variance of the parameters through time, and a discount factor is again applied to determine the amount of prior data used in the estimation at each time step.

The discount factor allows the model to change the importance of recent observations when making predictions of model parameters and variance for the next time step. Theoretically, discount factors can range from 0 (no prior data are

Fig. 3. Stock–recruit relationship for bloater (*Coregonus hoyi*) in Lake Michigan. Each data point represents the average of three consecutive years of data; the numbers represents the last two digits of the median year class for those three years (e.g., “88” represents the average of the 1987–1989 year-classes. The arrow was added to demonstrate the “loop” or nonstationarity in the relationship (see Walters 1987).



considered) to 1 (all prior data are considered), but Pole et al. (1994) recommend setting discount factors to be at least 0.8. In addition, we always set the discount factor for the regression parameters to be greater than that for the trend parameters (i.e., level and growth parameters), but the difference between the two discounts was never greater than 0.1, as recommended by Pole et al. (1994).

Before fitting each model, we (i) \log_e -transformed the response variables such that they were normalized and (ii) standardized (mean deleted and divided by the standard deviation) the explanatory variables to improve the estimation of the level parameter and allow direct comparison of the explanatory variable coefficients (Pole et al. 1994). For each model, we systematically varied the discount factors until the combination that maximized the log-likelihood in the forecast model was identified. Once the discount factors were determined, we then fit the data retrospectively with the appropriate discount factors and used the residuals to calculate the negative log-likelihood (NLL) for that model:

$$(3) \quad NLL = n[\log_e(\sigma) + 0.5 \log_e(2\pi)] + SSE/2\sigma^2$$

where n is the number of observations, SSE is the sum of the squared residuals, and σ^2 is SSE divided by n (Hilborn and Mangel 1997). We conducted all of our analyses using the BATS statistical package (Pole et al. 1994). For all models, we evaluated whether serial correlation of the residuals existed, as indicated by a nonrandom pattern in the residuals of the forecast model. Those that were identified to have serial correlation were not considered in the model rankings (see below).

We used two different response variables: the abundance of age-3 recruits (i.e., $\log_e(\text{recruits})$) and reproductive success (i.e., $\log_e(\text{recruits}/\text{population egg production})$, sensu Wada and Jacobson 1998). When modeling abundance of recruits as the response, we considered 17 different models (each model contained population egg production), and then we considered every possible combination of the four poten-

tial explanatory variables (bloater sex ratio, adult bloater condition, adult alewife biomass, and winter and spring temperatures). In addition, we included a reference model that contained only the level and growth trend parameters and no explanatory variables. When modeling reproductive success as the response variable, we considered 16 different models. None of the models contained population egg production because it was already considered in the response variable. Within each response variable, we ranked competing models according to the Bayes information criterion (BIC):

$$(4) \quad \text{BIC} = 2(\text{NLL}) + m[\log_e(n)]$$

where m is the number of estimated parameters (level, growth, regression parameters) plus the observation variance estimate (v_i), NLL is the negative log-likelihood, and n is the sample size (Box et al. 1991). The model with the smallest BIC was ranked highest, as it provided the most parsimonious fit to the data. To make a pairwise comparison between models i and j , where the $\text{BIC}_i < \text{BIC}_j$, we used the Schwarz criterion (Kass and Raftery 1995):

$$(5) \quad S_{ij} = (\text{BIC}_j - \text{BIC}_i)/2$$

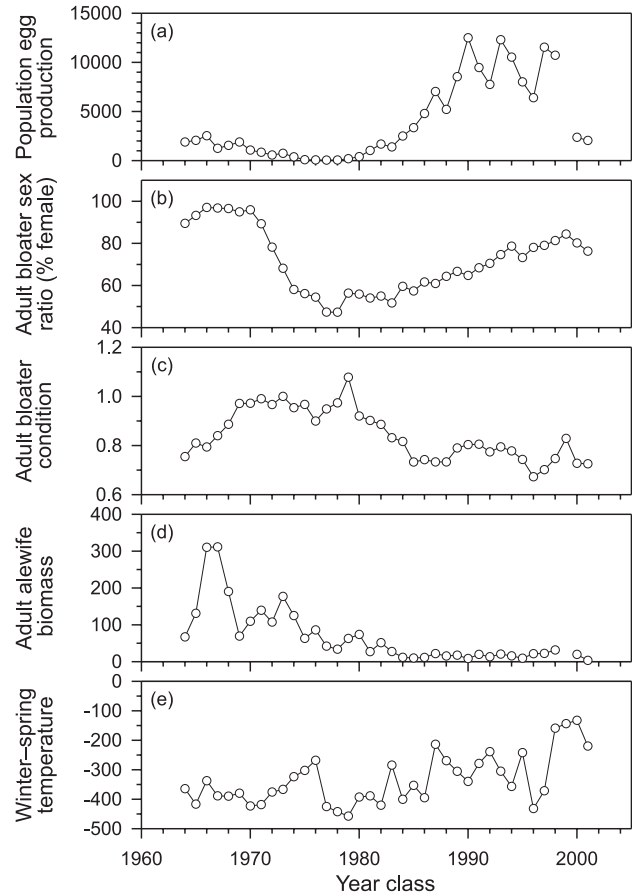
According to Kass and Raftery (1995), when $2S_{ij}$ is between 0 and 2, the evidence for the higher ranked model is “not worth more than a bare mention”; as the difference increases, the evidence for the higher ranked model becomes “positive” (2–6), “strong” (6–10), and even “very strong” (>10).

Results

The explanatory variables demonstrated dynamic trends over the three decades (Fig. 4). Population egg production lagged a few years behind the abundance of age-3 recruits: declining through the 1977 year class, increasing through the 1990 year class, and then fluctuating before declining in the final years (Fig. 4a). The sex ratio of the population was nearly always skewed toward females (Fig. 4b). In the 1960s, more than 85% of adults were females, but that percentage gradually declined to reach 47% for the 1977 year class. As recruitment increased, however, the sex ratio steadily increased through the 1999 year class, attaining levels of more than 80% female. Condition of adults increased early in the time series until generally stabilizing through the 1970s (Fig. 4c). During the 1980s through the mid-1990s, condition declined as the bloater population increased in size, because of strong recruitment. Condition increased slightly in the final years of the time series but did not reach levels as high as in the early 1970s. Biomass of adult alewife peaked in the late 1960s, declined through the early 1980s, and has remained consistently low since then (Fig. 4d). Finally, winter and spring temperatures have fluctuated considerably, but the overall trend appears to suggest warmer years in the latter half of the time series (Fig. 4e).

The time series of the two response variables were somewhat similar in that both declined through the 1960s, then increased, and subsequently declined again (Figs. 5a, 6a). Age-3 recruits increased through the 1989 year class before stabilizing and declining, whereas reproductive success increased through only the 1978 year class and then declined.

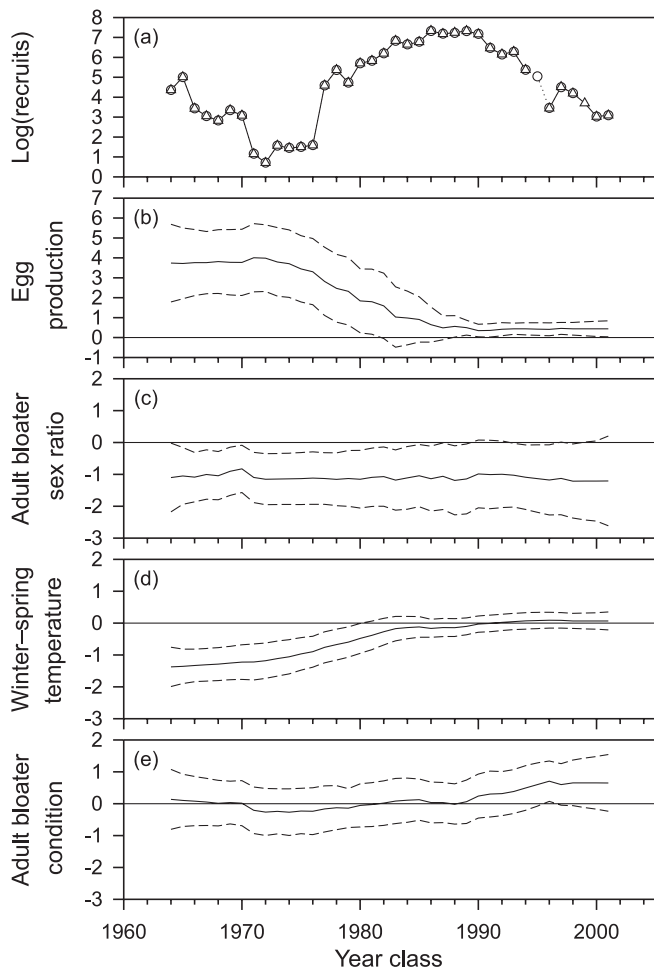
Fig. 4. Time series of the explanatory variables (raw values) that were used in the dynamic linear models: (a) population egg production, in billions of eggs; (b) adult bloater (*Coregonus hoyi*) sex ratio; (c) Fulton's condition factor of adult bloaters; (d) biomass of adult alewife (*Alosa pseudoharengus*), in kilotonnes; and (e) index of winter and spring temperatures (1 January through 30 June) between depths of 40 m and 100 m in Lake Michigan (more negative values equals colder temperatures).



Reproductive success increased slightly in the final years of the time series, whereas the abundance of age-3 recruits did not.

When abundance of age-3 recruits was the response variable, the top-ranked model included population egg production, sex ratio, bloater condition, and winter and spring temperatures (i.e., every explanatory variable except alewife; Table 1). The retrospectively fit model explained nearly all of the variation in the observed data (Fig. 5a; the coefficient of determination, r^2 , from plot of predicted versus observed, equaled 0.999). As expected, the coefficient for population egg production was positive throughout the time series, but the high value of the coefficient through the 1960s and 1970s indicates that population egg production had its greatest effect during this time period (Fig. 5b). Among the other explanatory variables, sex ratio had the greatest impact during the time series with its 90% credible intervals different from zero for the majority of the time series (Fig. 5c). Overall, sex ratio was inversely associated with recruitment (i.e., stronger recruitment occurred when sex ratios were more balanced).

Fig. 5. Time series results of the top-ranked dynamic linear model when the abundance of age-3 bloater (*Coregonus hoyi*) recruits was the dependent variable. (a) The observed (open triangles) and model-predicted (open circles) abundance (\log_e -transformed) of age-3 recruits. (b–e) The coefficient (solid line) and 90% Bayesian credible intervals (broken lines) for explanatory variables population egg production, adult bloater sex ratio, winter and spring temperatures, and adult bloater condition, respectively. Note that the y axes are equal in c–e and are unique in a and b.



Winter and spring temperatures also were inversely associated with recruitment until the early 1980s when the coefficient began hovering around 0 (Fig. 5d). Opposite from the Rice et al. (1987) hypothesis, recruitment was higher during years of colder temperatures relative to warmer ones. Finally, adult bloater condition appeared to have the least impact on recruitment as its 90% credible intervals were not different from zero for nearly the entire time series (Fig. 5e). Late in the time series, adult condition was positively related to recruitment, as we had hypothesized. The second-ranked model included all variables of the top-ranked model except bloater condition, but the Schwarz criterion revealed a difference of 18, indicating very strong evidence for the top-ranked model over the second-ranked one. Compared with the reference model with no explanatory variables, however, the Schwarz criterion found very strong evidence that all

Table 1. Summary of dynamic linear models to explain variation in abundance of age-3 bloater (*Coregonus hoyi*) recruits in Lake Michigan over the 1964–2001 year classes.

Explanatory regressor variable(s)	<i>m</i>	NLL	BIC
EGG, SEX, WIN, CON	7	-144.5	-264.0
EGG, SEX, WIN	6	-133.8	-246.1
EGG, WIN, ALE, CON	7	-125.0	-224.9
EGG, SEX, WIN, ALE, CON	8	-119.6	-210.5
EGG, WIN, CON	6	-114.5	-207.5
EGG, SEX, CON	6	-101.0	-180.5
EGG, SEX, WIN, ALE	7	-88.4	-151.7
EGG, SEX, ALE, CON	7	-77.4	-129.7 ^a
EGG, ALE, CON	6	-70.6	-119.6
EGG, WIN, ALE	6	-68.4	-115.3
EGG, CON	5	-55.3	-92.6
EGG, ALE	5	-36.7	-55.4 ^a
EGG, WIN	5	-34.8	-51.6
EGG, SEX, ALE	6	-34.6	-47.6 ^a
EGG, SEX	5	-27.3	-36.6
EGG	4	-19.6	-24.9
	4	17.0	48.4

Note: Codes for explanatory regressor variables: EGG, population egg production; SEX, adult bloater sex ratio; CON, adult bloater condition; WIN, winter temperatures; ALE, adult alewife biomass. All models also included the level and trend parameter estimates. *m*, number of parameters; NLL, negative log-likelihood; BIC, Bayes information criterion. ^aSerial autocorrelation in the residuals was identified.

models provided better support. Only three of the models, each ranked far below the top-ranked model, exhibited serial autocorrelation in the forecast residuals (Table 1).

When reproductive success was the response variable, the top-ranked model included every explanatory variable: sex ratio, bloater condition, winter and spring temperatures, and alewife (Table 2). The second-ranked model included all of the explanatory variables of the top-ranked model except alewife. The Schwarz criterion revealed a difference of 5.9 between the top two models, offering positive evidence for the top-ranked model over the second-ranked one. Although there was BIC evidence to favor the top-ranked model, we chose the second-ranked model as the best model because the 90% credible intervals for the alewife coefficient were never different from zero in the top-ranked model. The retrospectively fit model explained nearly all of the variation in the observed data (Fig. 6a; r^2 from plot of predicted versus observed equaled 0.999). The trends in coefficients were very similar to the trends of coefficients for the top-ranked model when abundance of age-3 recruits was the response variable. The coefficient for sex ratio was always negative (Fig. 6b) and was most strongly inversely associated with reproductive success during the late 1970s and early 1980s. Winter and spring temperatures were inversely associated with reproductive success in the late 1960s and early 1970s (Fig. 6c); later in the time series, its effects were minimal. Finally, adult bloater condition (Fig. 6d) was positively related to reproductive success early (1960s) and late (late 1990s) in the time series; during the other periods, the effects of adult bloater condition were minimal. Using the Schwarz criterion, all 15 models with explanatory variables provided were found to have very strong support for a better

Table 2. Summary of dynamic linear models to explain variation in reproductive success (abundance of age-3 bloater (*Coregonus hoyi*) recruits divided by population egg production) in Lake Michigan over the 1964–2001 year classes.

Explanatory regressor variable(s)	<i>m</i>	NLL	BIC
SEX, WIN, ALE, CON	7	-131.4	-237.7
SEX, WIN, CON	6	-126.6	-231.8
SEX, WIN	5	-112.3	-206.6
SEX, WIN, ALE	6	-102.2	-182.9
SEX, CON	5	-99.6	-181.3
SEX, ALE, CON	6	-99.9	-178.2
WIN, CON	5	-91.1	-164.3
WIN, ALE, CON	6	-83.8	-146.1 ^a
SEX, ALE	5	-70.6	-123.3
ALE, CON	5	-40.8	-63.7
CON	4	-29.6	-44.8
SEX	4	-22.0	-29.8
WIN, ALE	5	-5.8	6.4
WIN	4	0.4	15.2
ALE	4	10.0	34.4 ^a
	3	26.9	64.6

Note: Codes for explanatory regressor variables: SEX, adult bloater sex ratio; CON, adult bloater condition; WIN, winter temperatures; ALE, adult alewife biomass. All models also included the level and trend parameter estimates. *m*, number of parameters; NLL, negative log-likelihood; BIC, Bayes information criterion.

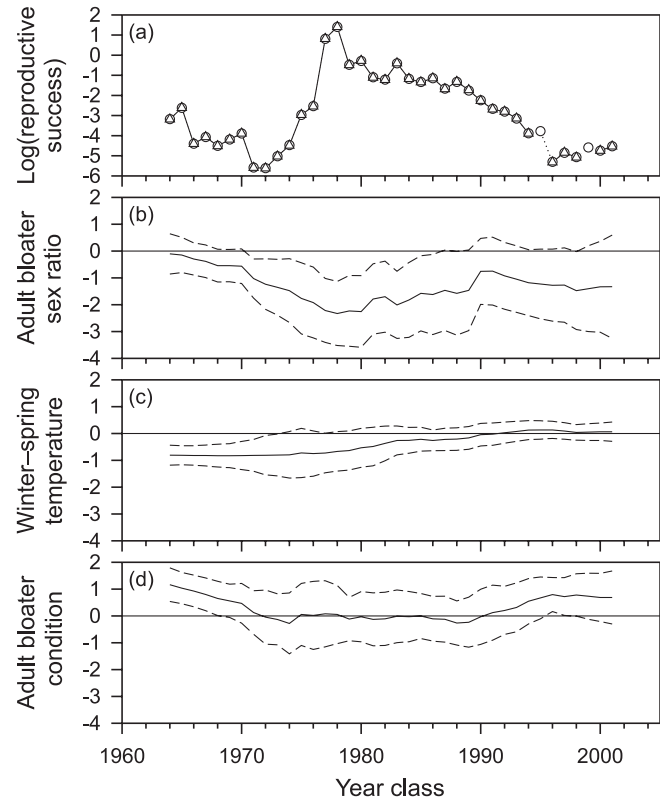
^aSerial autocorrelation in the residuals was identified.

fit to the data than the reference model without any explanatory variables. Only two of the models, each ranked far below the top-ranked models, exhibited serial autocorrelation in the forecast residuals (Table 2).

Discussion

In the 1964 through 2001 year classes, bloater recruitment and bloater reproductive success (abundance of recruits divided by population egg production) followed a fairly smooth trend without the high interannual variability typically observed in fish species. Recruitment went through three phases: declining from the early 1960s through the early 1970s, increasing through the late 1980s, and then declining again through the early 2000s. Because each phase occurred over intervals of 15 years or so, our 38-year time series is insufficient to document regular bloater recruitment (and adult population abundance) cycling; additional years of GLSC surveys will determine whether bloaters undergo regular cycles (as proposed by Madenjian et al. 2002). Our objective was to use Bayesian time series analyses to determine whether the variation in bloater recruitment and reproductive success was explained by factors extrinsic or intrinsic to the population. Unlike most studies that have explained long-term trends with extrinsic factors, our analyses revealed that adult sex ratio, an intrinsic factor, explained more variation in recruitment than extrinsic factors. Another intrinsic factor, an index of adult bloater physiological condition, explained some of the variation early and late in the time series. With regards to extrinsic factors, biomass of adult alewives failed to explain variation in the time series, and winter and spring temperatures during the period of bloater

Fig. 6. Time series results of the second-ranked dynamic linear model when reproductive success ($\log_e(\text{recruits}/\text{population egg production})$) was the dependent variable. We considered this model superior to the top-ranked model for two reasons: (i) the top-ranked model included an additional variable (adult alewife biomass) for which the 90% Bayesian credible intervals were never above or below the zero line; and (ii) the difference in BIC (Bayes information criterion) between the top-ranked models was minimal. (a) The observed (open triangles) and model-predicted (open circles) abundance (\log_e -transformed) of reproductive success. (b–d) The coefficient (solid line) and 90% Bayesian credible intervals (broken lines) for explanatory variables adult bloater (*Coregonus hoyi*) sex ratio, winter and spring temperatures, and adult bloater condition, respectively. Note that the y axes are equal in c and d and are unique in a and b.



egg and larval development explained some of the variation, but only early in the time series.

The most important explanatory variable throughout the time series, adult sex ratio, demonstrated a smooth trend of declining and then increasing female predominance across the Lake Michigan time series. Bloater female predominance is caused primarily by higher longevity among females than males (TeWinkel et al. 2002), as initial sex ratios are roughly equal. Among age-2 bloaters, the earliest age for which we have reliable data, 53% (average of annual percentages, range = 35–78%) are females since 1973. Although this average percentage is greater than 50% ($t_{30} = 2.41$, $P = 0.02$), it is not sufficient to explain the increasing percentage of females among older age classes (e.g., 73% for age 5, 81% for age 7, 91% for age 9). Additional evidence that initial sex ratios are not biased comes from a laboratory study that found equal sex ratios at hatching across a range of tempera-

tures (Eck and Allen 1995), indicating that abiotic factors do not influence sex ratio as found for some other animals (Charnov and Bull 1977).

Why males die sooner than females is unclear. In Lake Michigan, male bloater condition, measured as Fulton's condition factor, is slightly lower than female bloater condition for a given age (paired *t* tests: age 2, $t_{36} = -1.92$, $P = 0.03$; age 3, $t_{37} = -2.88$, $P = 0.003$; age 4, $t_{37} = -7.36$, $P < 0.0001$), suggesting that males are at an energetic disadvantage that could make them more susceptible to natural mortality than females. One potential explanation for low male condition or high male natural mortality is that males mature slightly earlier than females, but the difference is generally not greater than 1 year (TeWinkel et al. 2002; D.B. Bunnell, unpublished data). The energetics associated with building gonads is likely insufficient to explain the differences between sexes because building testes requires little energy relative to ovaries. In other fishes, however, male spawning behavior can require more energy than female spawning behavior (e.g., Jonsson et al. 1991), which could explain differences in their mortality rates. Unfortunately, bloater spawning behavior has not been characterized.

A dynamic bloater sex ratio that includes periods of female predominance is not just a recent phenomenon in Lake Michigan. Using bottom-set gillnets, Jobes (1949) reported a bias towards females in 1930 (69%), 1931 (65%), and 1932 (80%). In 1919, however, males predominated (36% female; Jobes 1949). Female predominance also was observed by Brown (1970) between 1954 and 1955 in both bottom-set gillnets (82%) and bottom trawls (72%) and then again between 1960 and 1961 (90% in bottom trawls, 87% in gillnets). To address concerns that female predominance is an artifact of seasonal changes in bottom distribution among the sexes, Jobes (1949) observed female predominance in May, June, July, August, and September of 1931 and 1932. Additionally, Brown (1970) allayed concerns that females may occupy deeper depths than males by reporting 99% predominance of females in mid-water trawls ($N = 347$ fish) and 97% predominance among bottom trawls ($N = 4348$ fish) in 1967. Bloaters also have exhibited periods of female dominance in Lake Huron (Schaeffer 2004; Dobiesz et al. 2005) and in Lake Ontario (Stone 1944). Finally, other deep-water ciscos also have demonstrated high percentages of females across the Great Lakes basin (see summary by Brown 1970).

Can female predominance mechanistically influence bloater recruitment and population dynamics as our time series analyses have suggested? One potential mechanism is inbreeding caused by too few male parents, which may lead to long-term suppression of population size until outbreeding can resume (Maynard Smith and Stenseth 1978). We know of no genetic evidence of inbreeding within the Lake Michigan bloater population, however. A second potential mechanism is too few males limiting the number of eggs that are actually fertilized during periods of female predominance (Brown et al. 1987). Using GLSC Lake Michigan bloater data through 1984, when the adult population was about 60% female, Brown et al. (1987) predicted that female predominance would continue to rise and bloater recruitment would ultimately decline. Indeed, their predictions were borne out. We are unaware of other studies that have indicated that the

number of male fishes can limit recruitment. Even though the statistical link between sex ratio and bloater recruitment is strong, unanswered questions regarding the mechanism by which sex ratio influences recruitment remain. First, during the period of strong recruitment (1977–1994), sex ratio linearly increased from around 47% to 80% female. However, during 1973–1976 when recruitment success (which accounts for differences in population egg production) was relatively low, sex ratio ranged from 54% to 68% female, within the range of sex ratios during the strong recruitment phase. Given the relatively balanced sex ratio during 1973–1976, it is unclear why recruitment success was not higher. Second, the resurgence of bloater recruitment in 1977 coincided with a bloater sex ratio just under 50%. In the early 2000s, females have comprised at least 70% of the adult population. Must the sex ratio decrease to less than 50% female, as it did in 1977, before bloater recruitment will return to a high phase in the coming years? Increased knowledge of bloater reproductive behavior and population model simulations may provide further insight into how bloater sex ratio influences recruitment. Without this understanding, we cannot exclude the possibility that sex ratio simply covaries with the factor that is truly critical to bloater recruitment success.

When recruitment was the response variable, the coefficient for population egg production in the top-ranked model was always positive. The value of the coefficient, however, was up to four times greater during the 1960s and early 1970s than it was during the 1980s and later. The time series of population egg production revealed relatively high levels of production during the mid-1980s through late 1990s compared with earlier years. Taken together, we interpret the lower coefficients during the mid-1980s and later as a consequence of the density-dependent recruitment that likely was occurring when population egg production reached high levels. This is consistent with general stock–recruitment theory (Hilborn and Walters 1992).

Although not explicitly included in our model, the commercial fishery likely influenced intrinsic variables that were included. First, the nadir in population egg production in the mid-1970s was likely enabled by a fishery targeting larger, older (age 4 and older) bloaters with their gillnets (Brown et al. 1985) at a much higher exploitation fraction than occurred in later years (exploitation fraction means: 1962–1977, 0.23; 1978–2003, 0.02). Second, because these larger, older individuals were primarily female, it is also possible that the fishery contributed to the nearly equal sex ratios that occurred during the mid-1970s. Coincidentally or not, the first strong year class in 10 years occurred in 1977, the year after the closure of the commercial fishery (Brown et al. 1985). Over the next 15 or so years, several consecutive strong year classes were produced but exploitation fractions remained at such low levels that the fishery could not have had any direct or indirect role in the poor recruitment levels that were observed in the late 1990s and early 2000s.

Because bloater recruitment began to increase in the late 1970s as alewife densities were reduced, many biologists hypothesized that adult alewives, which are known to prey on pelagic larvae (Krueger et al. 1995), had been suppressing bloater recruitment in the 1960s and early 1970s (Wells and McLain 1973; Eck and Wells 1987). This hypothesis lost support in the late 1990s, however, when bloater recruitment

worsened in the face of relatively low alewife densities (Madenjian et al. 2002). Our time series analysis further discredited the role of alewife as effectors of bloater recruitment. Models with alewife generally ranked low in terms of explanatory power, and credible intervals around the alewife coefficients were never different from zero. Although alewife may negatively influence other native fish species in the Great Lakes (Madenjian et al. 2002), our analyses suggest that alewives do not negatively influence bloomers.

Many recent studies have found regional climate patterns to explain variation in long-term trends of population abundance (Beamish and Bouillon 1993; Wada and Jacobson 1998; Clark and Hare 2002). Rice et al. (1987) hypothesized that warmer winter and spring temperatures (and subsequently faster egg development and larval growth) would enhance recruitment by reducing the period of vulnerability to egg and larval predators. The Lake Michigan temperature models that we used revealed winter and spring temperatures to have generally warmed, with considerable variation, over the course of our time series. Our dynamic linear models revealed an inverse relationship between temperatures and recruitment during the 1964–1980 year classes: colder temperatures were associated with stronger recruitment. It is possible that this result is a spurious correlation. However, the Rice et al. (1987) hypothesis focused on the period of fertilized egg incubation and larval growth. The critical temperature effect could occur earlier, during the period of gonadal maturation. Temperatures outside of the optimal range for gonadal maturation have been linked to resorption of their eggs (Tanasichuk and Ware 1987; Sandström et al. 1997). In yellow perch, for example, warmer winter temperatures reduce fecundity and egg viability (Jones et al. 1977; Sandström et al. 1997). Although the negative effect of warmer winter temperatures on bloater gonad maturation is untested, it is one possible mechanism that could explain the unexpected temperature effect found in our model.

The final explanatory variable that we evaluated was adult condition, hypothesizing that years in which adults were in higher condition would translate to years of higher quality offspring production which, in turn, have a higher probability of surviving and recruiting to age 3. Our analyses revealed marginal support for the positive effect of adult condition on recruitment. During the late 1960s and late 1990s, bloater condition was increasing, likely because of decreasing bloater population size and reductions in density-dependent effects. During these time periods only, the coefficients for adult condition in the top-ranked models were greater than zero. One concern for future recruitment, however, is that adult condition achieved considerably higher levels in the 1970s (before the resurgence in recruitment) than in the late 1990s and early 2000s (prior to when recruitment should resurge if bloater recruitment cycles). The recent decline of *Diporeia* spp. in Lake Michigan (Nalepa et al. 1998), one of the two primary prey items (along with *Mysis*) for adult bloomers (Crowder and Crawford 1984; TeWinkel and Fleischer 1999), likely explains the lower-than-expected adult condition in recent years. If bloomers resume a phase of high recruitment in spite of relatively low adult condition factors, then the hypothesis for adult condition as an internal factor regulating bloater recruitment will have even less empirical support.

Over the next 5–10 years, our annual GLSC bottom trawl surveys will reveal whether bloater recruitment in Lake Michigan returns to a high phase. If it does, then the proposed 30-year population cycle for bloomers (Madenjian et al. 2002) would be validated. If it does not, then we should consider the possibility that a “regime shift” in Lake Michigan has occurred (sensu Beamish et al. 1999) such that strong bloater recruitment is no longer supported in this ecosystem. Regardless of the findings of future surveys, however, our current study marked the first attempt to rigorously identify the important factors affecting bloater recruitment. Over a 38-year time series, a strong positive linkage between a balanced sex ratio and bloater reproductive success was revealed. Hence, bloomers are relatively unique among fish populations in that they appear to be regulated by a factor intrinsic, rather than extrinsic, to their population. However, additional research will be required to elucidate the mechanisms underlying this linkage.

Acknowledgments

We thank the many biologists, technicians, captains, and crew for their many hours and days spent on Lake Michigan maintaining this long-term data set. Jeff Holuszko, Tom Todd, and two anonymous reviewers provided very helpful reviews to the manuscript. We thank Tim Desorcie for preparation of Fig. 2. Mark Scheuerell helped us understand and apply the BATS software. This article is Contribution 1347 of the US Geological Survey Great Lakes Science Center.

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