

ARTICLE

Energy Density of Bloaters in the Upper Great Lakes

Steven A. Pothoven*

National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory,
1431 Beach Street, Muskegon, Michigan 49441, USA

David B. Bunnell and Charles P. Madenjian

U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor,
Michigan 48105, USA

Owen T. Gorman

U.S. Geological Survey, Great Lakes Science Center, Lake Superior Biological Station,
2800 Lake Shore Drive East, Ashland, Wisconsin 54806, USA

Edward F. Roseman

U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor,
Michigan 48105, USA

Abstract

We evaluated the energy density of bloaters *Coregonus hoyi* as a function of fish size across Lakes Michigan, Huron, and Superior in 2008–2009 and assessed how differences in energy density are related to factors such as biomass density of bloaters and availability of prey. Additional objectives were to compare energy density between sexes and to compare energy densities of bloaters in Lake Michigan between two time periods (1998–2001 and 2008–2009). For the cross-lake comparisons in 2008, energy density increased with fish total length (TL) only in Lake Michigan. Mean energy density adjusted for fish size was 8% higher in bloaters from Lake Superior than in bloaters from Lake Huron. Relative to fish in these two lakes, small (<125 mm TL) bloaters from Lake Michigan had lower energy density, whereas large (>175 mm TL) bloaters had higher energy density. In 2009, energy density increased with bloater size, and mean energy density adjusted for fish size was about 9% higher in Lake Michigan than in Lake Huron (Lake Superior was not sampled during 2009). Energy density of bloaters in Lake Huron was generally the lowest among lakes, reflecting the relatively low densities of opossum shrimp *Mysis diluviana* and the relatively high biomass of bloaters reported for that lake. Other factors, such as energy content of prey, growing season, or ontogenetic differences in energy use strategies, may also influence cross-lake variation in energy density. Mean energy density adjusted for length was 7% higher for female bloaters than for male bloaters in Lakes Michigan and Huron. In Lake Superior, energy density did not differ between males and females. Finally, energy density of bloaters in Lake Michigan was similar between the periods 2008–2009 and 1998–2001, possibly due to a low population abundance of bloaters, which could offset food availability changes linked to the loss of prey such as the amphipods *Diporeia* spp.

Changes in fish physiological condition have important consequences for fisheries ecology and management. From a population perspective, declines in physiological condition can affect whether a fish will reproduce (Rijnsdorp 1990; Rideout et al.

2005) and the quality of its gametes (Chambers and Waiwood 1996; Ouellet et al. 2001; Bunnell et al. 2007) and have even been linked to declines in year-class strength (Marshall et al. 1999). From a community perspective, reduced condition of a

*Corresponding author: steve.pothoven@noaa.gov
Received July 20, 2011; accepted December 28, 2011

prey species has consequences for its predator; that is, to maintain similar levels of growth, the predator would have to consume more prey if the prey's energy density has declined (Rand et al. 1994; Madenjian et al. 2006b). Changes in the physiological condition of a predator are generally associated with intraspecific, density-dependent factors or with some dramatic change in the densities of its preferred prey (Shearer 1994; Madenjian et al. 2000).

Planktivorous and benthivorous fish populations in many of the Laurentian Great Lakes have undergone changes, especially over the past 15 years, associated with proliferation of invasive species (Mills et al. 1993; Vanderploeg et al. 2002) and declining productivity (Fahnenstiel et al. 2010; Mida et al. 2010; Evans et al. 2011). In addition to some abrupt declines in abundance for some fish species (Riley et al. 2008), several species have also endured declines in physiological condition as measured by their energy density. These declines have largely been attributed to the decline of the amphipods *Diporeia* spp. (Pothoven et al. 2001; Madenjian et al. 2006b; Pothoven et al. 2011), which are energy-rich prey in the Great Lakes. *Diporeia* numbers in Lakes Michigan and Huron have declined dramatically (Nalepa et al. 2007, 2009) and are now similar to Lake Superior *Diporeia* numbers, which have changed little (Barbiero et al. 2011).

The bloater *Coregonus hoyi* is a native planktivore in Lakes Superior, Huron, and Michigan (extirpated from Lake Ontario), and *Diporeia* spp. have historically been among its primary prey (Wells and Beeton 1963; Crowder and Crawford 1984; Rand et al. 1995; reviewed by Clemens and Crawford 2009). Ecologically, bloaters play an important role in the food web dynamics of these lakes. As juveniles, bloaters are epilimnetic and eat zooplankton (reviewed by Clemens and Crawford 2009). As adults, they shift to the profundal zone, where they undergo diel vertical migrations to feed on opossum shrimp *Mysis diluviana* (hereafter, *Mysis*) and large calanoid copepods (in addition to *Diporeia*), thus integrating the pelagic and benthic profundal food web (Hondorp et al. 2005; Davis et al. 2007; Bunnell et al. 2011; reviewed by Clemens and Crawford 2009). Bloaters also provide a food source for Chinook salmon *Oncorhynchus tshawytscha*, lake trout *Salvelinus namaycush*, and burbot *Lota lota*, although they are generally not a predominate prey item for these piscivores (Madenjian et al. 1998, 2006a; Gamble et al. 2011; reviewed by Clemens and Crawford 2009). Bloaters are also commercially harvested in Lakes Superior, Huron, and Michigan (Baldwin et al. 2009).

From a population perspective, bloaters exhibit unique dynamics and sex-specific differences in life history characteristics. The population dynamics of bloaters in these systems are highly variable, with years of consistently strong recruitment followed by years of relatively weak recruitment (Bunnell et al. 2010). In each system, recruitment of bloaters appears to be trending upward in recent years (Bunnell et al. 2010). Whether this recruitment success will reach the high levels that were obtained in the 1980s may, in part, depend on the energy content of the fish, which is often associated with fitness. Recent work

in Lake Michigan, for example, revealed fecundity of bloaters to be 24% lower in the mid-2000s than in the late 1960s, a reduction attributed to a 41% decline in adult condition between the two time periods (Bunnell et al. 2009). From a life history perspective, male bloaters have a higher mortality rate, attain a smaller length at age after maturity, and also may deplete somatic lipids more rapidly than females over the course of the spawning season (January–March; Bunnell et al. 2012).

Historically, energy content of bloaters has varied across the upper three Great Lakes. In the early 1990s, energy density of bloaters in Lake Superior was approximately 30% lower than the energy density of bloaters in Lake Michigan from the 1970s, a difference attributed to lower productivity in Lake Superior (Vondracek et al. 1996) as well as an unprecedented population expansion in Lake Superior. Similarly, Clemens and Stevens (2003) compared the percentage of total lipids in bloaters from Lake Huron in 2000 to previously published values for the upper Great Lakes and generally found percent lipids of bloaters to be highest in Lake Michigan, intermediate in Lake Huron, and lowest in Lake Superior. In recent years, however, the trophic state of Lakes Michigan and Huron has changed so that phosphorus concentrations, primary production, nutrient depletion rates, zooplankton communities, and *Diporeia* densities are now more similar among all three lakes (Barbiero et al. 2009a, 2009b; Fahnenstiel et al. 2010; Evans et al. 2011). Given these changes, we hypothesized that bloater energy density would now be more similar among these three lakes.

Our objective was to estimate the energy density of bloaters across Lakes Michigan, Huron, and Superior in 2008–2009 and to assess factors (including lakewide bloater abundance and prey availability) that may explain any observed differences. A second objective was to compare the energy density of male and female bloaters within each lake to determine whether the sex-specific differences in percent total lipids that were recently observed in Lake Michigan could be occurring in Lakes Huron and Superior. Finally, a third objective was to compare energy density of bloaters between two time periods (1998–2001 and 2008–2009) in Lake Michigan. We hypothesized that energy density would be greater in 1998–2001 than in 2008–2009 because *Diporeia* were still relatively abundant in the late 1990s (Nalepa et al. 2009).

METHODS

Bloaters were collected in 2008 and 2009 as part of U.S. Geological Survey bottom trawl surveys (Figure 1). In Lake Michigan, samples were collected at approximately 9-m depth contour increments between 9 and 110 m using a 12-m-long bottom trawl. Between September 23 and October 9, 2008, collections were made offshore of Frankfort and Ludington, Michigan; Port Washington, Wisconsin; Saugatuck, Michigan; and Waukegan, Illinois. Between September 14 and October 1, 2009, collections were made at the same Lake Michigan sites except Waukegan. In Lake Huron, samples were also collected

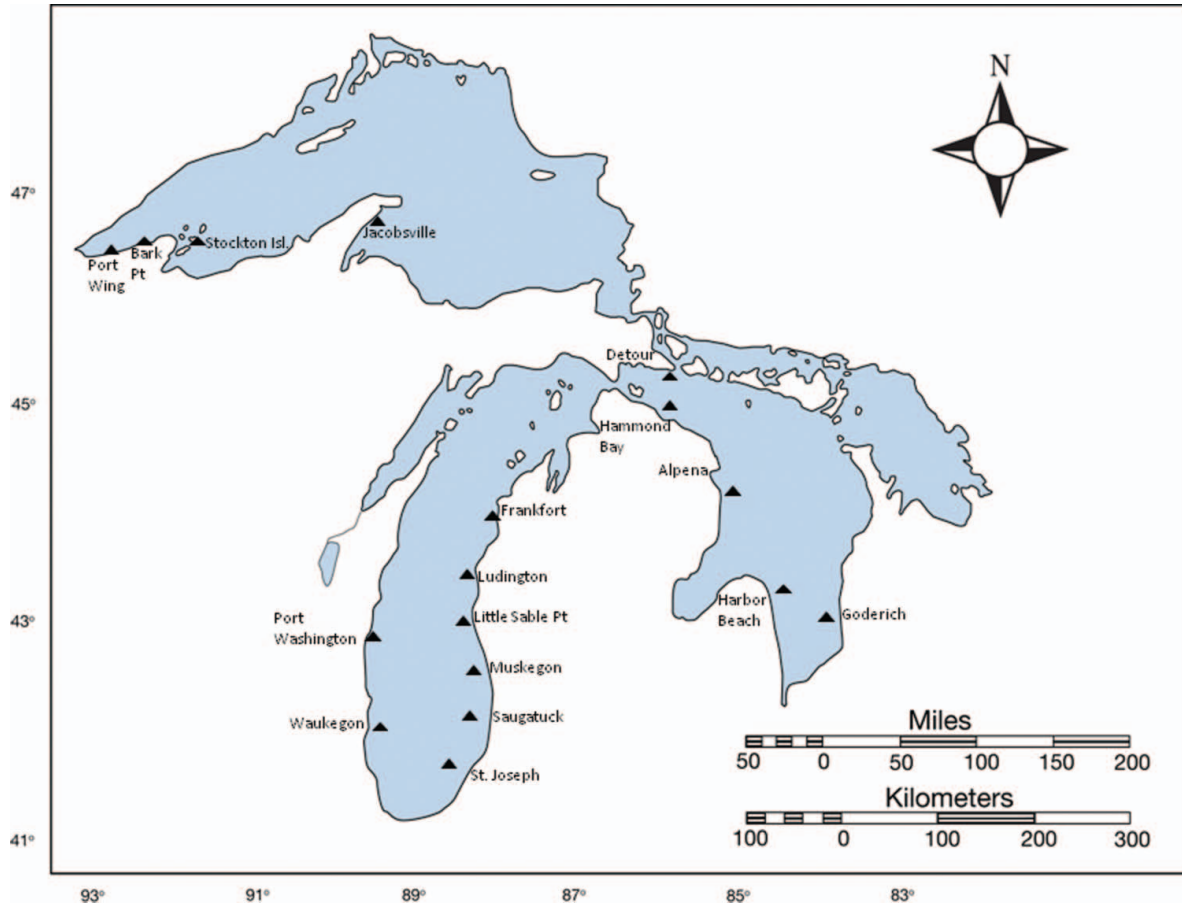


FIGURE 1. Map of Lakes Huron, Michigan, and Superior, showing locations of sampling sites for bloaters (Pt = Point; Isl = Island). [Figure available online in color.]

at approximately 9-m depth contour increments between 9 and 110 m using a 21-m-long bottom trawl. In 2008, bloaters were collected offshore of Alpena, Detour, and Hammond Bay, Michigan, between October 25 and November 4. These same sites were sampled in 2009 (between October 20 and November 4), with the addition of Goderich, Ontario, and Harbor Beach, Michigan. In Lake Superior, bloaters were collected only during 2008. Between May 6 and May 31, a 12-m-long bottom trawl was towed across contours between 12- and 130-m depths offshore of Bark Point, Port Wing, and Stockton Island, Wisconsin, and Jacobsville, Michigan. Upon capture, all bloaters were frozen in water aboard the vessel until they were subsequently analyzed.

In the laboratory, fish were thawed, measured (total length [TL], nearest mm), and weighed (nearest 0.01 g). Sex was determined for individuals larger than 120 mm. Individual fish were homogenized, dried at 65–75°C for approximately 60 h, and reweighed. After fish were dried, a subsample of individual fish from each year and site was used for direct energy density determinations (Table 1). The subsampled fish were chosen to account for the range of fish lengths in each sample and ranged

in number at each site between 10 and 25 individuals in 2008 and between 10 and 15 individuals in 2009. These subsampled fish were further ground with a mortar and pestle after drying. A 1-g subsample of the dried, ground material was combusted in a Parr 1261 isoperibol bomb calorimeter that was standardized with benzoic acid. Energy density for each individual fish was converted to joules per gram of wet weight using the known dry weight : wet weight ratio ($D:W$) for that fish. Triplicate

TABLE 1. Number of bloaters for which energy density was directly determined using bomb calorimetry (direct n) or indirectly determined using regression of energy density versus the dry weight : wet weight ratio (indirect n); fish were sampled in Lakes Huron, Michigan, and Superior during 2008 and 2009.

Lake	Year	Direct n	Indirect n
Huron	2008	45	264
Michigan	2008	105	176
Superior	2008	74	117
Huron	2009	62	429
Michigan	2009	42	326

energy density determinations were made for 10 bloaters to estimate within-fish variability. Because the mean coefficient of variation ($100 \times [\text{SD}/\text{mean}]$) within a sample was 0.56%, only a single 1-g subsample was used to directly determine energy density for each fish thereafter.

Energy density of bloaters was regressed as a function of $D:W$ for 147 individuals from Lake Michigan, 107 individuals from Lake Huron, and 74 individuals from Lake Superior. Energy densities were compared across lakes by using analysis of covariance (ANCOVA) after testing whether regression slopes were homogeneous by confirming that there was no significant interaction ($P > 0.05$) between the covariate and the main factor (lake, in this case) using a general linear model. The regressions (see Results) predicting energy density as a function of $D:W$ were then used to predict energy density for the 1,312 remaining dried fish (Table 1) as has been done in previous studies (Hartman and Brandt 1995; Pothoven et al. 2011).

The sampling unit in our analyses was the average energy density for bloaters in a given 25-mm size-bin (i.e., 75–100, >100–125 mm, and so on) from a given site in a lake during a given year. We chose to pool fish from a given site within a size-bin to avoid pseudoreplication, as we did not view each individual fish (especially those of similar sizes) as independent. In our view, an analysis that included a sample size of 1,640 fish would have resulted in significant effects for nearly every variable and would have made determination of biological significance more difficult. Further, previous studies have documented that fish size explains a significant amount of the variation in energy density of bloaters (Madenjian et al. 2000). To that end, we believed that a 25-mm size-bin would be small enough to permit the relationship between size and energy density to be revealed but yet be large enough to include as many “replicate” fish of similar sizes as possible. We did not test for differences between sites within a given lake because we were interested in the broad-scale variation in bloater energy content across lakes. Furthermore, bloater populations in the three upper Great lakes have broad synchrony in population dynamics, both within and across lakes (Bunnell et al. 2010). We chose to analyze the data separately for 2008 and 2009 owing to differences in sites sampled during each year. We used ANCOVA to evaluate whether variation in energy density could be explained by lake in each year, with the mean length of fish in each 25-mm grouping as the covariate. For this and all other ANCOVA tests, we first tested whether slopes were homogeneous by confirming that there was no significant interaction ($P > 0.05$) between the covariate and the main factor (lake) using a general linear model; if the interaction term was not significant, ANCOVA was used, and we report the F -statistic, P -value, and the least-squares (LS) mean energy density (which adjusts for differences in the covariates) for the main factors. To ensure that similar-sized fish were compared in a given year across the lakes, sizes were restricted to 75–225 mm TL in 2008 and 75–200 mm TL in 2009 for cross-lake comparisons.

We used a similar ANCOVA approach to determine whether energy density differed between males and females within a lake (i.e., sex as the main factor). To compare energy density between sexes, bloaters of a given sex from both years (where relevant) were pooled into 25-mm size-bins for each sampling site within each lake. To ensure similar size ranges, we restricted our analysis to bloaters ranging from 125 to 175 mm TL in Lake Huron and from 125 to 250 mm TL in Lakes Michigan and Superior.

An ANCOVA approach was also used to determine whether energy density of bloaters differed in Lake Michigan between 1998–2001 and 2008–2009 (i.e., period as the main factor). When comparing between time periods in Lake Michigan, bloaters were pooled into 25-mm size-bins for each sampling site across years within each period. Data for 1998–2001 were collected in the fall with a 7.6-m-long bottom trawl at depths of 15–110 m off St. Joseph, Muskegon, and Little Sable Point, Michigan (Figure 1), as part of various National Oceanic and Atmospheric Administration studies. The years 1998–2001 represent the period when *Diporeia* were in decline but still relatively abundant in Lake Michigan (Hondorp et al. 2005). For these analyses, data were restricted to bloaters ranging from 75 to 250 mm TL.

RESULTS

There was a significant interaction between the covariate $D:W$ and lake ($F_{2,322} = 7.03$, $P = 0.001$), indicating that slopes were not homogeneous (Figure 2). Although the differences in the relationships across lakes appeared slight and were perhaps not biologically significant, we took a conservative approach and used a separate regression equation to predict energy density (J/g wet weight) for fish within each lake as follows: energy density

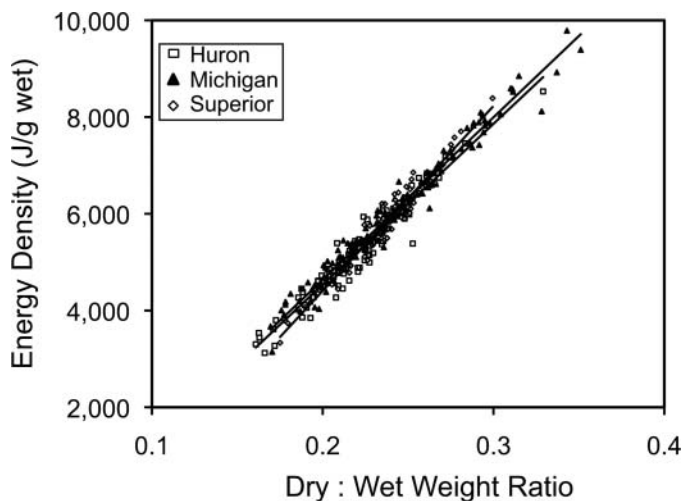


FIGURE 2. Energy density (J/g wet weight) as a function of the dry weight : wet weight ratio in bloaters sampled from Lakes Huron, Michigan, and Superior in 2008–2009.

$= (33,598 \times D:W) - 2,084$ ($r^2 = 0.97$; Lake Michigan); energy density $= (33,224 \times D:W) - 2,107$ ($r^2 = 0.93$; Lake Huron); and energy density $= (38,206 \times D:W) - 3,233$ ($r^2 = 0.94$; Lake Superior). These regressions were then used to predict energy density for the 1,312 remaining dried fish (Table 1).

For 2008, there was a significant interaction between the covariate (length) and the main factor (lake; $F_{2,51} = 21.7$, $P < 0.001$), indicating that slopes were not homogeneous (Figure 3). A visual inspection of the data suggested that the difference was related to Lake Michigan data; when these data were removed, the slopes were indeed homogeneous between Lakes Superior and Huron, and energy density did not vary with bloater length. A difference was found for these two lakes (ANCOVA: $F_{1,29} = 7.6$, $P = 0.01$): the LS mean energy density for bloaters differed by 8% between Lake Superior (5,832 J/g) and Lake Huron (5,360 J/g). In Lake Michigan, energy density of bloaters increased with bloater length (energy density [J/g wet weight] $= [22.5 \times TL] + 2,397$) in 2008. As a result, energy density of small (<125 mm TL) bloaters in Lake Michigan was low compared with small bloaters in the other two lakes. Among larger bloaters (>175 mm TL), however, energy density of fish from Lake Michigan was higher than that of fish from Lakes Huron and Superior.

For 2009 (with no data from Lake Superior), energy density increased with fish length for Lakes Huron and Michigan, and slopes were homogeneous (Figure 3). A difference between

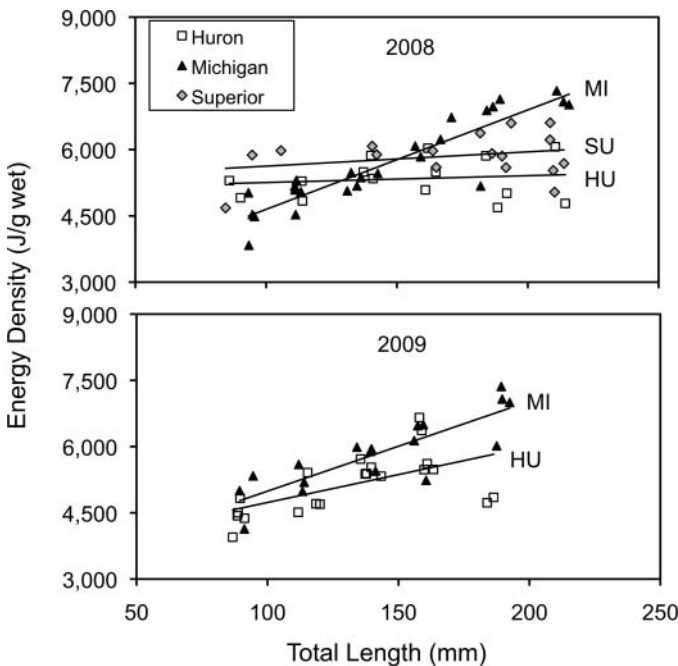


FIGURE 3. Energy density (J/g wet weight) as a function of total length for bloaters sampled from Lake Huron (HU), Lake Michigan (MI), and Lake Superior (SU) in 2008–2009. Fish from each sampling location in each lake were assigned to 25-mm length-bins, and average energy density was plotted as a function of the average total length of fish in each length-bin.

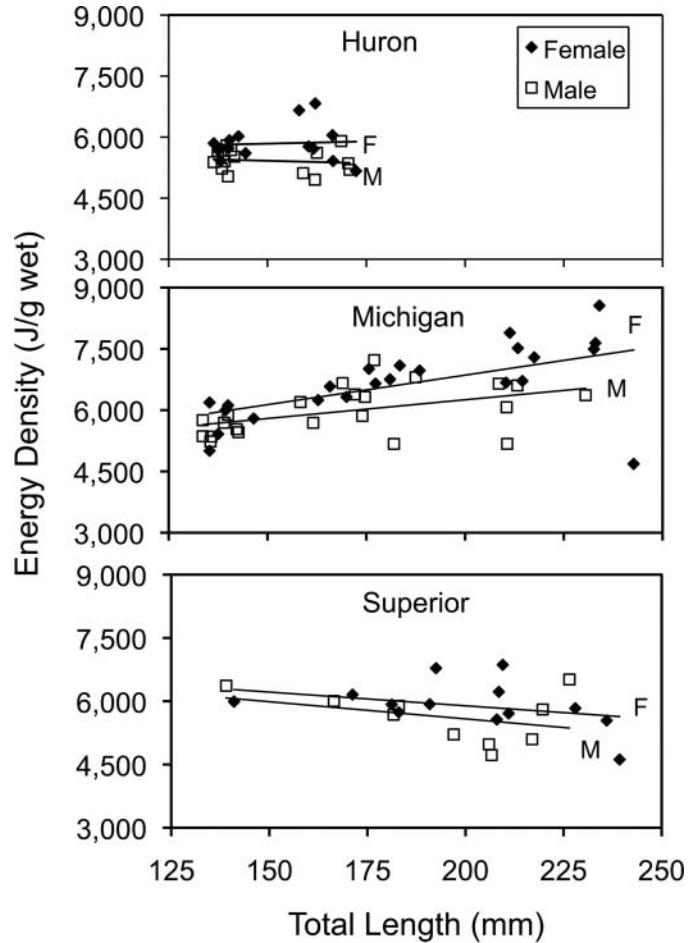


FIGURE 4. Energy density (J/g wet weight) as a function of total length for male (M) and female (F) bloaters sampled in Lakes Huron, Michigan, and Superior during 2008–2009 (data combined for the two years). Fish from each sampling location and year were assigned to 25-mm length-bins, and average energy density was plotted as a function of the average total length of fish in each length-bin.

these two lakes was found (ANCOVA: $F_{1,36} = 10.3$, $P < 0.01$), as the LS mean energy density for bloaters differed by 10% between Lake Michigan (5,760 J/g) and Lake Huron (5,218 J/g).

We found significant differences in energy density between male and female bloaters in Lake Huron (ANCOVA: $F_{1,25} = 8.4$, $P = 0.008$) and Lake Michigan (ANCOVA: $F_{1,42} = 5.4$, $P = 0.025$), although the difference was not a large percentage of the overall energy content; there was about an 8% difference in LS mean energy density between females (Lake Michigan: 6,545 J/g; Lake Huron: 5,844 J/g) and males (Lake Michigan: 6,070 J/g; Lake Huron: 5,418 J/g; Figure 4). In Lake Superior, energy density did not differ between males and females (ANCOVA: $F_{1,21} = 1.8$, $P = 0.19$).

Energy density did not differ (ANCOVA: $F_{1,83} = 0.004$, $P = 0.95$) between time periods (1998–2001 and 2008–2009) in Lake Michigan (Figure 5). Mean energy density adjusted for

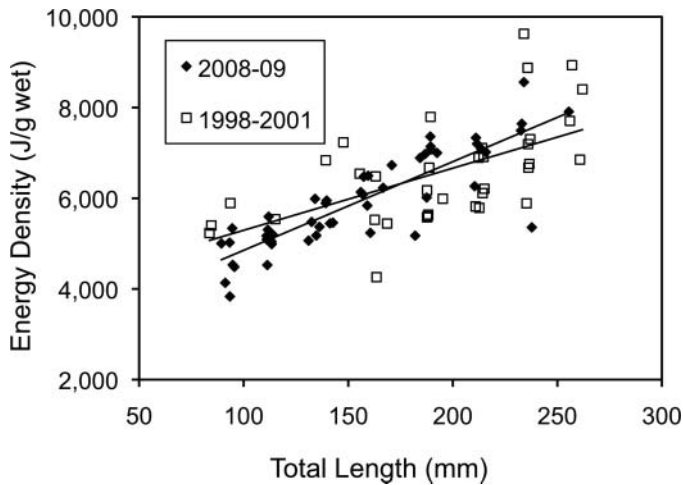


FIGURE 5. Energy density (J/g wet weight) as a function of total length for bloaters sampled in Lake Michigan during fall 1998–2001 and 2008–2009. Fish from each sampling location and year were combined into 25-mm length-bins, and average energy density was plotted as a function of the average total length of fish in each length-bin.

fish length was nearly identical for 1998–2001 (6,210 J/g) and 2008–2009 (6,221 J/g) in Lake Michigan.

DISCUSSION

We were able to detect small (i.e., generally < 10% difference) but significant differences in energy density of bloaters among Lakes Huron, Michigan, and Superior. Thus, despite increasing trophic similarities among these lakes, our hypothesis that bloater energy density would be similar among lakes was not entirely supported. One factor behind cross-lake energy density differences was the consistent increase in energy density with bloater length in 2008 and 2009 for Lake Michigan. In contrast, energy density did not vary with bloater length in Lakes Huron and Superior during 2008, although energy density did increase with bloater length in Lake Huron during 2009. Previous work in Lakes Michigan and Huron demonstrated that fish lipids or energy density increased with bloater size over the same general size range as we examined (Rudstam et al. 1994; Madenjian et al. 2000; Clemens and Stevens 2003). Small fish should be more focused on allocating energy toward growth rather than storage, which would help to explain the increase in energy with increasing size of fish in Lakes Huron and Michigan (Shearer 1994). Metabolic costs are probably also proportionately lower for larger fish, allowing them to allocate more energy toward storage (Post and Lee 1996).

Differences in the relationship between bloater energy density and size between lakes (or years within the same lake) may be due to differences in the energy density of the prey consumed by different-sized bloaters. Madenjian et al. (2000) documented that lipid content (closely related to energy density; Rottiers and Tucker 1982) of most fishes in Lake Michigan increased with increasing fish size; however, the lipid content

of Lake Michigan rainbow smelt *Osmerus mordax* decreased with increasing fish size. These researchers proposed that the decrease may have been due to the prey of larger rainbow smelt having lower lipid content. We presume that since the decline of *Diporeia*, the main prey of bloaters have become relatively similar across lakes, with small bloaters feeding primarily on zooplankton and then incorporating increasing amounts of *Mysis* into their diet over ontogeny (Rand et al. 1995; Johnson et al. 1998; Hondorp et al. 2005; Bunnell et al. 2011). Perhaps the energy density of the zooplankton eaten by small bloaters was higher in Lake Superior than in Lake Michigan, whereas the energy density of *Mysis* eaten by large bloaters was higher in Lake Michigan than in Lake Superior. Consequently, the differences in energy density of the prey of bloaters between the two lakes may be such that the energy density of bloaters in Lake Michigan would continue to increase with increasing bloater size, while the energy density of bloaters in Lake Superior would remain constant or even decrease (Vondracek et al. 1996) with increasing bloater size. Similarly, differences in energy density of the prey of bloaters between years within the same lake (e.g., Lake Huron) may explain the phenomenon of increasing energy density of bloaters with increasing size in one year but constant energy density of bloaters with increasing size in another year.

Prey abundance and fish density can both affect the feeding rates and thus the energy content of fish (Madenjian et al. 2000). As noted, the main prey types eaten by bloaters are zooplankton, *Mysis*, and *Diporeia*. In the past, abundances of prey such as zooplankton and *Diporeia* were reportedly higher in Lake Michigan (*Diporeia*; Nalepa et al. 2007, 2009; Barbiero et al. 2011) or Lake Huron (zooplankton; Barbiero et al. 2001) than in Lake Superior. However, more recent data suggest that after large-scale food web changes, abundances of these prey are now similar across Lakes Michigan, Huron, and Superior (Barbiero et al. 2009a, 2009b, 2011; Yurista et al. 2009). In contrast, historical differences in *Mysis* abundance among lakes appear to persist (Carpenter et al. 1974; Grossnickle and Morgan 1979; McDonald et al. 1990), with higher abundances occurring in Lakes Michigan and Superior than in Lake Huron (Jensen et al. 2009; Mida 2010). Given the similarities in *Diporeia* densities across lakes, we assume that interlake differences in *Mysis* could influence any interlake differences in bloater energy density.

In terms of fish abundance, lakewide acoustic surveys indicated that biomass density of bloaters was at least three times higher in Lake Huron than in Lake Michigan during 2008–2009, although total biomass density of all fish was similar between the two lakes (Schaeffer et al. 2010; Warner et al. 2010). Acoustic estimates from Lake Superior in 2001–2004 indicated that biomass density of bloaters was similar to or slightly lower than that in Lake Michigan (Stockwell et al. 2007). Based on bottom trawl data, it appears safe to assume that bloater biomass in Lake Superior was generally unchanged or in decline between 2001–2004 and 2008 (Gorman and Bunnell 2011); thus, available data suggest that the highest biomass of bloaters occurred in Lake Huron during our study period.

The consistently low energy density of bloaters in Lake Huron probably results from the lake's relatively low densities of *Mysis* and relatively high biomass of bloaters. Further, the lipid content of *Mysis* in Lake Huron is reported to be less than that in Lake Michigan (Mida 2010) and also probably contributes to the relatively low energy density of bloaters in Lake Huron. Considering all the factors favoring low energy content for bloaters in Lake Huron, it is perhaps somewhat surprising that the difference among lakes is not even greater.

Differences in water temperature may also help to explain some of the differences in bloater energy density between Lakes Superior and Michigan. Epilimnetic water temperatures are colder and the growing season is more limited in Lake Superior than in Lake Michigan (McCormick and Fahnenstiel 1999). Bloaters occupy the epilimnion during the first year or two of life (reviewed by Clemens and Crawford 2009), and these young bloaters in Lake Superior may allocate more energy toward storage to enhance survival in a harsher environment relative to that in Lake Michigan. This would be consistent with previous work indicating that young fish at higher latitudes allocate energy toward storage rather than growth in length under certain conditions (Schultz and Conover 1997; Garvey and Marschall 2003); however, it provides little insight into why larger fish had such relatively low energy content. The shorter growing season and cooler temperatures could certainly contribute to lower secondary production in Lake Superior despite similarities in standing stock of prey (Stockwell and Johannsson 1997). Finally, interactions with other species cannot be discounted. For example, other coregonid species (e.g., kiyi *C. kiyi* and cisco *C. artedii*) are relatively abundant in Lake Superior and may influence feeding by bloaters differently than in Lake Michigan, where these coregonid species are rare or absent.

Energy density can vary with season for some Great Lakes fishes (Madenjian et al. 2006b), so energy content differences in fish from Lake Superior relative to the other two lakes could simply be a function of collecting fish in the spring rather than in the fall. More subtly, differences in bloater energy between Lakes Michigan and Huron could be affected by later sampling in the fall in Lake Huron. Bloaters could accumulate energy in the fall in preparation for spawning during winter (Vondracek et al. 1996). However, previous work in Lake Superior indicated that energy density of bloaters was similar in spring and fall (Vondracek et al. 1996). Similarly, lipid content of bloaters did not vary seasonally in Lake Michigan (Madenjian et al. 2000). Finally, the energy density of bloaters collected in spring 2010 at a single site in Lake Michigan increased with fish size (S. A. Pothoven, unpublished data), so the constant energy density as a function of fish size as observed in Lake Superior is not necessarily related to the collection of fish in the spring. Further, given the absence of seasonal trends in energy or lipid content in previous studies (Vondracek et al. 1996; Madenjian et al. 2000), it seems that the later sampling during fall in Lake Huron relative to that in Lake Michigan is a relatively minor factor behind the observed differences in energy density.

Energy density was slightly higher for female bloaters than for males in Lakes Huron and Michigan. In a previous study, results from a small sample of bloaters from Lake Huron indicated that there were no differences in lipids between males and females (Clemens and Stevens 2003). In Lake Superior, Vondracek et al. (1996) found that energy density generally did not differ between male and female bloaters, but in instances when it did, the energy density was higher for females. Likewise, Bunnell et al. (2012) found that the percent total lipids of somatic tissue in bloaters sampled between December and April was generally higher for females than for males. Relative to males, a higher energy density for females is consistent with a higher female survival rate (Bunnell et al. 2012) if higher energy density contributes to a lower probability of mortality (because of increased physiological condition). One plausible explanation for the higher energy density in females is that females grow faster than males (Bunnell et al. 2012), and higher lipid content (and energy density) is often associated with higher growth rates (Madenjian et al. 2000). Finally, the interlake differences in energy density do not appear to be linked to differences in energy density for male and female bloaters, as energy density for large bloaters was highest in Lake Michigan, where the proportion of females (i.e., higher-energy fish) in the sample was lower (56%) than the proportion in the other two lakes (63–65%).

The comparison between 1998–2001 and 2008–2009 for Lake Michigan provides some further insight into energy density dynamics of bloaters. One might expect that energy density would be higher in 2008–2009 than in 1998–2001 given the lower overall population abundance of bloaters during the latter time period (D. B. Bunnell, unpublished data). However, *Diporeia* also declined between these time periods (Nalepa et al. 2009). Similarly, bloater lipids did not increase between 1994 and 2005–2006, despite a substantial decline in population abundance of bloaters (Bunnell et al. 2009). Bloater growth in length and mass also declined despite relatively low abundances of bloaters after the disappearance of *Diporeia* (Szalai et al. 2003). Thus, despite low population abundance of bloaters in Lake Michigan, expected increases in energy density appear to have not taken place owing to concurrent declines in *Diporeia* abundance.

The absence of changes in energy density of bloaters over time is somewhat in contrast to changes observed for other Great Lakes fish species. Energy content of alewives *Alosa pseudoharengus* and deepwater sculpins *Myoxocephalus thompsonii* declined by more than 23% after the decline of *Diporeia* despite the fact that the abundance of these fish species exhibited no change or even decreased (Madenjian et al. 2006b; Pothoven et al. 2011). Dramatic declines in condition for another coregonid fish, the lake whitefish *C. clupeaformis*, were linked to both increasing abundance as well as changes in the food web after the dreissenid mussel invasion and the *Diporeia* decline (Pothoven et al. 2001; Rennie et al. 2009). These observations contrast with bloater results indicating that abundance has decreased and energy density has remained relatively constant.

Bloater recruitment in Lake Michigan has improved recently (Warner et al. 2010). If bloater abundance in Lake Michigan continues to increase and approaches the levels recently observed in Lake Huron (or higher), energy content may well be affected. For example, energy density of large bloaters in Lake Michigan would probably decrease as the adult bloater population increases and would become more similar to the energy density levels observed in bloaters from Lake Huron. Density-dependent declines in energy content for adult bloaters could be exacerbated by increasing predation pressures on *Mysis* after declines in *Diporeia* (Pothoven et al. 2010).

Overall, we were able to find differences in energy density of bloaters across Lakes Superior, Michigan, and Huron despite ongoing convergences in lake productivity. Some differences, such as the relatively low energy density in Lake Huron, could be attributed to relatively low densities of mysids as well as a relatively high bloater biomass. On the other hand, these factors do not appear to fully explain differences between other lakes, such as Lakes Superior and Michigan, where ontogenetic differences in energy accumulation, prey energy content, growing season, and interspecific competition may be important factors as well. Ongoing assessments of the food web in these lakes and evaluations of the potential changes in dependency from benthic to pelagic food sources would further our understanding of energy flow through bloaters and other fishes in these lakes.

ACKNOWLEDGMENTS

This article is Contribution Number 1610 of the Great Lakes Science Center, U.S. Geological Survey, and is Contribution Number 1679 of the Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration. Use of trade, product, or firm names does not imply endorsement by the U.S. Government.

REFERENCES

- Baldwin, N. S., R. W. Saalfeld, M. R. Dochoda, H. J. Buettner, and R. L. Eshenroder. 2009. Commercial fish production in the Great Lakes 1867–2006. Great Lakes Fishery Commission, Ann Arbor, Michigan. Available: www.glfsc.org/databases/commercial/commerc.php. (July 2011).
- Barbiero, R. P., M. Balcer, D. C. Rockwell, and M. L. Tuchman. 2009a. Recent shifts in the crustacean zooplankton community of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences* 66:816–828.
- Barbiero, R. P., D. B. Bunnell, D. C. Rockwell, and M. L. Tuchman. 2009b. Recent increases in the large glacial-relict calanoid *Limnocalanus macrurus* in Lake Michigan. *Journal of Great Lakes Research* 35:285–292.
- Barbiero, R. P., R. E. Little, and M. L. Tuchman. 2001. Results from the U.S. EPA's biological open water surveillance program of the Laurentian Great Lakes: III. crustacean zooplankton. *Journal of Great Lakes Research* 27: 167–184.
- Barbiero, R. P., K. Schumde, B. M. Lesht, C. M. Riseng, G. J. Warren, and M. L. Tuchman. 2011. Trends in *Diporeia* populations across the Laurentian Great Lakes, 1997–2009. *Journal of Great Lakes Research* 37:9–17.
- Bunnell, D. B., J. V. Adams, O. T. Gorman, C. P. Madenjian, S. C. Riley, E. F. Roseman, and J. S. Schaeffer. 2010. Population synchrony of a native fish across three Laurentian Great Lakes: evaluating the effects of dispersal and climate. *Oecologia* 162:641–651.
- Bunnell, D. B., S. R. David, and C. P. Madenjian. 2009. Decline in bloater fecundity in southern Lake Michigan after decline of *Diporeia*. *Journal of Great Lakes Research* 35:45–49.
- Bunnell, D. B., B. M. Davis, D. M. Warner, M. A. Chriscinkse, and E. F. Roseman. 2011. Planktivory in the changing Lake Huron zooplankton community: *Bythotrephes* consumption exceeds that of *Mysis* and fish. *Freshwater Biology* 56:1281–1296.
- Bunnell, D. B., C. P. Madenjian, M. W. Rogers, J. D. Holuszko, and L. J. Begnoche. 2012. Exploring mechanisms underlying sex-specific differences in mortality of Lake Michigan bloaters. *Transactions of the American Fisheries Society* 141:204–214.
- Bunnell, D. B., S. E. Thomas, and R. A. Stein. 2007. Prey resources before spawning influence gonadal investment of female, but not male, white crappie. *Journal of Fish Biology* 70:1838–1854.
- Carpenter, G. F., E. L. Mansey, and N. H. F. Watson. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. *Journal of the Fisheries Research Board of Canada* 31:319–325.
- Chambers, R. C., and K. G. Waiwood. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1986–2003.
- Clemens, B. J., and S. S. Crawford. 2009. The ecology of body size and depth use by bloater (*Coregonus hoyi* Gill) in the Laurentian Great Lakes: patterns and hypotheses. *Reviews in Fisheries Science* 17:174–186.
- Clemens, B. J., and E. D. Stevens. 2003. Buoyancy range, gas bladder volume, and lipid content of adult bloater, *Coregonus hoyi* Gill, in the Laurentian Great Lakes. *Environmental Biology of Fishes* 68:175–182.
- Crowder, L. B., and H. L. Crawford. 1984. Ecological shifts in resource use by bloaters in Lake Michigan. *Transactions of the American Fisheries Society* 113:694–700.
- Davis, B. M., J. F. Savino, and L. M. Ogilvie. 2007. Diet niches of major forage fish in Lake Michigan. *Advances in Limnology* 60:261–275.
- Evans, M. A., G. L. Fahnenstiel, and D. Scavia. 2011. Incidental oligotrophication of North American Great Lakes. *Environmental Science and Technology* 45:3297–3303. DOI: 10.1021/es103892w.
- Fahnenstiel, G. L., S. A. Pothoven, H. A. Vanderploeg, D. Klarer, T. F. Nalepa, and D. Scavia. 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *Journal of Great Lakes Research* 36:20–29.
- Gamble, A. E., T. R. Hrabik, J. D. Stockwell, and D. L. Yule. 2011. Trophic connections in Lake Superior part I: the offshore fish community. *Journal of Great Lakes Research* 37:541–549.
- Garvey, J. E., and E. A. Marschall. 2003. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. *Canadian Journal of Fisheries and Aquatic Sciences* 60:938–948.
- Gorman, O. T., and D. B. Bunnell. 2011. Great Lakes prey fish populations: a cross-basin overview of status and trends from bottom trawl surveys, 1978–2010. Great Lakes Fishery Commission, Upper and Lower Lakes Committee Meetings, Report, Ypsilanti, Michigan. Available: www.glfsc.usgs.gov/_files/reports/2010xbasinpreyfish.pdf. (November 2011).
- Grossnickle, N. E., and M. D. Morgan. 1979. Density estimates of *Mysis relicta* in Lake Michigan. *Journal of the Fisheries Research Board of Canada* 36:694–698.
- Hartman, K. J., and S. B. Brandt. 1995. Estimating the energy density of fish. *Transactions of the American Fisheries Society* 124:347–355.
- Hondorp, D. W., S. A. Pothoven, and S. B. Brandt. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. *Transactions of the American Fisheries Society* 134:588–601.
- Jensen, O. P., P. M. Yurista, T. R. Hrabik, and J. D. Stockwell. 2009. Densities and diel vertical migration of *Mysis relicta* in Lake Superior: a comparison of optical plankton counter and net-based approaches. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 30: 957–963.

- Johnson, T. B., D. M. Mason, C. R. Bronte, and J. F. Kitchell. 1998. Estimation of invertebrate production from patterns of fish predation in western Lake Superior. *Transactions of the American Fisheries Society* 127:496–506.
- Madenjian, C. P., T. J. DeSorcie, and R. M. Stedman. 1998. Ontogenetic and spatial patterns in diet and growth of lake trout in Lake Michigan. *Transactions of the American Fisheries Society* 127:236–252.
- Madenjian, C. P., R. F. Elliot, T. J. DeSorcie, R. M. Stedman, D. V. O'Connor, and D. V. Rottiers. 2000. Lipid concentrations in Lake Michigan fishes: seasonal, spatial, ontogenetic, and long-term trends. *Journal of Great Lakes Research* 26:427–444.
- Madenjian, C. P., J. D. Holuszko, and T. J. DeSorcie. 2006a. Spring-summer diet of lake trout on Six Fathom Bank and Yankee Reef in Lake Huron. *Journal of Great Lakes Research* 32:200–208.
- Madenjian, C. P., S. A. Pothoven, J. D. Dettmers, and J. D. Holuszko. 2006b. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. *Canadian Journal of Fisheries and Aquatic Sciences* 63:891–902.
- Marshall, C. T., N. A. Yarina, Y. Lambert, and O. S. Kjesbu. 1999. Total lipid energy as a proxy for total egg production by fish stocks. *Nature (London)* 402:288–290.
- McCormick, M. J., and G. L. Fahnenstiel. 1999. Recent climatic trends in nearshore water temperatures in the St. Lawrence Great Lakes. *Limnology and Oceanography* 44:530–540.
- McDonald, M. E., L. B. Crowder, and S. B. Brandt. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in the fish community. *Limnology and Oceanography* 35:220–227.
- Mida, J. L. 2010. Status and condition of *Mysis diluviana* in Lakes Michigan and Huron, 2007–2008. Master's thesis. University of Michigan, Ann Arbor.
- Mida, J. L., D. Scavia, G. L. Fahnenstiel, S. A. Pothoven, H. A. Vanderploeg, and D. M. Dolan. 2010. Long-term and recent changes in southern Lake Michigan water quality with implications for present trophic status. *Journal of Great Lakes Research* 36(Supplement 3): 42–49.
- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19:1–54.
- Nalepa, T. F., D. L. Fanslow, and G. A. Lang. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. *Freshwater Biology* 54:466–479.
- Nalepa, T. F., D. L. Fanslow, S. A. Pothoven, A. J. Foley III, and G. A. Lang. 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. *Journal of Great Lakes Research* 33:421–436.
- Ouellet, P., Y. Lambert, and I. Berube. 2001. Cod egg characteristics and viability in relation to low temperature and maternal nutritional condition. *ICES Journal of Marine Science* 58:672–686.
- Post, J. R., and J. A. Lee. 1996. Metabolic ontogeny of teleost fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:910–923.
- Pothoven, S. A., G. L. Fahnenstiel, and H. A. Vanderploeg. 2010. Temporal trends in *Mysis relicta* abundance, production, and life-history characteristics in southeastern Lake Michigan. *Journal of Great Lakes Research* 36(Supplement 3): 60–64.
- Pothoven, S. A., D. W. Hondorp, and T. F. Nalepa. 2011. Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* in Lakes Huron and Michigan. *Ecology of Freshwater Fish* 20:14–22.
- Pothoven, S. A., T. F. Nalepa, P. J. Schneeberger, and S. B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. *North American Journal of Fisheries Management* 21:876–883.
- Rand, P. S., B. F. Lantry, R. O'Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. *Transactions of the American Fisheries Society* 123:519–534.
- Rand, P. S., D. J. Stewart, B. F. Lantry, L. G. Rudstam, O. E. Johannsson, A. P. Goyke, S. B. Brandt, R. O'Gorman, and G. W. Eck. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1546–1563.
- Rennie, M. D., W. G. Sprules, and T. B. Johnson. 2009. Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences* 66:2096–2108.
- Rideout, R. M., G. A. Rose, and M. P. M. Burton. 2005. Skipped spawning in female iteroparous fishes. *Fish and Fisheries* 6:50–72.
- Rijnsdorp, A. D. 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. *Netherlands Journal of Sea Research* 25:279–290.
- Riley, S. R., E. F. Roseman, S. J. Nichols, T. P. O'Brien, C. S. Kiley, and J. S. Schaeffer. 2008. Deepwater demersal fish community collapse in Lake Huron. *Transactions of the American Fisheries Society* 137:1879–1890.
- Rottiers, D. V., and R. M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish and Wildlife Service Technical Papers 108.
- Rudstam, L. G., F. P. Binkowski, and M. M. Miller. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. *Transactions of the American Fisheries Society* 123:344–357.
- Schaeffer, J. S., D. M. Warner, T. O'Brien, and S. A. Farha. 2010. Status and trends of pelagic prey fishes in Lake Huron, 2009. Great Lakes Fishery Commission, Lake Huron Committee, Report, Windsor, Ontario.
- Schultz, E. T., and D. O. Conover. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). *Oecologia* 109:516–529.
- Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. *Aquaculture* 119:63–88.
- Stockwell, J. D., and O. E. Johannsson. 1997. Temperature dependent, allometric models to estimate zooplankton production in temperate, freshwater lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2351–2360.
- Stockwell, J. D., D. L. Yule, T. R. Hrabik, J. V. Adams, O. T. Gorman, and B. V. Holbrook. 2007. Vertical distribution of fish biomass in Lake Superior: implications for day bottom trawl surveys. *North American Journal of Fisheries Management* 27:735–749.
- Szalai, E. B., G. W. Fleischer, and J. R. Bence. 2003. Modeling time-varying growth using a generalized von Bertalanffy model with application to bloater (*Coregonus hoyi*) growth dynamics in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 60:55–66.
- Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1209–1228.
- Vondracek, B., B. D. Giese, and M. G. Henry. 1996. Energy density of three fishes from Minnesota waters of Lake Superior. *Journal of Great Lakes Research* 22:757–764.
- Warner, D. M., R. M. Claramunt, and J. D. Holuszko. 2010. Status of pelagic prey fishes and pelagic macroinvertebrates in Lake Michigan, 2009. Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Report, Windsor, Ontario. Available: www.glsc.usgs.gov/files/reports/2009LakeMichiganAcoustic.pdf. (July 2011).
- Wells, L., and A. M. Beeton. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan. *Transactions of the American Fisheries Society* 92:245–255.
- Yurista, P. M., J. R. Kelly, and S. E. Miller. 2009. Lake Superior zooplankton biomass: alternative estimates from a probability-based net survey and spatially extensive LOPC surveys. *Journal of Great Lakes Research* 35:337–346.

This article was downloaded by: [Noaa Glerl Library]

On: 25 May 2012, At: 08:51

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Energy Density of Bloaters in the Upper Great Lakes

Steven A. Pothoven^a, David B. Bunnell^b, Charles P. Madenjian^b, Owen T. Gorman^c & Edward F. Roseman^b

^a National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 1431 Beach Street, Muskegon, Michigan, 49441, USA

^b U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan, 48105, USA

^c U.S. Geological Survey, Great Lakes Science Center, Lake Superior Biological Station, 2800 Lake Shore Drive East, Ashland, Wisconsin, 54806, USA

Available online: 25 May 2012

To cite this article: Steven A. Pothoven, David B. Bunnell, Charles P. Madenjian, Owen T. Gorman & Edward F. Roseman (2012): Energy Density of Bloaters in the Upper Great Lakes, Transactions of the American Fisheries Society, 141:3, 772-780

To link to this article: <http://dx.doi.org/10.1080/00028487.2012.675911>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.