Diet shifts by planktivorous and benthivorous fishes in northern Lake Michigan in response to ecosystem changes

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ABSTRACT

In Lake Michigan, diets of planktivorous and benthivorous fishes have varied over the past decades, in part owing to food web changes. To update diet information and compare them to a similar effort in 1994–1995, we analyzed the diets of seven benthivorous and planktivorous fish species collected along two northern Lake Michigan transects that spanned nearshore (18 m), intermediate (46 m), and offshore (91, 110, 128 m) bottom depths during spring, summer, and autumn of 2010. Calanoid copepods (e.g., *Limnocalanus macrurus*, *Leptodiaptomus sicilis*, and *Senecella calanoides*) comprised a majority of the diets in at least one season for all sizes of alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), and rainbow smelt (*Osmerus mordax*). Similarly, *Mysis diluviana* was the highest proportion in at least one season for large sizes of alewife, bloater, and rainbow smelt, as well as slimy sculpin (*Cottus cognatus*) and deepwater sculpin (*Myoxocephalus thompsonii*). The diets of the remaining two species, ninespine stickleback (*Pungitius pungitius*) and round goby (*Neogobius melanostomus*), were dominated by herbivorous cladocerans or dreissenid mussels, respectively. Interspecific diet overlap was minimal at 18 and 46 m. In offshore waters, however, overlap was relatively high, driven by frequent consumption of *Mysis*. Relative to 1994–1995, 2010 diets revealed increased feeding on calanoid copepods and *Mysis*, with corresponding declining consumption of *Diporeia* spp. and herbivorous cladocerans. Relative diet weight was also higher in 1994–1995 than in 2010 for small and large bloater and both sculpin species. We hypothesize that the shifts in diets are reflective of community-level changes in invertebrate prey availability.

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Introduction

Over the last 30 years, benthivorous and planktivorous fishes in the Laurentian Great Lakes (hereafter, Great Lakes) have experienced a multitude of changes in biotic and abiotic factors that can influence their population dynamics, including increasing water clarity, the introduction of new invertebrate and vertebrate competitors, and declines in several invertebrate prey species. In Lake Michigan, for example, mean spring Secchi depth increased 36% between 1983–2003 and 2004–2010 (Bunnell et al., 2014). Theoretically, clearer water could improve the foraging efficiency for all visual feeders, such as planktivorous fishes (Barton, 2007). Several nonindigenous species that have proliferated in recent decades also have had lakewide food web effects. The predatory zooplankters *Bythotrephes longimanus* (hereafter, *Bythotrephes*) and *Cercopagis pengoi* (hereafter, *Cercopagis*)

invaded in the 1980s and 1990s, respectively (Charlebois et al., 2001; Evans, 1988). Their relatively high consumption rates (e.g., Yurista et al., 2010) and ability to reach high seasonal densities could limit the types or amounts of food available to planktivorous fishes, although they also serve as a prey item themselves. Likewise, nonindigenous and benthivorous round goby *Neogobius melanostomus* arrived in the 1990s (Clapp et al., 2001). Unlike other benthivorous fishes, they can consume a relatively high proportion of nonindigenous dreissenid mussels *Dreissena polymorpha* and *D. bugensis*. Furthermore, native logperch *Percina caprodes* (Balshine et al., 2005) and mottled sculpin *Cottus bairdii* (Janssen and Jude, 2001) likely declined in abundance owing to interactions with round gobies. Finally, the proliferation of these nonindigenous species is believed to underlie the declines of many key invertebrate prey, including the amphipod *Diporeia* spp. (hereafter, *Diporeia*, Nalepa et al., 2009) in the benthos and several *Daphnia* spp. in the pelagia (Barbiero and Tuchman, 2004).

Not all of the potential prey taxa available to benthivorous and planktivorous fishes have declined over the past several decades. For example, *Mysis diluviana* (hereafter, *Mysis*) appears to have exhibited no changes in lakewide abundance since 1985 (Madenjian et al., 2015). Similarly, biomass of calanoid copepods has been unchanged

since the mid to late 1990s, while the biomass of cyclopoid copepods and herbivorous cladocerans has declined (Barbiero et al., 2012; Vanderploeg et al., 2012). In fact, one particularly large calanoid copepod that occupies the hypolimnion, *Limnocalanus macrurus*, has even increased in abundance over this time period (Barbiero et al., 2009; Vanderploeg et al., 2012).

Some Lake Michigan fish species have responded to these and other perturbations through changes in growth, condition, and diet composition. For example, the growth and condition of alewife *Alosa pseudoharengus*, one of the most well-studied planktivorous fish species, declined in 1995 (Madenjian et al., 2003, 2006). Furthermore, between 1983–1994 and 1995–2005, alewife diet composition shifted to include more cladocerans and *Mysis* and fewer *Diporeia* and copepods (Pothoven and Madenjian, 2008). The diet of lake whitefish *Coregonus clupeaformis* shifted from a preponderance of *Diporeia* in 1998 to one dominated by *Mysis*, ostracods, oligochaetes, and zooplankton just 2 years later (Pothoven et al., 2001). Given the changing abiotic and biotic factors within the Lake Michigan ecosystem over the past decades, new information on fish diets is needed for mass-balance ecosystem (e.g., Christensen and Walters, 2004) and bioenergetics models (e.g., Hanson, 1997). New data are derived at the lakewide level and from multiple depths and seasons provide the greatest utility to these modeling efforts.

The primary objective of this paper was to comprehensively describe the diets of seven planktivorous and benthivorous fish species sampled from northern Lake Michigan in 2010. Fish were collected seasonally along two transects (e.g., near Sturgeon Bay, Wisconsin, and Frankfort, Michigan) that each included nearshore (18 m), intermediate (46 m), and offshore (110 m) sampling stations. Although our design was limited to two sites in one basin of the lake, similarly comprehensive studies are relatively rare. Furthermore, comparing our results to those of previous studies allowed us to determine whether the diets of slimy sculpin *Cottus cognatus* and deepwater sculpin *Myoxocephalus thompsonii* (Davis et al., 2007; Hondorp et al., 2005, 2011; Mychek-Londer et al., 2013), bloater *Coregonus hoyi* (Davis et al., 2007; Hondorp et al., 2005), rainbow smelt *Osmerus mordax* (Davis et al., 2007; Lantry and Stewart, 1993), and alewife (Hondorp et al., 2005; Pothoven and Madenjian, 2008) have shifted in response to the changing food web in Lake Michigan. We hypothesized that fish diets would change in accordance with the changing invertebrate community (i.e., Nalepa et al., 2009; Vanderploeg et al., 2012). Specifically, diets of benthivorous fishes in 2010 should include more *Mysis* and fewer *Diporeia*, while the diets of planktivorous fish would include more calanoid copepods and fewer herbivorous cladocerans and cyclopoid copepods. We were able to explore this hypothesis directly by comparing the diets of fishes collected at one transect (Sturgeon Bay) in 2010 with those collected and analyzed with identical field and laboratory techniques in 1994–1995 (Davis et al., 2007).

Beyond describing 2010 diet proportions and the extent to which they have changed over the past decades, our study afforded an opportunity to explore two other ecological questions. First, we evaluated the extent to which diets overlapped at each sampling site, depth, and season in 2010. We hypothesized that overlap would remain high among at least those species that consumed large proportions of *Mysis* (e.g., slimy sculpin, deepwater sculpin, bloater). These overlap analyses also took advantage of our protocol to identify prey to a relatively fine taxonomic resolution (e.g., zooplankton to the species level). For example, overlap was based on relative consumption of *Epischura lacustris*, *Leptodiaptomus ashlandi*, *L. minutus*, *L. sicilis*, *Limnocalanus macrurus*, and *Senecella calanoides*, rather than just a coarse grouping of calanoid copepods. Second, we evaluated whether the total weight of prey items in fish diets had changed between 1994–1995 and 2010 near Sturgeon Bay. We hypothesized that the decline in *Diporeia* would result in lower diet weights in 2010 for the sculpins, bloater, and even alewife, which each have historically had varying levels of reliance on this key invertebrate prey.

Methods

Fish sampling and diet laboratory processing

In spring (April and May), summer (July), and autumn (September) 2010, planktivorous and benthivorous fishes were collected at nearshore (18 m), intermediate (46 m), and offshore (110 m) bottom depths near Sturgeon Bay, Wisconsin (44.75°, −87.28°; 44.73°, −87.26°; and 44.69°, −87.15°), and Frankfort, Michigan (44.52°, −86.26°; 44.48°, −86.30°; and 44.48°, −86.33°). At each depth, season, and site, fish were sampled during the day with two replicate bottom trawl (12-m headrope, 13-mm cod end mesh) tows and during the night with at least one midwater trawl (15-m headrope, 6-mm cod end mesh) tow. Vertical depth of midwater trawls ranged 2–6 m at 18-m bottom depth, 8–30 m at 46-m bottom depth, and 10–80 m at 110-m bottom depth. Bottom trawls were towed for up to 10 min and midwater trawls were towed for up to 35 min; each was towed at a speed of 3.5–4.0 km · hour^{-1}. We also used bottom-trawl caught fish collected from 91 m and 128 m bottom depths at these same sites during spring from a companion study (see Mychek-Londer et al., 2013), and classified these fish as "offshore." Fish from each tow were sorted to species and immediately preserved in a −20 °C freezer aboard the research vessel.

Our goal was to preserve up to 15 individuals per species and size class for each month, depth, site, and sampling gear. For both gear types, fish were preserved from the first tow and only preserved from the second tow if they were needed to reach the sample size goal. Small- and large-size classes were delineated for alewife [delineation threshold, 110 mm total length, (TL)], bloater (140 mm TL), rainbow smelt (90 mm TL), and round goby (75 mm TL). Some species were only captured during the day with a bottom trawl (deepwater sculpin, slimy sculpin, round goby, ninespine stickleback), whereas other species that presumably spend at least part of the night in the pelagia were sampled with both gears (small rainbow smelt = 64% day, large rainbow smelt = 49% day; small bloater = 88% day; large bloater = 80% day; small alewife = 40% day; large alewife = 93% day). A comparison of diets between day and night (within a given depth and site) was outside the scope of this study, in large part because we were limited by pairs of tows (N = 6) within a 24-hour period where we had at least three individuals of the same species sampled during both day and night.

In the laboratory, fish were thawed (but kept cold on ice) and measured for TL and wet weight (nearest 0.1 g). Stomachs were dissected by removing the digestive tract from the esophagus to pyloric caeca for all fishes but round goby, for which the entire digestive tract was removed, and then preserved in 80% ethanol. To identify and enumerate diet items, stomach contents were teased apart in a Ward counting wheel under a dissecting microscope. Prey items were identified to species, where possible (see Electronic Supplementary Material (ESM) Table S1). For benthivores (sculpins and gobies), all diet items were always counted. For planktivores, however, subsampling was considered an option under one of two scenarios: 1) if the total number of prey items appeared to exceed 200, or 2) if the prey contents were highly digested (occurred mainly with bloater and alewife). For all diets (independent of subsampling), all large prey such as *Mysis*, predatory cladocerans, amphipods, and fish were counted and measured. If subsampling was required, the stomach contents were diluted to 100 ml, gently stirred, and then a known volume was removed with a pipette. All smaller prey items within the subsample were identified to the lowest possible taxon, enumerated, and up to ten individuals per species were measured with an ocular micrometer. For subsample scenario 1, we counted at least 100 total individual prey items from a known volume of the sample. For subsample scenario 2, we counted 10% of the total volume of the sample.

To avoid the double-counting of partially digested or non-intact prey, we counted only specific body parts (e.g., caudal rami of copepods,