**Research Article**

# Feeding ecology of invasive age-0 white perch and native white bass after two decades of co-existence in Saginaw Bay, Lake Huron

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## Abstract

The diets and energy content of sympatric populations of invasive age-0 white perch *Morone americana* and native age-0 white bass *Morone chrysops* were evaluated in Saginaw Bay, Lake Huron following >20 years of coexistence. Fish were collected during July-November in 2009 and 2010 to assess seasonal and interannual patterns of diet composition, diet similarity, feeding strategy and energy density for the two species. The diet composition by weight of age-0 white bass was dominated by various zooplankton taxa, fish, or emergent insects, depending on the month and year. Although fish occasionally comprised a large fraction of the diet biomass, they were eaten by <24% of white bass each month. The diet composition of age-0 white perch shifted from one dominated by chironomids and other benthic macroinvertebrates in 2009 to one largely consisting of *Daphnia* spp. in 2010. There was more overlap in standardized diet assemblages in 2010 than in 2009 due to the increased importance of *Daphnia* spp. in white perch diets in 2010. Contrary to expectations, complete separation of diets was not a requirement that enabled the long-term coexistence of invasive white perch and native white bass in Saginaw Bay. Both age-0 white bass and white perch had a mixed feeding strategy with varying degrees of specialization and generalization on different prey. The inter-annual variation in prey, i.e., higher densities of zooplankton in 2009 and chironomids in 2010, is directly opposite of the pattern observed in white perch diets, i.e., diets dominated by chironomids in 2009 and zooplankton in 2010. Energy density increased from July into autumn/fall for both species suggesting that food limitation was not severe.

**Key words:** sympatry, *Morone*, planktivory, benthivory, competition

## Introduction

The introduction of invasive species into aquatic systems is known to cause profound ecological changes. In some cases, invasions lead to situations where closely related species that were formerly geographically isolated now interact in the same system. One example is the invasion of white perch *Morone americana* (Gmelin, 1789) into the Laurentian Great Lakes where white bass *Morone chrysops* (Rafinesque, 1820) are native. White bass are a freshwater fish native to the St. Lawrence-Great Lakes, Hudson Bay (Red River), and Mississippi River basins, whereas white perch is a euryhaline species native to the Atlantic coast region (Page and Burr 1991). Both species have been introduced outside their native range either through intentional or accidental stockings resulting in situations where these two congeners, once formerly isolated from each, other now overlap (Irons et al. 2002; Kuklinski 2007; Feiner et al. 2013a). For example, in the Laurentian Great Lakes region, white perch were found in lakes Ontario and Erie in the 1950s and spread to Lake Huron by the early 1980s (Boileau 1985; Johnson and Evans 1990).

Phylogenetic analysis suggests that there are two sets of sister taxa of the *Morone* complex in North America, *M. chrysops*: striped bass *M. saxatilis* (Walbaum, 1792) and *M. americana*: yellow bass *M. mississippiensis* (Jordan and Eigenmann, 1887) (Leclerc et al. 1999). The native range of *M. americana* overlaps that of *M. saxatilis*, whereas that of *M. chrysops* overlaps

that of *M. mississippiensis* (Page and Burr 1991). Despite this native range overlap with their respective sister taxa, introductions of white perch are generally associated with declines in white bass populations. Specifically, invasions of white perch appear to affect white bass during early life, through direct predation of white bass eggs or competition for food during the juvenile period (Gopalan et al. 1998; Madenjian et al. 2000; Eckmayer and Margraf 2004; Feiner et al. 2013a). The early life period was identified as a potential bottleneck for recruitment of white bass in Lake Erie (Gopalan et al. 1998; Madenjian et al. 2000; Eckmayer and Margraf 2004), where competition with invasive white perch led to food limitation, decreased growth rates and lower energy stores for age-0 white bass (Eckmayer and Margraf 2004). These declines in growth and condition are thought to have contributed to the decline of white bass through increased risk of predation, reduced ability to switch to energetically profitable food sources such as fish, and higher likelihood of overwinter mortality (Eckmayer and Margraf 2004). Other studies in reservoirs have also documented that the juvenile period constitutes the highest trophic overlap between white perch and white bass (Kuklinski 2007; Feiner et al. 2013a).

Most studies of white perch in the Great Lakes took place in Lake Erie soon after an initial population explosion in the early 1980s (Schaeffer and Margraf 1986; Parrish and Margraf 1990, 1991; Eckmayer and Margraf 2004). Although white perch have been a part of the fish community of Saginaw Bay, Lake Huron since 1983 (Boileau 1985), almost no information exists on their life history or ecology even though they became a numerically important species in the system by the late 1980s (Fielder et al. 2000). Often, ecological interactions and population biology of invasive species are evaluated relatively soon after the invasion period before the long-term interactions between native and non-native species have become established. Field studies conducted in Saginaw Bay during 2009–2010 provided the opportunity to assess diets and condition of age-0 white perch and age-0 white bass in a large system where the two species have coexisted for over two decades.

In general, native species with the greatest diet or habitat overlap with invasive species are most at risk for declines (Crowder et al. 1981; Olden et al. 2006). When closely related species coexist over a long period of time, they generally have complementary diets to minimize overlap

(Werner and Hall 1979; Bøhn and Amundsen 2001; Bøhn et al. 2008). For example, the invasion of white perch in Lake Erie was expected to have negative impacts on yellow perch *Perca flavescens* (Mitchill, 1814) because of competition for shared resources (Parrish and Margraf 1990, 1991), but after 30 years of coexistence, the two species appear to have developed an ecological divergence with only a moderate degree of diet overlap (Guzzo et al. 2013).

In this study, we evaluated the diet composition, diet overlap, feeding strategy and condition of sympatric populations of age-0 invasive white perch and age-0 native white bass in Saginaw Bay, Lake Huron following >20 years of coexistence. Diet composition was determined during July-November in 2009 and 2010 to assess seasonal and interannual patterns of feeding ecology for the two species. Diet overlap was evaluated using nonparametric multivariate analyses (Clarke and Warwick 2001). We expected that there would be little diet overlap between the two species given their prolonged coexistence in Saginaw Bay. We evaluated feeding strategy using a graphical approach (Amundsen et al. 1996). Based on results from other systems, we expected white perch diet would be more generalized than that of white bass (Feiner et al. 2013a, b). We evaluated the condition of both species by determining their whole-body energy density. Considering that both species have persisted together in Saginaw Bay, we did not expect that food resources would be limiting and that energy density would increase for both species over their first growing season.

## Methods

Age–0 white bass and white perch were collected at four sites from inner Saginaw Bay, Lake Huron (Figure 1) during July–November 2009 and 2010 using a 7.6 m semi–balloon bottom trawl with a 13 mm mesh cod liner. Fish were placed in bags with water, and immediately put on ice in coolers. Upon returning to shore, bags of fish were frozen at –20°C. Immediately before or after fish collections, zooplankton samples were collected at the trawl start or end points. Zooplankton were collected with duplicate vertical net tows from just above bottom to the surface using a 0.3 m diameter, 64 µm mesh net and were narcotized and preserved using 10% sugar buffered formaldehyde. Benthic macroinvertebrates were collected with duplicate sediment grabs immediately after zooplankton collections using a standard 0.052 m$^2$ PONAR dredge with 500–µm

mesh. Samples were concentrated through a 500–µm mesh screen and preserved with a 10% formaldehyde solution with Rose Bengal.

Fish were sorted by species, and total length and wet weight were measured to the nearest mm and 0.01 g, respectively. Age-0 fish were chosen based on size distributions which clearly tracked the age-0 cohort across months. Stomach contents were removed for all age-0 fish or a subsample of fish from larger catches. After stomach contents were removed, individual fish were ground and dried for three days at 70° C. To evaluate diets, whole invertebrates or fish in stomachs were identified and counted. For partial invertebrates, only individuals with heads attached were identified and counted. For partially digested fish, structures such as cleithra or otoliths were used to determine species where possible, and the number of fish in a stomach was determined based on pairs of these structures. For diet analysis, zooplankters were classified as Copepoda, *Daphnia* spp., Chydoridae, other herbivorous cladocerans (Bosminidae, *Diaphanosoma* spp.), and predatory cladocerans (e.g., *Leptodora kindtii* (Lilljeborg, 1861) and *Bythotrephes longimanus* (Leydig, 1860)). Nauplii were not found in diets and therefore excluded from analysis. Benthic macroinvertebrates were classified as Chironomidae (larvae and pupae combined) and other benthos (mainly Amphipoda). Other prey categories included fish and emergent insects (mostly Ephemeroptera). Whole organisms were measured using a microscope-mounted digital camera and image analysis software (Image Pro V. 6.2). Depending on the prey type, weight-length regressions or a published mean weight were used to estimate the mean dry weight for each prey type (Nalepa and Quigley 1980; Culver et al. 1985; Makarewicz and Jones 1990; Benke et al. 1999). The mean weight of a given prey type was multiplied by the total number of that respective prey to determine its dry weight contribution to the diet. Diets were expressed as percent occurrence of each prey type and as the percent of the total dry weight summed across all fish within each species for a given month and year. Zooplankton from net tows were sub-sampled using a Hensen-Stempel pipette and a minimum of 600 individuals were identified to species and summarized at the same taxonomic level as prey items in diets (see Pothoven et al. 2013 for details). Benthic samples were observed under magnification (1.5×), and all animals in a sample were removed, identified to family, enumerated, and summarized at the same taxonomic level as prey items in diets.
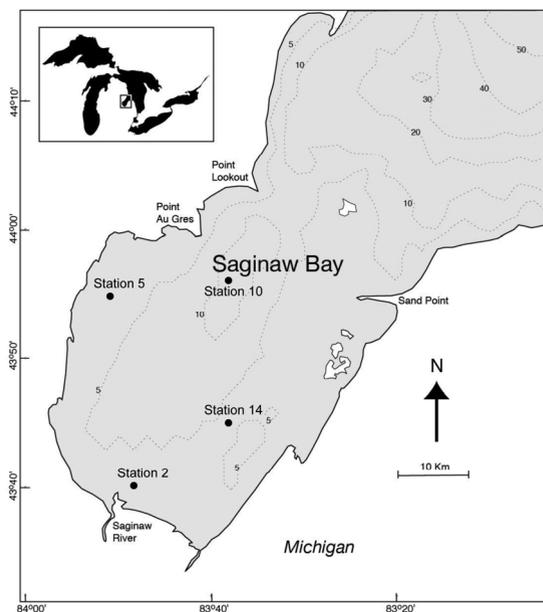


**Figure 1.** Map showing location of 4 sampling stations in inner Saginaw Bay.

Zooplankton and chironomid abundance was compared across months or years with ANOVA.

Energy density was determined to evaluate fish condition. For energy density analysis, a subsample of individual dried fish was selected and further homogenized with a mortar and pestle. Entire homogenized individual fish or a 1 g subsample for fish > 1 g dry weight were combusted in a Parr 1261 isoperibol calorimeter that had been standardized with benzoic acid. Each individual fish's percent dry to wet weight and energy density on a wet weight basis were determined. Energy density was regressed as a function of percent dry weight for each species and these regressions were used to estimate energy density for all dried fish as done in other studies (e.g., Pothoven et al. 2011; Jacobs et al. 2012). Mean energy density for each species was compared among months within each year using ANOVA with $p<0.05$ considered significant.

Analysis of similarities (ANOSIM) was used to test for differences in standardized diet percent weight composition between white perch and white bass for each month. This approach is analogous to an ANOVA, with a non-parametric permutation applied to a rank similarity matrix of samples (Clarke and Warwick 2001). Diet composition, standardized as percent of total dry weight, was square root transformed to down-
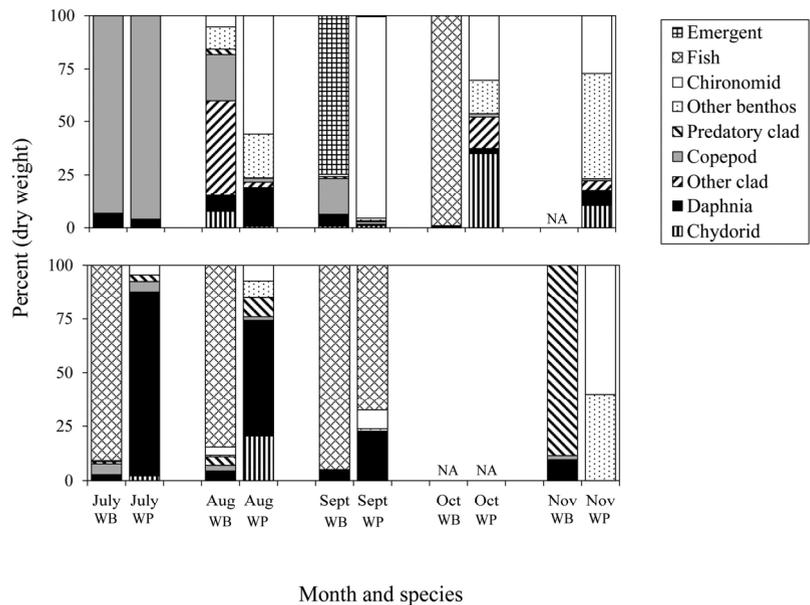
**Figure 2**. Diet composition (percent dry weight) for age-0 white bass (WB) and age-0 white perch (WP) in Saginaw Bay during July-November in 2009 (top) and 2010 (bottom). See Table 2 for number of fish used for diet evaluations in each month.

weight highly abundant species (Clarke and Warwick 2001) and used to create a Bray-Curtis similarity matrix for ANOSIM. R-values from ANOSIM were used as a measure of absolute separation of diet assemblages between white perch and white bass for each month and year. R-values range from -1 to +1, and generally lie between 0 where groups are indistinguishable and +1 where all similarities within groups are less than any similarity between groups (Clarke and Gorley 2001). Negative R-values indicate greater dissimilarity among replicates within a sample than between samples (Chapman and Underwood 1999). R-values provide an absolute measure of how separated groups are, with R-values <0.25 indicating almost no separation between groups, R-values of 0.5 to 0.75 indicating some overlap between groups, and R-values >0.75 indicating clear separation between groups (Clarke and Gorley 2001). A similarity percentage routine (SIMPER) was applied to determine which prey typified the diet of white perch and white bass within each month and year. ANOSIM and SIMPER were performed using Primer v5.2.9.

To evaluate the feeding strategy of age-0 fish, an approach proposed by Amundsen et al. (1996) was used, where the prey specific abundance ($P_i$) is plotted against the frequency of occurrence. Prey specific abundance is the percentage a prey type comprises of all prey items in only those predators in which the prey occurs (Amundsen et

al. 1996). We used dry weight diet biomass to determine prey specific biomass. The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and rare prey in the lower left. The vertical axis represents the feeding strategy of the predator in terms of specialization and generalization. Predators specialize on prey types on the upper half of the plot, whereas prey types on the lower half of the plot represent a generalized feeding strategy. Prey points in the upper left indicate specialization by individuals whereas points in the upper right indicate a dominant prey of the overall population (Amundsen et al. 1996).

**Results**

We evaluated diets of 346 age-0 white bass and 349 age-0 white perch, of which 343 and 342, respectively, contained prey in their stomachs. The diet composition (by weight) of age-0 white bass was dominated by fish, various zooplankton taxa, or emergent insects, depending on the month and year (Figure 2). Zooplankton were consumed by at least 91% of the white bass each month, with various zooplankton groups being eaten more or less frequently depending on the month and year (Figure 3 and 4). Although fish comprised a large fraction of the diet biomass, especially in 2010 (Figure 2), they were eaten by <24% of

**Table 1.** Mean CPUE of age-0 white bass and white perch for each site and year, percent contribution of total diet dry weight for zooplankton, benthic invertebrates, and fish, and number of stomachs used to determine diet composition from each site.

| Year | Species | Site | CPUE #/10 min | Zooplankton % | Benthos % | Fish % | n |
|------|---------|------|---------------|---------------|-----------|--------|---|
| 2009 | White bass | 10 | 1.5 | 1 | 0 | 99 | 21 |
| 2009 | White bass | 14 | 3 | 40 | 1 | 0 | 24 |
| 2009 | White bass | 2 | 8.8 | 89 | 11 | 0 | 79 |
| 2009 | White bass | 5 | 1.0 | 71 | 29 | 0 | 20 |
| 2010 | White bass | 10 | 4.6 | 48 | 2 | 50 | 37 |
| 2010 | White bass | 14 | 7.2 | 2 | 0 | 98 | 49 |
| 2010 | White bass | 2 | 7.3 | 73 | 26 | 0 | 61 |
| 2010 | White bass | 5 | 0.7 | 2 | 0 | 98 | 52 |
| 2009 | White perch | 10 | 2.8 | 54 | 46 | 0 | 54 |
| 2009 | White perch | 14 | 17.5 | 10 | 88 | 0 | 40 |
| 2009 | White perch | 2 | 2.5 | 2 | 98 | 0 | 31 |
| 2009 | White perch | 5 | 0.5 | 12 | 88 | 0 | 9 |
| 2010 | White perch | 10 | 12.5 | 9 | 91 | 0 | 58 |
| 2010 | White perch | 14 | 9.1 | 99 | 1 | 0 | 63 |
| 2010 | White perch | 2 | 12.8 | 11 | 0 | 89 | 50 |
| 2010 | White perch | 5 | 5.9 | 74 | 26 | 0 | 37 |

**Table 2.** Mean ± SE total length of age-0 white bass and white perch (number of fish examined for diets in parentheses), mean surface temperature, mean zooplankton abundance, mean *Daphnia* spp. abundance, and mean chironomid (larvae and pupae) density at 4 sites in inner Saginaw Bay, Lake Huron.

| Year | Month | White bass mm | White perch mm | Temp. °C | All zoopl. #/m$^3$ | *Daphnia* #/m$^3$ | Chironomids #/m$^2$ |
|------|-------|---------------|----------------|----------|-------------------|-------------------|---------------------|
| 2009 | July | 39 ± 2 (10) | 39 ± 1 (3) | 20 | 8709 | 3049 | 215 |
|  | Aug | 50 ± 1 (99) | 52 ± 1 (19) | 21 | 21834 | 1856 | 246 |
|  | Sept | 64 ± 2 (14) | 70 ± 1 (66) | 20 | 87170 | 1597 | 172 |
|  | Oct | 97 ± 4 (21) | 85 ± 2 (38) | 14 | 116214 | 12463 | 341 |
|  | Nov | - | 64 ± 5 (8) | 10 | 9503 | 701 | 324 |
| 2010 | July | 43 ± 1 (77) | 40 ± 1 (30) | 26 | 4962 | 1320 | 1034 |
|  | Aug | 75 ± 1 (79) | 71 ± 1 (77) | 25 | 22827 | 652 | 536 |
|  | Sept | 102 ± 1 (39) | 95 ± 1 (75) | 17 | 47966 | 2787 | 441 |
|  | Nov | 114 ± 2 (4) | 102 ± 2 (26) | 6 | 8537 | 831 | 596 |

**Table 3.** R-values from ANOSIM comparing standardized diet composition (% dry weight) between age-0 white bass and age-0 white perch in Saginaw Bay, and percent contribution of dominant (>10%) prey groups to the characterization of diets for each species within each month and year based on SIMPER analysis. R values generally range from 0 (complete overlap) to + 1 (no overlap). R-values <0.25 indicate almost no separation between groups, R-values of 0.5 to 0.75 indicate some overlap between groups, and R-values >0.75 indicate clear separation between groups (Clarke and Gorley 2001).

| Month and Year | R-value | White bass | White perch |
|----------------|---------|------------|-------------|
| Aug 2009 | 0.566 | Copepod (42%), other cladocerans (39%), chydorid (15%) | Chironomid (52%), Daphnia (16%), copepod (13%) |
| Sept 2009 | 0.683 | Copepod (49%), emergent (34%), *Daphnia* (13%) | Chironomid (73%, copepod (10%) |
| Oct 2009 | 0.611 | Other cladoceran (36%), fish (16%), copepod (14%), chydorid (13%) | Chironomid (32%, chydorid (31%), other cladoceran (18%), other benthos (11%) |
| July 2010 | 0.117 | Copepod (64%), *Daphnia* (23%), fish (10%) | *Daphnia* (94%) |
| Aug 2010 | 0.141 | Predatory cladoceran (45%), *Daphnia* (29%), copepod (19%) | *Daphnia* (81%), predatory cladoceran (14%) |
| Sept 2010 | 0.126 | *Daphnia* (74%), predatory cladoceran (24%) | *Daphnia* (84%), chironomid (12%) |

white bass each month (Figure 4). The few fish found in stomachs that were identifiable to species were emerald shiners *Notropis atherinoides* (Rafinesque, 1818) and gizzard shad *Dorosoma cepedianum* (Lesueur, 1818). Chironomids and other benthic macroinvertebrates were a relatively minor part of white bass diets by weight (Figure 2) and occurred relatively infrequently in diets (Figure 3 and 4).

The diet composition by weight of age-0 white perch in 2009 shifted from one dominated by copepods in July to one dominated by chironomids
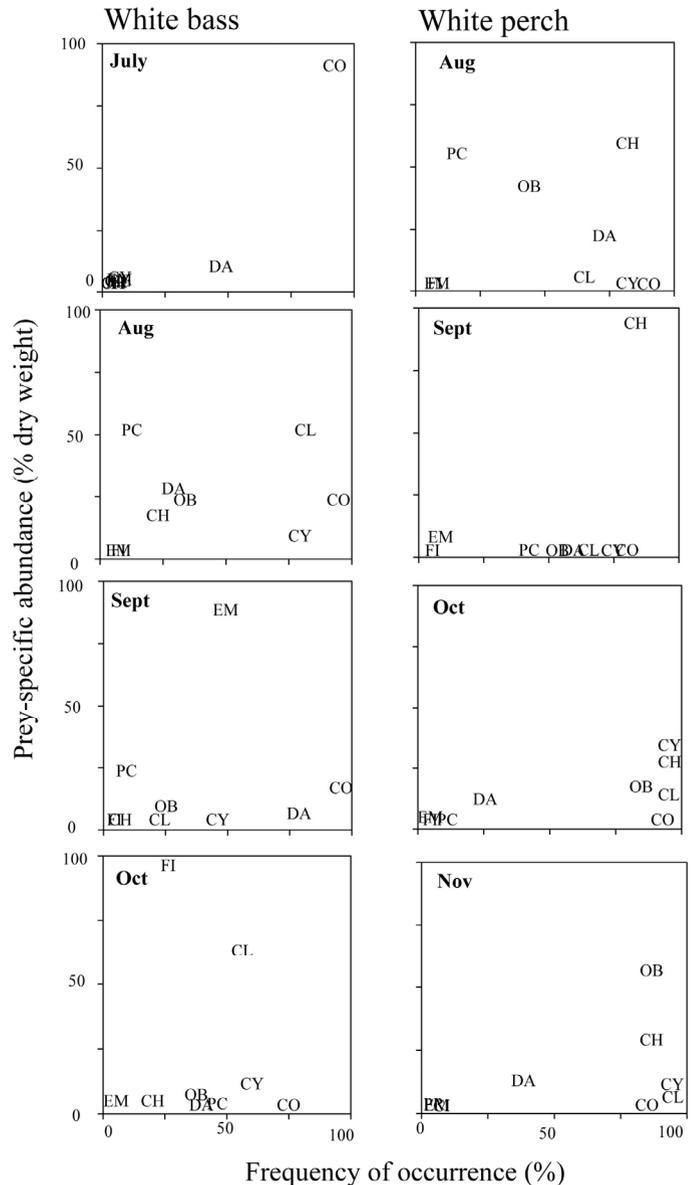
**Figure 3.** Feeding strategy plot (prey specific abundance on a percent dry weight basis plotted against frequency of occurrence, Amundson et al. 1996) for age-0 white bass and white perch during 2009. CH=Chironomidae, OB=other benthic invertebrates, CY=Chydoridae, *DA=Daphnia*, PC=predatory Cladocera, CO=Copepoda, CL=other Cladocera, FI=fish, EM=emergent Insecta. The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and unimportant prey in the lower left. The vertical axis represents the feeding strategy of the fish in terms of specialization (upper part of plot) and generalization (lower part of plot). Prey points in the upper left indicate specialization by individuals whereas points in the upper right indicate a dominant prey of the overall population (Amundsen et al. 1996).

and other benthic macroinvertebrates in August-November (Figure 2). In 2010, chironomids and other benthic prey dominated the diet by weight in November, but *Daphnia* spp. or fish were the dominant prey in July/August or September, respectively (Figure 2). For example, in 2009 at least 79% of white perch ate chironomids in each month except July, whereas <35% of white perch ate chironomids in July-September 2010 (Figure 3 and 4). Despite the importance of chironomids and other benthic prey in diets in 2009, all white perch examined had also eaten zooplankton, and in 2010, zooplankton were eaten by >92% of

age-0 white perch each month except November 2010 (Figure 3 and 4). Fish were generally not eaten by white perch except in September 2010, when 4% of the white perch had eaten fish (Figure 3 and 4), which accounted for 68% of the diet biomass (Figure 2).

Percent dry weight diet composition differed somewhat across sites during each year for both species (Table 1). Diets of white bass were mainly zooplankton or fish depending on site. Benthic invertebrates composed white perch diets at each site in 2009, and zooplankton or fish composed diets in 2010, except at station 10, where benthic
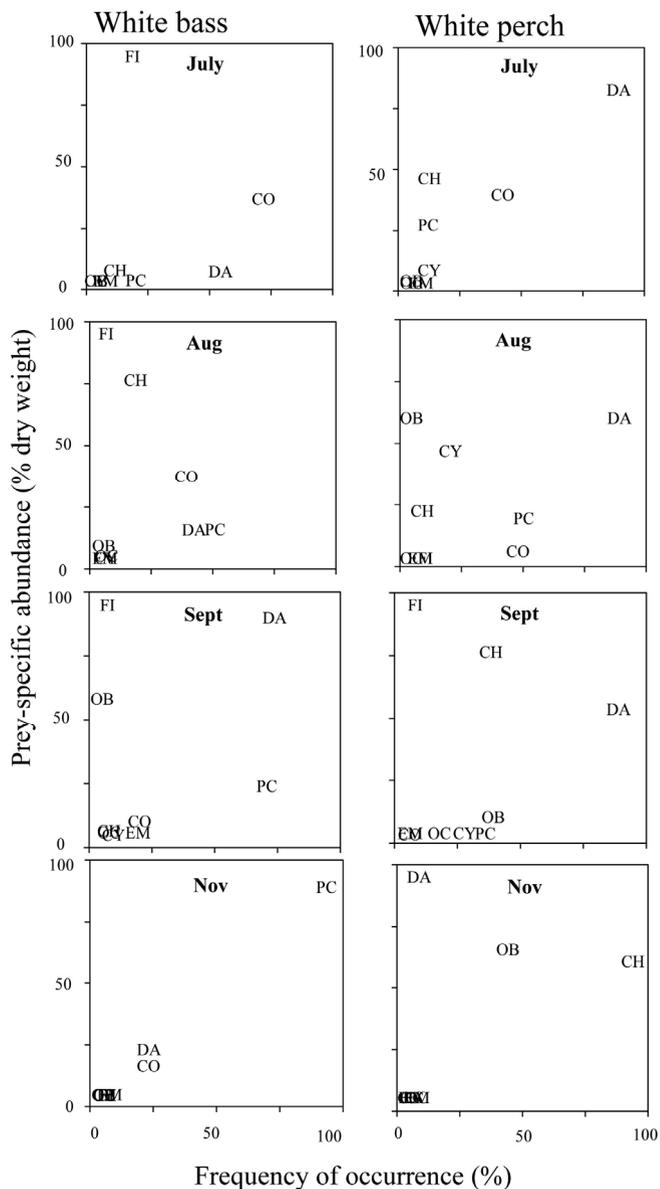
**Figure 4.** Feeding strategy plot (prey specific abundance on a percent dry weight basis plotted against frequency of occurrence, Amundson et al. 1996) for age-0 white bass and white perch during 2010. See Figure 3 legend for abbreviations.

invertebrates remained important (Table 1). Catches of both species were highly variable and did not differ across sites ($p>0.37$) or between years ($p>0.22$) (Table 1). Total lengths of white perch and white bass were similar in July each year, but by fall, white bass were slightly larger than white perch (Table 2).

The R-values from ANOSIM indicated that diet overlap between age-0 white bass and white perch was fairly substantial during 2009 based on R-values between 0.57 and 0.68 (Table 3). In contrast, diet assemblages in 2010 were barely separated between species based on R-values of 0.12 to 0.13 (Table 3). SIMPER results indicated that different prey generally characterized each species' diet in 2009, with chironomids having a large influence on white perch diet composition and various zooplankton groups generally characterizing white bass diets (Table 3). By contrast, there was more overlap in diet assemblages between species in 2010 because of the importance of *Daphnia* spp. and predatory cladocerans (mainly
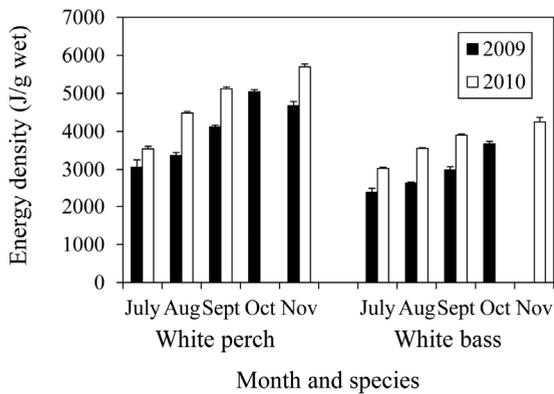
**Figure 5.** Mean ± SE energy density of age-0 white bass and age-0 white perch in Saginaw Bay during July-November 2009 and 2010.

*Bythotrephes*) for both species (Table 3). July 2009 and November 2010 were not used for ANOSIM or SIMPER analysis due to small samples sizes (<4) of either white perch or white bass.

Both white bass and white perch had a mixed feeding strategy with varying amounts of generalized and specialized feeding on different prey types (Figure 3 and 4). In 2009, white bass demonstrated population level specialization on Copepoda, other Cladocera, or emergent insects, depending on the month (Figure 3). Individual white bass specialized on predatory Cladocera or fish in August and October 2009, respectively (Figure 3). Chironomids or other benthic prey dominated the diet at the population level for white perch in 2009 except in October, when all prey were eaten occasionally (Figure 3). White perch demonstrated little individual specialization in 2009 except on predatory Cladocera in August (Figure 3).

In 2010, white bass demonstrated population specialization on *Daphnia* spp. and predatory Cladocera in September and November, respectively (Figure 4). White bass also demonstrated individual specialization on fish or benthic prey during some months (Figure 4). In 2010, white perch specialized on *Daphnia* spp. at the population level except during November, when it was specialized upon by a few individuals (Figure 4). Chironomids and other benthos were specialized upon by individual white perch in August and September, respectively, and by the population in November. Fish were specialized upon by a few individual white perch in September (Figure 4).

The total abundance of zooplankton and the abundance of *Daphnia* spp. differed among months each year ($p<0.04$), with the highest abundances occurring in October and September in 2009 and 2010, respectively (Table 2). In contrast, the densities of chironomids did not differ significantly among months in either year ($p>0.58$) (Table 2). Although the mean abundance of zooplankton was 55,597/$m^3$ and 22,871/$m^3$ in 2009 and 2010, respectively, there was no significant difference between years ($F_{1,29}=3.92$, $p=0.06$) due to the high variation among months. In contrast, chironomid density differed significantly between years ($F_{1,32}=6.70$, $p=0.01$), with mean densities of 253/$m^2$ and 660/$m^2$ in 2009 and 2010, respectively. The annual variation in prey (i.e., trend for higher densities of zooplankton in 2009 and chironomids in 2010) is directly opposite of the pattern observed in white perch diets (i.e., diets dominated by chironomids in 2009 and zooplankton in 2010).

The regressions relating % dry weight vs energy density were: white bass; $J/g = (192.59 \times$ % dry weight) + 162.37 ($R^2=0.89$, n=52) and white perch; $J/g = (245.62 \times$ % dry weight) - 648.77 ($R^2=0.96$, n=96). These regressions were subsequently used to determine energy density for all fish that had been dried. Energy density differed among months for both species in 2009 and 2010 ($p<0.001$). Energy density for both species increased each month over the growing season, peaking in October or November each year (Figure 5).

## Discussion

The magnitude of the separation in diet assemblages for age-0 white perch and white bass in Saginaw Bay varied greatly between years largely due to strong interannual variation in white perch feeding ecology. The importance of benthic prey in white perch diets decreased dramatically between 2009 and 2010, so that in 2010, there was considerably more overlap between white perch and white bass diet assemblages. Age-0 white perch and white bass both had a mixed feeding strategy, with various degrees of generalization and specialization on individual prey. However, the ability of white perch to shift from specialization on benthic prey to specialization on pelagic prey between years highlights the flexibility that has made them a successful invader. This is consistent with the idea that white perch generally exploit a much larger niche and are

more capable of switching between pelagic and benthic prey items than age-0 white bass, which tend to be more specialized when in sympatry with white perch (Gopalan et al. 1998; Feiner et al. 2013a, b). Nonetheless, somewhat contrary to our expectations, complete separation of diets is apparently not a requirement for long-term coexistence of these closely related species in Saginaw Bay.

Other studies have found some diet overlap between both juvenile and adult white perch and white bass, although the shared prey groups appear to vary between systems, and include zooplankton, benthic invertebrates, and insects (Bur and Klarer 1991; Gopalan et al. 1998; Kuklinski 2007; Feiner et al. 2013a). Results from a reservoir in North Carolina indicated that invasive white perch were probably not exploiting an underutilized resource, but rather sharing resources with other fish (Feiner et al. 2013 a, b). The invasion of white perch in Lake Erie is thought to have increased competition for food for white bass (Gopalan et al. 1998; Madenjian et al. 2000; Eckmayer and Margraf 2004) as well as benthic oriented fish such as yellow perch (Parrish and Margraf 1990). Although age-0 white bass in Saginaw Bay appear to be largely oriented toward pelagic prey, other studies where white bass and white perch do not co-occur or where white perch invasions are in the early stages indicate that white bass can also be opportunistic and utilize benthic resources (Van Den Avyle et al. 1983; Feiner et al. 2013a). Perhaps the current focus of white bass on pelagic prey in Saginaw Bay is a "ghost of competition past" (Connell 1980) and before the white perch invasion, white bass would have had more access to benthic resources. Unfortunately, we do not have white bass diet data available for the pre-white perch period for comparison. However, age-0 yellow perch in Saginaw Bay during 2009–2010 did not demonstrate the expected shift from zooplanktivory to benthivory, suggesting that competition for benthic resources was high (Roswell et al. 2014). Another more recent invasive species, round goby *Neogobius melanostomus* (Pallas, 1814), is also dependent on benthic prey in Saginaw Bay (T. Höök, unpubl. data).

Previous work with white perch documented shifts in their diet depended on prey availability (Prout et al. 1990; Gopalan et al. 1998; Couture and Watzin 2008; Feiner et al. 2013a). However, the shifts in white perch diets in this study are the opposite of trends we noted in prey availability. For example, chironomids were more prevalent in white perch diets in 2009 even though their abundance in the environment was higher in 2010. Similarly, zooplankton, were more important in white perch diets in 2010 even though zooplankton abundance was higher in 2009. Thus, factors other than shifts in prey availability alone must have influenced the annual variability of white perch diets.

One factor that might have led to interannual shifts in diets was changes in inter-species interactions between years. For example, a smaller year class of yellow perch in 2010 (M. Thomas, Michigan Department of Natural Resources, unpubl. data) could have led to reduced competition for *Daphnia* spp. Age-0 yellow perch are one of the most abundant planktivores in Saginaw Bay, and *Daphnia* spp. composed much of their diets (Roswell et al. 2014). In Oneida Lake, Prout et al. (1990) found that large year classes of yellow perch compete with white perch for *Daphnia* spp. resulting in slower white perch growth and heightened vulnerability to predation.

The difference in the size of fish between years may have also influenced interannual variation in diets. Both white bass and white perch were larger in 2010 than in 2009. One factor that might have contributed to larger sizes in 2010 than in 2009 is earlier warming and higher temperatures that can contribute to more rapid growth. Both species were slightly larger on July 6–8, 2010 than they were on July 23, 2009, and by August 2010, both species were as large as or larger than they were in September 2009. Perhaps the larger white perch were more pelagic oriented in their diets in 2010 than in 2009. Feiner et al. (2013a, b) indicated that diets of medium sized perch were more pelagic oriented than those of small white perch, suggesting that there could be a shift toward increased pelagic foraging as white perch grow larger. Similarly, it seems likely that faster growing white bass were more likely to shift toward piscivory, although the proportion of white bass that ate fish was relatively low even in 2010.

Even though diets varied somewhat across sites, a site bias is not an underlying factor behind the dramatic interannual variation in white perch diets. White perch diets were dominated by benthic invertebrates at all sites in 2009, but at only one site in 2010. Thus, even though site can contribute to variation in diets, our overall conclusion of a shift from benthic prey to pelagic prey appears robust for white perch. Clearly, understanding diet shifts for both age-0 white perch and age-0 white bass is complex and requires

information on abiotic factors was well as biotic factors other than simple prey abundance.

Energy density increased steadily between July and October/November for both age-0 white perch and white bass in Saginaw Bay. By contrast, lipid content decreased between July and September for age-0 white bass that were considered food limited in Lake Erie (Eckmayer and Margraf 2004). This suggests that conditions in Saginaw Bay were favorable enough for both species to allocate energy toward storage and that neither species was suffering from undue food limitation or competition. On the other hand, white bass growth in Saginaw Bay was slower than that observed in other northern lakes (Priegel 1970; Eckmayer and Margraf 2004). White bass shift toward piscivory as they grow (Tubb 1973) and they need to grow fast enough to maintain their ability to consume forage fish which are also increasing in size over the summer (Eckmayer and Margraf 2004). The comparatively slow growth could have contributed to low frequency of piscivory by white bass, especially in 2009.

Minimal diet overlap during the juvenile period is apparently not an absolute prerequisite for a native species and a closely related introduced species to coexist. Perhaps resources in Saginaw Bay were not limited to the point where age-0 white bass and white perch needed to develop more separate diet strategies. Saginaw Bay is a relatively productive system with phosphorus concentrations often exceeding water quality recommendations of 15 ug/L (Pothoven et al. 2013). Steadily increasing energy density over the growing season for both species provides some evidence that resources were not limiting. This study points to the complexity of understanding the impacts of competition when closely related species (one invasive and one native) that existed in isolation are put into sympatry in large freshwater systems.

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