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To cite this article: Steven A. Pothoven & David B. Bunnell (2016) A Shift in Bloater Consumption in Lake Michigan between 1993 and 2011 and Its Effects on Diporeia and Mysis Prey, Transactions of the American Fisheries Society, 145:1, 59-68, DOI: [10.1080/00028487.2015.1094130](https://doi.org/10.1080/00028487.2015.1094130)

To link to this article: <http://dx.doi.org/10.1080/00028487.2015.1094130>



Published online: 08 Jan 2016.



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ARTICLE

A Shift in Bloater Consumption in Lake Michigan between 1993 and 2011 and Its Effects on *Diporeia* and *Mysis* Prey

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Abstract

Bioenergetics modeling was used to determine individual and population consumption by Bloater *Coregonus hoyi* in Lake Michigan during three time periods with variable Bloater density: 1993–1996 (high), 1998–2002 (intermediate), and 2009–2011 (low). Despite declines in Bloater abundance between 1993 and 2011, our results did not show any density-dependent compensatory response in annual individual consumption, specific consumption, or proportion of maximum consumption consumed. *Diporeia* spp. accounted for a steadily decreasing fraction of annual consumption, and Bloater were apparently unable to eat enough *Mysis diluviana* or other prey to account for the loss of *Diporeia* in the environment. The fraction of production of both *Diporeia* and *Mysis* that was consumed by the Bloater population decreased over time so that the consumption-to-production ratio for *Diporeia* + *Mysis* was 0.74, 0.26, and 0.14 in 1993–1996, 1998–2002, and 2009–2011, respectively. Although high Bloater numbers in the 1980s to 1990s may have had an influence on populations of *Diporeia*, Bloater were not the main factor driving *Diporeia* to a nearly complete disappearance because *Diporeia* continued to decline when Bloater predation demands were lessening. Thus, there appears to be a decoupling in the inverse relationship between predator and prey abundance in Lake Michigan. Compared with Alewife *Alosa pseudoharengus*, the other dominant planktivore in the lake, Bloater have a lower specific consumption and higher gross conversion efficiency (GCE), indicating that the lake can support a higher biomass of Bloater than Alewife. However, declines in Bloater GCE since the 1970s and the absence of positive responses in consumption variables following declines in abundance suggest that productivity in Lake Michigan might not be able to support the same biomass of Bloater as in the past.

Through consumption, predators can directly influence the distribution and abundance of their prey species (reviewed by Kerfoot and Sih 1987; Northcote 1988). When consumption exceeds the production capability of the prey species, the resultant decline in prey abundance can lead to numerous responses in individual predators, including reduced consumption, reduced growth rates, or declines in physiological condition (Hewett and Stewart 1989; Stewart and Ibarra 1991; Paterson et al. 2009). These density-dependent responses can

be best revealed when the predators undergo orders-of-magnitude changes in density.

In the Laurentian Great Lakes, populations of Bloater *Coregonus hoyi* have undergone order-of-magnitude changes in abundance over the past several decades (Bunnell et al. 2010). As the Bloater population density increased from 48 fish/ha in 1978 to 2,040 fish/ha in 1987, individual consumption, growth, and energetic condition concomitantly declined (Brown et al. 1987; Rudstam et al. 1994). Eventually, the density in Lake

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Received May 11, 2015; accepted September 8, 2015

Michigan peaked at 2,500 fish/ha in 1989 and then dropped steadily to levels less than 3 fish/ha by 2014 (Bunnell et al. 2015) owing to consistently poor recruitment after 1991. Although several hypotheses have been posited to explain the limited Bloater productivity and subsequent population decline, none has been confirmed as the primary factor (Bunnell et al. 2014). Despite the expectation that individual-level responses would rebound given the decline in population size, studies have reported that individual growth rates and condition have not increased (Szalai et al. 2003; Bunnell et al. 2012; Pothoven et al. 2012). These results suggest that Bloater consumption has also not increased despite fewer intraspecific competitors.

Adult Bloater are hypolimnetic benthivores that mainly eat large macroinvertebrates such as the glacial relicts *Mysis diluviana* and *Diporeia* spp., but they are able to consume zooplankton as well (Wells and Beeton 1963; Crowder and Crawford 1984; Hondorp et al. 2005). Bioenergetics models performed on the 1987 food-web suggested that Bloater consumption was more than what *Mysis* and *Diporeia* prey populations could sustain (Rand et al. 1995). Furthermore, McDonald et al. (1990) found declines in *Mysis* and *Diporeia* populations and shifts in prey size structure in the 1980s that were consistent with changes in Bloater abundance, although concurrent changes in nutrient loading complicate the analysis of *Diporeia* trends (Nalepa et al. 1998). Furthermore, several years following the decline in Bloater population density, *Diporeia* exhibited an unprecedented population decline in the late 1990s (Nalepa et al. 2006). Based on data from southeast Lake Michigan, *Mysis* abundance appeared to have increased between the 1980s and late 1990s as Bloater abundance declined, but then returned to 1980s levels in 2007–2008 despite continued declines in Bloater (Pothoven et al. 2010). The role of top-down control of *Diporeia* by Bloater (and other benthivorous species) has never been formally evaluated as a mechanism behind their declines, despite the indications in the 1980s that consumption demands were high. The more widely held hypothesis to explain the unambiguous decline of *Diporeia* in Lake Michigan (and Huron and Ontario) is a negative interaction with invasive dreissenid mussels, although the exact mechanism has yet to be identified (Dermott 2001; Nalepa et al. 2009).

To understand the changing food web in Lake Michigan, scientists and managers would benefit from an examination of the predator–prey dynamics that have occurred between Bloater and their two key prey species, *Diporeia* and *Mysis*, over the past several decades. These relationships have not been formally evaluated since the late 1980s (e.g., Rudstam et al. 1994; Rand et al. 1995), and bioenergetics models are excellent tools for determining the response of the individual predator (i.e., consumption rates) and exploring whether Bloater predation was underlying changes in *Diporeia* and *Mysis*. Our work has two broad objectives. First, we sought to determine whether different indicators of individual Bloater

consumption (e.g., consumption, specific consumption rate, proportion of maximum consumption, gross conversion efficiency [GCE]) varied between three periods that coincide with variable Bloater population density: 1993–1996 (high), 1998–2002 (intermediate), and 2009–2011 (low). We hypothesized that consumption indicators would be similar among periods, given the recent studies that revealed a lack of compensatory response for Bloater growth and condition (Szalai et al. 2003; Bunnell et al. 2012; Pothoven et al. 2012). Second, we sought to determine whether consumption by Bloater exceeded the production of *Diporeia* and *Mysis* in each of the three periods. We hypothesized that the fraction of production consumed would never exceed one (i.e., indicate that top-down control was minimal), given that declines for *Diporeia* and *Mysis* occurred after the Bloater population began declining in 1990. At the same time, we predicted the fraction of *Diporeia* and *Mysis* production that was consumed would decline with later periods given the marked declines in Bloater density.

METHODS

Bloater.—Three time periods were chosen to reflect variation in the density of Bloater and their prey and because corresponding data on Bloater diets and prey abundance were available: period 1 = 1993–1996 (high), period 2 = 1998–2002 (intermediate), and period 3 = 2009–2011 (low). Consumption was determined using the Wisconsin Fish Bioenergetics 3.1 Model, with species parameters for Bloater (Hanson et al. 1997). Fish initial and final weight, water temperature, fish diet composition, and fish and prey energy density were required inputs for the model to determine annual consumption by an average individual Bloater. To determine annual population consumption, annual mortality rate and age-specific Bloater density were also required. Available data were pooled over the entire lake within each time period for consistency with previous bioenergetics analyses of Bloater and other fish (Stewart and Binkowski 1986; Rudstam et al. 1994; Rand et al. 1995; Pothoven and Madenjian 2008).

The model inputs for Bloater density, mortality, and growth were derived from the U.S. Geological Survey (USGS) Great Lakes Science Center fall forage fish survey. Briefly, up to 11 depth strata in 9-m increments from 9 to 110 m were sampled at seven sites around the lake with a 12-m bottom trawl (13-mm cod end mesh) that was towed for about 10 min. Further survey details are available in Madenjian et al. (2003) and Bunnell et al. (2006). Density (fish/ha) was determined based on the area swept for each tow as a function of bottom depth and time of tow (Madenjian et al. 2010). Densities were averaged across all sites for a given depth and then averaged across all depths weighted by the representative area of the lake to determine age-specific numeric density (see below for age information). Age-specific density was averaged across years within each time period to provide a single age-specific

density for each time period (Table 1). Annual mortality was estimated for males and females for the 1990–2004 year-classes using the catch-curve analyses and mortality rates from Bunnell et al. (2012). Male and female mortality was averaged across year-classes, and finding no difference in mortality between periods 1 and 2 ($P = 0.21$), mortality ($A = 0.46$) was assumed to remain constant across the three time periods in our study. This assumption seemed reasonable given the lack of data in period 3 and because previous analyses of Bloater bioenergetics did not find variation in survival rates to be a major source of error in population consumption estimates (Rand et al. 1995).

Bloater were aged by counting the number of annuli on projected scale images and were used to produce age–length keys for each year (see Bunnell et al. 2012). Initial weight was input as the mean weight at age for a fish at the beginning of each time period, and the final weight was input as the mean weight at age of a fish for the successive age-class (Table 1). Simulations were run for each age-class for a period of 1 year using October 1 as a start date, e.g., consumption was

determined between October 1 as an age-1 fish through the following September 30 as an age-2 fish and is referred to hereafter as an age-1 fish, etc. For population simulations, all fish \geq age 9 were combined into a single age-9+ group because of limited weight-at-age data for fish $>$ age 9 and because at least 97% of all fish were \leq age 9 in each period.

To estimate the temperature occupied by Bloater, we used modeled data that incorporated evaporation and thermal fluxes (see Croley 1995) to predict water temperature at 1-m vertical depths for each day from 1994 to 2008 averaged across the entire basin of Lake Michigan. Because data beyond 2008 were not available, we assumed Bloater occupied the same annual temperature regime for each time period, which is not unreasonable for adult Bloater given that they primarily occupy hypolimnetic waters which have a more stable temperature regime. Furthermore, the bioenergetics model results are relatively insensitive to minor changes in temperature (Rand et al. 1995). We assumed that Bloater would occupy temperatures up to 6°C when it was available in the hypolimnion (Clemens and Crawford 2009; Harford et al. 2012).

TABLE 1. Initial and final weight at age, density for each age-group, annual consumption for an average individual in each age-group (C), and GCE for each age-group of Bloaters during three time periods in Lake Michigan. Period 1 = 1993–1996, period 2 = 1998–2002, and period 3 = 2009–2011. Density for age-9 Bloater includes all fish \geq age 9. Initial weight is for October 1, and final weight is for the following September 30.

Period	Age	Initial weight (g)	Final weight (g)	Density (number/ha)	C (g/year)	GCE (%)
1	1	14.8	28.6	8	169	8.18
	2	28.6	46.9	62	279	6.56
	3	46.9	60.3	162	370	3.63
	4	60.3	84.3	185	530	4.53
	5	84.3	105.0	141	665	3.11
	6	105.0	127.2	78	816	2.72
	7	127.2	140.3	123	895	1.46
	8	140.3	157.6	35	1,021	1.69
	9	157.6	169.9	4	1,093	1.13
2	1	17.8	35.5	3	184	9.63
	2	35.5	56.8	5	297	7.18
	3	56.8	73.7	13	398	4.24
	4	73.7	88.0	19	477	3.00
	5	88.0	96.0	29	517	1.55
	6	96.0	110.0	27	602	2.33
	7	110.0	128.2	14	712	2.56
	8	128.2	134.0	10	732	0.79
	9	134.0	141.6	7	778	0.98
3	1	17.1	24.9	14	141	5.55
	2	24.9	43.6	19	249	7.50
	3	43.6	51.0	12	297	2.49
	4	51.0	63.2	6	372	3.28
	5	63.2	78.2	3	465	3.23
	6	78.2	77.3	1	447	-0.20
	7	77.3	85.6	1	506	1.64
	8	85.6	94.7	<1	562	1.62
	9	94.7	124.0	<1	770	3.81

TABLE 2. Adult Bloater diet inputs (percent total wet weight) for the bioenergetics model during three time periods: 1 = 1993–1996, 2 = 1998–2002, and 3 = 2009–2011.

Period	Season	<i>Diporeia</i>	<i>Mysis</i>	Copepod	Cladoceran	Predatory cladoceran	Diptera	Other
1	Spring	30	35	29	0	0	1	5
	Summer	50	13	28	0	0	7	2
	Fall	22	31	8	23	15	0	1
2	Spring	62	27	1	0	0	6	4
	Summer	42	30	4	13	0	10	1
	Fall	15	72	0	1	10	0	2
3	Spring	0	36	61	0	0	2	1
	Summer	0	60	22	4	2	10	2
	Fall	0	60	16	12	12	0	0
	Winter	0	87	13	0	0	0	0

Diet information on a dry weight (DW) basis was available from various studies (Hondorp et al. 2005; Davis et al. 2007; Bunnell et al., in press; S. A. Pothoven, unpublished data) from several sites throughout Lake Michigan within each time period. Diets were converted to a wet weight (WW) basis using published WW:DW ratios for each prey type. Available diet information was divided into seasons, with spring = April, May, June; summer = July, August; fall = September, October, November; and winter = December, January, February, March. Diet proportions for each season and site combination were averaged across years within each time period to produce a single diet composition for each season within each time period (Table 2).

The energy density of Bloater did not vary for fish collected between 1998 and 2009, and was described by the equation

$$J/g = 24.075 g + 5,043.4$$

(Pothoven et al. 2012). This equation was used to determine Bloater energy density for all time periods because no additional information was available for 1993–1996. Using the same energy density for all periods seems reasonable considering that Bunnell et al. (2009) reported little change in Bloater lipid content between 1994 and 2005–2006.

Wet weight prey energy densities for *Diporeia* (4,185 J/g), *Mysis* (4,604 J/g), cladocerans (including *Bythotrephes*; 1,674 J/g), copepods (2,300 J/g), and Diptera (3,138 J/g) were taken from Stewart and Binkowski (1986) and Lantry and Stewart (1993), and remained constant across all periods. Bloater were assumed to spawn February 15 for each period at age 3 and older, with 10% of body mass shed as gametes (Rudstam et al. 1994).

Age-specific consumption (g/year) by an average individual Bloater and by the Bloater population was determined within each time period. Specific consumption was determined on a weight ($g \cdot g^{-1} \cdot d^{-1}$) and energetic ($J \cdot g^{-1} \cdot d^{-1}$) basis. Gross

conversion efficiency was determined as the change in fish weight (i.e., final weight – initial weight) per weight of food eaten on an annual basis. The proportion of maximum consumption (pCmax) eaten was determined iteratively to balance consumption with changes in fish weight. Individual responses were compared among periods using ANCOVA if there was no interaction between the covariate and time period. Fish age was the covariate for the analysis of consumption, and GCE and mean simulated fish weight over the year was the covariate for specific consumption and pCmax. Analyses were done using SYSTAT 11, with $P < 0.05$ considered significant.

Prey production.—To determine annual *Diporeia* production for each period, we used *Diporeia* densities from lakewide surveys in 1994–1995, 2000, and 2010 (Nalepa et al. 2009, 2014; T. Nalepa, University of Michigan, unpublished data). *Diporeia* densities were reported by depth zones of <30, 31–50, 51–90, and >90 m, which represented 12.7, 14.7, 31, and 41.5% of the lake area, respectively (see Nalepa et al. 2009). The average *Diporeia* length for each depth zone was converted to an average dry weight, which was used to determine biomass (B) density for each depth zone and time period (Nalepa et al. 2000, 2009, 2014). Dry weight production (P) from each zone was determined using P:B ratios for each depth zone (Winnell and White 1984), which was converted to WW production assuming a DW:WW ratio of 0.27 (Nalepa et al. 2009).

To determine annual *Mysis* production for each period, we used Menzie's (1980) size-frequency method that has previously been used for Lake Michigan (Sell 1982; Pothoven et al. 2010). We assumed that size-frequency and abundance data collected offshore of Muskegon, Michigan at 45- and 110-m bottom depths were representative of the entire lake given the absence of other monthly data, with the 45-m site representing 27.4% of lake area (<50 m) and the 110-m site representing the remainder of the lake (Nalepa et al. 2009). Dry weight production was converted to a WW basis assuming a DW:WW

ratio of 0.175 (Ricciardi and Bourget 1998). Production for 1995–1996 and 1998–2000 was available in Pothoven et al. (2010); production for 2009–2011 was based on unpublished data (Pothoven) using identical size-frequency methods as during the previous time periods.

RESULTS

Contrary to our expectations, consumption by an average individual Bloater differed among time periods, but the difference depended on fish age, i.e., there was a significant interaction between the factor (time period) and the covariate (age; $F_{2, 21} = 37.6$, $P < 0.001$; Figure 1). The slope of consumption as a function of fish age increased at a faster rate in period 1 than during the other two time periods, resulting in larger differences in consumption among time periods for older Bloater than for younger fish. On an energetic basis ($J/year$), there was also a significant interaction between the factor (time period) and the covariate (age; $F_{2, 21} = 23.7$, $P < 0.001$). Consumption on an energetic basis was higher for all ages in period 2 than in period 3, whereas for period 1, the gap in consumption relative to period 3 increased with fish age (Figure 1). Overall, *Diporeia*, *Mysis*, and copepods accounted for 78–87% of consumption among periods (Figure 2).

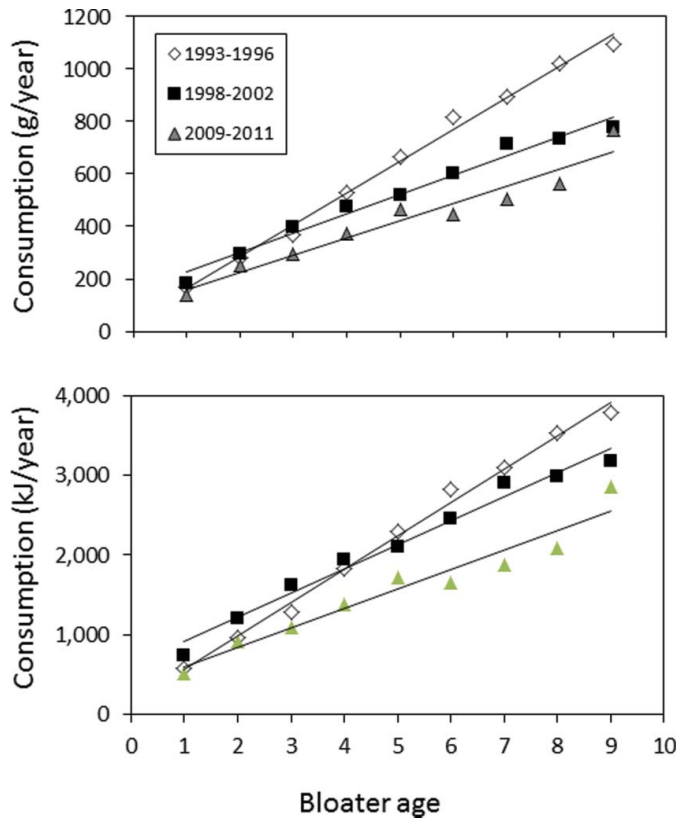


FIGURE 1. Annual consumption for an average individual Bloater by weight (top) and energy (bottom) as a function of fish age during three time periods in Lake Michigan.

Specific consumption ($g \cdot g^{-1} \cdot d^{-1}$) was highest in the fall, decreased through late winter, and then increased through spring before leveling off each year (Figure 3). Specific consumption ($g \cdot g^{-1} \cdot d^{-1}$) for Bloater differed among time periods ($F_{2, 23} = 44.0$, $P = 0.001$), with mean values of 0.020, 0.017, and 0.018 $g \cdot g^{-1} \cdot d^{-1}$ in periods 1, 2, and 3, respectively. Specific consumption on an energetic basis ($J \cdot g^{-1} \cdot d^{-1}$) also differed among periods ($F_{2, 23} = 3.9$, $P = 0.001$), but differences among years were small, with values ranging between 70 $J \cdot g^{-1} \cdot d^{-1}$ in period 1 and 66 $J \cdot g^{-1} \cdot d^{-1}$ in period 3.

The pCmax increased with fish weight during all time periods (Figure 4). There was a significant interaction between the factor (time period) and the covariate (weight; $F_{2, 22} = 10.7$, $P = 0.001$). The pCmax for period 1 was generally higher than in periods 2 and 3. Gross conversion efficiency generally decreased with fish age (Table 1) and did not differ among time periods ($F_{2, 23} = 0.2$, $P = 0.80$), ranging between 3.7% in period 1 and 3.2% in period 3.

Overall consumption by the Bloater population was 359, 52, and 11 $kg \cdot ha^{-1} \cdot year^{-1}$ in periods 1, 2, and 3, respectively. Consumption by Bloater \geq age 5 contributed the most to annual population consumption in period 1 (64%) and period 2 (77%), but only accounted for 16% of the population consumption in period 3 (Table 3). Peak consumption by the Bloater population was in the fall, and the lowest consumption was in early March during each period. Peak population consumption in the fall was three times higher than the lowest population consumption in periods 1 and 2, and 2.8 times higher in period 3.

Both *Diporeia* and *Mysis* production decreased over time, but the declines for *Diporeia* production were more drastic and occurred sooner (Figure 5). In period 1, *Diporeia* production was more than twice that of *Mysis*, but by period 2, *Diporeia* and *Mysis* production had nearly converged, and in period 3, *Mysis* production was almost eight times that of *Diporeia*. Consumption of *Diporeia* was just over 50% of production estimates in period 1, but only 20% of production in period 2, and negligible in period 3 (Figure 5). Consumption of *Mysis* was about equal to production estimates in period 1, about 33% of production in period 2, and 16% of production in period 3. Over the three time periods, the consumption to production ratio for *Diporeia* + *Mysis* steadily declined from 0.74 to 0.26 to 0.14.

DISCUSSION

Despite declines in Bloater density between 1993 and 2011 (Table 1; Bunnell et al. 2015), our results did not show any compensatory response in individual consumption. This supports the hypothesis that a fundamental shift has occurred in density-dependent responses for Bloater in Lake Michigan. In the past, Bloater consumption rates were density dependent, with low consumption rates during periods of high abundance and high consumption rates during periods of low abundance

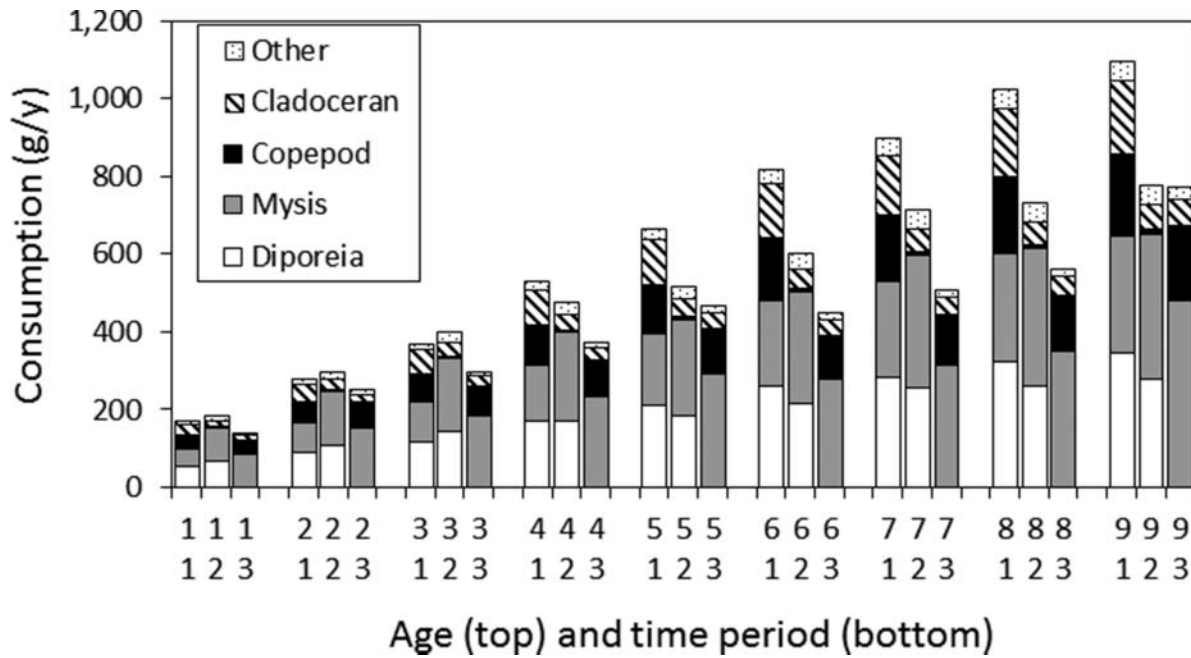


FIGURE 2. Annual consumption of specific prey by an average individual Bloater as a function of fish age during three time periods in Lake Michigan. Time period 1 = 1993–1996, 2 = 1998–2002, 3 = 2009–2011.

(Rudstam et al. 1994). Our results not only revealed no increase in consumption indices with declining Bloater abundance, they also provided some evidence that individual consumption, specific consumption, and pCmax actually decreased, especially for older fish. The changes in Bloater consumption and growth dynamics have been linked to the drastic declines of *Diporeia* in Lake Michigan. Szalai et al. (2003) noted that after *Diporeia* declines in the 1990s, adult Bloater length and weight remained low despite decreased Bloater numbers. Other studies have found that following *Diporeia* declines, Bloater condition (Bunnell et al. 2006), lipid content (Bunnell et al. 2009), and energy density

(Pothoven et al. 2012) all remained low despite declining abundances of Bloater.

Diporeia and *Mysis* combined for the majority of consumption in each period, i.e., 59, 84, and 63% in periods 1, 2, and 3, respectively. However, *Diporeia* comprised a steadily decreasing fraction of consumption over the three time periods, whereas *Mysis* comprised an increasing fraction. Even though the amount of *Mysis* eaten by an individual Bloater increased on average 59% between period 1 and 3, this increase apparently was not enough to compensate for the complete loss of *Diporeia* in diets. The generally lower pCmax in period 3, especially for older fish, is consistent with the idea that Bloater

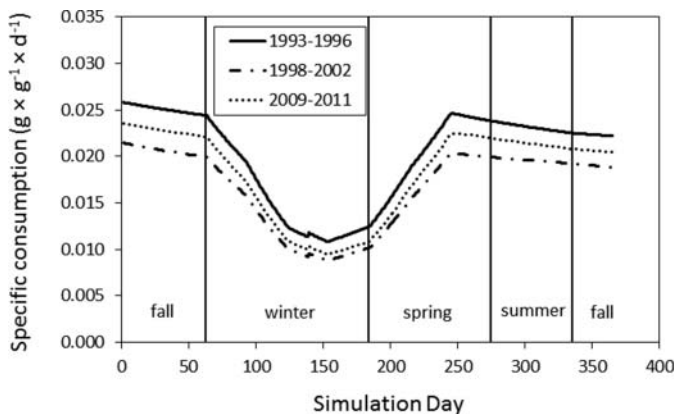


FIGURE 3. Specific consumption for Bloater during three time periods in Lake Michigan. Starting date for simulations is October 1.

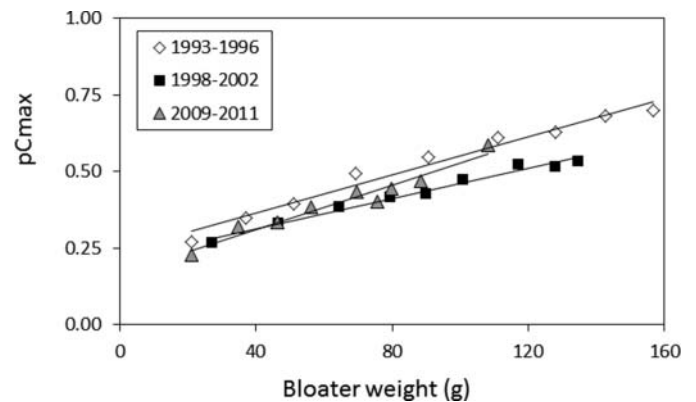


FIGURE 4. Proportion of maximum consumption eaten by Bloater as a function of mean annual weight during three time periods in Lake Michigan.

TABLE 3. Total amount ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) of various prey eaten by the Bloater population during three time periods in Lake Michigan. Period 1 = 1993–1996, period 2 = 1998–2002, and period 3 = 2009–2011. Consumption for age-9 Bloater includes all fish \geq age 9.

Period	Age	Consumption ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$)				Total
		<i>Diporeia</i>	<i>Mysis</i>	Zooplankton	Other	
1	1	0.3	0.3	0.3	<0.1	0.9
	2	3.9	3.6	4.7	0.5	12.6
	3	13.4	12.5	16.5	1.8	44.3
	4	22.0	20.4	26.9	3.0	72.3
	5	21.0	19.6	25.9	2.9	69.4
	6	14.3	13.4	17.7	2.0	47.3
	7	24.7	23.2	30.6	3.4	81.8
	8	8.0	7.5	9.9	1.1	26.5
	9	1.0	1.0	1.3	0.1	3.4
2	1	0.1	0.2	<0.1	<0.1	0.4
	2	0.3	0.5	0.1	0.1	1.0
	3	1.3	1.9	0.4	0.2	3.7
	4	2.3	3.5	0.6	0.4	6.9
	5	3.8	5.7	1.1	0.7	11.2
	6	4.1	6.0	1.1	0.7	12.0
	7	2.5	3.8	0.7	0.5	7.5
	8	1.8	2.7	0.5	0.3	5.4
	9	1.4	2.1	0.4	0.3	4.2
3	1	0.0	0.9	0.5	<0.1	1.5
	2	0.0	2.2	1.2	0.1	3.5
	3	0.0	1.7	0.9	0.1	2.7
	4	0.0	1.0	0.5	<0.1	1.6
	5	0.0	0.6	0.3	<0.1	1.0
	6	0.0	0.2	0.1	<0.1	0.3
	7	0.0	0.1	0.1	<0.1	0.2
	8	0.0	<0.1	<0.1	<0.1	0.1
	9	0.0	<0.1	<0.1	<0.1	0.1

were unable to eat enough *Mysis* (or other prey) to completely replace *Diporeia*. This is somewhat surprising, because although *Mysis* abundance was lower in period 3 than in period 1, the fraction of *Mysis* production that was eaten by Bloater was much lower in period 3. Furthermore, many of the planktivorous fish that potentially compete with Bloater for *Mysis* were in decline in period 3 (Bunnell et al. 2015). Perhaps the ability to efficiently find, capture, and consume *Mysis* reduced Bloaters' ability to further increase consumption. In a similar result, Pothoven and Madenjian (2008) noted that as *Diporeia* declined, Alewife *Alosa pseudoharengus* in Lake Michigan were unable to fully replace *Diporeia* with other prey and energy content subsequently declined (Madenjian et al. 2006). Similarly, the loss of *Diporeia* was associated with declines in both energy content and ration for Deepwater Sculpin *Myoxocephalus thompsonii* in Lake Michigan (Pothoven et al. 2011).

As expected, the fraction of both *Diporeia* and *Mysis* production that was consumed by the Bloater population decreased over time. Interestingly, the consumption-to-production ratio declined for both prey species even though production for both species declined across time periods. However, Bloater abundance also declined over time so that consumption by the Bloater population also decreased 85% between periods 1 and 2, and 79% between periods 2 and 3. In turn, the consumption-to-production ratio for *Diporeia* + *Mysis* was 0.74, 0.26, and 0.14 in periods 1, 2, and 3, respectively.

In 1987, when Bloater abundance was near its peak and almost twice as high as in 1993–1996, Rudstam et al. (1994) determined Bloater consumption was $533 \text{ kg} \times \text{ha}^{-1} \times \text{year}^{-1}$ and was split roughly equally between *Mysis* and *Diporeia*. Based on *Diporeia* abundance in the southern basin of the lake, we can roughly estimate production of *Diporeia* at

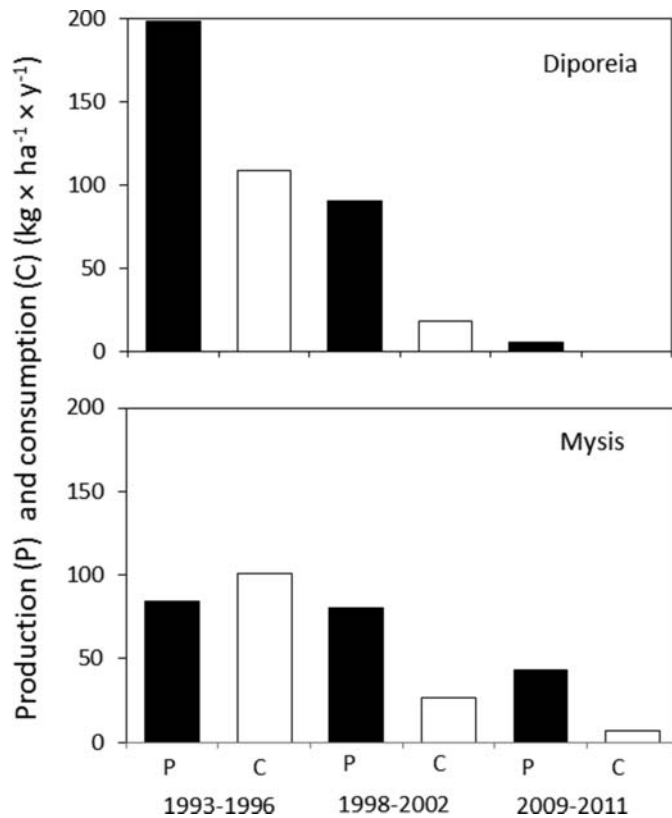


FIGURE 5. Annual production (P) of *Diporeia* and *Mysis* and consumption of each prey by the Bloater population (C) in Lake Michigan during three time periods.

266 kg × ha⁻¹ × year⁻¹ in 1987 (Nalepa et al. 1998). Thus, predation pressures on *Diporeia* and *Mysis* would have been even more intense in the late 1980s than in our earliest time period of 1993–1996. This is consistent with the results from Rand et al. (1995) noting that planktivory by Alewife and Bloater in Lake Michigan exceeded prey production in 1987. These high consumption rates are thought to have affected *Mysis* and *Diporeia* abundance and population structure in the late 1980s (McDonald et al. 1990). During this period of high Bloater abundance between the early 1980s to the early 1990s, *Diporeia* abundance decreased at a relatively high rate (Nalepa et al. 1998), and consumption by Bloater (and other fish species) may have contributed to those declines in *Diporeia* along with decreased nutrient loading. Even back to the 1960s and 1970s, *Diporeia* and Bloater appeared to be at least somewhat inversely related to one another (McDonald et al. 1990; Nalepa et al. 1998), but shifts in nutrient loading and other fish species were also influencing trends in *Diporeia*, so the exact relationship is not entirely clear (Nalepa et al. 1998). Since 1998, however, any potential inverse relationship between predator and prey appears to be decoupled, given that *Diporeia* abundance has not responded favorably to reductions in Bloater abundance. Furthermore, although high Bloater numbers in the 1980s–1990s likely had some influence on

populations of *Diporeia*, Bloater do not appear to be the main factor that ultimately led to *Diporeia*'s nearly complete disappearance. However, the prolonged period of high predation relative to production likely put the population of *Diporeia* in a state of greater vulnerability to environmental factors more commonly associated with their decline, such as decreased nutrient loading and dreissenid mussel invasions (Nalepa et al. 1998, 2006).

Limited data on *Mysis* production throughout Lake Michigan further complicates the efforts to understand predator–prey relationships between *Mysis* and planktivores. As with *Diporeia*, Rand et al. (1995) and McDonald et al. (1990) indicated that Bloater was likely exerting top-down control on *Mysis* in the 1980s. Similarly, our results indicate that Bloaters were consuming over 100% of *Mysis* production in period 1. When one considers that Bloater is only one of several species to consume *Mysis*, it is very surprising that *Mysis* densities may have actually increased between the 1980s and 1990s (Pothoven et al. 2010). In fact, *Mysis* densities did not decline back to 1980s levels until 2007–2008 (Pothoven et al. 2010), when Bloaters were already at relatively low densities, and they were eating only a small fraction of the *Mysis* production. Hence, despite bioenergetics models revealing a relatively high predation pressure on *Mysis* densities in the 1980s and 1990s, populations of *Mysis* persisted over this time period and have only recently begun to demonstrate some indications of population decline (Pothoven et al. 2010).

Our analyses involved a number of assumptions that could influence the conclusions. When evaluating population consumption by Bloater, this type of modeling can be quite sensitive to changes in fish growth and density (Rand et al. 1995). For fish growth, we erred on the side of overestimating weight at age because we assumed that ages determined by scales were accurate up to age 9. In reality, if scales underestimate bloater ages older than age 6 (see Szalai et al. 2003), then we are biasing the weight at age for older fish to be high and therefore overestimating consumption of older fish. For Bloater density, we used data from the USGS bottom trawl survey that takes place at fixed sites and depths and was assumed to represent Bloater density across the lake. Because catchability was not 100% (i.e., some Bloaters are off the bottom during the day or some Bloaters on the bottom could avoid the net), we know that we underestimated Bloater density. This would have the greatest impact on our consumption estimates in period 1, when Bloater consumption was highest relative to prey production. For example, if Bloater density was actually twice what we observed, then Bloater consumption would increase by roughly the same factor, suggesting a much higher top-down influence by Bloater during this period of high density than what we reported. On the other hand, estimates of *Diporeia* and *Mysis* production are also underestimated due to sampling inefficiencies (Nalepa et al. 1988; Chipps and Bennett 1996).

From a Lake Michigan food web perspective, the other dominant planktivore is Alewife, and it is interesting to compare their consumption patterns with those of Bloater. Bioenergetics analyses for the late 1980s indicated that the lake could support a higher biomass of Bloater than Alewife, based on Bloater's higher GCE and lower specific consumption demands (Rudstam et al. 1994). Based on the same indicators, our results indicated that Lake Michigan can still support a higher biomass of Bloater than Alewife. For example, the GCE of Bloater averaged 3.5% for 1993–2011, compared with 2.1% for Alewife in 1995–2005 (Pothoven and Madenjian 2008), and mass specific consumption was $0.018 \text{ g} \times \text{g}^{-1} \times \text{d}^{-1}$ for Bloater compared with $0.039 \text{ g} \times \text{g}^{-1} \times \text{d}^{-1}$ for Alewife. Therefore, the annual consumption by a Bloater is lower than that of a similar age Alewife due to lower ration requirements. For example, annual consumption by an age-4 Bloater was 14% lower than that of an age-4 Alewife, even though the Bloater would weigh 58% more and have an annual growth rate 180% higher than that of the Alewife.

Even though productivity in Lake Michigan can support a higher biomass of Bloater than Alewife, other factors suggest fundamental changes in the lake that have affected Bloater. For example, GCE was lower in period 3 (3.2%) than during a previous period of low Bloater abundance in the 1970s (6.8%; Rudstam et al. 1994). A decrease in GCE suggests that productivity in Lake Michigan might not be able to support the same production of Bloater as in the past. This is consistent with the absence of positive responses in consumption, growth, and energy content for Bloater despite declines in abundance. Furthermore, prey production for *Diporeia* and *Mysis* has not rebounded despite decreases in predation pressure. Thus, past paradigms used to understand and manage Bloater in Lake Michigan may no longer be valid.

ACKNOWLEDGMENTS

We thank C. Madenjian for his constructive comments that improved the manuscript. This article is contribution 1778 of the National Oceanic and Atmospheric Administration (NOAA) Great Lakes Environmental Research Laboratory and contribution 1971 of the USGS Great Lakes Science Center. Reference to trade names does not imply endorsement by the U.S. Government.

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