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**Do models parameterized with observations from the system predict larval yellow perch
(*Perca flavescens*) growth performance better in Lake Erie?**

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Abstract: Growth performance can influence survival during early life. As such, a range of statistical to mechanistic modeling approaches has been used to predict growth performance, with few studies evaluating prediction accuracy. We tested the ability of three models to estimate observed larval yellow perch (*Perca flavescens*) growth and length in western Lake Erie (USA-Canada). We found that a General Linear Model developed using yellow perch data from western Lake Erie performed best, followed closely by a semi-mechanistic Individual-Based Model (IBM) specific to Lake Erie yellow perch and worst by a General multi-species IBM. We suspect the Statistical Model performed better because, unlike IBMs, it does not require prey availability data, probably poorly represented by zooplankton samples, and because the IBMs are imperfectly parameterized. Our findings indicate that caution should be exercised when using general IBMs given that the models parameterized with observations from the system of interest outperformed the general IBM in providing accurate fish growth and length estimates, pointing to the need for research that can improve existing mechanism-based models of larval growth.

Keywords: Great Lakes, early life stages, planktivory, recruitment, physical-biological modeling

Introduction

The probability of fish surviving to adulthood has been hypothesized to largely depend on growth performance during early life stages (Anderson 1988; Miller et al. 1988; Houde 2008). Specifically, larger and faster-growing fish have been generalized to be faster swimmers and less prone to predation because they can: (a) more successfully avoid predators (i.e., bigger is better hypothesis, Butler and Pickett 1988; Miller et al. 1988), (b) fewer predators should be able to ingest them (i.e., gape-limited predation hypothesis, Zaret 1980), and (c) they remain susceptible to predation for a shorter period of time (i.e., stage-duration hypothesis, Houde 1987). Larger fish also should be less prone to starvation because, if they are faster swimmers, they can more efficiently capture prey and accumulate more energy reserves that will enable them to survive the less-productive winter months (i.e., Growth-mortality hypothesis, Ware 1975; Shepherd and Cushing 1980).

Because of how important size and growth can be for fish survival, many modeling approaches have been developed to measure and predict these performance metrics, ranging from purely mechanistic to purely statistical. Mechanistic models are commonly employed tools in population ecology. Such models often explicitly include known mechanistic factors important for controlling population dynamics with varying degrees of statistical input (reviewed in Ellner et al. 1998; Kendall et al. 1999). The incorporation of individual traits and performance into these mechanistic models has increased during recent decades, which has improved our understanding of population-level phenomena (see Grimm 1999; Grimm et al. 1999 for review). Such Individual-based models (IBMs) are often considered semi-mechanistic because the high degree of mechanistic detail that they require is often incomplete for most ecosystems. In turn, parameters are commonly statistically estimated, “borrowed” from other species or ecosystems,

and generalized processes are used to describe individual-level behavior (e.g., energetics, foraging, movement), performance (e.g., growth, survival) or other attributes (e.g., predation risk) (Grimm 1999; Hartman and Kitchell 2008). Further, because empirical observations typically are lacking from ecosystems that use “general” IBMs (*sensu* Grimm 1999), the accuracy of these semi-mechanistic models is often difficult to discern, thus causing uncertainty in the results (North et al. 2009). While some have warned about the dangers of using such practices in developing mechanistic models to understand and predict population-level phenomena for a given species in a particular ecosystem (Brandt et al. 1992; Trudel et al. 2004; Watkins and Rose 2014), investigators are often in a position where empirical data on the species or location of interest is lacking. The commonality of this situation helps to explain why “general” IBMs that incorporate borrowed data to fill knowledge gaps is pervasive in the peer-reviewed literature, particularly the aquatic literature (reviewed in Hartman and Kitchell 2008; North et al. 2009).

Another method commonly used to estimate fish growth and length are phenomenological or statistical (Sokal and Rohlf 1995). These models are often developed using data on factors or processes known to influence population dynamics (e.g., environmental variables, prey availability, competition, predation; Power and van den Heuvel 1999; Tomaro et al. 2012; Manning et al. 2013). Statistical models can be advantageous in that they do not require prior time- or labor-intensive mechanistic studies or observations, they can be developed easily using *in situ* data collected at multiple spatial and temporal scales, and they can be developed with even a cursory understanding of the modeled system or species. However, the predictions generated from statistical models may not match the qualitative and quantitative characteristics of ecological systems because they do not require, but can incorporate, any previous knowledge,

and they do not allow scientists to determine the exact causes affecting population variation since they are based on statistical relationships.

As with other freshwater (Graeb et al. 2004; Roseman et al. 2005) and marine (Houde 1987; Anderson 1988) ecosystems, larval growth is thought to be important for understanding recruitment of individuals to the age-0 juvenile stage for many ecologically and economically important Laurentian Great Lakes fishes (Ludsin et al. 2014). As an example, survival to the juvenile stage appears growth-dependent for Lake Erie yellow perch (*Perca flavescens*, Carreon-Martinez et al. 2014), which is our focal species. In this system, slower-growing larvae do not recruit as well as faster-growing ones, owing to growth-dependent predation (e.g., invasive White perch, *Morone americana*) during the spring (Ludsin et al. 2014; Carreon-Martinez et al. 2014). Thus, developing modeling approaches that can reliably describe and forecast larval growth performance has been strongly encouraged in Lake Erie and other large lakes of the world (Ludsin et al. 2014).

Given that yellow perch is common throughout north-temperate waters of North America and supports important recreational and commercial fisheries in the Great Lakes basin (Clapp and Dettmers 2004), much effort has been directed at determining the factors that influence larval yellow perch foraging behavior and growth in lake ecosystems, both large and small. Towards this end, Fulford et al. (2006) developed a “general” IBM, which was based on a series of laboratory experiments. This IBM also included a previously developed bioenergetics model that was parameterized using data from yellow perch and other fresh- and salt-water fish species including *Scomber scombrus*, *Morone saxatilis*, *Engraulis mordax*, *Clupea harengus*, *Pleuronectes platessa*, *Achirus lineatus*, *Spartus aurata* and *Anchoa mitchilli* (Kitchell et al. 1977; Post 1990; Letcher et al. 1996; Hanson 1997). Fulford et al. (2006) evaluated the diet

predictions of this IBM in the laboratory using water samples from one small (Lake Nagawicka, WI, USA) and large lake (Lake Michigan, MI, USA), but growth estimates were not assessed. Other IBMs have been developed for yellow perch (Rose et al. 1999), including a model for larval and juvenile yellow perch in Lake Erie (Manning et al. 2014). However, these models were not included in the present study because they primarily focused on performance of juvenile fish in Lake Erie and were developed for use in a much smaller ecosystem (i.e., Oneida Lake, New York, USA, Rose et al. 1999; Manning et al. 2014).

Towards improving our ability to reliably estimate growth and length of larval yellow perch in Lake Erie, as well as assess the relative value of semi-mechanistic individual-based versus statistical modeling approaches, we developed two new predictive models of yellow perch growth, compared them to a general, existing IBM (Fulford et al. 2006), and evaluated the predictive capability of the three models. The “general” model was the semi-mechanistic IBM developed for yellow perch but parameterized using information from multiple species and lakes, both small and large (Fulford et al. 2006, referred to as *General IBM*), and the two new models were a modified version of the *General IBM*, which was parameterized with locally obtained data from western Lake Erie (referred to as *Lake Erie IBM*) and a purely statistical General Linear Model (GLM) developed using environmental variables and larval yellow perch data measured in western Lake Erie (referred to as *Statistical GLM*). We tested our ability to estimate growth rates and length because they provide short- (last 3 days of life) and long-term (larval stage) cumulative measures. The accuracy of these models was verified using independent observational yellow perch data from western Lake Erie. To our knowledge, this study is one of the few in fisheries ecology to explicitly compare and test the predictive power of varying types of ecological models.

Methods

To evaluate the three models, growth rates and total lengths (TLs) of larval yellow perch from western Lake Erie were studied during 2006-2008. Data on larval yellow perch diet composition, growth rates, TLs, and of abiotic variables (temperature and turbidity), prey availability (zooplankton prey densities, length and mass), competition (yellow perch larval densities) and predation (potential predator densities) from 2006 and 2008 were used as potential factors to develop the *Lake Erie IBM* and *Statistical GLM*. These environmental variables were considered because previous studies have found them to be related to larval fish foraging behavior and growth (Post and Prankevicius 1987; Post and McQueen 1988; Post and Johannes 1997; Power and van den Heuvel 1999; Pangle et al. 2012). We also included day of year because it can be related to factors such as cumulative degree-days or number of days in which water temperature allowed for positive growth (Post and McQueen 1988) and/or a synchronization with their prey cycles (Wu and Culver 1994) both of which are more difficult to quantify. To determine the predictive accuracy of the *General* and *Lake Erie IBMs*, and *Statistical GLM*, model results were compared to 2007 observational data. We chose the years 2006 and 2008 to develop, and 2007 to evaluate the models because it allowed sample sizes for each process to be balanced (~20 data points each, see Methods and Results) and similar larval length ranges for the development years compared to the test year (5.2 to 15.6 mm vs. 5.6 vs. 19.6 mm TL). We also examined the use of different year combinations to develop and test the models and found no differences in our results (see discussion section); therefore only the results from the best fit models are shown.

Study species and system

Yellow perch is distributed throughout North America, including the Laurentian Great Lakes basin, which includes Lake Erie (Clapp and Dettmers 2004). The western basin of Lake Erie (waters west of an imaginary line extending from Point Pelee, Ontario Canada to Huron, Ohio USA, Fig. 1) is an important area for yellow perch spawning, supported by numerous local-spawning populations (Reichert et al. 2010, Brodnik et al. 2015). First-feeding larvae typically hatch during mid-April through May and become obligate zooplanktivores (Gopalan et al. 1998; Reichert et al. 2010). Pelagic yellow perch larvae undergo an ontogenetic shift in their diet from rotifers and small cyclopoids to larger calanoids and eventually larger cladocerans (Bremigan et al. 2003; Graeb et al. 2004; Fulford et al. 2006). The larval phase is approximately 30-45 days and ends with the acquisition of juvenile characteristics, which occurs slightly before the fish transition to their demersal habitat (Auer 1982; Wu and Culver 1992; Gopalan et al. 1998). Recruitment to the fishery is set by the early juvenile stage (Farmer et al. 2015), with larval growth being critical to understanding recruitment to this stage (Ludsin et al. 2014).

The western basin of Lake Erie exhibits several distinct physical and biological characteristics that may influence the accuracy of the *General IBM*. Western Lake Erie is a shallow body of water (average 7.4 m in depth) that exhibits high primary and secondary production (mesotrophic to eutrophic, Ludsin et al. 2001; Fahnenstiel et al. 2010; Allinger and Reavie 2013). Unlike most large lakes, the waters of the western basin of Lake Erie do not vertically stratify during the summer due to its shallow nature, but exhibit strong horizontal spatial heterogeneity due to outflows from the Detroit and Maumee rivers (Pangle et al. 2010; Reichert et al. 2010; Marin Jarrin et al. 2015). In the text, we refer to areas receiving waters

primarily from the Maumee River as the Maumee River plume, while other areas of the west basin are referred to as the non-Maumee River plume.

Empirical data used to drive, develop, and verify model accuracy

Collections occurred at eight fixed locations in the Maumee River plume (primarily in Michigan and Ohio, USA waters along the south shore) and eight in non-Maumee River plume waters (primarily in Ontario, Canada waters along the north shore), which differed predictably in their water temperature and turbidity (DiToro and Connolly 1980; DePinto et al. 1986; Reichert et al. 2010; Fig. 1). Except for potential predator collections, sampling at these 16 sites occurred 5-7 times each year on a weekly or biweekly basis from mid-April to June, 2006-2008 (total of 284 collections) when larval yellow perch are usually present (Gopalan et al. 1998; Reichert et al. 2010; Marin Jarrin et al. 2015). Methodology for measuring and sampling abiotic variables, zooplankton prey, yellow perch larvae and potential predators inside and outside Maumee River plume waters are described in detail elsewhere (Reichert et al. 2010; Carreon-Martinez et al. 2011; Ludsins et al. 2014). A brief description is presented below.

Temperature (nearest 0.1 °C) and turbidity (transmissometry, unitless measurement) were measured using vertical casts of a SeaBird SBE 19 Conductivity-Temperature-Depth (CTD, Seabird Electronics, Inc., Bellevue, WA) and a 5 cm path transmissometer. Zooplankton prey were collected using replicate vertical tows (1 m from bottom to surface) with a metered 0.5 m diameter net with 64 µm mesh. Samples were preserved in a 10% buffered sugar-formalin solution. We counted all prey groups, but for development of the *Lake Erie IBM* and *Statistical GLM*, we only included zooplankton prey groups that were >1% of total number of diet items. Zooplankton prey densities (ind. m⁻³) were calculated by subsampling using a wide-bore pipette

until 100 individuals for each group were counted or 20% of the entire sample volume was processed (Reichert et al. 2010).

Larval yellow perch were collected using paired, metered bongo nets, with 500 and 1000 μm mesh, each. Samples were taken beginning ~ 2 m from the bottom of the lake to the surface (~ 8 min. average tow duration). Larvae were preserved in 100% ethanol until sample processing. In the laboratory, yellow perch individuals were identified using diagnostic features that included myomere counts (Auer 1982), and measured for TL (nearest 0.1 mm) under a dissecting microscope (5-6.3x magnification) coupled with image analysis software (MediaCybernetics, Inc. Bethesda, Maryland).

Potential larval yellow perch predator densities were estimated using a bottom trawl (7.6-m semi-balloon design, 13-mm stretched-mesh cod-end liner) towed at $\sim 1.5 \text{ m s}^{-1}$. Samples were collected weekly at an offshore and nearshore site in both Maumee River plume and non-plume waters. Trawl times averaged 18 min. (range: 5-31 min). Trawl duration was largely variable due to changes in catch size, weather conditions, and depth. Fish were immediately euthanized, identified, counted, and measured. Those considered potential predators were age 1 or older white bass *Morone chrysops*, White perch, and yellow perch, as well as age-1 walleye *Sander vitreus* (Carreon-Martinez et al. 2011, 2014; Ludsine et al. 2014).

Diet and growth analysis

Consumption of zooplankton (μg) was evaluated by quantifying prey items in the entire digestive tract of larvae using a dissecting microscope (5-6.3x magnification). Recent growth (last 3 d of life) of larval yellow perch was estimated by measuring the width of the last three (complete) daily growth increments of sagittal otoliths (i.e., the edge increment was not

considered in analysis because it might have not been fully formed). Ring counts and measurements were conducted under 50-100x magnification with the image analysis system along the longest readable transect, with at least two independent measurements made by at least two readers (Reichert et al. 2010). Daily increments have been validated for laboratory-reared yellow perch up to 63 d old (Post and Prankevicius 1987; Powels and Warlen 1988; Ludsins 2000). Because otolith radius was highly correlated with TL ($r = 0.96$, $p < 0.001$, $n = 154$ larvae, Reichert et al. 2010), we estimated recent growth rates by using a direct back-calculation approach (see Francis 1990 for review of method).

Description of *General Individual-Based Model*

Larval yellow perch growth rates were estimated using the *General* (Fulford et al. 2006) and *Lake Erie IBMs* (see below). These models were both run using a one day time-step. The *General IBM* was composed of foraging and growth submodels adapted for yellow perch larvae (Letcher et al. 1996; Fulford et al. 2006; Beletsky et al. 2007, Table A1). The foraging submodel estimates daily gut content biomass by incorporating (1) an encounter rate with each prey item that depends on larval yellow perch swimming speed and reactive distance, as well as prey density, (2) a handling time that depends on prey type and length, as well as individual larval yellow perch length, and (3) the probability of attack and capture, which depends on foraging selectivity for each prey type (Letcher et al. 1996; Fulford et al. 2006). The growth submodel uses a mass-balance bioenergetics modeling framework (Kitchell et al. 1977) to estimate growth. This framework essentially estimates growth (mm d^{-1}) as a function of energy intake (consumption) minus energy expended on metabolism (respiration, specific dynamic action) and energy lost as waste products (egestion and excretion). The consumption and growth submodels

use parameters from multiple species adapted for yellow perch larvae (Post 1990; Letcher et al. 1996; Hanson 1997).

Development of *Lake Erie Individual-Based Model*

The *Lake Erie IBM* was developed by modifying the *General IBM* in two ways (Table A2). First, the foraging selectivity for each prey item was re-estimated using a new submodel that was developed using data from western Lake Erie (see below). Second, instead of having a single growth function that was applied to all larvae, regardless of their location of capture, our modified model applied a location-specific growth coefficient that depended on whether larvae were collected inside or outside Maumee River plume waters. We also attempted to develop coefficients for gut content biomass and metabolism; however, final growth estimates were most accurate when only varying the growth coefficient (JRMJ, unpublished data). The growth coefficient was developed because larvae present in the Maumee River plume can experience lower predation pressure than those present in non-Maumee River plume waters (Carreon-Martinez et al. 2014); therefore, Maumee River plume yellow perch may spend less energy avoiding predators, which could in turn influence their metabolism, consumption, and growth rates (Pangle et al. 2012). The components of this model were built using 2006 and 2008 data from western Lake Erie.

Prey Selectivity

To estimate larval foraging selectivity in the *Lake Erie IBM*, we used Chesson's (1983) selectivity index, assuming no food depletion:

$$\alpha = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j}, i = 1 \dots, m \quad (1)$$

where r_i is the proportion of prey type i in the larva's diet, n_i is the proportion of prey type i in the zooplankton available, and m is the total number of prey types. We pooled larval yellow perch data from each site within each date due to their lack of independence and only used sites (on any given day) for which at least three fish were collected to reduce random variability. The same pooling procedure was also followed in future analyses. We calculated coefficients of Chesson's α for our pooled data points and then developed multiple regression models to predict selectivity (Chesson's α) from collection-site information and larval yellow perch attributes, including which area larvae were collected (Maumee or non-Maumee River plume, categorical variable), temperature, turbidity, total zooplankton density, individual zooplankton prey group densities, collection day of year, yellow perch TL, yellow perch density, predator density, and selectivity towards cyclopoid copepods (for non-cyclopoid foraging selectivity calculations). We also included all possible combinations of explanatory variables including polynomial, square and cubic factors and second degree interactions to allow for the possibility that relationships were not linear or that they were not similar in Maumee or non-Maumee River plume waters. Selectivity for cyclopoids was included as an explanatory variable because they are the preferred prey item of larval yellow perch in Lake Erie (Ludsin 2000; Marin Jarrin et al. 2015), and therefore, selectivity towards other prey items may be dependent on cyclopoid availability. Data were $\log_{10}(\alpha+1)$ transformed to meet parametric assumptions, which were tested using normal probability (quantile–quantile) plots and boxplots of residuals versus fitted values (Sokal and Rohlf 1995). The most parsimonious model was selected using Akaike Information Criterion scores for small sample sizes (Anderson 2008) for which we compared all possible models based on ΔAIC_c and AIC_c weights (w_i). Analyses were performed using the R Core software (v. 2.15.3; <http://www.r-project.org>) and dredge function in the MuMIn package (Barton and Barton 2015).

Growth Coefficient

We developed a location-specific growth coefficient using multiple linear regression modeling. To do so, we developed models that predicted observed growth (mm d^{-1}) as a function of growth originally estimated by the *Lake Erie IBM* and the same set of potential predictor variables used to estimate foraging selectivity (per above). We followed similar statistical procedures as above.

Development of Statistical General Linear Model

Growth Rate

Our *Statistical GLM* was developed to estimate growth rate (mm d^{-1}) using a similar approach to that used to estimate foraging selectivity and growth coefficients in the *Lake Erie IBM* where we used multiple linear regression and AICc to identify the most parsimonious predictive models (using the same set of potential explanatory variables described above). Data transformation, assumptions and model selection procedures were similar to those described above. Likewise, these models were developed using empirical data collected from western Lake Erie during 2006 and 2008.

Model Evaluation

To evaluate the performance of our three models, we compared their predictions of growth rate (mm d^{-1}) and TL (mm) to observed data from larval yellow perch collected in western Lake Erie during 2007. To evaluate TL, we subtracted observed growth rates obtained using otolith analysis from observed TL at capture to obtain the TL of larvae the day before capture. We then separately added the estimated growth rates from the three models to TL the day before capture and compared it to the TL at capture to evaluate the estimates. Similar to

above, we pooled larval yellow perch data from each site within each date due to their lack of independence and only used sites (on any given day) for which at least three fish were collected to reduce random variability. We evaluated TL to explore whether the accuracy of the growth rate estimates were similar at the captured yellow perch size ranges.

Accuracy of all models was evaluated by calculating the overall skill score (Willmott 1981), Percent Bias (PBIAS, Gupta et al. 1999), coefficient of determination (R^2), and conducting General Linear Models (i.e., ANCOVAs and ANOVAs). Skill score measures the degree to which the observed variate is accurately estimated by the simulated variable by providing an estimate of the degree to which the predictions of the model are error free. This index is currently favored in oceanographic and ecological studies because it complements AIC and R^2 measures (Warner et al. 2005; Moriasi et al. 2007; Munroe et al. 2013). Overall model skill score (skill) was calculated as:

$$skill = 1 - \frac{\sum |X_{est} - X_{obs}|^2}{\sum (|X_{est} - \bar{X}_{obs}| + |X_{obs} - \bar{X}_{obs}|)^2} \quad (2)$$

where X_{est} = model estimated values of growth and TL, and X_{obs} = observed values for these two parameters. In this analysis, a value of 0 and 1 signify complete disagreement and agreement, respectively. PBIAS estimates the average deviation of simulated from observed data relative to the observed data. The values in this analysis range from $-\infty$ to ∞ with 0 indicating no bias, and were calculated as:

$$PBIAS = \left[\frac{\sum_{i=1}^n (X_{est} - X_{obs}) * 100}{\sum_{i=1}^n (X_{obs})} \right] \quad (3)$$

We used a combination of ANCOVAs and ANOVAs to determine if the slope of the regressions between the observed vs. estimated values from all three models was significantly different from the 1:1 ratio line and if the intercept was significantly different from zero.

To determine which model was most parsimonious, we calculated AICs for the three models using the total number of parameters that each model incorporates, and residual sum of squares and sample sizes from the observed vs. estimated values regression. We did not correct the AIC for small sample sizes because this method assumes the number of samples will be higher than the number of parameters. This was not the case for IBMs since they had five times as many parameters as there were samples for evaluation, and therefore, the correction factor would artificially favor the *General and Lake Erie IBMs* (Table 1). We included multiple measures of predictive power (overall skill score, PBIAS, R^2 , p-values) and parsimony (AIC) to provide broader measures of accuracy, which we developed by comparing model predictions against observational data, and the three models amongst each other.

Results

Summary of empirical data used to drive, develop, and verify model accuracy

Temperature and transmissometry varied from 8.5 to 23.6 °C (mean $\pm$ SD = 16.3 ± 3.4 °C) and 0.6 to 59.9 (8.3 ± 9.8), respectively, during 2006-2008. Potential prey densities ranged from 1,192 to 168,762 ind. m^{-3} ($14,682 \pm 22,158$ ind. m^{-3}). A total of 373 yellow perch larvae were collected in 71 tows (108 fish in 2006, 144 in 2007 and 121 in 2008), with densities ranging from 1 to 59 ind. m^{-3} (8 ± 12 ind. m^{-3}). Larvae were collected from late April to mid-June 2006-2008 and had mean TLs that ranged from 5.2 to 19.6 mm (8.0 ± 2.4 , 9.5 ± 2.7 and 7.0 ± 0.5 mm

TL during 2006, 2007, and 2008, respectively). We analyzed the stomach contents and otoliths of 265 yellow perch of which 46% had prey items in their stomachs and had been collected at one to four Maumee and non-Maumee River plume sites per day. Yellow perch larvae mostly fed on cyclopoid copepods ($50 \pm 34\%$ of total prey items), followed by small cladocerans ($22 \pm 30\%$), calanoid copepods ($20 \pm 28\%$) and dreissenid veligers ($8 \pm 13\%$). Observed growth rates ranged from 0.04 to 1.58 mm d⁻¹ (0.27 ± 0.23 mm d⁻¹). Potential predator densities ranged from 10 to 75 ind. 1000 m⁻³ (47.9 ± 15.0 ind. 1000 m⁻³). See Marin Jarrin et al. 2015 for more details of environmental variables, potential prey, and yellow perch diet and consumption data, and Carreon-Martinez et al. 2011, 2014 for potential predator details.

Development of *Lake Erie IBM*

Prey Selectivity

For cycloid copepods, the most parsimonious predictive model included only yellow perch larval TL (Equation 1 in Table 2, Table A2 and A3). In this way, selectivity for copepods increased with increasing larval yellow perch TL (range = 6-15 mm). Interestingly, selectivity for calanoid copepods, small cladocerans, and veligers depended on (a) their selectivity for cyclopoids (their selectivity was negatively related to selectivity for cyclopoids), (b) whether larvae were collected inside versus outside of the Maumee River plume (positively or negatively related, depending on taxon), and (c) the interaction of these two variables (Equations 2-4 in Table 2, Table A2 and A3). These models accounted for 10 to 52% of the variability in individual yellow perch selectivity towards the four prey items (Table 2).

Growth Coefficient

The model that best fit observed growth data included growth values from the IBM, location relative to the Maumee River plume (inside or outside of it), and an interaction between these two factors (Equation 5 in Table 2, Table A2 and A3). This model accounted for 52% of the variability in observed yellow perch growth rates (Table 2).

Development of *Statistical GLM*

Growth Rate

The most parsimonious *Statistical GLM* to estimate growth rates included location relative to the Maumee River plume, day of the year, and the square term of day of year (Equation 6 in Table 2, Table A4). This model accounted for 93% of the variability in larval yellow perch growth rates (Table 2).

Model Performance Evaluation

Growth rate

Evaluation of the three models demonstrated that the best fit between observed and predicted values were obtained using the *Statistical GLM* (highest skill and R^2 , and PBIAS closest to) followed by the *Lake Erie IBM*. The worst fit came from using the *General IBM* (Table 1, Fig. 2). The *General IBM* tended to over and underestimate growth rate with no obvious pattern (by $192 \pm 240\%$). By contrast, the *Lake Erie IBM* and *Statistical GLM* tended to only underestimate values (by 51 ± 14 and $45 \pm 23\%$). None of the slopes or intercepts of the three models differed from a 1:1 line, with the intercept of all three not being different from zero (Slopes: ANCOVA, $t < 0.29$, $p > 0.45$; Intercepts: $t < 1.7$, $p > 0.10$). The *Statistical GLM* also was the most parsimonious model with the lowest AIC value followed by the *Lake Erie* and *General IBMs*, respectively (Table 1).

Total length

Total length findings were similar to growth rates but less definitive. The *Statistical GLM* estimated TL best (highest Skill and R^2 , and PBIAS closest to 0), followed closely by the *Lake Erie IBM* and the *General IBM* performing slightly worse (Fig. 3). When comparing observed and estimated values on a 1:1 ratio we observed that TL estimates from the three models were slightly overestimated for larvae <8 mm TL (by 5 ± 4 , 2 ± 1 , $3 \pm 1\%$ for *General* and *Lake Erie IBMs*, and *Statistical GLM*) and underestimated for larger individuals (by 9 ± 11 , 2 ± 1 , $1 \pm 1\%$, respectively, Fig. 3). The slope and intercept of the *General IBM*, and the intercept of the *Statistical GLM* differed from the 1:1 line and zero, respectively (Slope: estimates $\pm$ SE: 1.37 ± 0.09 , $t = -2.68$, $p = 0.009$; Intercepts: -2.93 ± 0.88 and -0.34 ± 0.07 , $t < -3.30$, $p < 0.004$) (Figure 3). The *Statistical GLM* also was the most parsimonious model with the lowest AIC value followed by the *Lake Erie* and *General IBMs*, respectively (Table 1).

Discussion

Our results demonstrate that a statistical model developed using locally collected data (*Statistical GLM*) better or equally estimated yellow perch larval growth rate and cumulative TL than a modified general IBM that incorporated local yellow perch foraging behavior and growth rate information (*Lake Erie IBM*), and markedly better than a general IBM developed for use in small and large lakes with borrowed data from other species/locations (*General IBM*; Fulford et al. 2006). Thus, caution should be exercised in using a general IBM given that models parameterized with observations from the system of interest can outperform in providing accurate fish growth and length estimates.

Our result of the statistical model being more accurate than the semi-mechanistic IBM is contrary to what has been observed in previous studies of ecological model comparisons (Ellner et al. 1998; Kendall et al. 1999) where semi-mechanistic models were found to be more accurate than statistical models. The difference between our results and those of previous studies may have occurred because mechanistic and semi-mechanistic models in these previous studies had fewer parameters (<10) and authors had longer time series (>180 data points) at their disposition, allowing for the use of more powerful statistical techniques (nonlinear feed-forward neural networks and forecasting, and seminonparametric models) to alter their mechanistic models (Ellner et al. 1998; Kendall et al. 1999). Therefore, at present, our *Statistical GLMs* provide the most accurate estimates of larval yellow perch short-term growth rate and long-term TL. However, the small difference observed between the TL estimates of the three models and the poor fit we observed when evaluating individual prey consumed in the IBM foraging submodel ($R^2 = 0.16 \pm 0.13$, JRMJ, unpublished data) suggests that in the future the accuracy of both semi-mechanistic models could be further improved and could surpass the *Statistical GLM*.

Our analysis does not provide a strong test as to why the *Statistical GLM* produced a better fit than the IBMs. However, the fact that statistical models do not force inclusion of specific variables and allow for easy inclusion of environmental factors without additional laboratory experiments, may have improved their fit. Another difference among models that could have influenced their performance is that, unlike the two IBMs used herein, the pure *Statistical GLM* did not include prey variables such as zooplankton density, size, or biomass. The reliance of the two IBMs on prey attributes might limit performance in Lake Erie because our estimates of prey availability may differ from what is actually perceived by the fish as has been found in a previous study (Luo et al. 1996). The fact that we may not be accurately measuring

prey availability is further supported by our poor estimates of prey consumed. Furthermore, since larval yellow perch do not appear limited by zooplankton prey availability in western Lake Erie (Marin Jarrin et al. 2015) this variable may not be necessary to accurately estimate their growth. Statistical models can be based on spurious correlations; however, in our models this is not likely because all of the factors included in the analysis can influence fish behavior, physiology and growth (Post and Prankevicius 1987; Post and McQueen 1988; Post and Johannes 1997; Power and van den Heuvel 1999; Pangle et al. 2012). Therefore, in western Lake Erie information on the potential prey community may not be required to accurately estimate larval yellow perch growth and length. We evaluated whether our choice of using 2006 and 2008 data to develop and 2007 to evaluate the models may have also influenced our conclusions. However, similar results were observed when we developed the *Lake Erie IBM* and *Statistical GLM* using 2006 and 2007 or 2007 and 2008 data, and when we evaluated the models using 2006 or 2008 data, with the *Statistical GLM* exhibiting the most accurate estimates in 75% of comparisons (JRMJ, data not presented). Consequently, these results suggest our conclusion that the *Statistical GLM* provides better estimates of larval yellow perch growth and TL were not due to chance.

In contrast to the *General IBM*, the *Lake Erie* and *Statistical* models included where larvae were collected (i.e. Maumee or non-Maumee River plume waters) in growth estimates. While both the Maumee and non-Maumee River plume waters provide habitat for yellow perch larvae, lower mortality rates were observed in the more turbid Maumee River plume waters than in the less turbid non-Maumee River plume waters (Reichert et al. 2010). Manning et al. (2014) were able to modify the Fulford et al. (2006) model and included turbidity as a variable to predict juvenile yellow perch TL. However, we did not include the Manning et al. (2014) model in our study because it comprises life stages outside of the larval period, and pilot analysis found their

fit to be poorer than the models used herein ($R^2 \leq 0.20$, JRMJ and KLP, unpublished data).

Previous research has also suggested that turbidity may influence larval yellow perch consumption rates (Wellington et al. 2010; Pangle et al. 2012). For example, Pangle et al. (2012) found that under predation risk, larval yellow perch foraging increases with increasing turbidity (and hence, reduced predation risk), until turbidity levels became too high. Further work looking at western Lake Erie yellow perch larvae found that larvae in more turbid Maumee River plume waters had similar or lower consumption and growth, and lower predation rates than larvae from less turbid non-Maumee River plume waters (Reichert et al. 2010; Carreon-Martinez et al. 2014; Marin Jarrin et al. 2015). We further tested the importance of including where the fish were collected in the *Lake Erie IBM* by re-running 2007 and found that without the growth coefficient this model performed only slightly better than the *General IBM* ($R^2 = 0.23$ vs. 0.22). Therefore, including where yellow perch larvae were collected may have improved the fit of the *Lake Erie* and *Statistical* models because growth is likely influenced by predation risk, which has been found to be lower in more turbid (e.g., Maumee River plume) than in less turbid waters (e.g., non-Maumee River plume, Carreon-Martinez et al. 2014).

Water temperature is included in the two IBMs but was not a part of the *Statistical GLM*. The influence of temperature on fish behavior, physiology, and growth is well documented (reviewed in Miller 1988; Wootton 1998). In recent years, the influence of water temperature on fish biology has received particular attention because of the potential impacts of predicted changes in climate on fish populations around the world (Thresher et al. 2007; Vinagre et al. 2012; IPCC 2013). For yellow perch, studies have predicted that future increases in Great Lakes water temperature would positively affect yellow perch growth and expand their spatial distribution unless prey became limiting (Hill and Magnuson 1990; Magnuson et al. 1990; Shuter

and Post 1990), or reduce growth if increases in water temperature strengthen stratification of lake water column during the summer, which could vertically separate fish and their prey (De Stasio et al. 1996). More recently, Farmer et al. (2015) found a strong positive relationship between length of winter and yellow perch juvenile recruitment in Lake Erie. These authors provided evidence that this was because shorter winters do not allow for proper ovary development and lead to smaller eggs, larvae that hatch earlier, at a smaller size and potentially out of sync with zooplankton blooms making them less likely to survive to the juvenile stage. Consequently, the *Statistical GLM* may not perform as well in the near future if water temperature changes drastically, unless the model is updated with new empirical data to capture this change.

Both IBMs and statistical models have disadvantages that cannot be overlooked. The main disadvantages of statistical models is that they do not permit us to test which mechanisms are driving observed relationships. Future laboratory experiments will still be required to fully understand the mechanisms behind larval fish foraging and growth. Because statistical models are not mechanistic, they can break down with no prior notice if relationships change over time. By not pinpointing the mechanisms, statistical models also do not allow administrators to manage the factor limiting fish growth, if the variable limiting growth is manageable (e.g., harvest, nutrient runoff, predation risk). On the other hand because IBMs are so complex, they often require “parameter borrowing” (Grimm 1999; Hartman and Kitchell 2008). For example, the *General* and *Lake Erie IBMs* employed in our study use parameters that were originally developed for other species and habitats, and adapted for yellow perch (Letcher et al. 1996; Fulford et al. 2006). Additionally, because of the amount of work required to determine model parameters, the way in which they interact is often overlooked. The unknown nature of these

interactions could also influence IBM accuracy since some parameters, such as maximum consumption, can vary under the influence of variables such as prey type and larval fish densities (Hartman and Brandt 1993).

To our knowledge, our study is one of the first to compare and evaluate the ability of completely different models to estimate larval fish growth and length. Our results suggest that models fit with observations specifically obtained from the system of interest can provide better estimates, particularly short-term growth estimates, and that investigators should be careful when applying models developed from one system to another or borrowing parameters from other species. However, because of the need to study the mechanisms behind larval fish growth and length, researchers should continue to develop and improve semi- and pure mechanistic models. In the case of western Lake Erie, data availability only allowed us to modify two parts (prey selectivity and larval growth) of the *General IBM*. Future work could continue to evaluate parameters borrowed from other habitats and species in order to make the *General IBM* more specific to this dynamic shallow body of water.

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Tables and Figures:

Fig. 1. Collection sites for zooplankton prey and larval yellow perch in western Lake Erie during 2006-2008. Sites within the Maumee River plume (denoted by an x) and outside of it (denoted by an o) were sampled during late April through mid-June, 2006-2008.

Fig. 2. Observed versus predicted growth rate (mm d^{-1}) of western Lake Erie yellow perch larvae (ranging 6 - 15 mm in total length) during spring 2007. Growth rate was predicted with a fully mechanistic general individual-based model for yellow perch (Fulford et al. 2006, *General IBM*; closed circles, dot-dash regression line), a modified version of the *General IBM* using data collected in Lake Erie (*Lake Erie IBM*; open circles, dotted line) and a purely *Statistical GLM* (closed triangles, dashed line). A 1:1 continuous line between observed and predicted values is provided.

Fig. 3. Observed versus predicted total length (TL, mm) of western Lake Erie yellow perch larvae (ranging 6 - 15 mm in TL) during spring 2007. Total lengths were predicted with a fully mechanistic general individual-based model for yellow perch (Fulford et al. 2006, *General IBM*; closed circles, dot-dash regression line), a modified version of the *General IBM* using data collected in Lake Erie (*Lake Erie IBM*; open circles, dotted line) and a purely *Statistical* model

(closed triangles, dashed line). A 1:1 continuous line between observed and predicted values is provided.

Table 1. Performance evaluation of a fully mechanistic general individual-based model (Fulford et al. 2006, *General IBM*), a modified version of the *General IBM* using data collected in Lake Erie (*Lake Erie IBM*) and a purely statistical model (*Statistical GLM*) in predicting growth rate (mm d^{-1}), and total length (mm) of larval yellow perch in western Lake Erie during 2007.

Reported are sample sizes used for regression (n), number of parameters for each model (Parameters), the Skill score (Skill), Percent Bias (PBIAS), the coefficient of determination (R^2), the slope of the relationship between predicted and observed values (a), the intercept value of the regression and AIC values. Slope and intercept in bold signify significant difference from 1:1 line and zero, respectively (p-value < 0.05).

Table 2. Description of most parsimonious (lowest AIC_c values and AIC_c weights, w_i) statistical models used in the *Lake Erie IBM* and *Statistical GLM* (only growth rates) to predict selectivity (Chesson's α) for zooplankton prey taxa (cyclopoids = CYCL; calanoids = CALA; small cladocerans = CLAD; VELI = dreissenid mussel veligers), location-specific growth coefficient, and growth rates of Lake Erie larval yellow perch in relation to environmental variables. These models were developed using empirical diet and environmental data collected in western Lake Erie during April through June 2006 and 2008. DOY = Day of year, TL = yellow perch larval total length (mm), MRP = categorical variable describing if larvae were collected inside versus outside of the Maumee River plume; and IBM = growth rate estimate obtained with *Lake Erie IBM* (see text for details). Included are the P-value, coefficient of determination (R^2), and sample size (n) for each model. Performance of these models relative to others can be found in Table A3 and A4.

Fig. 1. Collection sites for zooplankton prey and larval Yellow Perch in western Lake Erie during 2006-2008. Sites within the Maumee River plume (denoted by an x) and outside of it (denoted by an o) were sampled during late April through mid-June, 2006-2008.

182x156mm (96 x 96 DPI)

Fig. 2. Observed versus predicted growth rate (mm d^{-1}) of western Lake Erie Yellow Perch larvae (ranging 6 - 15 mm in total length) during spring 2007. Growth rate was predicted with a fully mechanistic general individual-based model for Yellow Perch (Fulford et al. 2006, *General Model*; closed circles, dot-dash regression line), a modified version of the *General Model* using data collected in Lake Erie (*Lake Erie Model*; open circles, dotted line) and a purely *Statistical Model* (closed triangles, dashed line). A 1:1 continuous line between observed and predicted values is provided.

298x239mm (150 x 150 DPI)

Observed versus predicted total length (TL, mm) of western Lake Erie Yellow Perch larvae (ranging 6 - 15 mm in TL) during spring 2007. Total length was predicted with a fully mechanistic general individual-based model for Yellow Perch (Fulford et al. 2006, *General Model*; closed circles, dot-dash regression line), a modified version of the *General Model* using data collected in Lake Erie (*Lake Erie Model*; open circles, dotted line) and a purely *Statistical Model* (closed triangles, dashed line). A 1:1 continuous line between observed and predicted values is provided.

300x237mm (150 x 150 DPI)

Table 1. Performance evaluation of a fully mechanistic general individual-based model (Fulford et al. 2006, *General Model*), a modified version of the *General Model* using data collected in Lake Erie (*Lake Erie Model*) and a purely statistical model (*Statistical Model*) in predicting growth rate (mm d^{-1}), and total length (mm) of larval Yellow perch in western Lake Erie during 2007. Reported are sample sizes used for regression (n), number of parameters for each model (Parameters), the Skill score (Skill), Percent Bias (PBIAS), the coefficient of determination (R^2), the slope of the relationship between predicted and observed values (a), the intercept value of the regression and AIC values. Slope and intercept in bold signify significant difference from 1:1 line and zero, respectively (p-value < 0.05).

Estimate	Model	n	Parameters	Skill	PBIAS	R^2	a	b	AIC
Growth rates	General	21	120	0.13	153.19	0.22	1.31	6.23	243.31
	Lake Erie	21	121	0.48	69.8	0.29	0.07	0.30	186.42
	Statistical	21	4	0.56	-43.65	0.37	0.03	0.64	-36.83
Total Length	General	21	120	0.94	5.74	0.92	-2.92	1.37	239.29
	Lake Erie	21	121	1.00	-1.95	0.99	-0.11	0.99	196.90
	Statistical	21	5	1.00	-1.64	0.99	-0.34	1.02	-36.10

Table 2. Description of most parsimonious (lowest AIC_c values and AIC_c weights, w_i) statistical models used in the *Lake Erie Model* and *Statistical Model* (only growth rates) to predict selectivity (Chesson’s α) for zooplankton prey taxa (cyclopoids = CYCL; calanoids = CALA; small cladocerans = CLAD; VELI = dreissenid mussel veligers), location-specific growth coefficient, and growth rates of Lake Erie larval Yellow perch in relation to environmental variables. These models were developed using empirical diet and environmental data collected in western Lake Erie during April through June 2006 and 2008. DOY = Day of year, TL = Yellow perch larval total length (mm), MRP = categorical variable describing if larvae were collected inside versus outside of the Maumee River plume; and IBM = growth rate estimate obtained with *Lake Erie Model* (see text for details). Included are the P-value, coefficient of determination (R²), and sample size (n) for each model. Performance of these models relative to others can be found in Table A3 and A4.

Eq. Model	Response variable	Predictive Model	P	R ²	n
1 Lake Erie	CYCL	0.11 + 0.06*TL	0.002	0.10	15
2	CALA	0.18 - 0.17*CYCL + 0.46*MRP - 0.49*CYCL(MRP)	<0.001	0.44	15
3	CLAD	0.32 - 0.32*CYCL - 0.22*MRP + 0.22*CYCL(MRP)	<0.001	0.20	15
4	VELI	0.49 - 0.51*CYCL - 0.25*MRP + 0.27*CYCL(MRP)	<0.001	0.33	15
5	Growth coefficient	0.14 + 0.14*IBM - 0.02*MRP - 0.13*IBM(MRP)	0.02	0.52	25
6 Statistical	Growth	14.76 - 0.21*DOY + 0.00077*DOY ² - 0.013*MRP	<0.001	0.93	25

Table A1. Equations of *General* (Fulford et al. 2006) and *Lake Erie IBMs* describing foraging and growth submodels of yellow perch larvae. Equations in which the models differ are detailed in Table A2.

Table A2. Comparison of equations in which *General* and *Lake Erie IBMs* differ. Both models describe foraging and growth of yellow perch larvae.

Table A3. Description of statistical models used in the *Lake Erie IBM* to predict selectivity (Chesson's α) for zooplankton prey taxa (cyclopoids = CYCL; calanoids = CALA; small cladocerans = CLAD; VELI = dreissenid mussel veligers) and a location-specific growth coefficient of Lake Erie larval yellow perch in relation to environmental variables. These models were developed using empirical diet and environmental data collected in western Lake Erie during April through June 2006 and 2008. TL = yellow perch larval total length (mm), MRP = categorical variable describing if larvae were collected inside versus outside of the Maumee River plume; and IBM = growth rate estimate obtained with *Lake Erie IBM* (see text for details). Included are the coefficient of determination (R^2), F statistic, degrees of freedom (df), log Likelihood (logLik), Akaike Information Criteria modified for small sample sizes (AIC_c), difference between model with lowest AIC_c and other models (delta) and model weight. Only models with delta <5 are presented.

Table A4. Description of statistical models used to estimate growth rates (mm d^{-1}) of Lake Erie larval yellow perch in relation to environmental variables. These models were developed using empirical diet and environmental data collected in western Lake Erie during April through June 2006 and 2008. DOY = Day of year and MRP = categorical variable describing if larvae were collected inside versus outside of the Maumee River plume (see text for details). Included are the

coefficient of determination (R^2), F statistic, degrees of freedom (df), log Likelihood (logLik), Akaike Information Criteria modified for small sample sizes (AIC_c), difference between model with lowest AIC_c and other models (delta) and model weight is also presented. Only models with delta <5 are presented.

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Table. A1. Equations of *General* (Fulford et al. 2006) and *Lake Erie* models describing foraging and growth submodels of Yellow perch larvae. Equations in which the models differ are detailed in Table A2.

Equation	Description
$ER_{i,k} = SS_k \cdot RA_{i,k} \cdot d_i$	Encounter rate (individuals $\cdot$ s $^{-1}$)*
SS_k : Hatch – 8 mm = 1 body length $\cdot$ s $^{-1}$ >8 mm = 3 body lengths $\cdot$ s $^{-1}$	Larval swimming speed (mm $\cdot$ s $^{-1}$)
$RA_{i,k} = \left[\frac{TL_i}{2 \tan(a_k/2)} \right]^2 \pi \cdot 0.5$	Larval reactive area for prey type i (mm 2)
$HT_{i,k} = e^{0.264 \cdot 10^{7.0151(TL_i/L)}}$	Handling time (s)
$Q_{i,k} = \frac{\alpha_{i,k}}{\sum_{j=1}^m \alpha_{k,j} \cdot p_j}$	Probability of attach and capture

See Selectivity Indexes in Table A2

$C_k = \frac{\sum_i (B_{i,k} \cdot m_i)}{1 + \sum_i E_{i,k} \cdot Q_{i,k} \cdot HT_{i,k}} \cdot \text{Seconds} \cdot \text{day}^{-1}$	Daily consumption ($\mu\text{g} \cdot \text{day}^{-1}$)
$C_{lim} = Ca \cdot wt^{Cb} \cdot f_c(T)$	Consumption limit ($\text{gg}^{-1} \text{d}^{-1}$)
$\max_{ration} = 100 \cdot C_{lim} \cdot KA \cdot KB$	Maximum Ration ($\text{gg}^{-1} \text{d}^{-1}$)
$C_{max} = W_k \cdot C_{lim} \cdot p_{max} \cdot KA \cdot KB$	Maximum Consumption ($\text{gg}^{-1} \text{d}^{-1}$)
$p_{max} = 18/24$	Maximum proportion of day with daylight
$KA = \frac{CK1 \cdot L1}{1 + CK1 \cdot (L1 - 1)}$	Increasing portion of the temperature dependence function
$KB = \frac{CK4 \cdot L2}{1 + CK4 \cdot (L2 - 1)}$	Decreasing portion of the temperature dependent function
$L1 = e^{(G1 \cdot (T - CQ))}$	Consumption multiplier
$L2 = e^{(G2 \cdot (CTL - T))}$	Consumption multiplier
$CA = 0.8464$	Intercept for C_{max} ($\text{gg}^{-1} \text{d}^{-1}$)
$CB = -0.3$	Exponent for C_{max}
$CQ = 5$	Slope for temperature-dependence of consumption
$CTO = 24$	Optimum temperature for consumption ($^{\circ}\text{C}$)
$CTM = 26$	Maximum temperature for consumption ($^{\circ}\text{C}$)

Equation	Description
CTL = 29	Temperature at which dependence is some reduced fraction (°C)
CK1 = 0.17	Fraction of maximum rate
CK4 = 0.01	Fraction of maximum rate
G1 = 0.288286714	Exponent of L1
G2 = 2.828980049	Exponent of L2
If consumption is $> C_{\max}$ than $C_k = C_{\max}$, otherwise $C_k = C_k$	
$G = (C_k \cdot AE_k) - R_k - [C_k \cdot (U + SDA)]$	Daily growth ($\mu\text{g} \cdot \text{day}^{-1}$)**
$R_k = W_k \cdot RA \cdot W_k^{RB} \cdot f(t) \cdot ACT$	Daily metabolic cost ($\mu\text{g} \cdot \text{day}^{-1}$)
$f(t) = V^x e^{x(l-V)}$	Temperature-dependent function
$V = \frac{RTM - t}{RTM - RTO}$	
$x = \left\{ Z^2 \left[1 + \left(1 + \frac{40}{Y} \right)^{0.5} \right]^2 \right\} \frac{1}{400}$	
$Z = \ln(RQ) (RTM - RTO)$	
$Y = \ln(RQ) (RTM - RTO + 2)$	
$AE_k = 0.8(1 - 0.25e^{-0.002(W_k^{-10})})$	Assimilation efficiency
$W_k = 0.519 \cdot l^{3.293}$	Length – dry mass relationship
RA = 0.035	Intercept for maximum std respiration
RB = -0.2	Exponent for maximum std respiration
RQ = 2.1	Slope for temperature-dependence of std respiration
RTO = 32	Optimum temperature for std respiration
RTM = 35	Maximum temperature for std respiration
ACT = 4.4	Activity multiplier
U and SDA = 0.15	Daily costs of excretion and specific dynamic action

d_i = density of prey type i ($\text{ind.} \cdot \text{mm}^{-3}$)

TL_i = length of prey type i (mm)

l = length of individual larva (mm)

p_i = relative abundance of prey type i

$B_{i,k}$ = stochastic estimate of number of prey type i consumed by larval k based on binomial calculation with $E_{i,k}$ as total trials and $Q_{i,k}$ as success probability

m_i = individual mass of prey type i

MRP = Larva collected in Maumee River Plume

*Realized encounter rate ($E_{i,k}$) calculated with Poisson distribution with $ER_{i,k}$ as rate parameter

**If using *Lake Erie model*, see Table A1 for growth coefficient

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Table A2. Comparison of equations in which *General* and *Lake Erie* Models differ. Both models describe foraging and growth of Yellow perch larvae.

<i>General Model</i>	<i>Lake Erie Model</i>	Description
$\alpha_{CY,k} = 193.499 \cdot TL_i^{-7.64}$	$\alpha_{CY,k} = 0.11 + 0.06 \cdot TL_i$	Selectivity of larva k for cyclopoid
$\alpha_{CA,k} = 0.272 \cdot \ln(TL_i) - 0.3834$	$\alpha_{CA,k} = 0.18 - 0.17 \cdot \alpha_{CY,k} + 0.46 \cdot MRP - 0.49 \cdot \alpha_{CY,k} \cdot MRP$	Selectivity for calanoid
$\alpha_{CL,k} = \frac{0.40}{\left[1 + \left(\frac{0.40}{0.09} - 1\right)e^{-20 \cdot 0.031 \cdot l}\right]^{1/0.031}}$	$\alpha_{SC,k} = 0.32 - 0.32 \cdot \alpha_{CY,k} - 0.22 \cdot MRP - 0.22 \cdot \alpha_{CY,k} \cdot MRP$	Selectivity for small cladocerans
$\alpha_{CL,k} = \frac{0.40}{\left[1 + \left(\frac{0.445}{0.092} - 1\right)e^{-20 \cdot 0.029 \cdot l}\right]^{1/0.029}}$	n/a	Selectivity for <i>Daphnia</i> spp.
n/a	$\alpha_{V,k} = 0.49 - 0.51 \cdot \alpha_{CY,k} - 0.25 \cdot MRP + 0.27 \cdot \alpha_{CY,k} \cdot MRP$	Selectivity for veliger larvae
$G_{IBM} = (C_k \cdot AE_k) - R_k - [C_k \cdot (U + SDA)]$	$G_{IBM} = (C_k \cdot AE_k) - R_k - [C_k \cdot (U + SDA)]$	Daily Growth (ug·day ⁻¹)*
n/a	$G = 0.14 + 0.14 \cdot G_{IBM} - 0.02 \cdot MRP - 0.13 \cdot IBM \cdot MRP$	Daily Growth with growth coefficient

TL_i = length of prey type i (mm)

MRP = Larva collected in Maumee River Plume

*Further description of equation in Table A1

Table A3. Description of statistical models used in the *Lake Erie Model* to predict selectivity (Chesson's α) for zooplankton prey taxa (cyclopoids = CYCL; calanoids = CALA; small cladocerans = CLAD; VELI = dreissenid mussel veligers) and a location-specific growth coefficient of Lake Erie larval Yellow perch in relation to environmental variables. These models were developed using empirical diet and environmental data collected in western Lake Erie during April through June 2006 and 2008. TL = Yellow perch larval total length (mm), MRP = categorical variable describing if larvae were collected inside versus outside of the Maumee River plume; and IBM = growth rate estimate obtained with *Lake Erie Model* (see text for details). Included are the coefficient of determination (R^2), F statistic, degrees of freedom (df), log Likelihood (logLik), Akaike Information Criteria modified for small sample sizes (AIC_c), difference between model with lowest AIC_c and other models (delta) and model weight. Only models with delta <5 are presented.

Response	Explanatory	R^2	F	df	logLik	AIC_c	delta	weight
CYCL	$0.11 + 0.06*TL$	0.10	10.59	3.00	-48.08	102.40	0.00	0.25
CYCL	$0.07 + 0.06*TL + MRP$	0.10	5.35	4.00	-47.98	104.40	1.97	0.09
CYCL	$0.14 + 0.06*TL - 0.03*TURBID$	0.10	5.28	4.00	-48.04	104.50	2.10	0.09
CYCL	$0.05 + 0.05*TL + 0.01*TEMP$	0.10	5.27	4.00	-48.05	104.50	2.12	0.09
CYCL	$0.12 - 0.001*DENSITY + 0.06*TL$	0.10	5.25	4.00	-48.07	104.60	2.15	0.09
CYCL	$0.13 + 0.06*TL - 0.0004*PRED$	0.10	5.25	4.00	-48.07	104.60	2.16	0.09
CYCL	$-0.37 + MRP + 0.06*TEMP + MRP:TEMP$	0.12	4.21	5.00	-47.02	104.70	2.29	0.08
CYCL	$-0.57 + 0.01*DENSITY + MRP + 0.07*TEMP + DENSITY*MRP + MRP:TEMP$	0.16	3.39	7.00	-44.91	105.10	2.67	0.07
CYCL	$-0.10 + 0.05*TEMP$	0.07	6.94	3.00	-49.78	105.80	3.41	0.05
CYCL	$-0.32 + MRP + 0.07*TEMP - 0.10*TURBID + MRP:TEMP$	0.13	3.33	6.00	-46.65	106.20	3.83	0.04
CYCL	$0.13 + 0.06*TL + MRP - 0.07*TURBID$	0.11	3.65	5.00	-47.80	106.30	3.85	0.04
CYCL	$-0.25 + 0.03*TL + MRP + 0.01*TEMP + MRP*TEMP$	0.13	3.31	6.00	-46.69	106.30	3.90	0.04
CALA	$0.18 - 0.17*CYCL + MRP + CYCL:MRP$	0.44	24.15	5.00	4.25	2.20	0.00	0.05
CALA	$-0.21 - 0.17*CYCL + MRP + 0.002*PRED + 0.40*TURB + CYCL:MRP + MRP:TEMP$	0.48	13.67	8.00	7.74	2.20	0.01	0.05
CALA	$-0.06 - 0.18*CYCL - 0.002*TL + MRP + 0.37*TURB + CYCL:MRP + MRP:TEMP$	0.47	13.45	8.00	7.35	2.90	0.79	0.04
CALA	$-0.04 - 0.16*CYCL + 0.01*TL + MRP + 0.003 + CYCL:MRP$	0.46	15.45	7.00	6.12	3.00	0.86	0.04
CALA	$0.08 - 0.15 + MRP + 0.002*PRED - 0.05*TURB + CYCL:MRP$	0.46	15.43	7.00	6.10	3.10	0.91	0.03
CALA	$-0.08 - 0.16*CYCL + MRP + 0.004*PRED + 0.01*TEMP + CYCL:MRP$	0.46	15.41	7.00	6.05	3.20	1.00	0.03
CALA	$0.05 - 0.15*CYCL + 0.001*DENS + MRP + 0.003*PRED + CYCL:MRP$	0.46	15.37	7.00	6.00	3.30	1.09	0.03
CALA	$0.03 - 0.15*CYCL + MRP + 0.003*PRED + CYCL:MRP + DENS:MRP$	0.46	15.36	7.00	5.98	3.30	1.14	0.03
CALA	$0.24 - 0.16*CYCL + 0.002*DENS + MRP - 0.12*TURB + CYCL:MRP$	0.46	15.24	7.00	5.81	3.60	1.48	0.03
CALA	$0.06 - 0.16*CYCL + 0.01*TL + MRP - 0.02*TEMP + 0.46*TURB + CYCL:MRP + MRP:TEMP$	0.48	11.82	9.00	8.20	3.70	1.52	0.03
CALA	$0.001 - 0.16*CYCL + MRP - 0.01*TEMP + 0.43*TURB + CYCL:MRP + MRP:TEMP + MRP:TURB$	0.48	11.78	9.00	8.11	3.80	1.69	0.02

CALA	-0.49 - 0.15*CYCL + MRP + 0.01*PRED + 0.48*TURB + CYCL:(MRP) + DENS:(MRP) + MRP:TEMP	0.48	11.77	9.00	8.10	3.90	1.72	0.02
CALA	-0.04 - 0.16*CYCL + 0.002*DENS + MRP - 0.01*TEMP + 0.45*TURB + CYCL:MRP + MRP:TEMP	0.48	11.75	9.00	8.05	4.00	1.82	0.02
CALA	0.32 - 0.15*CYCL + MRP - 0.004*TEMP - 0.11*TURB + CYCL:MRP	0.45	15.12	7.00	5.64	4.00	1.83	0.02
CALA	-0.22 - 0.17*CYCL + 0.002 + MRP + 0.001*PRED + 0.41*TURB + CYCL:MRP + MRP*TEMP	0.48	11.74	9.00	8.02	4.00	1.87	0.02
CALA	0.24 - 0.17*CYCL + 0.003*TL + MRP - 0.11*TURB + CYCL:MRP	0.45	15.09	7.00	5.59	4.10	1.92	0.02
CALA	0.27 - 0.15*CYCL + MRP - 0.01*TEMP + CYCL:MRP	0.44	18.05	6.00	4.40	4.10	1.98	0.02
CALA	-0.07 - 0.15*CYCL + MRP + 0.001*PRED - 0.01*TEMP + 0.45*TURB + CYCL:TURB + MRP:TEMP	0.48	11.68	9.00	7.92	4.20	2.08	0.02
CALA	0.17 - 0.17 + 0.001*DENS + MRP + CYCL:MRP	0.44	18.00	6.00	4.34	4.30	2.10	0.02
CALA	-0.12 - 0.18*CYCL + 0.003*DENS + MRP + 0.39*TURB + CYCL:MRP + DENS:MRP + MRP*TEMP	0.48	11.66	9.00	7.87	4.30	2.17	0.02
CALA	0.16 - 0.18*CYCL + 0.003*TL + MRP + CYCL:MRP	0.44	17.95	6.00	4.28	4.40	2.21	0.02
CALA	-0.14 - 0.18*CYCL + 0.003*DENS + 0.002*TL + MRP + 0.38*TURB + CYCL:MRP + MRP:TEMP	0.48	11.65	9.00	7.85	4.40	2.22	0.02
CALA	-0.21 - 0.17*CYCL + 0.0001*TL + MRP + 0.002*PRED + 0.40*TURB + CYCL:MRP + MRP:TEMP	0.48	11.59	9.00	7.74	4.60	2.44	0.02
CLAD	0.32 - 0.32*CYCL + MRP + CYCL:MRP	0.20	7.82	5.00	7.21	-3.80	0.19	0.06
CLAD	0.18 - 0.26*CYCL - 0.002*DENS + MRP + 0.16 + DENS:MRP	0.24	5.59	7.00	9.30	-3.30	0.61	0.05
CLAD	0.34 - 0.33*CYCL - 0.002*DENS + MRP + CYCL:MRP + DENS:MRP	0.23	5.52	7.00	9.15	-3.00	0.90	0.04
CLAD	0.36 - 0.33*CYCL - 0.004*DENS + MRP + CYCL:MRP + DENS:MRP	0.21	6.23	6.00	7.93	-2.90	1.01	0.04
CLAD	0.47 - 0.34*DENS - 0.001*TL + MRP - 0.003*PRED + CYCL:MRP + DENS:MRP	0.25	5.00	8.00	10.25	-2.90	1.09	0.04
CLAD	0.42 - 0.33*CYCL + MRP - 0.002*PRED + CYCL:MRP	0.21	6.17	6.00	7.83	-2.70	1.23	0.04
CLAD	0.29 - 0.25*CYCL - 0.002*DENS + MRP + DENS:MRP	0.21	6.10	6.00	7.71	-2.50	1.45	0.03
CLAD	0.31 - 0.31*CYCL - 0.003*DENS - 0.01*TL + MRP + 0.16*TURB + CYCL:MRP + DENS:MRP	0.26	4.52	9.00	11.07	-2.10	1.88	0.03
CLAD	0.26 - 0.23*CYCL + MRP	0.17	9.47	4.00	5.21	-2.00	1.96	0.02
CLAD	0.29 - 0.24*CYCL - 0.003*DENS - 0.01*TL + MRP + 0.16*TURB + DENS:MRP	0.24	4.81	8.00	9.78	-1.90	2.02	0.02
CLAD	0.24 - 0.34*CYCL + MRP + 0.01*TEMP + CYCL:MRP	0.20	5.89	6.00	7.36	-1.80	2.17	0.02
CLAD	0.40 - 0.26*CYCL - 0.001*DENS + MRP - 0.002*PRED + DENS:MRP	0.22	5.20	7.00	8.50	-1.70	2.21	0.02
CLAD	0.15 - 0.34*CYCL - 0.002*DENS + MRP + 0.27*TURB + CYCL:MRP + DENS:MRP + TURB:MRP	0.26	4.46	9.00	10.90	-1.70	2.22	0.02
CLAD	0.35 - 0.31*CYCL - 0.004*TL + MRP + CYCL:MRP	0.20	5.83	6.00	7.26	-1.60	2.36	0.02
CLAD	0.45 - 0.34*CYCL - 0.003*DENS + MRP - 0.002*PRED + CYCL:MRP	0.22	5.17	7.00	8.42	-1.60	2.36	0.02
CLAD	0.28 - 0.34*CYCL - 0.002*DENS + MRP - 0.001*PRED + 0.13*TURB + CYCL:MRP + DENS:MRP	0.26	4.44	9.00	10.82	-1.60	2.38	0.02
CLAD	0.27 - 0.33*CYCL - 0.002*DENS + MRP - 0.003*TEMP + 0.16*TURB + CYCL:MRP + DENS:MRP	0.26	4.43	9.00	10.81	-1.60	2.39	0.02
CLAD	0.32 - 0.25*CYCL - 0.003*DENS + MRP - 0.01*TEMP + 0.17*TURB + DENS:MRP	0.24	4.73	8.00	9.59	-1.60	2.39	0.02
CLAD	0.31 - 0.32*CYCL + MRP + 0.02*TURB + CYCL:MRP	0.20	5.82	6.00	7.24	-1.50	2.40	0.02
CLAD	0.22 - 0.23*CYCL	0.14	15.93	3.00	3.82	-1.40	2.56	0.02
CLAD	0.45 - 0.31*CYCL - 0.004*DENS - 0.01*TL + MRP + CYCL:MRP	0.22	5.09	7.00	8.27	-1.30	2.67	0.02

CLAD	0.42 - 0.31*CYCL - 0.003*DENS - 0.008*TL + MRP + CYCL:MRP + DENS:MRP	0.24	4.65	8.00	9.41	-1.20	2.76	0.02
CLAD	0.57 - 0.32*CYCL - 0.002*DENS - 0.01*TL + MRP - 0.003*PRED + CYCL:MRP + DENS:MRP	0.26	4.37	9.00	10.63	-1.20	2.76	0.02
CLAD	0.30 - 0.24*CYCL - 0.004*DENS + MRP	0.18	6.78	5.00	5.90	-1.10	2.80	0.02
CLAD	0.40 - 0.23*CYCL - 0.003*DENS - 0.01*TL + MRP + DENS:MRP	0.22	5.04	7.00	8.16	-1.10	2.87	0.02
CLAD	0.13 - 0.26*CYCL - 0.002*DENS + MRP + 0.23*TURB + DENS:MRP + TURB:MRP	0.24	4.63	8.00	9.35	-1.10	2.88	0.02
CLAD	0.17 - 0.26*CYCL - 0.002*DENS + MRP + 0.0001*PRED + 0.16*TURB + DENS:MRP	0.24	4.61	8.00	9.30	-1.00	2.98	0.02
CLAD	0.53 - 0.34*CYCL + MRP - 0.003*PRED - 0.07*TURB + CYCL:MRP	0.22	5.00	7.00	8.08	-0.90	3.05	0.01
CLAD	0.63 - 0.32*CYCL - 0.002*DENS + MRP - 0.003*PRED - 0.01*TEMP + CYCL:MRP + DENS:MRP	0.25	4.31	9.00	10.45	-0.80	3.11	0.01
CLAD	0.34 - 0.33*CYCL - 0.004*DENS + MRP + 0.03*TURB + CYCL:MRP	0.21	4.98	7.00	8.04	-0.80	3.13	0.01
CLAD	0.70 - 0.24*CYCL - 0.003*DENS + MRP - 0.003*PRED - 0.02*TEMP + DENS:MRP	0.23	4.57	8.00	9.20	-0.80	3.19	0.01
CLAD	0.32 - 0.33*CYCL - 0.002*DENS + MRP + 0.002*TEMP + CYCL:MRP + DENS:MRP	0.23	4.55	8.00	9.16	-0.70	3.25	0.01
CLAD	0.19 - 0.33*CYCL - 0.02*TL + MRP + 0.02*TEMP + CYCL:MRP	0.21	4.95	7.00	7.97	-0.70	3.27	0.01
CLAD	0.47 - 0.32*CYCL - 0.01*TL + MRP - 0.002*PRED + CYCL:MRP	0.21	4.94	7.00	7.95	-0.60	3.31	0.01
CLAD	0.36 - 0.33*CYCL - 0.004 + MRP + 0.0002*TEMP + CYCL:MRP	0.21	4.93	7.00	7.93	-0.60	3.34	0.01
CLAD	0.53 - 0.35*CYCL + MRP - 0.004*PRED + CYCL:MRP + MRP:PRED	0.21	4.93	7.00	7.92	-0.60	3.36	0.01
CLAD	0.53 - 0.24*CYCL - 0.002*DENS - 0.01*TL + MRP - 0.002*PRED + DENS:MRP	0.23	4.53	8.00	9.11	-0.60	3.36	0.01
CLAD	0.34 - 0.24*CYCL - 0.003*DENS - 0.02*TL + MRP + 0.17*TURB + DENS:MRP + TL:MRP	0.25	4.26	9.00	10.31	-0.50	3.40	0.01
CLAD	0.30 - 0.33*CYCL + MRP + 0.002*TEMP + CYCL:MRP	0.21	4.91	7.00	7.90	-0.50	3.41	0.01
CLAD	0.49 - 0.34*CYCL - 0.001*DENS + MRP - 0.003*PRED + CYCL:MRP + DENS:MRP + MRP:TEMP	0.25	4.24	9.00	10.25	-0.40	3.52	0.01
CLAD	0.42 - 0.34*CYCL + MRP - 0.002*PRED + 0.0002*TEMP + CYCL:MRP	0.21	4.88	7.00	7.83	-0.40	3.55	0.01
CLAD	0.37 - 0.25*CYCL - 0.002*DENS + MRP - 0.005*TEMP + DENS:MRP + MRP:PRED	0.21	4.87	7.00	7.80	-0.30	3.60	0.01
CLAD	0.12 - 0.33*CYCL + MRP + 0.28*TURB + CYCL:MRP	0.21	4.86	7.00	7.79	-0.30	3.62	0.01
CLAD	0.33 - 0.23*CYCL + MRP - 0.001*PRED	0.17	6.46	5.00	5.49	-0.30	3.63	0.01
CLAD	0.32 - 0.22*CYCL - 0.01*TL + MRP	0.17	6.40	5.00	5.40	-0.10	3.80	0.01
CLAD	0.43 - 0.22*CYCL - 0.01*DENS - 0.01*TL + MRP + MRP:TURB	0.19	5.40	6.00	6.53	-0.10	3.81	0.01
CLAD	0.12 - 0.33*CYCL - 0.04*TL + MRP + 0.04*TEMP + CYCL:MRP + TL:MRP	0.23	4.44	8.00	8.88	-0.10	3.83	0.01
CLAD	0.55 - 0.32*CYCL - 0.004*DENS - 0.01*TL + MRP - 0.002*PRED + CYCL:MRP	0.23	4.43	8.00	8.86	-0.10	3.85	0.01
CLAD	0.34 - 0.31*CYCL - 0.003*DENS - 0.01*TL + MRP + 0.16*TURB + CYCL:MRP + DENS:MRP + TL:MRP	0.27	3.98	###	11.29	0.00	3.93	0.01
CLAD	0.21 - 0.32*CYCL - 0.003*DENS - 0.01*TL + MRP + 0.31*TURB + CYCL:MRP + DENS:MRP + TURB:MR	0.27	3.98	###	11.27	0.00	3.97	0.01
VELI	0.50 - 0.51*CYCL + MRP + CYCL:MRP	0.33	15.18	5.00	-5.08	20.80	0.00	0.62
VELI	0.43 - 0.40*CYCL + MRP	0.30	19.83	4.00	-7.35	23.10	2.30	0.20
VELI	0.39 - 0.39*CYCL	0.28	36.97	3.00	-8.47	23.20	2.38	0.19

GROWTH												
COEFFICIENT	0.14 + 0.14*IBM - 0.02*MRP - 0.13*IBM(MRP)	0.5	7.24	5	36.23	-59.1	0	0.14				

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Table A4. Description of *Statistical Models* used to estimate growth rates (mm d^{-1}) of Lake Erie larval Yellow perch in relation to environmental variables. These models were developed using empirical diet and environmental data collected in western Lake Erie during April through June 2006 and 2008. DOY = Day of year and MRP = categorical variable describing if larvae were collected inside versus outside of the Maumee River plume (see text for details). Included are the coefficient of determination (R^2), F statistic, degrees of freedom (df), log Likelihood (logLik), Akaike Information Criteria modified for small sample sizes (AIC_c), difference between model with lowest AIC_c and other models (delta) and model weight is also presented. Only models with delta <5 are presented.

Response	Explanatory	R^2	F	df	logLik	AIC_c	delta	weight
Growth	$14.76 - 0.212 \cdot \text{DOY} + 0.00077 \cdot \text{DOY}^2 + \text{MRP}$	0.93	90.21	5	61.64	-110.10	0.00	0.25
Growth	$14.9 - 0.21 \cdot \text{DOY} + 0.00078 \cdot \text{DOY}^2 + \text{MRP} + \text{DOY}:\text{MRP} + \text{DOY}^2:\text{MRP}$	0.95	65.25	7	65.00	-109.40	0.71	0.18
Growth	$14.27 - 0.21 \cdot \text{DOY} + 0.00074 \cdot \text{DOY}^2 + \text{MRP} + \text{DOY}^2:\text{MRP}$	0.93	66.63	6	62.03	-107.40	2.73	0.06
Growth	$14.29 - 0.21 \cdot \text{DOY} + 0.00075 \cdot \text{DOY}^2 + \text{MRP} + \text{DOY}:\text{MRP}$	0.93	66.40	6	61.99	-107.30	2.81	0.06