

Modeling turbidity type and intensity effects on the growth and starvation mortality of age-0 yellow perch

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Abstract: We sought to quantify the possible population-level influence of sediment plumes and algal blooms on yellow perch (*Perca flavescens*), a visual predator found in systems with dynamic water clarity. We used an individual-based model (IBM), which allowed us to include variance in water clarity and the distribution of individual sizes. Our IBM was built with laboratory data showing that larval yellow perch feeding rates increased slightly as sediment turbidity level increased, but that both larval and juvenile yellow perch feeding rates decreased as phytoplankton level increased. Our IBM explained a majority of the variance in yellow perch length in data from the western and central basins of Lake Erie and Oneida Lake, with R^2 values ranging from 0.611 to 0.742. Starvation mortality was size dependent, as the greatest daily mortality rates in each simulation occurred within days of each other. Our model showed that turbidity-dependent consumption rates and temperature are key components in determining growth and starvation mortality of age-0 yellow perch, linking fish production to land-based processes that influence water clarity. These results suggest the timing and persistence of sediment plumes and algal blooms can drastically alter the growth potential and starvation mortality of a yellow perch cohort.

Résumé : Nous avons voulu quantifier l'influence possible au niveau de la population des panaches de sédiments et des proliférations d'algues sur la perchaude (*Perca flavescens*), un prédateur visuel qui occupe des systèmes présentant une clarté de l'eau dynamique. Nous avons utilisé un modèle basé sur l'individu (MBI) qui nous a permis d'inclure la variance de la clarté de l'eau et la répartition de la taille des individus. Notre MBI a été élaboré avec des données de laboratoire qui montrent que les taux d'alimentation des perchaudes larvaires augmentent légèrement avec l'augmentation du degré de turbidité associée aux sédiments, mais que les taux d'alimentation des perchaudes tant larvaires que juvéniles diminuent à mesure que la quantité de phytoplancton augmente. Notre MBI explique la majeure partie de la variance de la longueur des perchaudes observée dans des données des bassins ouest et central du lac Érié et du lac Oneida, les valeurs de R^2 allant de 0,611 à 0,742. La mortalité par inanition dépend de la taille, les taux de mortalité quotidienne les plus élevés dans chaque simulation se produisant dans un intervalle de quelques jours seulement. Notre modèle montre que les taux de consommation dépendants de la turbidité et la température sont des éléments clés pour la détermination de la croissance et de la mortalité par inanition pour les perchaudes de moins d'un an, reliant la production de poissons à des processus terrestres qui influencent la clarté de l'eau. Ces résultats donnent à penser que le moment et la persistance des panaches de sédiments et des proliférations d'algues peuvent modifier radicalement le potentiel de croissance et la mortalité par inanition d'une cohorte de perchaudes. [Traduit par la Rédaction]

Introduction

Turbidity events, such as sediment plumes and algal blooms, are increasing owing to changes in land use and climate (Allan 2004) across a range of aquatic ecosystems (Johnson and Rejmánková 2005; Hoegh-Guldberg et al. 2007). Alterations to the observable environment are of particular importance to visually foraging fish species (McMahon and Holanov 1995; Turesson and Brönmark 2007) because many of the factors affecting the growth, survival, and ultimately the recruitment success of age-0 fish are influenced by water clarity (Crowder et al. 1987; Post and Evans 1989; Sogard 1997; Bergenius et al. 2002). Therefore, quantifying the relationship between water clarity and age-0 fish growth and survival may help predict year class strength, especially under changing environmental conditions.

Yellow perch (*Perca flavescens*) are visual predators often found in systems with dynamic water clarity regimes and therefore provide a good model to illustrate the possible population-level influence of sediment plumes and algal blooms on fish. Age-0 yellow perch transition from pelagic larvae that feed primarily on zooplankton to demersal juveniles that feed on zooplankton and benthos (Wu and Culver 1992). During this ontogenic transition, visual focal length and acuity increase (Wahl et al. 1993), possibly resulting in developmental-stage-dependent effects of water clarity on foraging ability. Growth and survival of age-0 yellow perch are subject to a number of environmental factors, such as zooplankton availability (Mills et al. 1989), predation pressure (Reichert et al. 2010), and water temperature (Clady 1976), many of which are influenced by turbidity type (sediment or algae) and intensity. The

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type and intensity of turbidity often change throughout the year while age-0 yellow perch are undergoing physiological and behavioral changes. This suggests that the effect of water clarity on age-0 yellow perch growth and mortality is seasonal and that temporal effects must be considered when describing the potential influence of water clarity.

Sediment turbidity can increase feeding by larval fish, possibly because of increased visual contrast of prey items at the small perceptive scale used by these fish (Boehlert and Morgan 1985; De Robertis et al. 2003; Wellington et al. 2010). In contrast, light scattering caused by particulates reduces the feeding rate of juveniles and adults owing to their longer focal lengths (Benfield and Minello 1996). Sediment turbidity may also increase larval survival by reducing predation risk from fish with longer focal lengths (Reichert et al. 2010) and reducing starvation mortality during the critical period after yolk-sac absorption (Houde 1975; Munk and Kiørboe 1985). However, increasingly rapid and frequent flooding of tributaries due to climatic and land-use changes may alter the timing of sediment plumes (Cooper 1995; Friedl and Wüest 2002; Pfister et al. 2004), producing turbid conditions during periods that have historically been clear-water phases (Sutherland et al. 2002). Late-season age-0 fish decrease feeding as sediment turbidity increases (Wellington et al. 2010), and the growth of juvenile and adult fish is likely to be reduced by late-season sediment plumes (Wellington et al. 2010), possibly having population-level effects.

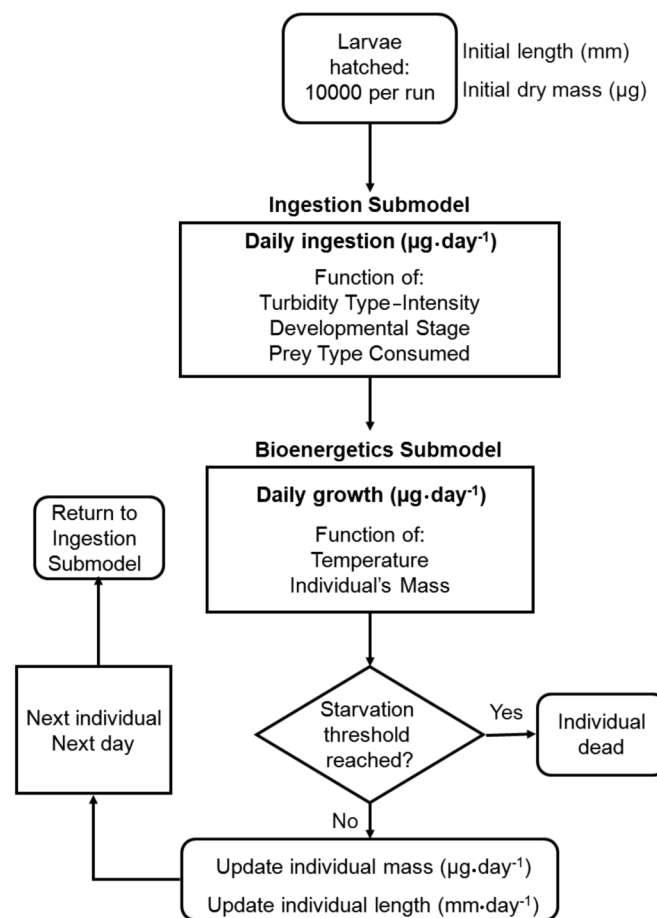
In contrast with sediment turbidity, algal turbidity both scatters incoming light and selectively absorbs photosynthetically active radiation, thus reducing light levels more than sediment turbidity of the same intensity (Gallegos et al. 1990). Additionally, algal cells form colonies and thus produce larger particles relative to sediment (Yang and Kong 2012), which may interfere with successful prey detection. Algal blooms reduce the foraging rate of both larvae and juveniles, even at low intensities (Diehl 1988; Radke and Gaupisch 2005; Wellington et al. 2010), suggesting that there is no developmental-stage-dependent effect of algal turbidity, unlike with sediment turbidity. Globally, algal blooms are increasing in intensity and duration (Hallegraeff 1993; Landsberg 2002) and have become problematic in many aquatic systems (Dyble et al. 2008; Bridgeman and Penamon 2010; Bridgeman et al. 2012), making it increasingly important to quantify how these blooms affect fish populations.

In this study, we utilized an individual-based model (IBM) of bioenergetics and starvation mortality, which allowed us to include both variance in water clarity conditions over time and variance in the population's response due to the distribution of fish size. We included laboratory-measured larval and juvenile feeding rates to estimate daily consumption and modeled the growth and starvation mortality of age-0 yellow perch. We validated our model using observed environmental data from three different systems and created an array of scenarios that predict how age-0 yellow perch are likely to respond to potential alterations in sediment plume and algal bloom dynamics.

Methods

We modified existing IBMs describing generalized growth and survival of larval fish (Letcher et al. 1996b) and larval yellow perch (Fulford et al. 2006a, 2006b) by explicitly including the effects of turbidity based on laboratory-derived ingestion rates (Wellington et al. 2010). These measured feeding rates replaced encounter and consumption rates that are traditionally indirectly calculated using swimming speed, light levels, and prey densities. Our model simulated the daily ingestion, growth, and starvation mortality of larval and juvenile yellow perch through the first 124 days post-hatch. This period covered the majority of the first growing season and corresponded to when juvenile yellow perch were regularly cap-

Fig. 1. Flow diagram of the individual-based model.



tured by the Ohio Department of Natural Resources' (ODNR) trawls, which is one of the data sets used for model validation.

Model description

General

Our base model was constructed using the simecol package in R version 2.15.1 and consisted of an initial cohort of individuals that passed through a series of submodels over a course of daily time steps. The submodels included (i) daily ingestion, (ii) daily bioenergetic growth, and (iii) starvation mortality (Fig. 1). Each model trial was initiated with a cohort of 10 000 individuals and run for 124 time steps (i.e., days). The initial length of each individual was drawn from a normal distribution (Table 1) and mass was then calculated using a length-mass regression (Table 1). For the first 4 days, individuals were considered yolk-sac larvae and did not feed; they grew at a standardized rate of 0.02 g·day⁻¹ (Gordon 1982) and did not experience starvation mortality. After the yolk-sac period, individuals were passed through the three submodels (ingestion, growth, starvation) each day, and size and survival status were updated for all individuals. Each trial continued for 124 days or until all individuals were dead. Using our base model, we altered parameters within the daily ingestion submodel to create hypothetical scenarios or historical scenarios that mimic real-world conditions (see below).

Daily ingestion

The daily ingestion submodel estimated the total mass of prey ingested (I) by each individual fish each day as

$$(1) \quad I = \sum (i_{th} \cdot c_{mass})$$

Table 1. Variable and parameter names, values, and sources.

Variable or parameter name	Value	Source
Initial number of individuals	10 000 (per cohort)	
Initial length distribution	$\mu = 5.3$ mm, SD = 0.3 mm	Fulford et al. 2006a
Length to mass equation	$W_k = 0.519 \times (\text{length})^{3.293}$	Fulford et al. 2006a
Ingestion rate, larva in sediment (no.·h ⁻¹)	$i_{LS} = 0.120 \times \text{NTU} + 29.248$	Wellington et al. 2010
Ingestion rate, larva in algae (no.·h ⁻¹)	$i_{LA} = -0.265 \times \text{NTU} + 31.104$	Wellington et al. 2010
Ingestion rate, juvenile in sediment (no.·h ⁻¹)	$i_{JS} = -0.359 \times \text{NTU} + 86.975$	Wellington et al. 2010
Ingestion rate, juvenile in algae (no.·h ⁻¹)	$i_{JA} = -0.449 \times \text{NTU} + 35.919$	Wellington et al. 2010
Secchi depth to NTU equation	$\text{NTU} = 5847.4 \times (\text{Secchi depth})^{-1.371}$	T.B. Bridgeman (unpublished data)
Mean prey mass (planktonic)	8.70×10^{-5} g	Rose et al. 1999
Mean prey mass (small benthic)	3.81×10^{-3} g	Rose et al. 1999
Mean prey mass (large benthic)	8.52×10^{-3} g	Schloesser and Nalepa 2001
Starvation threshold	0.53	Fulford et al. 2006a
C_{max} intercept	2.8275	Letcher et al. 1996a
C_{max} exponent	0.8496	Letcher et al. 1996a

Note: NTU, nephelometric turbidity unit; W_k , mass of an individual larva.

where i_{ih} is the total number of prey items consumed by an individual in a given hour and c_{mass} is the mean mass of individual items consumed. We assumed a 12 h period of active feeding (daylight hours) as a simplification for modeling purposes (Fulford et al. 2006b). The 12 values for i_{ih} were converted to hourly consumed mass by multiplying i_{ih} by the mean mass of the prey consumed (c_{mass} , Table 1) and then summed across the 12 h to determine I . I varied as a function of three factors: turbidity type and intensity, life stage of the individual, and prey types consumed (Fig. 1). Turbidity type and intensity were assigned based on values derived from our hypothetical and historical scenarios described below. The life stages of yellow perch include an ontogenetic shift from pelagic larvae and postlarvae to more benthic juveniles at >30 mm total length (TL) (Wu and Culver 1992). The 12 hourly ingestion rates, i_{ih} (Table 1), were drawn from a normal distribution based on the results of Wellington et al. (2010), in which ingestion rates varied hourly depending on turbidity type and intensity, zooplankton density, and life stage. The range used to calculate the distribution included the numbers of prey consumed by larvae and juveniles at low (10 zooplankton·L⁻¹), medium (100 zooplankton·L⁻¹), and high (300 zooplankton·L⁻¹) zooplankton densities at a given turbidity type-intensity combination. If a nephelometric turbidity unit (NTU) value used in the model was equal to an NTU value in the experimental data, then the observed standard deviation was used in the normal distribution; otherwise, the standard deviation of the distribution was the mean of the two nearest observed NTU values. Converting the laboratory data into a normal distribution in this way allowed for stochasticity in feeding rates based on turbidity intensity and type, fish developmental stage, and zooplankton density within day, between days, and between individuals.

The shift from pelagic larvae to benthic juveniles in yellow perch typically results in a switch from an entirely zooplankton-based diet to one composed of both zooplankton and benthic macroinvertebrates (Wu and Culver 1992). Thus, in our model, c_{mass} for individuals smaller than 30 mm TL consisted entirely of planktonic prey, while for individuals larger than 30 mm TL, diet composition was partitioned into 70% zooplankton (*Daphnia* sp.), 20% small benthic invertebrates (chironomids), and 10% large benthic invertebrates (mayfly larvae), and c_{mass} was determined by multiplying those percentages by the respective prey masses (Table 1). The partitions were set to be representative of the typical diet composition of yellow perch juveniles in Lake Erie (Parrish and Margraf 1994; Tyson and Knight 2001).

Because our ingestion submodel had the potential to allow an individual fish to feed at or near its maximum feeding rate for multiple hours, it was necessary to limit daily ingestion to a size-specific daily maximum (C_{max}). If an individual's projected con-

sumption exceeded maximum consumption, the mass of food eaten was set to C_{max} , defined as

$$(2) \quad C_{\text{max}} = \text{CmaxInt} \cdot \text{Mass}^{\text{CmaxExp}}$$

where CmaxInt and CmaxExp were derived from Letcher et al. (1996a) (Table 1). This function decreased C_{max} as a percentage of an individual's body mass as fish size increased, from a maximum of 200% of body mass per day for small larvae to approximately 60% of body mass per day for larger juveniles.

Bioenergetic growth

The bioenergetics submodel determined individual gains or losses (ΔM) in a day, defined as

$$(3) \quad \Delta M = (I \cdot \text{AE}) - \text{TC}$$

where I ($\mu\text{g}\cdot\text{day}^{-1}$) is the ingestion rate from above and AE is the assimilation efficiency, which was set at 0.8, the asymptotic maximum identified in Letcher et al. (1996a). Total costs (TC) was a function of routine metabolism (RM, $\mu\text{g}\cdot\text{day}^{-1}$), activity metabolism (AM, $\mu\text{g}\cdot\text{day}^{-1}$), specific dynamic action (SDA), and egestion (E):

$$(4) \quad \text{TC} = \text{RM} + 0.5 \cdot \text{AM} + I(\text{SDA} + E)$$

RM was a function of fish mass and temperature and was calculated as in Kitchell et al. (1977) and Post (1990). AM equaled 4.4 times RM during active feeding hours and 0 during nonfeeding times (Post 1990). SDA + E was defined as a constant proportion of I (0.30; Letcher et al. 1996a). The value of ΔM was applied to the individual, and the individual's mass was increased or decreased for the next day cycle. Length could increase as a result of mass gain, but it could not decrease as a result of mass loss. If the individual attained a new maximum mass (W_{max}), it was recorded for comparison with subsequent masses in the starvation submodel.

Starvation

Individuals in the model were subject to starvation mortality if they lost a predetermined proportion of their previous maximum body mass. In the model,

$$(5) \quad W_s = \text{Thresh} \cdot W_{\text{max}}$$

where W_s is the mass at which death is caused by starvation, and Thresh is the proportion of W_{max} at which an individual starved. Individuals that attained W_s for any value of W_{max} died of starvation (Letcher et al. 1996a). The starvation threshold for this model

was set to 0.53, a value that has been used for yellow perch (Fulford et al. 2006a) but is conservative in that it allows for a greater percentage of mass loss before mortality relative to values (0.58 to 0.87) used for other fish species (Letcher et al. 1996a).

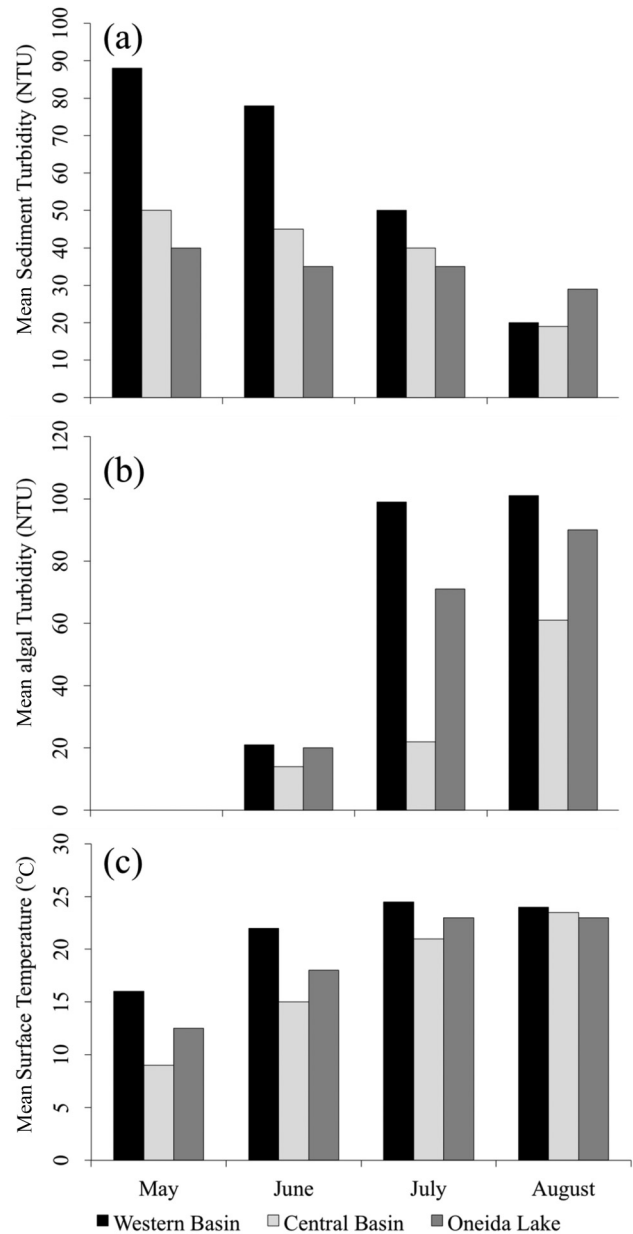
Model testing and application

Model evaluation

To evaluate the performance of our IBM, we compared model output (mean length at 124 days posthatch) with data collected in the field for three different systems: the western and central basins of Lake Erie, and Oneida Lake, New York. For each comparison, we used field observations of turbidity type, clarity, and temperature to set the parameters in the daily ingestion and bioenergetics submodels. Using these parameters, we generated model results that could be compared with corresponding field data on fish length.

Data from Lake Erie were collected by the ODNR interagency trawl surveys. For the western basin of Lake Erie, we considered the years 1987–2007, and for the central basin, the years 1990–2011. For both basins of Lake Erie, individual years were included if they had at least two observations for water clarity (Secchi depth) and surface and bottom temperatures in all months between May and September as well as fish length data from the last week of August and (or) the first 2 weeks of September. Monthly mean field observations of temperature as well as turbidity and (or) water clarity for each system were used to inform the model parameters for each year included in the comparison. In our model we used surface water temperatures for the pelagic larval stage and bottom temperatures after the ontogenetic shift to more demersal juveniles. The turbidity type was not specified in the water quality data, so to differentiate between sediment and algal turbidity, we used records of phytoplankton density and total suspended solids by date in the western basin of Lake Erie for the years 2002 through 2009 (Chaffin et al. 2011). In Lake Erie, there are two primary blooms: a spring bloom, which occurs between April and June, and a summer–fall bloom, which generally occurs between July and September. The spring bloom is primarily composed of diatoms and has a much lower intensity and shorter duration than the summer–fall bloom (Chaffin et al. 2011). The summer–fall bloom is primarily composed of buoyant cyanobacterial species, such as *Microcystis* and *Anabena* spp., which often form thick layers at or near the surface, potentially reducing light levels more than a comparable density of diatoms would (Chaffin et al. 2011). Owing to their timing, high density, and long duration, summer–fall blooms are likely to be more detrimental to fish growth than the shorter, low-intensity spring blooms; therefore, we focus on summer–fall blooms in this model. For the years that phytoplankton density data were unavailable, we needed to estimate the start date of the algal bloom. To estimate these bloom dates, we used the data from Chaffin et al. (2011) to identify environmental thresholds that best described the onset of cyanobacterial algal blooms. For the years 2002–2009, no blooms occurred when surface water temperatures were below 21 °C. When this temperature threshold was exceeded, observed Secchi depth was negatively correlated with phytoplankton density but not with sediment, suggesting that any reduction in water clarity observed in the ODNR data when surface water temperatures exceeded 21 °C was likely due to algal turbidity. This corresponds to the general pattern of turbidity observed in the western basin of Lake Erie, where sediment turbidity peaks in the spring and early summer months and algal blooms are more prominent later in the season (Figs. 2a–2c). For our IBM, an algal bloom was considered to have started if there was an observed decrease in water clarity from the ODNR data and the surface water temperature exceeded 21 °C, and it would end if the water temperature dropped below the threshold value. For both basins of Lake Erie, the hatch-out date was assumed to be 1 May, as that date generally

Fig. 2. Mean monthly values for (a) sediment turbidity, (b) algal turbidity, and (c) surface water temperatures for the western and central basins of Lake Erie and Oneida Lake for years included in the individual-based model. NTU, nephelometric turbidity unit.



falls within the first week in which temperature-days have exceeded the 90% hatch-out threshold (Guma'a 1978).

The Oneida Lake data were collected by the Cornell Biological Field Station, and we included the years 1981–2011. For Oneida Lake, sampling was conducted more frequently, which allowed us to use weekly field observations to set model parameters for each year included. Particular years were included if they contained at least one field record per week for temperature, turbidity level, and turbidity type in all months between May and September as well as mean fish masses for the 17th and 18th weeks posthatch. These masses were converted to length using regression (Schael et al. 1991) for comparison with model results. For Oneida Lake, hatch-out was assumed to be 1 week prior to the first records of 8 mm fish, which made hatch-out the last week of April or the first week of May, depending on the year.

The field-measured values for water clarity were converted to NTU values using a Secchi depth to NTU conversion equation (Table 1) to compare them with the laboratory-derived feeding rates (Table 1). Model output was obtained by running each year in each lake or basin five times, for a total of 50 000 individuals. The daily ingestion submodel was modified by using the weekly or bimonthly mean NTU values and turbidity types observed in the field. The daily records of individual length, mass, and survival status were averaged within each model run and then across the model runs to produce daily mean cohort length and survival values to allow for comparison with field data from Lake Erie and Oneida Lake.

Mean length of age-0 yellow perch at ~124 days posthatch from the field data was compared with the mean length of individuals from the model using linear regression to determine the precision with which the model predicted growth of yellow perch in conditions that mimic natural temporal variations in turbidity type and intensity. ANCOVA for parallel slopes was used to determine whether the slopes of the predicted regression lines were significantly different from 1, which would indicate a bias for over- or underprediction in the model.

Sensitivity analysis

We used the individual parameter perturbation and sensitivity calculations described in [Letcher et al. \(1996a\)](#) to test the sensitivity of our model outputs of growth and starvation mortality to changes in key parameters. We adjusted the following parameters by $\pm 10\%$ independently: larval and juvenile feeding rates in both sediment and algal turbidity, and temperature. The sensitivities were calculated as

$$(6) \quad (|y_+ - y_-|)/(y_0 \cdot 0.2)$$

where y_+ and y_- are the outputs with the individual parameters adjusted $\pm 10\%$ (five replicates), and y_0 is the mean output value (10 replicates) using the unadjusted parameter values. A sensitivity value >1 indicates that the selected parameter had a disproportionately large effect, while a value <1 indicates that the change in the individual parameter value had a less than proportional effect on the output.

Model scenarios

We designed 12 scenarios to predict age-0 yellow perch growth across a range of possible future turbidity conditions. First, we conducted “static” runs whereby four possible turbidity type-intensity combinations were held constant for the entire 124-day period: low sediment turbidity (~5 NTU), high sediment turbidity (~100 NTU), low algal turbidity, and high algal turbidity. These scenarios span the range observed in the systems and were designed to bracket the responses of both larval and juvenile fish. Growth and survivorship curves were generated for each scenario and examined to determine the relative effects of turbidity type and intensity on growth and starvation rates during the larval and juvenile stages. We also noted the number of days it took for the average individual to reach ≥ 30 mm TL and make the switch to the juvenile feeding regime. Temperature regimes for all 12 scenarios were set to the long-term mean in the western basin of Lake Erie for each week included.

Second, we developed eight dynamic scenarios that exposed yellow perch cohorts to hypothetical changes in the intensity and timing of sediment plumes and algal blooms. For these simulations, turbidity conditions were altered based on a series of environmental scenarios that were informed by locally downscaled climate change models for the Great Lakes Basin (e.g., [Mortsch and Quinn 1996](#); [Goyette et al. 2000](#)). These climate change models were used to broadly define generic scenarios that would correspond to potential changes in turbidity regime, such as an espe-

cially wet spring prolonging the sediment plumes from surface runoff, or extended periods of high temperatures and low precipitation allowing algal blooms to start earlier in the season. These dynamic scenarios included the following:

- A. A hypothetical “best-case” scenario in which the results of the static, single-condition model scenarios were used to determine a sequence of turbidity conditions that would result in maximal growth and survival at the end of the 124-day period (Scenario 5)
- B. High-intensity algal blooms (~100 NTU) lasting 2, 4, and 8 weeks during the juvenile phase (i.e., late summer) (Scenarios 6–8)
- C. A 1-week high-intensity algal bloom during the larval phase (i.e., late spring) (Scenario 9)
- D. High-sediment conditions (~100 NTU) 2, 4, and 8 weeks past the ontogenetic shift (Scenarios 10–12)

For Scenarios 6–12, time periods that were not specifically manipulated were set to the turbidity regime in Scenario 5 (i.e., the best-case scenario). Growth and survivorship curves were generated for each experimental perturbation and compared with the ideal growth curve to determine the reduction in growth, potential delay of the ontogenetic shift, and changes in the starvation mortality potential.

Results

Model evaluation

Our IBM explained a majority of the variance in yellow perch length for the data sets from the western and central basins of Lake Erie and Oneida Lake, with R^2 values ranging from 0.611 to 0.742 (Figs. 3a–3c). The slope of the regression line for the western basin was not significantly different from 1 (ANCOVA test for parallel slopes, $df = 15$, $P > 0.068$), indicating that model results for this system were balanced between over- and underprediction of observed fish lengths, but the mean predicted length was higher than observed mean values by an average of 6%. The slopes of the regression lines for the central basin of Lake Erie and for Oneida Lake, however, were significantly different from 1 (ANCOVA test for parallel slopes, $df = 10$, $P = 0.037$ and $df = 31$, $P = 0.021$, respectively). For the central basin, the model overpredicted mean length by 12% when observed individuals were, on average, smaller than 73 mm, and underpredicted by 8% for years in which mean length exceeded 73 mm. For Oneida Lake, the model overpredicted length by 11%, on average. The three underpredictions for Oneida Lake were for the years with the greatest observed lengths. It should be noted that while the long-term model fit for these systems is good, the within-year differences between predicted and observed lengths could represent a biologically significant amount of variation.

The patterns of starvation mortality of yellow perch predicted by the model were similar among all years and among all systems. Starvation mortality was highly size dependent, with the greatest daily mortality rates occurring within days of each other, regardless of year or system. Daily mortality rates peaked between 7 and 12 days posthatch and then rapidly declined until starvation mortality rates neared zero for individuals larger than 50 mm in length. The only significant starvation events for larger individuals occurred in years with prolonged, high-intensity algal blooms; however, these rates never exceeded 5% per day and were far less than the peak mortality rates of nearly 20% per day for smaller size classes.

Sensitivity analysis

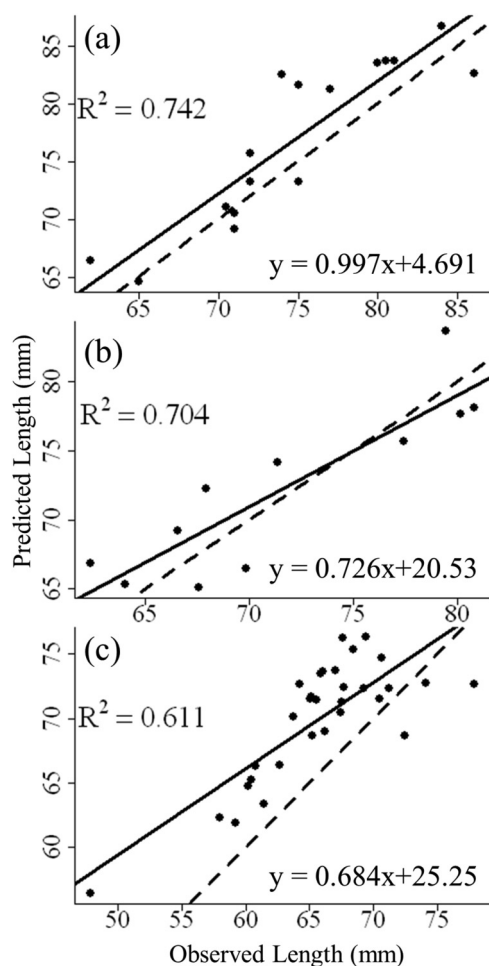
The sensitivity analysis indicated that both growth and starvation mortality were strongly influenced by algal turbidity during the larval phase (Table 2). Juvenile feeding rates in algal turbidity were the second most important determinant of growth but had

Table 2. Proportional sensitivities of the five parameters tested for both growth and starvation mortality.

Rank	Growth		Starvation	
	Parameter	Sensitivity	Parameter	Sensitivity
1	Larval algal turbidity	2.89	Larval algal turbidity	1.59
2	Juvenile algal turbidity	2.09	Larval sediment turbidity	1.41
3	Larval sediment turbidity	1.52	Juvenile algal turbidity	1.39
4	Temperature	0.87	Juvenile sediment turbidity	0.56
5	Juvenile sediment turbidity	0.71	Temperature	0.30

Note: A value >1 indicates a disproportionately large effect on the response variable (growth or starvation), and a value <1 indicates a less than proportional effect.

Fig. 3. Linear regressions of model predictions versus observed lengths (mm) 124 days posthatch for (a) the western basin of Lake Erie, (b) the central basin of Lake Erie, and (c) Oneida Lake, New York. The dashed lines have a slope of 1.



less effect on starvation mortality, indicating that while algal turbidity impaired the ability of juveniles to grow, the larger size of juveniles in the model made them less susceptible to starvation mortality. Sediment turbidity was important for both growth and starvation during the larval phase, but not for juveniles. Temperature had the lowest proportional effect on starvation and, surprisingly, had a proportional sensitivity <1 for growth as well. This relatively low proportional effect of temperature, particularly on growth, may have occurred because a 10% change in temperature would be within the normal daily range of conditions encountered. To produce proportional effects similar to algal turbidity, a change in temperature of more than 25%, or about 6 °C, would be required.

Model scenarios

Growth, timing of ontogenetic shifts, and starvation mortality differed substantially among the hypothetical IBM scenarios that simulated a static turbidity type and intensity. Cohorts modeled with high sediment turbidity had the highest larval growth rate and underwent the ontogenetic shift 5 days earlier, on average, than cohorts modeled with low sediment turbidity (Fig. 4a). However, the larval growth advantage did not continue into the juvenile phase when sediment turbidity remained high; the low-sediment fish quickly surpassed the high-sediment fish in length. Fish produced in low-sediment conditions were 25% larger than those produced in high-sediment conditions (82 versus 63 mm, Fig. 4a) at 124 days. Higher total growth, however, did not confer higher survival, as high-sediment conditions produced the lowest starvation mortality rate (Fig. 4b).

Fish in algal turbidity grew more slowly than those in sediment turbidity (Fig. 4a). Constant low-algae conditions produced fish that averaged 38 mm in length and that did not make the ontogenetic shift until approximately 100 days posthatch (Fig. 4a). Cohorts modeled with continuous high-algae conditions averaged only 24 mm in length, and these individuals generally never achieved the size associated with the ontogenetic shift (Fig. 4a). The algal cohorts also had significantly increased starvation mortality when compared with the sediment cohorts. Individuals in low-algae conditions experienced nearly 80% mortality, and those in high-algae conditions experienced over 99% mortality owing to starvation (Fig. 4b). Because survival was very poor in the high-algae conditions, additional runs were completed to improve the sample size of survivors to estimate growth.

Using the relationships observed in the static-condition scenarios, we developed a “best growth” model that would represent growth of yellow perch under ideal turbidity conditions. The best growth model applied high sediment turbidity until the mean cohort length exceeded the threshold to switch to the juvenile feeding regime. Turbidity was then switched to low sediment to maximize juvenile-stage growth through the remaining days. No algal turbidity was applied to this group, as even low levels of algal turbidity reduced growth rates in both developmental stages. The cohorts in this model averaged 96 mm in length at 124 days posthatch, which was approximately 4% larger than the largest observed length (western basin, 1987, 92.4 mm, Fig. 3a).

Our algal turbidity scenarios, which simulated algal blooms lasting for 2, 4, and 8 weeks at the end of the season, produced reductions in growth of 11%, 23%, and 45.5%, respectively, compared with the best-case scenario (Fig. 5a). Additionally, starvation mortality increased from <10% in the best growth model to >60% in the 8-week algal bloom treatment (Fig. 5b). A 1-week algal bloom during the second week of the larval stage produced results similar to a 2-week bloom during the juvenile phase, with a 10% reduction in mean cohort length (Fig. 5a) and starvation mortality of 19% (Fig. 5b). An algal bloom during the larval phase also delayed the ontogenetic shift in these cohorts by approximately 12 days (Fig. 5a).

Our IBM showed that prolonged sediment turbidity after the ontogenetic shift had less severe effects than algal turbidity but still produced reductions in growth and increases in starvation

Fig. 4. Predicted (a) growth (measured as length) and (b) survivorship curves for yellow perch cohorts modeled with four static turbidity conditions for 124 days posthatch. The four scenarios were low sediment, high sediment, low algae, and high algae. The grey box denotes fish that have not yet made the ontogenetic shift.

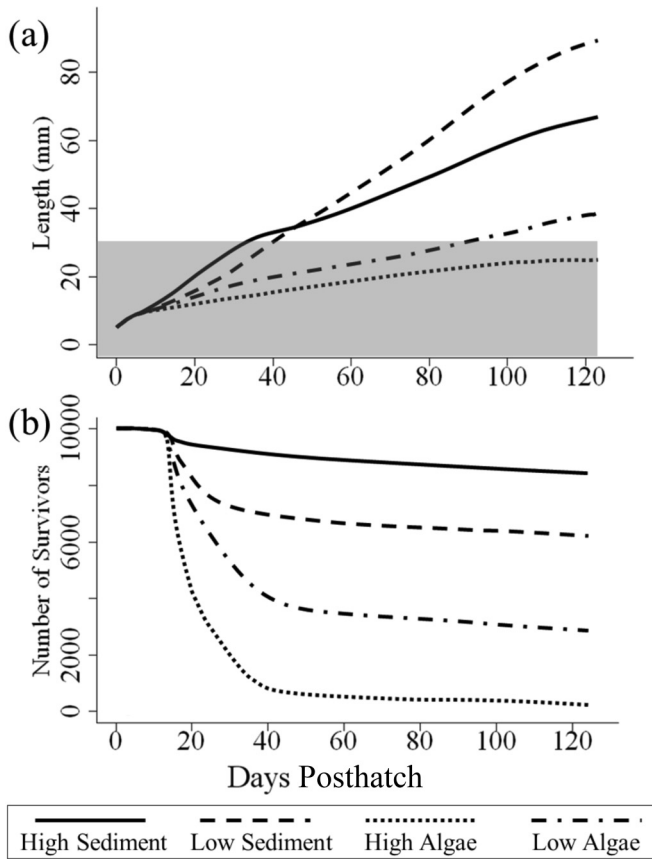
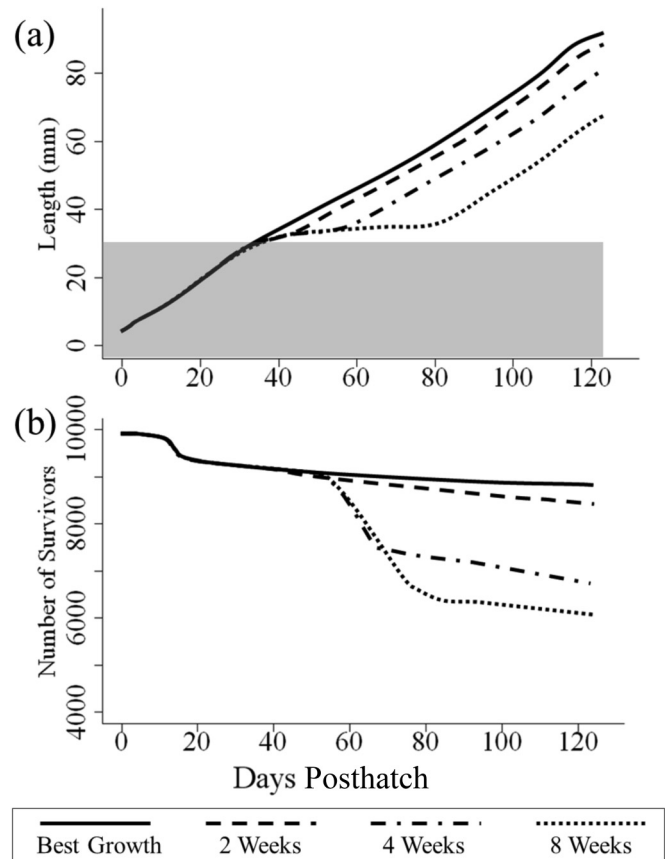


Fig. 5. Predicted (a) growth (measured as length) and (b) survivorship curves for the best growth model and models of high-algae conditions for the final 2 weeks, 4 weeks, and 8 weeks of 124 days and high-algae conditions for 1 week during the larval phase. The grey box denotes fish that have not yet made the ontogenetic shift.



mortality when compared with the best growth model. The 2-week extension of high-sediment conditions produced only a 3% reduction in mean cohort length at 124 days posthatch (Fig. 6a) and a 2% increase in starvation mortality (Fig. 6b). The 4-week extension of high-sediment conditions produced a 12.5% reduction in growth (Fig. 6a) and a 22% increase in starvation mortality (Fig. 6b); these results are similar to those obtained with a 2-week algal bloom late in the season (Figs. 5a and 5b). The 8-week sediment turbidity treatment resulted in a 26% reduction in mean cohort length (Fig. 6a) and a 28% increase in starvation mortality (Fig. 6b).

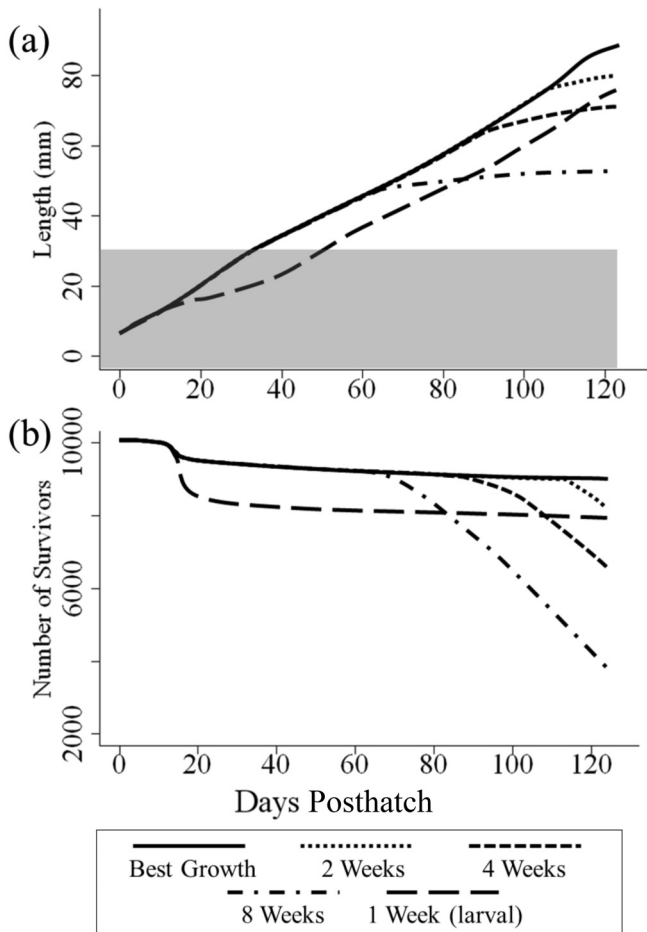
Discussion

Our bioenergetics IBM showed that turbidity-dependent consumption rates and temperature are key components in determining growth and starvation mortality of age-0 yellow perch, thereby linking fish production to land-based processes that influence water clarity. Our model validation showed that in Lake Erie and Oneida Lake, the visual environment encountered by age-0 yellow perch, and its effects on prey consumption, explained substantial variability in growth. Furthermore, the results of our water-clarity scenarios suggested that the timing and duration of sediment turbidity may have a strong influence on larval fish growth, as early-season but not late-season sediment turbidity increased larval growth and reduced starvation mortality. In contrast, there were no developmental-stage-dependent effects with algal turbidity, as growth decreased and starvation mortality increased for both larval and juvenile fish in our model, even at low algal concentrations. Recruitment of a cohort is strongly influ-

enced by growth and survival of age-0 individuals (Miller et al. 1988; Madenjian et al. 1996; Schlosser 1998; MacKenzie 2000). Therefore, our results help connect the potential year class success of an economically important fish species to the timing and intensity of sediment plumes and algal blooms, which are often due to anthropogenic actions (Nicholls and Hopkins 1993; Anderson et al. 2002; Otero and Siegel 2004).

While our model was successful at explaining mean fish length at the end of the growing season in several systems, other factors likely contribute variability to fish growth. For example, density-dependent growth may explain some of the deviation of our model results from observed growth (Sable and Rose 2010), particularly for Oneida Lake, a system in which yellow perch has been shown to exhibit strongly density-dependent growth (Mayer et al. 2000; Irwin et al. 2009). Our model consistently overpredicts size at date for this system, which is consistent with a system in which there are high levels of intraspecific competition for prey items. Size-dependent predation is another factor not considered in our model that can shape size distributions of yellow perch, favoring the survival of the fastest-growing individuals (Brandt et al. 1987; Post and Evans 1989; Rice et al. 1993). However, the effect of size-dependent predation mortality may be reduced in our models. Size-dependent predation and starvation mortality interact through compensatory processes (Letcher et al. 1996a) such that many of the individuals in our models that succumbed to starvation would likely be in poor condition and would have been consumed by predators prior to reaching their starvation threshold. It is often difficult to identify the cause of mortality in a natural system, and

Fig. 6. (a) Growth and (b) mortality curves for the best growth model and for individuals exposed to high-sediment conditions for 2 weeks, 4 weeks, and 8 weeks after the ontogenetic shift. The grey box denotes fish that have not yet made the ontogenetic shift.



so determining an actual starvation mortality rate for comparison is not feasible. However, the estimates produced with this model are similar to the starvation mortality rates and timing of starvation events found in other modeling efforts (Letcher et al. 1996a, 1996b). Additionally, spring diatom blooms are often associated with increased zooplankton densities, which may offset some of the negative impacts of the reduction in visual foraging ability in larval fish (Kalf and Knoechel 1978). Because of the short duration and low intensities of these blooms, the positive effect of sediment turbidity during this time is likely a more significant factor in the growth and survival of larval fish. While there are multiple sources of variability not included in our model that may influence our results, we believe the inclusion of natural variability in fish size distributions and zooplankton densities, in conjunction with the laboratory-derived feeding rates, makes this a robust model for predicting the growth and starvation mortality potential of age-0 yellow perch.

The effects of sediment turbidity on yellow perch growth in our model depended primarily on the developmental stage of the individuals. While increased fish growth has been linked to increased water clarity (Mayer et al. 2000; Idrisi et al. 2001; Lathrop et al. 2002), these studies often focus on a specific life stage and so do not distinguish how turbidity may affect a succession of developmental stages of fish. In our model, high sediment turbidity increased the feeding ability and thus the growth rate of larval fish, and these fish underwent their ontogenetic shift 4 days earlier than their low-sediment counterparts. The rapid early growth

experienced by larvae in high-sediment conditions also resulted in lower starvation mortality and thus may contribute to higher survival and numerically larger cohorts. The increased survival in high-sediment conditions supports previous studies that have shown that both higher survival (Reichert et al. 2010) and higher abundances (Manning et al. 2013) of age-0 yellow perch are associated with the sediment-rich outflow of the Maumee River into the western basin of Lake Erie. Therefore, larval yellow perch that experience an early-season sediment plume are likely to grow faster than fish in clear water and will also be less vulnerable to predation because predators, with relatively large reactive distances, may forage less efficiently in turbid water.

While our model predicts that sediment plumes are beneficial to the growth and survival of larval yellow perch, late-season plumes may reduce growth and increase starvation during the juvenile phase. Yellow perch are often associated with river mouths, which are historically turbid systems (Mulder et al. 1998; Moorhead et al. 2008), particularly during spring runoff. The higher larval growth rate in high-sediment conditions may be indicative of natural adaptation to historic turbidity regimes in these systems that have higher sediment turbidity during the spring. However, anthropogenic activity has increased sediment transportation in many systems (McDonnell and Pickett 1990; Waters 1995; Li and Zhang 1998) and has likely extended the duration and altered the timing of high-sediment conditions (Uncles et al. 1994; Prosser et al. 2001; Sutherland et al. 2002; Paul and Meyer 2008). This anthropogenic alteration of sediment plume dynamics has the potential to change the role of river-associated sediment plumes, with the implication that longer periods of sediment turbidity may reduce growth rates in juvenile fish and ultimately reduce survival.

In contrast to the developmental-stage-dependent effects of sediment turbidity, algal turbidity reduced foraging ability and thus reduced growth and increased starvation of both larval and juvenile fish in our model. For larval fish, algal turbidity has the potential to reduce growth and delay the ontogenetic shift (Wu and Culver 1992; Graeb et al. 2006), which can have serious repercussions for the growth and survival of age-0 fish as well as the long-term success of a population (Forseth et al. 1994; Olson 1996; Post 2003). However, this negative effect may only occur in a worst-case scenario in which cyanobacterial blooms begin to replace the diatom blooms generally seen in Lake Erie and Oneida Lake during the larval stage of development. Algal blooms during the juvenile phase also reduced growth, but perhaps more importantly, they increased susceptibility to starvation in these larger fish. However, age-0 fish may experience lower predation mortality when algal turbidity is high. For example, in western Lake Erie at the end of August, age-0 yellow perch were more abundant but smaller in highly turbid areas, suggesting a turbidity-mediated trade-off between growth and survival (Manning et al. 2013). Therefore, the effects of algal blooms on recruitment are likely complex. Blooms should increase rates of starvation and lower the condition of surviving juveniles, thereby increasing overwinter mortality (Post and Evans 1989) and size-based vulnerability to predation (Rice et al. 1993; Lundvall et al. 1999). However, predators should also forage inefficiently during algal blooms, possibly contributing to a pattern of small but abundant fish in turbid water (Irwin et al. 2009; Reichert et al. 2010; Manning et al. 2013). Larval fish may also experience some benefit from increased zooplankton densities during the low-intensity spring blooms. Ultimately, high mortality and poor condition of fish are associated with large algal blooms (Burkholder 1998; Malakoff 1998; Kempton et al. 2002), and it is likely that the balance of effects of algal blooms on yellow perch and other fish populations is highly negative.

Our model suggests that the timing and persistence of sediment plumes and algal blooms can drastically alter the growth potential and starvation mortality of a yellow perch cohort. The timing and duration of algal blooms in particular can substantially re-

duce the growth and survival of a cohort and ultimately its recruitment success. Even short-duration algal blooms during the larval phase can significantly reduce the growth of a cohort. Long-duration blooms during the juvenile phase (mid- to late summer) have become increasingly frequent in many systems and can also have dire consequences for a population. While short-duration sediment plumes early in the season may not have a large effect on a cohort, plumes that occur later in the season, owing to resuspension events or dredging and dumping, could have a much larger negative effect. Sediment plumes and algal blooms are tied to land use and can be altered through directed management actions in the watershed. Therefore, the potentially negative effects of increased turbidity on fish should be considered when management actions are planned that may alter the turbidity regime of a system.

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References

- Allan, J.D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annu. Rev. Ecol. Syst.* **35**: 257–284. doi:10.1146/annurev.ecolsys.35.120202.110122.
- Anderson, D.M., Gilbert, P.M., and Burkholder, J.M. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuar. Coasts*, **25**: 704–726. doi:10.1007/BF02804901.
- Benfield, M.C., and Minello, T.J. 1996. Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environ. Biol. Fishes*, **46**: 211–216. doi:10.1007/BF00005223.
- Bergenius, M.A.J., Meekan, M.G., Robertson, D.R., and McCormick, M.I. 2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecologia*, **131**: 521–525. doi:10.1007/s00442-002-0918-4.
- Boehlert, G.W., and Morgan, J.B. 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasii*. *Hydrobiologia*, **123**: 161–170. doi:10.1007/BF00018978.
- Brandt, S.B., Mason, D.M., Macneill, D.B., Coates, T., and Gannon, J.E. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. *Trans. Am. Fish. Soc.* **116**: 641–645. doi:10.1577/1548-8659(1987)116<641:PBAOLO>2.CO;2.
- Bridgeman, T.B., and Penamon, W.A. 2010. *Lyngbya wollei* in western Lake Erie. *J. Gt. Lakes Res.* **36**: 167–171. doi:10.1016/j.jglr.2009.12.003.
- Bridgeman, T.B., Chaffin, J.D., Kane, D.D., Conroy, J.D., Panek, S.E., and Armenio, P.M. 2012. From River to Lake: Phosphorus partitioning and algal community compositional changes in Western Lake Erie. *J. Gt. Lakes Res.* **38**: 90–97. doi:10.1016/j.jglr.2011.09.010.
- Burkholder, J.M. 1998. Implications of harmful microalgae and heterotrophic dinoflagellates in management of sustainable marine fisheries. *Ecol. Appl.* **8**: S37–S62. doi:10.1890/1051-0761(1998)8[S37:IOHMAH]2.0.CO;2.
- Chaffin, J.D., Bridgeman, T.B., Heckathorn, S.A., and Mishra, S. 2011. Assessment of *Microcystis* growth rate potential and nutrient status across a trophic gradient in western Lake Erie. *J. Gt. Lakes Res.* **37**: 92–100. doi:10.1016/j.jglr.2010.11.016.
- Clady, M.D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. *J. Fish. Board Can.* **33**(9): 1887–1893. doi:10.1139/f76-241.
- Cooper, S.R. 1995. Chesapeake Bay Watershed historical land-use: impact on water-quality and diatom communities. *Ecol. Appl.* **5**: 703–723. doi:10.2307/1941979.
- Crowder, L.B., McDonald, M.E., and Rice, J.A. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. *Can. J. Fish. Aquat. Sci.* **44**(S2): 141–147. doi:10.1139/f87-317.
- De Robertis, A., Ryer, C.H., Veloza, A., and Brodeur, R.D. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Can. J. Fish. Aquat. Sci.* **60**(12): 1517–1526. doi:10.1139/f03-123.
- Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos*, **53**: 207–214. doi:10.2307/3566064.
- Dyble, J., Fahnenstiel, G.L., Litaker, R.W., Millie, D.F., and Tester, P.A. 2008. Microcystin concentrations and genetic diversity of *Microcystis* in the lower Great Lakes. *Environ. Toxicol.* **23**: 507–516. doi:10.1002/tox.20370. PMID: 18247416.
- Forseth, T., Ugedal, O., and Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of arctic charr, *Salvelinus alpinus*. *J. Anim. Ecol.* **63**: 116–126. doi:10.2307/5588.
- Friedl, G., and Wüest, A. 2002. Disrupting biogeochemical cycles — consequences of damming. *Aquat. Sci.* **64**: 55–65. doi:10.1007/s00027-002-8054-0.
- Fulford, R.S., Rice, J.A., Miller, T.J., and Binkowski, F.P. 2006a. Elucidating patterns of size-dependent predation on larval yellow perch (*Perca flavescens*) in Lake Michigan: an experimental and modeling approach. *Can. J. Fish. Aquat. Sci.* **63**(1): 11–27. doi:10.1139/f05-195.
- Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., Dettmers, J.M., and Belonger, B. 2006b. Foraging selectivity by larval yellow perch (*Perca flavescens*): implications for understanding recruitment in small and large lakes. *Can. J. Fish. Aquat. Sci.* **63**(1): 28–42. doi:10.1139/f05-196.
- Gallegos, C.L., Correll, D.L., and Pierce, J.W. 1990. Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. *Limnol. Oceanogr.* **35**: 1486–1502. doi:10.4319/lo.1990.35.7.1486.
- Gordon, T.C. 1982. Instantaneous growth rates and distribution of larval fish in the vicinity of Locust Point, western Lake Erie. CLEAR Technical Report.
- Goyette, S., McFarlane, N.A., and Flato, G.M. 2000. Application of the Canadian Regional Climate Model to the Laurentian Great Lakes region: implementation of a lake model. *Atmosphere-Ocean*, **38**: 481–503. doi:10.1080/07055900.2000.9649657.
- Graeb, B.D.S., Mangan, M.T., Jolley, J.C., Wahl, D.H., and Dettmers, J.M. 2006. Ontogenetic changes in prey preference and foraging ability of yellow perch: insights based on relative energetic return of prey. *Trans. Am. Fish. Soc.* **135**: 1493–1498. doi:10.1577/T05-063.1.
- Guma'a, S.A. 1978. The effects of temperature on the development and mortality of eggs of perch, *Perca fluviatilis*. *Freshw. Biol.* **8**: 221–227. doi:10.1111/j.1365-2427.1978.tb01443.x.
- Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia*, **32**: 79–99. doi:10.2216/i0031-8884-32-2-79.1.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., and Hatzioiols, M.E. 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, **318**: 1737–1742. doi:10.1126/science.1152509. PMID: 18079392.
- Houde, E.D. 1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea bream *Archosargus rhomboidalis* (L.) (Sparidae). *J. Fish Biol.* **7**: 115–127. doi:10.1111/j.1095-8649.1975.tb04581.x.
- Idrisi, N., Mills, E.L., Rudstam, L.G., and Stewart, D.J. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* **58**(7): 1430–1441. doi:10.1139/f01-070.
- Irwin, B.J., Rudstam, L.G., Jackson, J.R., VanDeValk, A.J., Forney, J.L., and Fitzgerald, D.G. 2009. Depensatory mortality, density-dependent growth, and delayed compensation: disentangling the interplay of mortality, growth and density during early life stages of yellow perch. *Trans. Am. Fish. Soc.* **138**: 99–110. doi:10.1577/T07-256.1.
- Johnson, S., and Rejmánková, E. 2005. Impacts of land use on nutrient distribution and vegetation composition of freshwater wetlands in northern Belize. *Wetlands*, **25**: 89–100. doi:10.1672/0277-5212(2005)025[0089:IOLUON]2.0.CO;2.
- Kalff, J., and Knoechel, R. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. *Annu. Rev. Ecol. Syst.* **9**: 475–495. doi:10.1146/annurev.es.09.110178.002355.
- Kempton, J.W., Lewitus, A.J., Deeds, J.R., McHugh Law, J., and Place, A.R. 2002. Toxicity of *Karlodinium micrum* (Dionophyceae) associated with a fish kill in a South Carolina brackish retention pond. *Harmful Algae*, **1**: 233–241. doi:10.1016/S1568-9883(02)00015-X.
- Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* **34**(10): 1922–1935. doi:10.1139/f77-258.
- Landsberg, J.H. 2002. The effects of harmful algal blooms on aquatic organisms. *Rev. Fish. Sci.* **10**: 113–390. doi:10.1080/20026491051695.
- Lathrop, R.C., Johnson, B.M., Johnson, T.B., Vogelsang, M.T., Carpenter, S.R., Hrabik, T.R., Kitchell, J.F., Magnuson, J.J., Rudstam, L.G., and Stewart, R.S. 2002. Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project. *Freshw. Biol.* **47**: 2410–2424. doi:10.1046/j.1365-2427.2002.01011.x.
- Letcher, B.H., Rice, J.A., Crowder, L.B., and Binkowski, F.P. 1996a. Size-dependent effects of continuous and intermittent feeding on starvation time and mass loss in starving yellow perch larvae and juveniles. *Trans. Am. Fish. Soc.* **125**: 14–26. doi:10.1577/1548-8659(1996)125<0014:SDEOCA>2.3.CO;2.
- Letcher, B.H., Rice, J.A., Crowder, L.B., and Rose, K.A. 1996b. Variability in sur-

- vival of larval fish: disentangling components with a generalized individual-based model. *Can. J. Fish. Aquat. Sci.* **53**(4): 787–801. doi:10.1139/f95-241.
- Li, J., and Zhang, C. 1998. Sediment resuspension and implications for turbidity maximum in the Changjiang Estuary. *Mar. Geol.* **148**: 117–124. doi:10.1016/S0025-3227(98)00003-6.
- Lundvall, D., Svanbäck, R., Persson, L., and Byström, P. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Can. J. Fish. Aquat. Sci.* **56**(7): 1285–1292. doi:10.1139/f99-058.
- MacKenzie, B.R. 2000. Turbulence, larval fish ecology and fisheries recruitment: a review of field studies. *Oceanol. Acta*, **23**: 357–375. doi:10.1016/S0399-1784(00)00142-0.
- Madenjian, C.P., Tyson, J.T., Knight, R.L., Kershner, M.W., and Hansen, M.J. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. *Trans. Am. Fish. Soc.* **125**: 821–830. doi:10.1577/1548-8659(1996)125<0821:FYGRAM>2.3.CO;2.
- Malakoff, D. 1998. Death by suffocation in the Gulf of Mexico. *Science*, **281**: 190–192. doi:10.1126/science.281.5374.190.
- Manning, N.F., Mayer, C.M., Bossenbroek, J.M., and Tyson, J.T. 2013. Effects of water clarity on the length and abundance of age-0 yellow perch in the Western Basin of lake Erie. *J. Gt. Lakes Res.* **39**: 295–302. doi:10.1016/j.jglr.2013.03.010.
- Mayer, C.M., VanDeValk, A.J., Forney, J.L., Rudstam, L.G., and Mills, E.L. 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the establishment of zebra mussels (*Dreissena polymorpha*). *Can. J. Fish. Aquat. Sci.* **57**(4): 742–754. doi:10.1139/f00-009.
- McDonnell, M.J., and Pickett, S.T.A. 1990. Ecosystem structure and function along urban–rural gradients: an unexploited opportunity for ecology. *Ecology*, **71**: 1232–1237. doi:10.2307/1938259.
- McMahon, T.E., and Holanov, S.H. 1995. Foraging success of largemouth bass at different light intensities: implications for time and depth of feeding. *J. Fish Biol.* **46**: 759–767. doi:10.1006/jfbi.1995.0069.
- Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* **45**(9): 1657–1670. doi:10.1139/f88-197.
- Mills, E.L., Sherman, R., and Robson, D.S. 1989. Effect of zooplankton abundance and body size on growth of age-0 yellow perch (*Perca flavescens*) in Oneida Lake, New York, 1975–86. *Can. J. Fish. Aquat. Sci.* **46**(5): 880–886. doi:10.1139/f89-113.
- Moorhead, D., Bridgeman, T.B., and Morris, J. 2008. Changes in water quality of Maumee Bay 1928–2003. In *Aquatic ecosystem health and management society*. Edited by M. Munwar and R.T. Heath. pp. 123–158.
- Mortsch, L.D., and Quinn, F.H. 1996. Climate change scenarios for Great Lakes Basin ecosystem studies. *Limnol. Oceanogr.* **41**: 903–911. doi:10.4319/lo.1996.41.5.0903.
- Mulder, T., Syvitski, J.P.M., and Skene, K.I. 1998. Modeling of erosion and deposition by turbidity currents generated at river mouths. *J. Sediment. Res.* **68**: 124–137. doi:10.2110/jsr.68.124.
- Munk, P., and Kjørboe, T. 1985. Feeding behaviour and swimming activity of larval herring (*Clupea harengus*) in relation to copepod nauplii. *Mar. Ecol. Progr. Ser.* **24**: 15–21. doi:10.3354/meps024015.
- Nicholls, K.H., and Hopkins, G.J. 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. *J. Gt. Lakes Res.* **19**: 637–647. doi:10.1016/S0380-1330(93)71251-4.
- Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. *Ecology*, **77**: 179–190. doi:10.2307/2265667.
- Otero, M.P., and Siegel, D.A. 2004. Spatial and temporal characteristics of sediment plumes and phytoplankton blooms in the Santa Barbara Channel. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **51**: 1129–1149. doi:10.1016/j.dsr2.2004.04.004.
- Parrish, D.L., and Margraf, F.J. 1994. Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. *J. Freshw. Ecol.* **9**: 29–35. doi:10.1080/02705060.1994.9664424.
- Paul, M.J., and Meyer, J.L. 2008. Streams in the urban landscape. *Annu. Rev. Ecol. Syst.* **32**: 333–365. doi:10.1146/annurev.ecolsys.32.081501.114040.
- Pfister, L., Kwadijk, J., Musy, A., Bronstert, A., and Hoffmann, L. 2004. Climate change, land use change and runoff prediction in the Rhine–Meuse basins. *River Res. Appl.* **20**: 229–241. doi:10.1002/rra.775.
- Post, D.M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology*, **84**: 1298–1310. doi:10.1890/0012-9658(2003)084[1298:IVITTO]2.0.CO;2.
- Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetics models. *Can. J. Fish. Aquat. Sci.* **47**(3): 554–560. doi:10.1139/f90-063.
- Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Can. J. Fish. Aquat. Sci.* **46**(11): 1958–1968. doi:10.1139/f89-246.
- Prosser, I.P., Rutherford, I.D., Olley, J.M., Young, W.J., Wallbrink, P.J., and Moran, C.J. 2001. Large-scale patterns of erosion and sediment transport in river networks, with examples from Australia. *Mar. Freshw. Res.* **52**: 81–100. doi:10.1071/MF00033.
- Radke, R., and Gaupisch, A. 2005. Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): possible implications for fish community structure in lakes. *Naturwissenschaften*, **92**: 91–94. doi:10.1007/s00114-004-0596-7.
- Reichert, J.M., Fryer, B.J., Pangle, K.L., Johnson, T.B., Tyson, J.T., Drelich, A.B., and Ludsins, S.A. 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. *Can. J. Fish. Aquat. Sci.* **67**(6): 987–1004. doi:10.1139/F10-036.
- Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A.S., and De Angelis, D.L. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Can. J. Fish. Aquat. Sci.* **50**(1): 133–142. doi:10.1139/f93-015.
- Rose, K.A., Rutherford, E.S., McDermot, D.S., Forney, J.L., and Mills, E.L. 1999. Individual-based model of yellow perch and walleye populations in Oneida Lake. *Ecol. Monogr.* **69**: 127–154. doi:10.1890/0012-9615(1999)069[0127:IBMOYP]2.0.CO;2.
- Sable, S.E., and Rose, K.A. 2010. Predicting yellow perch population responses using a density-dependent age-structured matrix projection model: how many annual data points are needed? *Trans. Am. Fish. Soc.* **139**: 1857–1871. doi:10.1577/T09-201.1.
- Schael, D.M., Rudstam, L.G., and Post, J.R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*) and black crappie (*Pomoxis nigromaculatus*). *Can. J. Fish. Aquat. Sci.* **48**(10): 1919–1925. doi:10.1139/f91-228.
- Schloesser, D.W., and Nalepa, T.F. 2001. Changing abundance of *Hexagenia* mayfly nymphs in western Lake Erie of the Laurentian Great Lakes: impediments to assessment of lake recovery? *Int. Rev. Hydrobiol.* **86**: 87–103.
- Schlosser, I.J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia*, **113**: 260–268. doi:10.1007/s004420050377.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* **60**: 1129–1157.
- Sutherland, A.B., Meyer, J.L., and Gardiner, E.P. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshw. Biol.* **47**: 1791–1805. doi:10.1046/j.1365-2427.2002.00927.x.
- Turesson, H., and Brönmark, C. 2007. Predator–prey encounter rates in freshwater piscivores: effects of prey density and water transparency. *Oecologia*, **153**: 281–290. doi:10.1007/s00442-007-0728-9.
- Tyson, J.T., and Knight, R.L. 2001. Response of yellow perch to changes in the benthic invertebrate community of Western Lake Erie. *Trans. Am. Fish. Soc.* **130**: 766–782. doi:10.1577/1548-8659(2001)130<0766:ROYPTC>2.0.CO;2.
- Uncles, R.J., Barton, M.L., and Stephens, J.A. 1994. Seasonal variability of fine-sediment concentrations in the turbidity maximum region of the Tamar Estuary. *Estuar. Coast. Shelf Sci.* **38**: 19–39. doi:10.1006/ecss.1994.1002.
- Wahl, C.M., Mills, E.L., McFarland, W.N., and DeGisi, J.S. 1993. Ontogenetic changes in prey selection and visual acuity of the yellow perch, *Perca flavescens*. *Can. J. Fish. Aquat. Sci.* **50**(4): 743–749. doi:10.1139/f93-085.
- Waters, T.F. 1995. Sediment in streams. In *Sources, biological effects, and control*. American Fisheries Society Monograph.
- Wellington, C.G., Mayer, C.M., Bossenbroek, J.M., and Stroh, N.A. 2010. Effects of turbidity and prey density on the foraging success of age 0 year yellow perch (*Perca flavescens*). *J. Fish Biol.* **76**: 1729–1741. doi:10.1111/j.1095-8649.2010.02612.x.
- Wu, L., and Culver, D.A. 1992. Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): a size-related response to zooplankton density. *Can. J. Fish. Aquat. Sci.* **49**(9): 1932–1937. doi:10.1139/f92-214, 10.1139/f92-214.
- Yang, Z., and Kong, F. 2012. Formation of large colonies: a defense mechanism of *Microcystis aeruginosa* under continuous grazing pressure by flagellate *Ochromonas* sp. *J. Limnol.* **71**: e5. doi:10.4081/jlimnol.2012.e5.