

ARTICLE

Biotic and Abiotic Factors Affecting Feeding Success of Early Juvenile Lake Whitefish in Lakes Michigan and Huron

Steven Pothoven* 

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

Chris Olds¹

U.S. Fish and Wildlife Service, Alpena Fish and Wildlife Conservation Office, Alpena, Michigan 49717, USA

Abstract

Feeding success is associated with increased growth and survival during early life stages for fish, and understanding the factors that influence feeding success is a critical step toward predicting future recruitment to the fishery. The goal of our study was to test whether various biotic and abiotic factors, including prey abundance, fish abundance, and water temperature, affected the feeding success of early juvenile Lake Whitefish *Coregonus clupeaformis* from Lakes Michigan and Huron. Higher feeding success, which was determined using residuals from average weights of consumed prey for a given length fish, was associated with more rapid growth rates in length and depended on multiple factors. Although the relationships were not overly strong, one factor that was most consistently associated with increased feeding success was available zooplankton biomass in combination with some other factor(s) such as water temperature and/or total fish or Lake Whitefish density. There was no difference in diet composition or the available zooplankton community composition among four different levels of feeding success. Feeding success measures help integrate complex environmental factors that can vary with fish ontogeny. In turn, feeding success has the potential to be an important metric for Lake Whitefish fishery management strategies that critically need to account for the myriad factors influencing survival and growth of prerecruits to the fishery.

Feeding success during early life is considered critical for fish survival, growth, and, ultimately, recruitment to older age-classes (Michaud et al. 1996; Pepin et al. 2015). Metrics of feeding success integrate multiple environmental factors, including prey density, temperature, light, and competition, making it a potentially useful predictor of year-class strength (Fortier et al. 1995). Studies of feeding success provide an understanding of the factors that limit fish growth and survival during early life (Michaud et al. 1996; Pepin et al. 2015). In turn, feeding success has been used to determine the influences of ecosystem changes on

early life stages (Schultz et al. 2019). Metrics of feeding success could also be used to help prioritize the most suitable nursery habitats that contribute to early life survival (Grecay and Targett 1996; Nunn et al. 2012; Wilson et al. 2013).

It has long been recognized that variation in population abundance is closely linked to recruitment success during early life stages (Houde 2008). Understanding the processes that influence survival and growth during the early life stages of a fish species is critical for understanding variability in fish populations and managing the fishery and

*Corresponding author: steve.pothoven@noaa.gov

¹Present address: U.S. Forest Service, Medicine Bow–Routt NF, Thunder Basin National Grassland–Parks District, 100 Main Street, Walden, Colorado 80480, USA.

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user expectations (Ludsin et al. 2014). Much of the research on recruitment bottlenecks has historically been focused on the egg and larval stages of fish that experience high mortality (Hjort 1914; Houde 2008). However, there are bottlenecks across multiple life stages (Houde 2008; Eckmann 2013), and subtle differences in the factors that limit the survival of late larval/early juvenile stages of fish can be critical for understanding year-class formation (Folkvord and Hunter 1986; Malloy and Targett 1991; Stige et al. 2019).

Although no single mechanism controls recruitment variability (Houde 2008; Ludsin et al. 2014; Pritt et al. 2014), survival during early life stages is clearly associated directly and indirectly with feeding success (Robert et al. 2009; Nunn et al. 2012; Stige et al. 2019). In particular, feeding success is generally linked to growth during early life stages (Pepin et al. 2015), and understanding the factors that affect feeding success is critical for predicting early life growth and survival (Folkvord and Hunter 1986; Robert et al. 2009; Pepin et al. 2015).

Lake Whitefish *Coregonus clupeaformis* are the primary target for commercial and subsistence fisheries in the Laurentian Great Lakes. In the upper Great Lakes, Lake Whitefish accounted for 67% of the commercial harvest in 2015, with a harvest of about 4.27 million kg (Baldwin et al. 2018). However, this level of harvest represents a decline from 7.3 million kg in 2010 and there is concern about the future of the fishery and whether harvest objectives are realistically obtainable (Gobin et al. 2015, 2016). Declines in adult Lake Whitefish growth and condition in Lakes Michigan and Huron have been associated with ecosystem changes following the invasion of dreissenid mussels and the loss of the benthic amphipod *Diporeia* (Pothoven et al. 2001; Brenden et al. 2010; Fera et al. 2015). Most recently, fishery managers have expressed concern that Lake Whitefish recruitment during early life stages is declining and that there has been a regime shift that threatens the yield capacity and sustainability of the fishery (Gobin et al. 2016).

Lake Whitefish spawn in the fall and fertilized eggs overwinter and hatch in early spring. Year-class strength in Lake Whitefish is thought to be largely determined early in their life history during the embryonic and larval stages (Taylor et al. 1987; Freeberg et al. 1990). However, Lake Whitefish undergo multiple ontogenetic diet shifts during the late larval/early juvenile stage (Claramunt et al. 2010a; Pothoven et al. 2014) as well as a morphological shift in mouth position from terminal to subterminal when they reach a length of about 40 mm (Claramunt et al. 2010a). A recent diet study in Lake Huron indicated that early juvenile Lake Whitefish may have broad flexibility in their diets, but this adaptability might not entirely buffer their feeding success across varying environmental conditions (Pothoven and Olds 2020). Another recent study at a single site in Lake Michigan indicated that feeding success increased with

preferred prey abundance for larval Lake Whitefish, but the relationship was less consistent for early juvenile fish, suggesting that other biotic or abiotic factors may be important (Pothoven 2020).

The goal of our study was to test whether various biotic and abiotic factors affected the feeding success of early juvenile Lake Whitefish, which was determined using residuals from the average weight of consumed prey for a given length fish. Specifically, we tested whether broad ranges in prey abundance, fish abundance, and water temperature interacted to affect feeding success for juvenile Lake Whitefish from Lakes Michigan and Huron during 2014–2019. We also tested whether diet composition or prey composition differed among different levels of feeding success. Feeding success is important for the development of models for predicting recruitment (Folkvord and Hunter 1986) and to better understand which environmental factors are most influential during the early juvenile life stage of Lake Whitefish.

METHODS

Field sampling.— Juvenile Lake Whitefish were collected as part of a regional age-0 coregonine seine survey program (Figure 1). In Lake Michigan, fish along with zooplankton and water temperature data were collected at five sites in eastern Lake Michigan by the National Oceanic and Atmospheric Administration during 2014–2019. In Lake Huron, collections were made by the U.S. Fish and Wildlife Service, with data available from four sites in western Lake Huron during 2018–2019. The sites were characterized by a sandy bottom with little to no bottom obstructions.

Juvenile Lake Whitefish were collected with a beach seine at each site. The seine was 45.7 m (length) \times 1.8 m (height) with a 1.8 \times 1.8 \times 1.8 m bag and 3.2-mm square delta mesh. One end of the seine was pulled perpendicular from shore until the seine was fully extended into the lake (45.7 m), and then the offshore end was pulled back to shore in a loop-like fashion. During each sampling event, three seine hauls were conducted with a distance of at least 50 m between tows. Fish from the three hauls were combined for diet analysis. Seining was done one to four times at each site during each year. The Lake Whitefish were preserved in 95% ethanol (Lake Michigan) or frozen (Lake Huron) upon collection. Lake Whitefish and other species relative abundance (CPE) was determined as number of fish/seine haul.

A single zooplankton tow was done at each site immediately after fish sampling using a 0.3 m (diameter) \times 0.9 m (length), 64- μ m mesh zooplankton net. The zooplankton net was attached to a pole and towed by hand off to the side of the individual wading in water about 0.5 m (depth) for a distance of 15.2 m (Lake Michigan) or 50 m (Lake Huron). The zooplankton were preserved using 10% buffered sugar formaldehyde (Lake Michigan) or ethanol

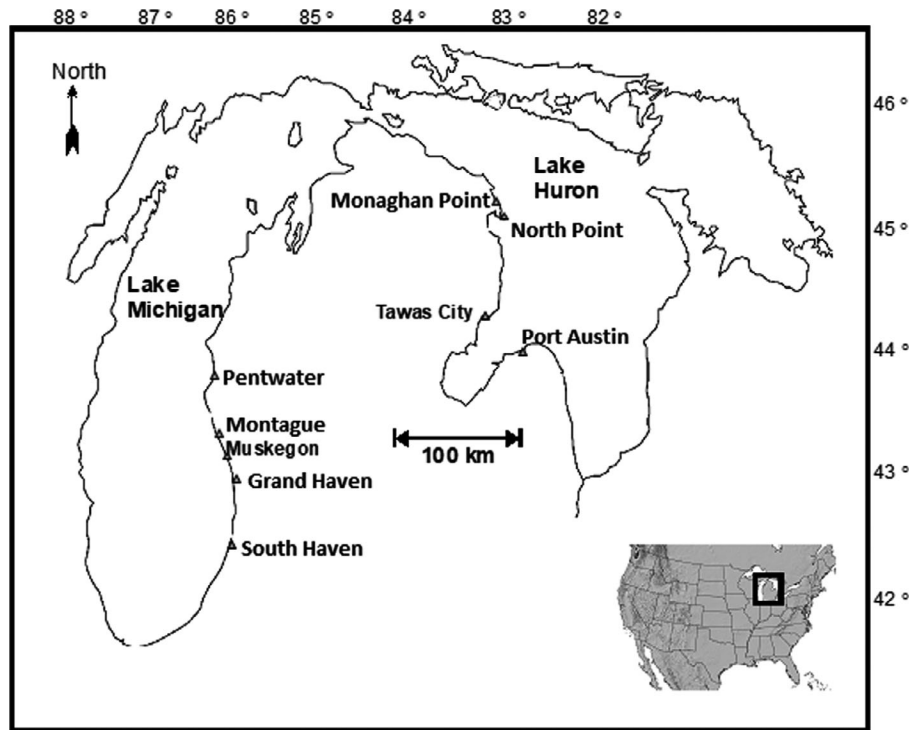


FIGURE 1. Map showing locations of five sampling sites in Lake Michigan and four sampling sites in Lake Huron.

(Lake Huron). The zooplankton catches were standardized based on the volume of water sampled, which was determined using the area of the net opening and distance towed. Water temperature was determined using a YSI Pro Plus probe or hand-held thermometer.

Analysis.—In the laboratory, total length (TL) of the Lake Whitefish was measured, the entire digestive tract removed, and the gut contents identified and enumerated. Whole prey organisms and partial organisms with heads attached were counted as individuals. The zooplankton were identified to varying levels of taxonomic resolution, specifically nauplii, calanoid copepod, cyclopoid copepod, *Daphnia*, *Bosminia*, Chydoridae, harpacticoid copepod, and other. Additional prey groups included chironomid pupae, benthic invertebrates (mostly chironomid larvae, as well as amphipods, ostracods, and mayflies), and terrestrial and emergent insects. Lengths of whole prey organisms were measured using Image Pro (v. 9.1). Weight-length regressions or prey specific mean weights were used to estimate the mean dry mass for each prey type from the stomachs (Hawkins and Evans 1979; Nalepa and Quigley 1980; Culver et al. 1985; Benke et al. 1999), which was then multiplied by the total number of that respective prey to determine its dry mass contribution to the diet for each fish.

For the zooplankton analysis, the whole sample was counted or a subsample was taken with a Hensen–Stemple

pipette so that at least 600 organisms (if available) were counted and identified. To determine zooplankton biomass, length measurements were obtained for a subsample of 10–25 individuals from taxa that made up at least 8% of the sample. Taxon-specific biomass was determined with dry mass-length regressions (Culver et al. 1985; Bowen et al. 2018). The mean calculated biomass for each taxon was used for samples when a particular taxon was not measured. For less common taxa that were not measured, a default mean mass was used (Hawkins and Evans 1979; Nalepa and Quigley 1980).

The amount of prey consumed per fish was used as a measure of feeding success (Fortier et al. 1995; Michaud et al. 1996; Robert et al. 2009). Diet mass increases with fish length, so a length independent index of feeding success was determined as the residuals of the regression of natural log-transformed prey biomass as a function of fish TL (see Figure 2). Positive residuals from the regression line indicated higher feeding success than average, and negative residuals indicated poorer feeding success than average for an individual fish (Michaud et al. 1996). The average residual across all fish from a given site and date were used to characterize feeding success for each sampling event. Only sampling events that had at least three fish collected were included in analyses. The average sample size was 35 fish/sampling event, with only 7% of the sample events having ≤ 5 fish.

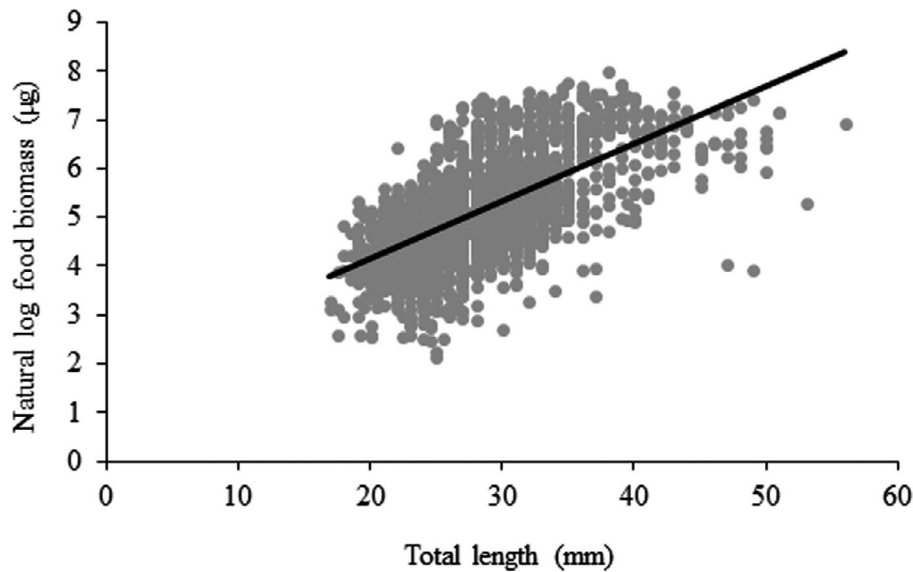


FIGURE 2. Consumed prey biomass (dry) in stomachs (natural log transformed) as a function of Lake Whitefish total length. Residuals from the regression line ($\ln \text{Prey biomass } \mu\text{g} = 1.79 + 0.118 \times \text{TL mm}$) were used to determine feeding success.

We tested whether Lake Whitefish growth varied as a function of feeding success. Sites that were sampled multiple times within a year and where at least three fish were collected during each sampling event were used for this analysis. The mean lengths of fish during each sampling event were used to determine instantaneous daily growth in length between sampling events, following Freeberg et al. (1990). If more than two sampling events occurred at a site, all of the growth rates for that site and year were averaged to provide a single growth estimate. Average feeding success for each site and year was determined, and we tested whether there was a linear relationship between growth and average feeding success with simple linear regression ($\alpha = 0.05$).

To test whether diet composition or zooplankton community composition differed among levels of feeding success, we used a nonparametric multivariate approach. To analyze diet composition, the prey were grouped as calanoid copepods, cyclopoid copepods, *Bosmina*, chironomid larvae, chironomid pupae, and other. Diet mass was standardized and square-root transformed to create a Bray–Curtis similarity matrix for an analysis of similarities (ANOSIM). Diet composition was compared across four levels of feeding success, based on quartiles of residuals, with the lowest quartile indicating the poorest feeding success and the highest quartile indicating the highest feeding success. R -values were used as an indication of separation in diet assemblages among feeding levels. R -values 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 2006). The R -values values provided a measure of how separated groups are, with R -values

<0.25 indicating almost no separation between groups, R -values of 0.25–0.5 indicating different groups but with considerable overlap, R -values of 0.5–0.75 indicating clearly different group with some overlap, and R -values >0.75 indicating clear separation between groups. We used R -values rather than P -values from the ANOSIM tests because this is the most useful measure of separation among groups (Clarke and Gorley 2006). A similar analysis was conducted to compare zooplankton prey composition among four levels of feeding success, with available zooplankton classified as nauplii, calanoid copepods, cyclopoid copepods, harpacticoid copepods, *Daphnia*, *Bosmina*, Chydoridae, veligers, and other cladocerans. The ANOSIM was performed using Primer 6.

The selectivity of various zooplankton groups was determined using the selectivity coefficient W' (Vanderploeg and Scavia 1979), using prey composition for diets and the environment from each sampling event. Only zooplankton prey were considered for selectivity because prey availability was not known for other prey types. The selectivity coefficient W' varies between 0 for no ingestion of a prey type to 1, the value for the most preferred prey type(s). We tested for a linear relationship between feeding success and selectivity for each zooplankton group with simple linear regression ($\alpha = 0.05$).

We tested for factors affecting feeding success using two different approaches. First, various factors were examined as predictors of feeding success with general linear modeling (GLM). Akaike information criteria for small samples (AIC_c) was used to select the “best” models. The lowest AIC_c value was subtracted from each AIC_c value to calculate relative AIC_c (i.e., ΔAIC_c), producing a ranked index

with the most parsimonious model having a ΔAIC_c value of zero. We considered models with $\Delta AIC_c < 2$ to have substantial support (Burnham and Anderson 2004). Akaike weights (w_i) were also determined to normalize model likelihoods following Burnham and Anderson (2004). The Akaike weights were used to determine the probability that a given model was the best model for the data. The factors that were included in GLM were total available zooplankton biomass, age-0 Lake Whitefish CPE (CPE_{LWF}), total fish CPE (CPE_{total}), ratio of zooplankton biomass to Lake Whitefish CPE ($ZP:CPE_{LWF}$), the ratio of zooplankton biomass to total fish CPE ($ZP:CPE_{total}$), and water temperature. All of the factors except water temperature were natural log transformed to help meet the assumptions of GLM. The $ZP:CPE$ ratios were not included in any models with multiple factors other than water temperature because this index is directly derived from the other factors.

We also performed a principal component analysis (PCA) on the above factors, with all factors except water temperature natural log transformed to meet PCA assumptions, and all factors were normalized to account for different units of measurement. The PCA was performed using Primer 6. We tested for a linear relationship between feeding success and each corresponding principal component score for each site and date with simple linear regression ($\alpha = 0.05$).

RESULTS

There were 69 sampling events and a total of 2,357 fish ranging in length from 17 to 56 mm used for analysis. Only one fish had an empty stomach and was excluded from analysis. Prey biomass in stomachs (natural log transformed) increased significantly with fish length ($F_{1,2255} = 1,627$, $R^2 = 0.41$, $P < 0.001$; Figure 2), and the residuals from this relationship were used to determine feeding success. Average growth in length significantly increased as feeding success increased ($F_{1,21} = 9.6$; $R^2 = 0.31$, $P = 0.005$; Figure 3).

Across all sampling events, zooplankton on average accounted for 85% of the diet biomass. Cyclopoid copepods were the most important diet item, with calanoid copepods, *Bosmina*, and chironomid pupae and larvae providing smaller contributions (Table 1). There was however, a wide range of contributions for all prey types across sampling events (Table 1). The ANOSIM indicated that there was no difference in diet assemblages among the four levels of feeding success (Global $R = 0.054$), with all pairwise comparisons having an R value ≤ 0.17 , indicating no separation in diet assemblages among four feeding success levels.

Cyclopoid copepods were the most highly selected prey group in 22 of 69 samples. *Daphnia*, calanoid copepods, *Bosmina*, and chydorids or other cladocerans were the most

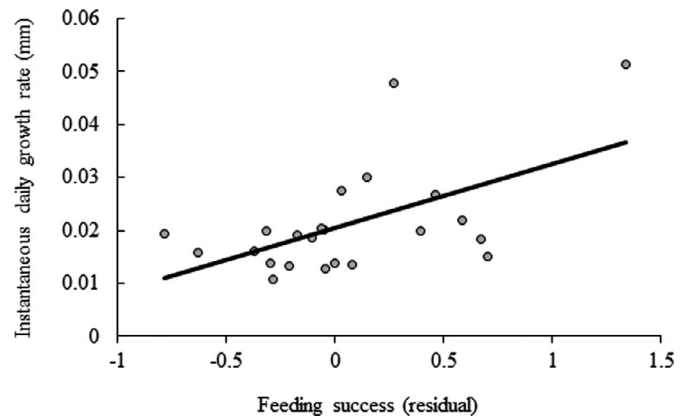


FIGURE 3. Relationship of instantaneous growth rate in length as a function of feeding success (i.e., $y = 0.012x + 0.0205$) for age-0 Lake Whitefish from Lakes Michigan and Huron.

TABLE 1. Average percentage of contribution across sampling events and range (in parentheses) of prey items to the dry diet biomass of early juvenile Lake Whitefish and to the available zooplankton community biomass in Lakes Michigan and Huron.

Prey group	Diet %	Zooplankton %
Cyclopoid copepod	59 (0–99)	38 (0–94)
Calanoid copepod	11 (0–99)	12 (0–88)
<i>Bosmina</i>	8 (0–62)	14 (0–47)
<i>Daphnia</i>	3 (0–30)	3 (0–60)
Chydoridae	2 (0–7)	4 (0–37)
Harpacticoid copepod	<1 (0–7)	2 (0–11)
Other cladoceran	1 (0–27)	<1 (0–6)
Nauplii	<1 (0–8)	16 (<1–51)
Veliger	<1 (0–1)	11 (0–91)
Chironomid larvae	6 (0–66)	–
Chironomid pupae	7 (0–99)	–
Other	2 (0–29)	–

highly selected prey in 19, 11, 9, and 8 samples, respectively. Feeding success decreased with increased selectivity for *Daphnia* ($y = -0.38X + 0.16$; $F_{1,66} = 5.7$; $R^2 = 0.08$, $P = 0.02$), and was not related to selectivity for all other prey groups ($P > 0.12$).

On average, cyclopoid copepods were the most abundant zooplankton group available, accounting for 38% of the zooplankton biomass. Nauplii, *Bosmina*, calanoid copepods, and veligers each accounted for >10% of the average zooplankton biomass across sampling events, but there was a wide range of importance for most zooplankton groups across sampling events (Table 1). The ANOSIM indicated that there was no difference in zooplankton assemblages among the four levels of feeding success (global $R = 0.035$), with all pairwise comparisons having $R < 0.08$, indicating no separation in zooplankton assemblages among four feeding success levels.

Five models from the GLM analysis had $\Delta AIC_c < 2$, indicating substantial support for these models (Table 2). Each of these models had a $w_i > 0.1$, indicating that there was at least a 10% probability that the model was the best model for the data. A model with available zooplankton biomass and water temperature was the top overall model, and all supported models included zooplankton biomass as a factor. Temperature was a factor in three of the top models, CPE_{total} in two of the top models, and CPE_{LWF} in one of the top models (Table 2). Feeding success increased with each of the factors that were found in supported models (Table 2; Figure 4).

For the PCA analysis, the first three principal components explained about 93% of the variation in the data, with 47, 25, 21, and 6% of variation explained by PC1, PC2, PC3, and PC4, respectively. Feeding success significantly increased with increases in PC2 ($F_{1,67} = 9.1$, $R^2 = 0.12$, $P = 0.004$; Figure 5), but there was no linear relationship between feeding success and PC1, PC3, or PC4 ($P > 0.41$). PC2 scores were most strongly positively related to available zooplankton biomass and CPE_{total} , with coefficients of 0.71 and 0.54, respectively. All other factors had coefficients < 0.34 for PC2.

DISCUSSION

The feeding ecology of young fish is influenced by a complex suite of factors (Nunn et al. 2012). In our study, we found that feeding success of early juvenile Lake Whitefish depended on multiple factors, but available zooplankton biomass was consistently an important factor to explain feeding success. It is generally assumed that higher prey availability leads to higher feeding success, but this relationship is often weak, difficult to evaluate in the field, and confounded by other factors (Robert et al. 2009). Feeding success for age-0 Lake Whitefish at a site in

TABLE 2. Factors from general linear models used to predict feeding success for age-0 Lake Whitefish, with the direction of the relationship with feeding success shown in parentheses. The Akaike information criteria for small samples (AIC_c) was used to rank the models, with relative AIC_c (i.e., ΔAIC_c) and Akaike weight (w_i) reported. Only models with $\Delta AIC_c < 2$ were considered supported and are presented. ZP = zooplankton biomass; CPE = catch/seine for total fish or Lake Whitefish (LWF).

Factors	R^2	P - value	ΔAIC_c	w_i
$\ln ZP$ (+), Temperature (+)	0.13	0.01	0.00	0.26
$\ln ZP$ (+)	0.08	0.02	1.42	0.13
$\ln ZP$ (+), $\ln CPE_{total}$ (+)	0.11	0.02	1.42	0.13
$\ln ZP$ (+), $\ln CPE_{LWF}$ (+), Temperature (+)	0.14	0.02	1.51	0.12
$\ln ZP$ (+), $\ln CPE_{total}$ (+), Temperature (+)	0.13	0.02	1.83	0.10

southeast Lake Michigan increased with the abundance of the preferred prey, cyclopoid copepods, but the relationship was strongest for larval fish, inconsistent among length-groups of early juvenile fish, and factors other than food availability were not examined (Pothoven 2020).

The highest ranked model to explain feeding success included water temperature along with zooplankton biomass, and water temperature was also a factor in other supported models. Water temperature was found to be a more important factor than food abundance for understanding early life growth and year-class strength of European Whitefish *C. lavaretus* (Eckmann and Pusch 1991; Anneville et al. 2009). Temperature can affect feeding

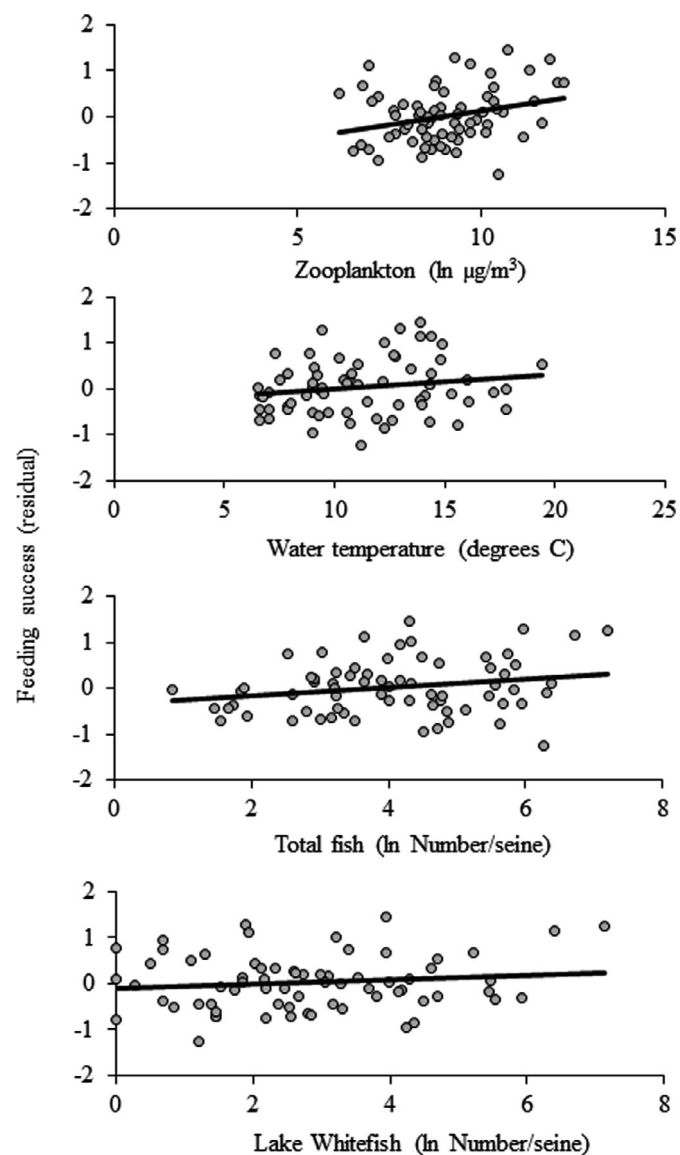


FIGURE 4. Relationship of feeding success for juvenile Lake Whitefish as a function of available zooplankton biomass, water temperature, total fish CPE, and Lake Whitefish CPE.

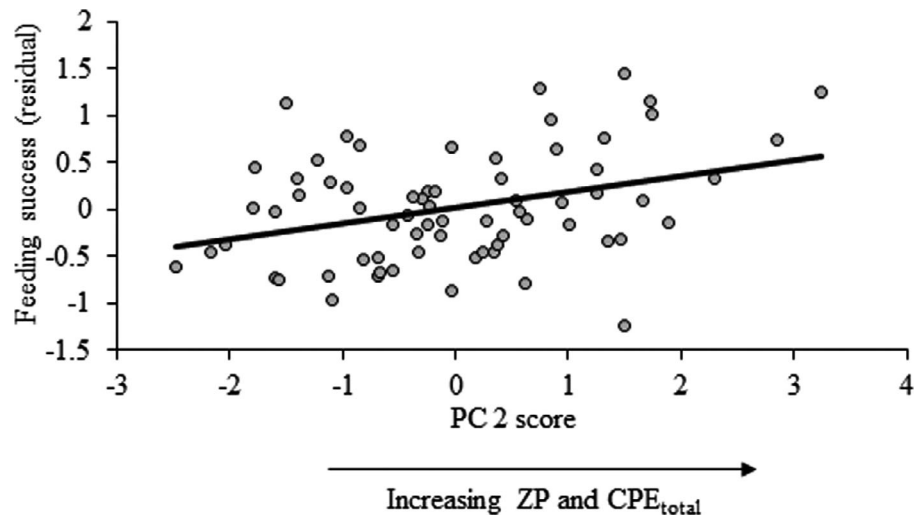


FIGURE 5. Relationship of feeding success as a function of principal component 2 (PC2). PC2 was the only PC with a significant relationship to feeding success and was most strongly related to the factors of available zooplankton (ZP) biomass and CPE_{total} .

success through a number of pathways. First, higher water temperatures lead to increased swimming speed, which leads to increased prey encounter rates and feeding success (Dabrowski 1989). Increased temperatures also can lead to decreased prey handling times that allow for higher feeding success, especially for small juvenile coregonines (Dabrowski 1989). On the other hand, increased temperatures lead to increased metabolic demands and digestion rates (Kitchell et al. 1977). Water temperatures also influence zooplankton phenology and, thus, can influence prey availability (Eckmann and Pusch 1991; Anneville et al. 2009). A later hatch date can lead to new recruits experiencing higher water temperatures and has been associated with better recruitment for Lake Whitefish (Dabrowski 1980; Patrick et al. 2013), possibly because of higher feeding success at higher water temperatures. However, early warming in the spring that leads to an early hatch has been associated with year-class failure (Ryan and Crawford 2014).

Fish density appeared to have some role in explaining feeding success, with feeding success increasing with either total or Lake Whitefish density, indicating that feeding success was not negatively influenced by higher fish densities in our study. Density-dependent effects vary with life stage and are assumed to be most important in the earliest stages (Stige et al. 2019), although there is evidence for density-dependent compensatory growth in juvenile fish that can be important for regulating recruitment (Houde 2008). If resources are not limited, then high numbers of fish will not affect feeding success, which could possibly improve if a larger shoal of fish is better able to locate patchy food (Nunn et al. 2012). On the other hand, fish density can affect effective feeding time of fish even if prey abundance is not reduced (Karjalainen 1992). Juvenile coregonine density

can be quite patchy even at a given site (Leonardsson et al. 2016). Although we were able to sample across a wide range of average fish relative abundances, the importance of density dependence might be obscured somewhat by this patchiness. Patchiness could also affect estimates of zooplankton abundance. Although the spatial variability makes it difficult to tease apart the importance of various factors on feeding success, this same variability may be important to the success of individual fish that experience superior feeding conditions (Pepin et al. 2015).

There was no difference in diet composition or available zooplankton community composition among different levels of feeding success. Furthermore, feeding success was generally not associated with the type of prey that was selected. Juvenile fish generally have a more diverse diet than larval fish (Nunn et al. 2012). Larval Lake Whitefish appear largely dependent on copepods (Freeberg et al. 1990; Hoyle et al. 2011; Pothoven 2020; Pothoven and Olds 2020), whereas early juvenile fish had a more diverse diet in Lakes Michigan and Huron, which may reflect not only greater ability to use more prey types, but also increasing availability of prey other than copepods (Claramunt et al. 2010a; Pothoven et al. 2014; Pothoven and Olds 2020). Pothoven and Olds (2020) found that despite differences in prey importance and selection across sites in Lake Huron, feeding success generally did not differ among sites, suggesting that juvenile Lake Whitefish can adapt to a variety of prey conditions. Interestingly, there was also no increase in feeding success for fish that had shifted to larger prey such as chironomid larvae or pupae in our study. In fact, there was no strong shift to benthic prey that has been noted for Lake Whitefish (Claramunt et al. 2010a; Pothoven et al. 2014). This might reflect adequate availability of zooplankton prey and low availability of benthic prey or that we

were sampling fish that had not yet shifted habitat from the shoreline to deeper waters.

We found that higher feeding success was associated with higher growth for juvenile Lake Whitefish. Although the relationship between feeding success and growth was relatively weak, it is fairly consistent among species and highlights the importance of understanding the factors that are affecting feeding success (Pepin et al. 2015). Growth, in turn, is linked to survival and recruitment success for most fish (Houde 2008), including Lake Whitefish (Taylor and Freeberg 1984; Claramunt et al. 2010b). In contrast to larval fish, starvation is likely not a major factor for juvenile Lake Whitefish (Dabrowski 1989), but poor growth is often associated with heightened vulnerability to predation for juvenile fish (Houde 2008) and even small changes in coregonine growth during early life can lead to large changes in recruitment to the reproductive stages (Eckmann 2013). We used a coarse growth measure based on mean length between sampling efforts (Freeberg et al. 1990). More detailed information on individual growth could be available from otolith analysis, but this methodology is still in development for young coregonines in the Great Lakes (Doerr 2019).

Feeding success, along with growth, can be important metrics to evaluate year-class strength (Fortier et al. 1995; Houde 2008). Despite the efforts required to determine feeding success, it seems important to continue to evaluate. Feeding success is considered a better measure of recruitment success than the individual components that can affect feeding success because it helps integrate multiple environmental factors that can also vary with age (Fortier et al. 1995). Lake Whitefish do not recruit to the fishery until at least age 5 or 6, so it is yet unclear how feeding success for the fish examined in our study will ultimately relate to year-class strength. Over time, the value of feeding success and growth of juvenile fish can be evaluated as measures of recruitment to the fishery. Considering the time that is required for Lake Whitefish to recruit to the fishery, prerecruit indices such as feeding success could prove to be valuable to managers who are determining harvest strategies. Furthermore, if information on the factors that affect feeding success is also collected, fishery managers should have a better understanding over time of whether various biotic and abiotic factors are affecting prerecruits and whether certain locations are more suitable nursery areas than others. This will enable managers to better adapt management strategies to environmental conditions that affect prerecruits to the Lake Whitefish fishery.

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ORCID

Steven Pothoven  <https://orcid.org/0000-0002-7992-5422>

REFERENCES

- Anneville, O., S. Souissi, J. C. Molinero, and D. Gerdeaux. 2009. Influences of human activity and climate on the stock recruitment dynamics of Whitefish, *Coregonus lavaretus*, in Lake Geneva. *Fisheries Management and Ecology* 16:492–500.
- Baldwin, N. A., R. W. Saalfeld, M. R. Dochoda, H. J. Buettner, R. L. Eshenroder, and R. O’Gorman. 2018. Commercial fish production in the Great Lakes 1867–2015. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to southeastern United States. *Journal of the North American Benthological Society* 18:308–343.
- Bowen, K. L., A. J. Conway, and W. J. S. Currie. 2018. Could veligers be the lost biomass of invaded lakes? *Freshwater Science* 37:315–329.
- Brenden, T. O., M. P. Ebener, T. M. Sutton, M. L. Jones, M. T. Arts, T. B. Johnson, M. A. Koops, G. M. Wright, and M. Faisal. 2010. Assessing the health of Lake Whitefish populations in the Laurentian Great Lakes: lessons learned and research recommendations. *Journal of Great Lakes Research* 36(Supplement 1):135–139.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304.
- Claramunt, R. M., A. M. Muir, J. Johnson, and T. M. Sutton. 2010a. Spatio-temporal trends in the food habits of age-0 Lake Whitefish. *Journal of Great Lakes Research* 36(Supplement 1):66–72.
- Claramunt, R. M., A. M. Muir, T. M. Sutton, P. J. Peeters, M. P. Ebener, J. D. Fitzsimmons, and M. A. Koops. 2010b. Measures of larval Lake Whitefish length and abundance as early predictors of year-class strength in Lake Michigan. *Journal of Great Lakes Research* 36(Supplement 1):8–91.
- Clarke, K. R., and R. N. Gorley. 2006. *Primer v6: user manual/tutorial*. Primer-E-LTD, Plymouth, UK.
- Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1380–1390.
- Dabrowski, K. 1989. Formulation of a bioenergetics model for coregonine early life history. *Transactions of the American Fisheries Society* 118:138–150.
- Doerr, L. 2019. Natal origins and daily age estimation in larval Lake Whitefish using otolith microstructure. Master’s thesis. University of Wisconsin–Green Bay, Green Bay.
- Eckmann, R. 2013. A review of the population dynamics of coregonids in European alpine lakes. *Advances in Limnology* 64:3–24.
- Eckmann, R., and M. Pusch. 1991. At what life stage is year-class strength of coregonids (*Coregonus lavaretus* L.) in Lake Constance

- determined? Verhandlungen des Internationalen Verein Limnologie 24:2465–2469.
- Fera, S. A., M. D. Rennie, and E. S. Dunlop. 2015. Cross-basin analysis of long-term trends in the growth of Lake Whitefish in the Laurentian Great Lakes. *Journal of Great Lakes Research* 41:1138–1149.
- Folkvord, A., and J. R. Hunter. 1986. Size-specific vulnerability of northern anchovy, *Engaulis mordax*, larvae to predation by fishes. U.S. National Marine Fisheries Service Fishery Bulletin 84:859–869.
- Fortier, L., D. Ponton, and M. Gilbert. 1995. The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered south-eastern Hudson Bay. *Marine Ecology Progress Series* 120:11–27.
- Freeberg, M. H., W. W. Taylor, and R. W. Brown. 1990. Effect of egg and larval survival on year-class strength of Lake Whitefish in Grand Traverse Bay, Lake Michigan. *Transactions of the American Fisheries Society* 119:92–100.
- Gobin, J., N. P. Lester, A. Cottrill, M. G. Fox, and E. S. Dunlop. 2015. Trends in growth and recruitment of Lake Huron Lake Whitefish during a period of ecosystem change, 1985–2012. *Journal of Great Lakes Research* 41:405–414.
- Gobin, J., N. P. Lester, A. Cottrill, M. G. Fox, and E. S. Dunlop. 2016. Effects of changes in density-dependent growth and recruitment on sustainable harvest of Lake Whitefish. *Journal of Great Lakes Research* 42:871–882.
- Greycay, P. A., and T. E. Targett. 1996. Spatial patterns in condition and feeding of juvenile Weakfish in Delaware Bay. *Transactions of the American Fisheries Society* 125:803–808.
- Hawkins, B. E., and M. S. Evans. 1979. Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. *Journal of Great Lakes Research* 5:256–263.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Proces-Verbaux des Reunions, Conseil Permanent International Pour L'Exploration de la Mer* 20.
- Houde, E. D. 2008. Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science* 41:53–70.
- Hoyle, J. A., O. E. Johannsson, and K. L. Bowen. 2011. Larval Lake Whitefish abundance, diet and growth and their zooplankton prey abundance during a period of ecosystem change on the Bay of Quinte, Lake Ontario. *Aquatic Ecosystem Health and Management* 14:66–74.
- Karjalainen, J. 1992. Food ingestion, density-dependent feeding and growth of Vendace (*Coregonus albula* (L.)) larvae. *Annales Zoologici Fennici* 29:93–103.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 34:1922–1935.
- Leonardsson, K., R. Hudd, A. Huhmarniemi, and E. Jokikokko. 2016. Optimal time and sample allocation for unichort fish larvae, sea-spawning Whitefish (*Coregonus lavaretus* L.) as a case study. *International Council for the Exploration of the Sea Journal of Marine Science* 73:374–383.
- Ludsin, S. A., K. M. DeVanna, and R. E. H. Smith. 2014. Physical-biological coupling and the challenge of understanding fish recruitment in freshwater lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 71:775–794.
- Malloy, K. D., and T. E. Targett. 1991. Feeding, growth and survival of juvenile Summer Flounder *Paralichthys denatus*: experimental analysis of the effects of temperature and salinity. *Marine Ecology Progress Series* 72:213–223.
- Michaud, J., L. Fortier, P. Rowe, and R. Ramseier. 1996. Feeding success and survivorship of Arctic Cod larvae, *Boreogadus saida*, in the Northeast Water polynya (Greenland Sea). *Fisheries Oceanography* 5:120–135.
- Nalepa, T. F., and M. A. Quigley. 1980. The macro- and meiobenthos of southeastern Lake Michigan near the mouth of the Grand River, 1976–77. National Oceanic and Atmospheric Administration, Data Report ERL GLERL-17, Ann Arbor, Michigan.
- Nunn, A. D., L. H. Tewson, and L. G. Cowx. 2012. The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries* 22:377–408.
- Patrick, P. H., E. Chen, J. Parks, J. Powell, J. S. Poulton, and C. L. Fietsch. 2013. Effects of fixed and fluctuating temperature on hatch of Round Whitefish and Lake Whitefish eggs. *North American Journal of Fisheries Management* 33:1091–1099.
- Pepin, P., D. Robert, C. Bouchard, J. F. Dower, M. Falardeau, L. Fortier, G. P. Jenkins, V. Leclerc, K. Leveque, J. L. Llopiz, M. G. Meehan, H. M. Murphy, M. Ringuette, P. Sirois, and S. Sponaugle. 2015. Once upon a larva: revisiting the relationship between feeding success and growth in fish larvae. *International Council for the Exploration of the Sea Journal of Marine Science* 72:359–373.
- Pothoven, S. A. 2020. The influence of ontogeny and prey abundance on feeding ecology of age-0 Lake Whitefish (*Coregonus clupeaformis*) in southeastern Lake Michigan. *Ecology of Freshwater Fish* 29:103–111.
- Pothoven, S. A., T. O. Höök, and C. R. Roswell. 2014. Feeding ecology of age-0 Lake Whitefish in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 40(Supplement 1):148–155.
- Pothoven, S. A., T. F. Nalepa, P. J. Schneeberger, and S. B. Brandt. 2001. Changes in diet and condition of Lake Whitefish in southern Lake Michigan associated with changes in benthos. *North American Journal of Fisheries Management* 21:876–883.
- Pothoven, S., and C. Olds. 2020. Spatial variation in feeding ecology of age-0 Lake Whitefish *Coregonus clupeaformis* in Lake Huron. *Journal of Freshwater Ecology* 35:349–366.
- Pritt, J. J., E. F. Roseman, and T. P. O'Brien. 2014. Mechanisms driving recruitment variability in fish: comparisons between the Laurentian Great Lakes and marine systems. *International Council for the Exploration of the Sea Journal of Marine Science* 71:2252–2267.
- Robert, D., M. Castonguay, and L. Fortier. 2009. Effects of preferred prey density and temperature on feeding success and recent growth in larval mackerel of the southern Gulf of St. Lawrence. *Marine Ecology Progress Series* 377:227–237.
- Ryan, K. M., and S. S. Crawford. 2014. Distribution and abundance of larval Lake Whitefish (*Coregonus clupeaformis*) in Stokes Bay, Lake Huron. *Journal of Great Lakes Research* 40:755–762.
- Schultz, E. T., M. G. Smircich, and D. L. Strayer. 2019. Changes over three decades in feeding success of young American Shad *Alosa sapidissima* are influenced by invading zebra mussels *Dreissena polymorpha*. *Marine Ecology Progress Series* 628:141–153.
- Stige, L. C., L. A. Rogers, A. B. Neuheimer, M. E. Hunsicker, N. A. Yaraina, G. Ottersen, L. Ciannelli, Ø. Langangen, and J. M. Durant. 2019. Density- and size-dependent mortality in fish early life stages. *Fish and Fisheries* 20:962–976.
- Taylor, W. W., and M. H. Freeberg. 1984. Effect of food abundance on larval Lake Whitefish, *Coregonus clupeaformis* Mitchill, growth and survival. *Journal of Fish Biology* 25:733–741.
- Taylor, W. W., M. A. Smale, and M. H. Freeberg. 1987. Biotic and abiotic determinants of Lake Whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Supplement 2):313–323.
- Vanderploeg, H. A., and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecological Modelling* 7:135–149.
- Wilson, M. T., K. L. Mier, and C. M. Jump. 2013. Effect of region on the food-related benefits to age-0 Walleye Pollock (*Theragra chalcogramma*) in association with midwater habitat characteristics in the Gulf of Alaska. *International Council for the Exploration of the Sea Journal of Marine Science* 70:1396–1407.