



Decline in bloater fecundity in Southern Lake Michigan after decline of *Diporeia*

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ABSTRACT

Population fecundity can vary through time, sometimes owing to changes in adult condition. Consideration of these fecundity changes can improve understanding of recruitment variation. Herein, we estimated fecundity of Lake Michigan bloater *Coregonus hoyi* during December 2005 and February 2006. Bloater recruitment has been highly variable from 1962 to present, and consistently poor since 1992. We compared our fecundity vs. weight regression to a previously published regression that used fish sampled in October 1969. We wanted to develop a new regression for two reasons. First, it should be more accurate because it uses fish collected closer to spawning, thus minimizing the potential for atresia (egg reabsorption) which could bias fecundity high. Second, we hypothesized that fecundity would be lower in 2006 because adult condition was 41% lower in 2006 compared to 1969, likely owing to the decline of *Diporeia* spp, a primary prey for bloater. Although the slope of the fecundity versus weight regression was similar between the years, fecundity was 24% lower in 2006 than in 1969 for bloater weighing between 70 and 240 g. Whether this was the result of the difference in sampling time prior to spawning or of differences in condition is unknown. We also found no relationship between maternal size and mature oocyte size. Incorporating our updated fecundity regression into a stock/recruit model failed to improve the model fit, indicating that the low bloater recruitment that has been observed since the early 1990s is not solely the result of reduced fecundity.

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Introduction

In the development of stock/recruit models, population egg production is the most appropriate measure for stock size (Hilborn and Walters, 1992). To calculate population egg production, biologists must first acquire estimates of population density and size distribution, the former of which can be difficult to attain with high precision or low uncertainty. Next, biologists must develop an accurate relationship between fecundity and fish size for the species under consideration or use a previously published relationship for that species from a different location or time period. Recent studies, however, have revealed that size-specific fecundity can vary temporally within a species or stock (Tanasichuk and Ware, 1987; Rijnsdorp, 1991; Kjesbu et al., 1998). Stock recruitment models that fail to consider this variation may be limited in their ability to explain variation in fish recruitment (Marshall et al., 1998; Scott et al., 2006).

Several factors can influence the relationship between fecundity and fish size. First, temperature influences the rate of gonadal development (Tveiten and Johnsen, 1999), and it has generally been observed that warmer than usual temperatures prior to spawning increase fecundity (Tanasichuk and Ware, 1987; Kjesbu et al., 1998).

Second, increased available prey resources can increase fecundity in some circumstances (Kjesbu et al., 1998; Lambert and Dutil, 2000). As an extension, biologists have hypothesized that adult condition can explain variation in fecundity that is not explained by fish size, and some results are consistent with this claim (Marshall et al., 1998; Blanchard et al., 2003). Other studies, however, have not supported this hypothesis (McIntyre and Hutchings, 2003; Trippel and Neil, 2004; Koops et al., 2004). Third, genotypic changes, perhaps associated with size-selective fishing mortality, could induce changes in the fecundity versus size relationship (Yoneda and Wright, 2004).

In this study, we investigate whether the fecundity of a native Lake Michigan planktivore, bloater (*Coregonus hoyi*), declined between 1969 and 2006 (see Emery and Brown, 1978) given a 41% decline in adult condition between these two time periods. Bloater is an important component of the Lake Michigan food web. The only one of six native deepwater ciscoes that remains extant, it appears in the diets of Chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*), although it is consumed far less frequently than non-native alewife (Madenjian et al., 1998; Warner et al., 2008). Its population abundance has oscillated dramatically since the early 1960s (Madenjian et al., 2002; Bunnell et al., 2006a), but has been declining since 1989 because of poor recruitment (Bunnell et al., 2006a).

As previously stated, we hypothesized that fecundity would be lower in 2006 than in 1969 because adult condition was considerably

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lower. Between 1969 and 1982, % total lipids (an excellent measure of adult condition) for Lake Michigan bloater averaged 22% ($N = 11$ years) without any trend (Hesselberg et al., 1990). In fact, % total lipids in 1969 equaled 22% (S.D. = 3.4, $N = 120$, Hesselberg et al., 1990). Subsequent, yet less frequent, % total lipids estimates dropped precipitously to 16% in 1984 (Hesselberg et al., 1990), 12% in 1986 (Hesselberg et al., 1990), and to 11% in 1994 (Madenjian et al., 2000), likely owing to density-dependent responses as the population biomass grew throughout the 1980s. Apparently, bloater lipid content remained relatively low from 1994 through 2005–2006, when lipid content was determined to be only 13% (S.D. = 2.7, $N = 44$, D. B. Bunnell, unpublished data). Based on population biomass alone, % total lipids should have been 18–20% in 2005–2006 given the relatively low bloater population biomass. This lower than expected condition was likely due to the 65% reduction in *Diporeia* densities that occurred in Lake Michigan between 1994 and 2000 (Nalepa et al., 2006). *Diporeia* has historically been an energy-rich (Gardner et al., 1985) prey resource for bloater (Wells and Beeton, 1963; Crowder and Crawford, 1984; Davis et al., 2007).

Fecundity estimated in 2006 also might be lower than fecundity estimated in 1969 because of a difference in sampling time. The 1969 fecundity versus weight regression was based on bloaters collected in October, three to five months before spawning occurred. Because this assumes that the number of mature oocytes to be spawned is fixed by October, this regression could be biased high if this assumption is incorrect. Indeed, for many other fish species the number of mature oocytes declines during the period of vitellogenesis before spawning owing to reabsorption (see Witthames and Walker, 1995; Kurita et al., 2003; Kennedy et al., 2007). In this study, we use bloater collected closer to spawning (i.e., in December and February) which should minimize the possibility of counting mature oocytes that ultimately will not be spawned. Hence, our study provides an updated, potentially more accurate, fecundity estimate for bloater in southern Lake Michigan for use in stock/recruitment models and other population-level analyses.

Methods

Bloaters in Lake Michigan typically mature by age 2 or 3 years, which corresponds to around 200 mm total length (TL) and 65 g (D. B. Bunnell, unpublished data). They are iteroparous, and spawn near the lake bottom between January and March (peak densities in late January and mid-February, Rice et al., 1987) in 40 to 110 m of water (Wells, 1966; Emery and Brown, 1978; Rice et al., 1987). Oocyte size distribution suggests that bloaters are group-synchronous spawners (i.e., the large mode of oocytes will be spawned during the current spawning season, whereas the small mode of oocytes will be spawned in future seasons, Murua and Saborido-Rey, 2003). Newly hatched larvae (i.e., those still containing yolk sacs) have been collected in profundal habitat during mid-April through mid-August, with the peak densities observed during May and June (Wells, 1966; Rice et al., 1987).

Bloaters were collected from commercial fisherman working out of Milwaukee, Wisconsin. On 20 December 2005 and 23 February 2006, fish were collected with gillnets (ranging 6.4–7.0 cm stretch-mesh) set for 3–4 nights 33–40 km east of Kenosha, WI in depths ranging 70–104 m. In the 1969 study, it is unclear whether the fish were collected off of Kenosha, WI or Saugatuck, MI (Emery and Brown, 1978); in either case they also were sampled in southern Lake Michigan. We met the fisherman at the dock, immediately placed the fish on ice, and returned to Ann Arbor, Michigan where the fish were frozen in water at -20°C . Approximately two months later, bloaters were thawed, weighed to the nearest 0.1 g, and measured to the nearest mm TL. Ovaries were dissected, weighed to the nearest 0.1 g, and preserved in 5% buffered formalin for 4–11 months.

We estimated fecundity only from bloaters that we were confident had not yet spawned, given that their body cavity was full of eggs.

From the February 2006 (putatively middle of spawning season) samples ($N = 91$ females), nearly 50% of the females had body cavities packed with eggs, whereas the remainder had body cavities that were nearly void of eggs (indicating previous spawning). From the December 2005 (putatively pre-spawning) samples ($N = 70$ females), 85% of the females had body cavities full of eggs.

We estimated fecundity from a subset of females that we presumed had not spawned in December 2005 ($N = 31$) and February 2006 ($N = 34$). To estimate fecundity, we first cut six cross-sections of tissue (~ 1 g) per ovary, three from each ovary lobe (anterior, middle, and posterior locations). Each cross-section, as well as the remainder of the ovary, was weighed separately to the nearest 0.001 g. For each cross-section, we counted all the mature oocytes with a dissecting microscope ($7\times$ magnification). As in Emery and Brown (1978), we observed two modes of oocyte sizes: primary (generally <0.4 mm) and mature (generally >1.4 mm). For each cross section, we then calculated oocyte density, as the number of oocytes per g of ovary tissue. We then calculated the mean oocyte density among the six cross-sections and multiplied this value times the total ovary mass (see Bunnell et al., 2005) to estimate total fecundity (total number of mature oocytes).

For up to two fish per cm size class from February 2006, we also measured the diameters of the first 20 encountered mature oocytes, and then the next 100 encountered oocytes (all maturity stages). We used image analysis software (Image Pro-Plus 6.0) to make linear measurements (nearest 0.01 mm) of oocyte images captured with a digital camera attached to the dissecting microscope.

To determine whether differences existed in the fecundity versus weight regressions for December 2005 and February 2006, and then for the regressions between 1969 and 2005–2006, we used Analysis of Covariance (ANCOVA). In both instances, we first tested for the homogeneity of slopes assumption by including the weight \times time period interaction term in a General Linear Model (SAS Institute, 1999). When that interaction was not significant ($\alpha = 0.05$), we assumed similar slopes between the time periods and removed the interaction term from the model and evaluated whether the time period (main effect) was significant. If time period was significant, we calculated the least-squares mean fecundity for each time period to reveal the overall difference. For the oocyte diameter data, we used linear regression to determine whether oocyte size was related to fish weight.

Results

For the December 2005 and February 2006 samples (Fig. 1a), the slopes from the fecundity versus weight regressions were not different (weight \times month: $F_{1,61} = 0.01$, $P = 0.92$), nor was month ($F_{1,62} = 0.00$, $P = 0.95$). This result suggested that fecundity is determined by at least late December. We then pooled 2005 and 2006 data into one time period (and herein refer to it as 2006). The 2006 regression line ($F_{1,63} = 196.40$, $P < 0.0001$, $r^2 = 0.76$) equaled Fecundity = $-1990.1 + 56.5(\text{weight})$ and included fish ranging 73–399 g (199–323 mm TL).

When comparing the 1969 and 2006 fecundity versus weight regressions we limited the samples to size ranges common to both years (i.e., 70–240 g), which eliminated only 1 fish from 1969 (345 g) but 17 fish from 2006 (range = 244–399 g). The slopes from the fecundity versus weight regressions were not different (weight \times year: $F_{1,108} = 1.08$, $P = 0.30$) over this size range (see Fig. 1b). When this interaction term was removed, the main effect of year was significant ($F_{1,109} = 33.06$, $P < 0.0001$). Least-squares mean fecundity for 2006 equaled 5757 eggs, which was a 24% reduction from the least-squares mean fecundity for 1969 (7604 eggs).

Among a subset of bloaters from February 2006, mean mature oocyte diameter was unrelated to fish size ($F_{1,22} = 1.49$, $P = 0.24$, Fig. 2a). The overall mean mature oocyte diameter across all females was 1.95 mm (standard deviation = 0.18). To describe the size distribution of all oocytes, we pooled the sizes of randomly encountered oocytes

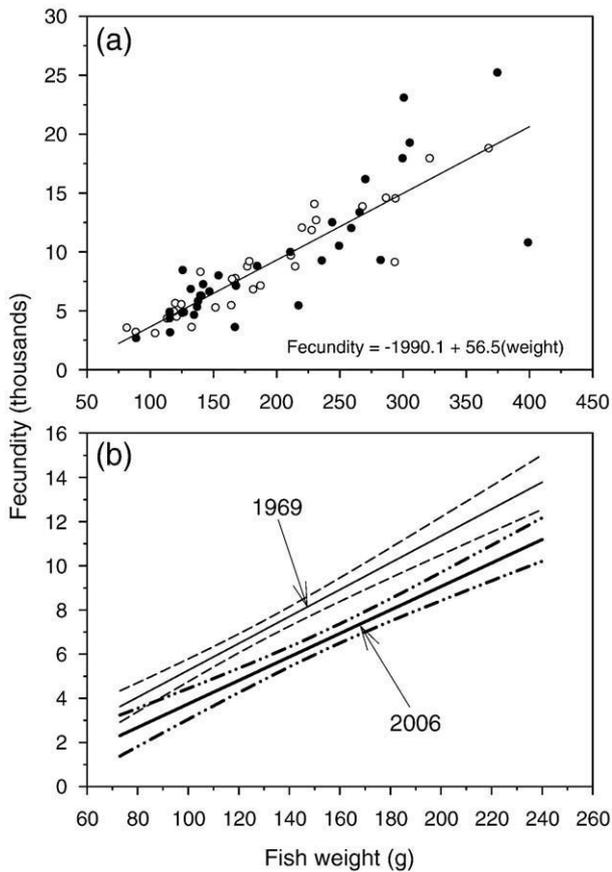


Fig. 1. (a) Fecundity (in thousands) of bloaters sampled from Lake Michigan during December 2005 (open circles) and February 2006 (closed circles) as a function of female weight (g). The solid regression line is for pooled 2005–2006 samples. (b) Regression line plus 95% confidence intervals for bloaters weighing 70–240 g and collected in October 1969 (Emery and Brown 1978; 95% CI = dashed line) and December 2005 and February 2006 (95% CI = dash-dot-dot-dash line). The 2006 regression line (and 95% CI) is thickened to help distinguish from the 1969 regression line.

across all 24 fishes, and found a bi-modal distribution (Fig. 2b): a smaller mode of presumably immature oocytes at 0.35 mm and a larger mode of presumably mature oocytes at 1.95 mm.

Discussion

We provided an updated weight-based regression to estimate bloater fecundity in Lake Michigan that can be used in stock/recruitment models and other population-level analyses. We also demonstrated that bloater fecundity is set as soon as late December, given that the fecundity regression based on fish sampled in late December 2005 was not different from the regression based on fish sampled in late February 2006. Finally, for bloaters smaller than 240 g, those sampled in 2006 were 24% less fecund than those sampled in 1969. Although we cannot rule out the possibility that this difference was the result of the difference of when bloaters were sampled (i.e., October versus December or February), our result is consistent with the hypothesis that bloater fecundity has declined with declining bloater condition. Bloater condition in 2006 was 41% lower than that measured in 1969, despite general similarity in population biomass between the two years. We expect that this lower than expected condition was the result of a general lakewide decline that has occurred in *Diporeia* (Nalepa et al., 2006), one of the historically important prey resources for bloater (Wells and Beeton, 1963; Crowder and Crawford, 1984; Davis et al., 2007). It should be noted, however, that *Diporeia* densities near our sample area in southwest Lake Michigan have maintained the highest densities throughout the

lake (Nalepa et al., 2006). As a result, bloater condition (and fecundity) could be even lower in other regions of the lake where *Diporeia* have completely disappeared.

Previous studies that have looked for linkages between condition and fecundity across years have focused on North Atlantic fishes. For example, North Sea cod (*Gadus morhua*) were 21% more fecund in 2002–2003 than in 1960–1970, and this increase was consistent with improved condition in later years (Yoneda and Wright, 2004). Similarly, Blanchard et al. (2003) found that size-specific fecundity and adult condition were generally higher in 1998 than in 1997 and 1999. Temporal variation in fecundity is not always explained by condition, however. Size specific fecundity of Atlantic cod in the Gulf of St. Lawrence was 42% lower in 1998 than in 1980 or 1999, but adult condition was unchanged among those time periods (McIntyre and Hutchings, 2003). The absence of a consistent condition effect on fecundity may be best explained by the hypothesis of McIntyre and Hutchings (2003), who argued that the positive relationship between fecundity and condition is asymptotic. As they suggest, only when condition falls below some threshold will the positive linkage between adult condition and fecundity be revealed. In our study, adult condition may have indeed crossed that threshold beyond which the effects of low condition on fecundity can be detected, although the 24% reduction in fecundity was perhaps not as large as would have been expected given the considerable 41% decline in adult condition.

Mean oocyte diameter varied among mature females in 2006, but that variation was unrelated to fish size, as has been commonly

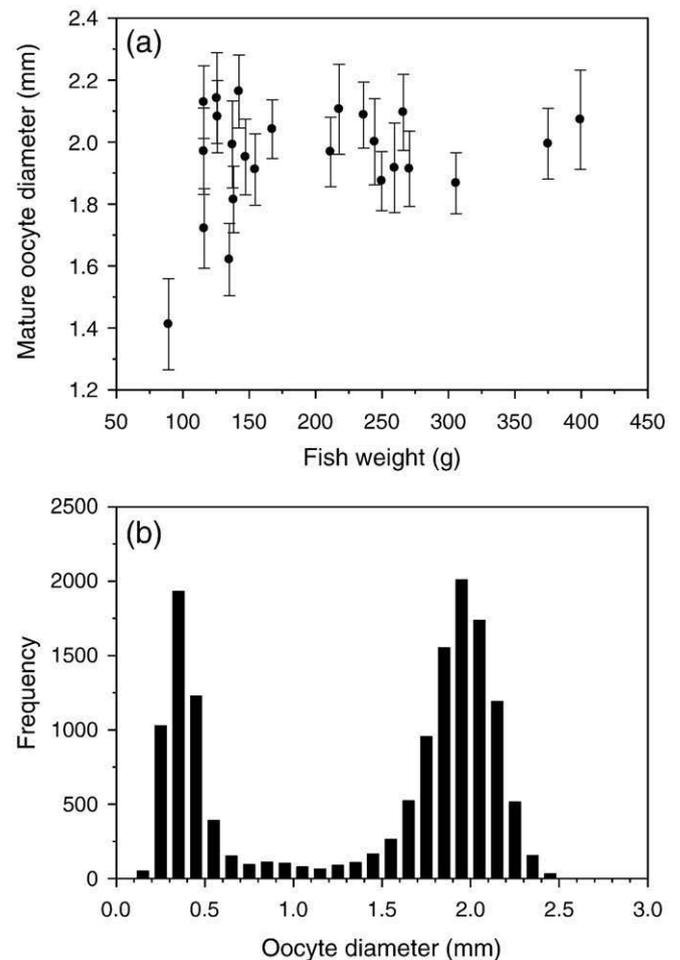


Fig. 2. Summary of oocyte size data from 24 mature Lake Michigan bloaters sampled in February 2006. Panel (a) depicts mature oocyte diameter (mean \pm standard deviation) as a function of female weight. Panel (b) depicts a size frequency histogram of all randomly encountered oocytes (600 per fish, includes primary (immature) and mature ones).

observed for several fish species (see review by Roff, 1992). In addition, variation in mean egg size for bloaters falls within the upper range of other benthic-spawning freshwater and marine species (Einum and Fleming, 2002). The modal size of primary oocytes in our February samples (i.e., 0.35 mm) was very similar to that measured by Emery and Brown (i.e., 0.30–0.40 mm) in February 1969. Conversely, the modal size for mature oocytes in our February samples (i.e., 1.95 mm) was slightly smaller than that measured by Emery and Brown (i.e., 2.05–2.25 mm). Because of differences in preservation between the two studies, however, we cannot confidently conclude that mature egg size has declined between 2006 and 1969. Unlike Emery and Brown (1978), we froze our fish prior to formalin preservation, which is known to cause nominal shrinkage in whole body sizes (e.g., 1–3%, Jones and Geen, 1977); effects on individual oocyte size are unknown, however. Second, Emery and Brown (1978) used 10% formalin, whereas we only used 5% formalin. The higher concentration of formalin for the 1969 samples may have shrunk oocytes more than the 2006 samples (Marteinsdottir and Able, 1988). Hence in both years, oocytes might have shrunk for different reasons, and the net effect of these differences limits our confidence that mature oocyte size has indeed declined between 1969 and 2006.

Given that our study revealed an updated fecundity versus weight regression, we conducted a post-hoc Ricker and Beverton–Holt stock/recruitment analysis where we explored whether incorporation of our new fecundity versus weight regression improved the model fit over using only the Emery and Brown (1978) regression that may overestimate population egg production when adult condition declines. Our previous attempts to fit these conventional stock/recruitment models failed because of non-stationarity in the relationship (i.e., the relationship changed through time, Bunnell et al., 2006a). Calculations of population egg production and density of age-3 recruits were identical to those outlined in Bunnell et al. (2006a) except that we were able to add 3 years of data from recent sampling. For our “new” population egg production estimate, we assumed that the shift to lower fecundity occurred after 1984 when the % total lipids declined to 16% after averaging 22% between 1969 and 1982. Hence, we use the Emery and Brown (1978) regression [Fecundity = $-580.6 + 58.88(\text{weight})$; note Emery and Brown (1978) failed to include the negative sign in front of the intercept] for the 1963–1984 year-classes, and our regression for 1985–2004 year-classes. To fit the Ricker ($R = Se^{(a-bS)}e^\epsilon$) and Beverton–Holt ($R = \{aS/[b+S]\}e^\epsilon$) models, where R equals age-3 bloater recruits (in millions of individuals), S equals population egg production (in billions of eggs), and e^ϵ equals the lognormal error term, we followed Bunnell et al. (2006b) where both sides of the equation were \log_e -transformed [Ricker: $\log_e(R) = \log_e(S) + a - bS + \epsilon$, Beverton and Holt: $\log_e(R) = \log_e(aS) - \log_e(b+S) + \epsilon$] and non-linear regression (Proc NLIN, SAS Institute, 1999) was used to estimate the parameters. For each model, r^2 was calculated as the model sum of squares divided by the corrected total sum of squares.

Developing a new estimate of population egg production based on reduced fecundity since 1984 failed to improve stock/recruitment model fits (Fig. 3). When the Emery and Brown (1978) fecundity regression was used for all years (Fig. 3a), r^2 ranged from 0.02–0.05, for the Ricker and Beverton and Holt models, respectively. When our equation was used for the 1985–2004 year-classes (Fig. 3b), r^2 was unchanged (0.02–0.05). Perhaps even more importantly, the non-stationarity of the stock/recruitment relationship remained. For example, recruitment in the late 1960s and early 2000s was much lower than in the early 1980s, despite similar estimates of population egg production. In fact, the reduction in fecundity would have had to have been far greater than 24% to shift those population fecundity estimates in the late 1990s and early 2000s farther to the left and remove the circularity or temporal autocorrelation in the relationship.

In conclusion, we provided an updated fecundity vs. weight regression based on southern Lake Michigan bloater collected in 2006 that indicated that fecundity was 24% lower in 2006 than in 1969. This

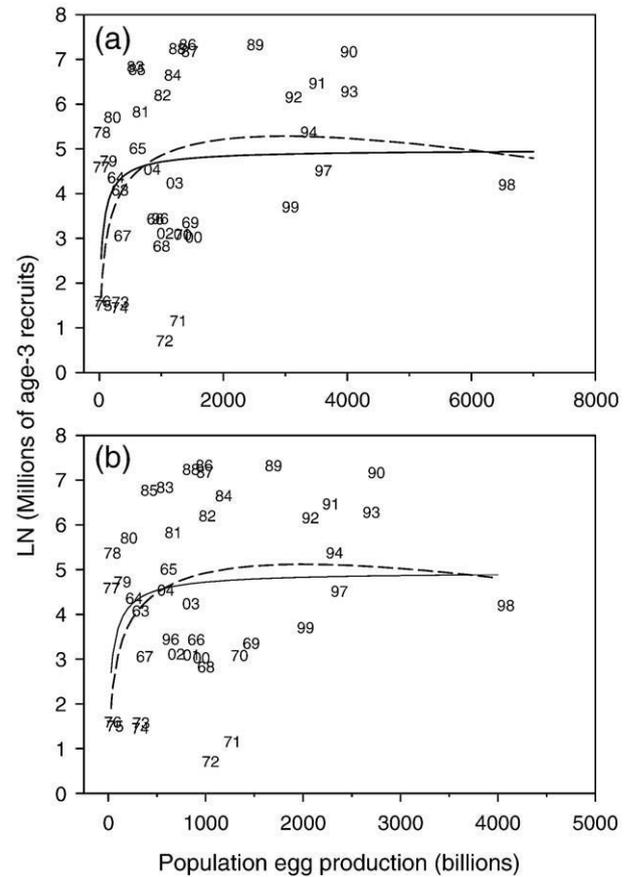


Fig. 3. Observed and predicted abundance of age-3 bloater recruits (ln-transformed) as a function of bloater population egg production. Predicted abundance of recruits is based on either the Ricker (dashed line) or Beverton and Holt (solid line) stock/recruitment model. Symbols indicate the last two digits of the year class (i.e., “97” symbolizes 1997). Panel (a) estimates population egg production using the fecundity vs. weight equation developed from Emery and Brown (1978), whereas panel (b) estimates population egg production by using the Emery and Brown (1978) fecundity equation for the 1963–1984 year-classes, and then our fecundity equation for the 1985–2004 year-classes.

could be the result of reduced condition in 2006 or the result of estimating fecundity from females sampled far closer to spawning. We had hypothesized that the consistently poor bloater recruitment observed since the early 1990s (relative to the 1980s) might have been due to a considerable reduction in fecundity. Post-hoc analyses of the bloater stock/recruit relationship that assumed bloater fecundity declined with reduced condition failed to support this hypothesis. Hence, despite a potential reduction in bloater fecundity in recent years, this decline is not sufficient to explain the poor recruitment observed in Lake Michigan since the early 1990s. As an extension, the failure to find an even more severe reduction in bloater fecundity despite a 41% reduction in adult condition suggests that a bloater recovery (or an increase in bloater recruitment) might still be possible despite the likely continued disappearance and decline of *Diporeia* spp in Lake Michigan. In fact, the years of strongest bloater recruitment (since 1962) were 1986–1990, when density dependent factors had reduced bloater condition to 15% total lipids (just above the 2006 level, Madenjian et al. 2000). Nonetheless, improved recruitment over the next five or so years will be critical to a bloater recovery, and we found no evidence that fecundity is or will be a recruitment bottleneck.

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