

TRACE Documentation:
Comprehensive aquatic systems model (CASMo_c)
for
Off-channel habitats

Steven M. Bartell
Cardno, Inc.
Greenback, TN 37742

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1. MODEL DESCRIPTION

1.1. Overview

The purpose of this report is to describe the Comprehensive Aquatic Systems Model (CASM) in a manner consistent with the TRACE reporting (Grimm et al. 2014).

1.1.1. Purpose

The CASM_{OC} is a version of the Comprehensive Aquatic Systems Model (CASM) developed to simulate the population dynamics of the Topeka shiner (*Notropis topeka*) and associated food web within a generalized Iowa off-channel (i.e., oxbow) habitat. The CASM_{OC} addresses the general biology and ecology of the Topeka shiner with an emphasis on characterizing the effects of competition, predation, and a dynamic physical-chemical oxbow environment on the biomass production of this endangered species. Additionally, the direct effects (effects on survival, growth or reproduction on this fish) and indirect (food web) effects of pesticides (e.g., benzovindiflupyr) and other environmental stressors (e.g., temperature) can be addressed by the CASM_{OC}. The CASM_{OC} also provides a coherent computational platform to examine population viability (colonization, sustainability, resilience) for Topeka shiner in oxbow and other off-channel habitats. The CASM_{OC} derives from the CASM_{TS} developed previously to examine the population dynamics of the Topeka shiner in Midwestern headwater pools (Bartell et al., 2019).

The CASM_{OC} has been developed to interact with an individual-based model (TS-IBM) also developed to model the populations dynamics of Topeka shiner (Schmolke et al., 2019.). The overall CASM approach is the same as used by the combination of the TS-IBM and the CASM_{TS} (Bartell et al. 2019, Schmolke et al. 2019). The major modifications for the CASM_{OC} include re-design of the food web to include populations representative of off-channel (e.g., oxbow) environments, specification of corresponding trophic interactions, and development of environmental input data representative of a generalized Iowa oxbow ecosystem. Using a hybrid modeling approach, the CASM_{OC} can provide daily values of prey biomass for the Topeka shiner TS-IBM. The two models can also be computationally linked and executed in tandem, where the TS-IBM provides daily biomass values of adult Topeka shiner to the CASM_{OC}. The CASM_{OC} computed the food web implications of the Topeka shiner biomass and communicates Topeka shiner prey biomass values back to the TS-IBM.

The CASM_{OC} has been constructed to explicitly examine the implications of parameter uncertainty and environmental variability on modeled impacts of environmental stressors (e.g., water temperature, pesticides).

1.1.2. Entities, state variables and scale

The following describes the derivation of the fish assemblage and other model attributes used in the hybrid modeling for off-channel habitats, primarily oxbows. The approach leverages the previous Waterborne (Nick Green) summary of Bakevich et al. (2013) and uses the 2016-2017 relative abundance data for Iowa and Minnesota oxbows reported by Bybel et al. (2019) and the Simpson (2018) MS thesis recently provided by Clay Pierce. Note that Table 3.1 in Simpson (2018) is identical to Table 22 in Bybel et al. (2019).

The percent occurrence data for fish species associated with either the presence or absence of Topeka shiner were taken from Table 22 (Bybel et al. 2019). Species were selected if either percentage was greater than 20 percent. This 20% threshold filtering is somewhat arbitrary, but was used to reduce the number of fish species. The CASM_{OC} can only include 18 fish species plus the two life stages of Topeka shiner. The challenge was to select a workable number of fish species that appear to convey information concerning the association (or lack thereof) with Topeka shiner. Selecting species identified as important by Bakevich et al. (2013) and Bybel et al. (2019) perhaps lends additional rigor to the selected assemblage.

To help with the selection process, a crude index was calculated for the fish species as the ratio of the percentages (TS_{present}/TS_{absent}). A ratio of 1.0 suggests that the fish species presence/absence carries minimal information concerning the presence/absence of TS. Very high or very low ratios identify species that are highly indicative of either TS presence or absence. Such species were recognized as useful for including in the CASM_{OC} food web. The underlying hypothesis is that the ecology (including trophic interactions) and habitat preferences/tolerances of the selected fish species would help discriminate among different environmental scenarios developed to challenge the hybrid model and simulated success/persistence of Topeka shiner for different oxbow conditions.

Selecting fish species for an “oxbow assemblage” also considered the overall ecology of these systems. There should be some balance among fishes in different trophic guilds (e.g., planktivores, omnivores, piscivores): the assemblage should not be all minnows and/or shiners. Therefore, the largemouth bass was included, despite its ratio of 0.83. Rock bass was included because of its diet breadth (i.e., insects, crustaceans, smaller fish) and ratio (4.41), even though it failed the 20% threshold criterion. Bakevich et al. (2013) identified rock bass as potentially informative. Similarly, golden redhorse was selected because of its 3.57 ratio, even though it fails the 20% criterion. Orangespotted sunfish was selected because of its higher ratio (1.58) compared to the green sunfish (1.18), even though the green sunfish was identified as important by Bakevich et al. (2013). Simpson (2018) highlighted the importance of orange-spotted sunfish to Topeka shiner presence in oxbows. The central stoneroller was selected instead of the hornyhead chub, despite their identical data. The assemblage already has the creek chub. Black bullhead was chosen over yellow bullhead because of its slightly higher ratio. The gizzard shad was not included even though its ratio is 0.24, potentially useful in discriminating test scenarios. However, it barely passed the 20% criterion and was only present in 5% of the oxbows that

included TS. Clearly, the resulting proposed assemblage represents an attempt (admittedly somewhat arbitrary) to balance the simple analysis of the data as well as considerations of oxbow trophic dynamics and ecology to define a reasonable/workable set of fish species for parameter estimation and model calibration.

The CASM_{OC} also includes the following attributes:

- The food web structure was informed by studies of off-channel habitats in west-central Iowa inhabited by the Topeka shiner (e.g., Bybel et al. 2019, Bakevich et al. 2013).
- The modeled Topeka shiner population is represented as two interconnected biomass (g C/m²) state variables: an aggregated early life stage biomass and an adult biomass pool. The early life stage state variable has not been used in applications of the CASM_{OC} to date. However, this variable is retained as part of the model structure to permit its inclusion in future modeling studies that might focus on TS reproduction. Populations of aquatic plants, invertebrates, and other fish populations included in the CASM_{OC} food web are each represented by a single biomass (g C/m²) state variable.
- The CASM_{OC} aquatic invertebrate food web was modified to include individual populations of ostracods (one of the zooplankton populations), corixids (water boatman), and coleopterans (water beetles) – organisms common to oxbows and other off-channel habitats.
- The basic CASM model is spatially explicit and provides the opportunity to define population initial biomass and values of environmental forcing data on a spatially explicit basis. As many as 100 contiguous spatial segments can be defined for CASM applications. However, the initial applications of the CASM_{OC} simply model an average m² of a generalized Iowa oxbow. The CASM_{OC} represents an Iowa oxbow as 75 x 15 m homogeneous system, with a constant daily water depth (~1.2 m) derived from Schilling et al. (2018, 2017).
- The model uses daily time steps for model output; the time step for model calculations was specified as 0.1 d for the CASM_{OC}. The initial duration of model simulations is 365 days; the model has the ability simulate longer time periods up to 50 years to address the 2-3 y lifespan of Topeka shiner, year-to-year variations in environmental conditions and time-varying environmental stressors.
- Environmental factors that influence population production in the CASM_{OC} food web include daily values of surface light intensity, water temperature, water depth, current velocity, dissolved oxygen, nutrient concentrations (N, P, Si), and concentrations of dissolved and particulate organic carbon (DOC, POC), and suspended inorganic sediments. Input values have been developed for these factors based on data relevant to reconstructed Iowa oxbow off-channel habitats and Midwestern off-channel aquatic habitats (e.g., Larimore et al. 1973, Jones 2015, Kalkhoff et al. 2016, Haines 2017, Schilling et al. 2018, 2017).

1.1.3. Process overview and scheduling

The CASM_{OC} includes the following:

- Biomass production for each population state variable is based on bioenergetics, trophic interactions (e.g., grazing, predation) and potential modifications by habitat quality parameters (e.g., water temperature and depth, current velocity, dissolved oxygen).
- Basic growth bioenergetics (i.e., photosynthesis, consumption, metabolism) are computed daily for each population in relation to environmental factors (e.g., water temperature, nutrients, dissolved oxygen) that directly influence growth in the model equations.
- Reproduction occurs for modeled populations according to life history characteristics of the modeled aquatic plants, invertebrates, and fish.
- Modeled fish life stages grow according to bioenergetics; consumption depends on specific feeding rate, prey availability, water temperature and average fish mass (i.e., bioenergetics submodel).
- Predation on TS by largemouth bass is modeled explicitly in the CASM_{OC}. Largemouth bass also prey on other CASM_{OC} fish and invertebrates. However, simulation scenarios to date using the CASM_{OC} have not included predation by largemouth bass; its initial biomass value has been set to zero.
- Environmental conditions are updated daily by input data and internal processing and recycling (e.g., decomposition, nutrient remineralization) of carbon and macronutrients (N, P, Si).

1.2. Design concepts

1.2.1. Basic principles

The CASM_{OC} represents a version of the comprehensive aquatic system model (e.g., Bartell et al. 2019, 2018, 2013) designed to address food web production dynamics in a generic Iowa oxbow, with particular emphasis on the federally listed Topeka shiner. The model is fundamentally a biomass (carbon) equivalent of bioenergetics-based growth of aquatic plants and consumer populations included in the modeled food web (Figure 1).

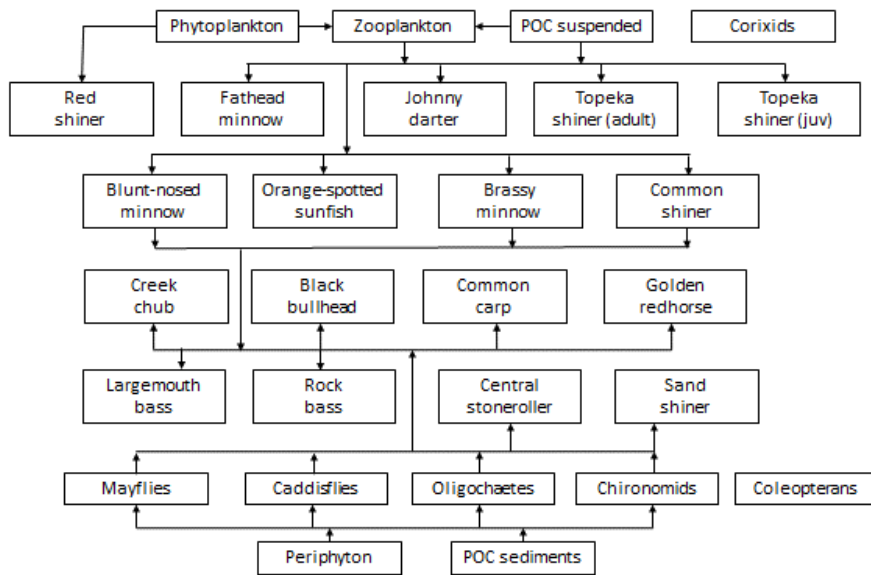


Figure 1. Illustration of the CASM_{OC} food web for generic Iowa oxbow. Not all populations interactions in the food web are shown for simplicity.

1.2.2. Emergence

Potential alterations in food web composition and ecosystem function can emerge from modeling of biomass of individual modeled populations in relation to a dynamic physical-chemical environment and potential impacts of environmental stressors, including pesticides (e.g., benzovindiflupyr). Model outputs that related to ecosystem function include daily concentrations of dissolved oxygen, dissolved and particulate organic carbon, and modeled macronutrients (e.g., N, P, silica).

1.2.3. Adaptation

No adaptation is included in the model.

1.2.4. Sensing

No sensing is included in the model.

1.2.5. Interaction

Modeled populations of aquatic plants, invertebrates, and fish in the CASM_{OC} are influenced by water quality conditions (e.g., temperature, nutrients), trophic interactions, and pesticide exposures. By tracking the daily consumption rate of the fish (as model output), the fish

populations can also indirectly affect the food web structure, for example through linkages with the TS-IBM (Schmolke et al. 2019).

1.2.6. Stochasticity

No stochastic elements were included in the CASM_{OC}.

1.2.7. Collectives

Individual populations of modeled aquatic plants and consumers are collected into trophic guilds (e.g., phytoplankton, periphyton, zooplankton, pelagic fishes, etc.) for computation of potential community-level impacts of environmental stressors. Community-level impacts are quantified as changes in absolute and relative species composition using the Steinhaus similarity index (SSI) (Bartell et al. 2013, Nair et al. 2015).

1.2.8. Observation

Model outputs are generated on a daily time step. Outputs include biomass of fish in each life stage, biomass of populations of aquatic plants and invertebrates, and values of water quality parameters (e.g., dissolved oxygen, N, P, dissolved silica, DOC, POC) tracked by the model.

1.3. Details

1.3.1. Initialization

Initial (January 1) biomass values for the CASM_{OC} populations of aquatic plants, invertebrates, and fish have been derived from data relevant to Iowa oxbow habitats for Topeka shiner (Table 1). Initial fish biomass values derive from analysis of off-channel habitat data presented by Bakevich et al. (2013). Values for aquatic plants and invertebrates were developed from simulations constructed to produce fish biomass values consistent with the Bakevich et al. (2013) data. Biomass and productivity data for the lower trophic levels were not discovered for off-channel habitats, including the modeled generic Iowa oxbow.

Table 1. Initial biomass values derived for CASM_{OC} populations for model day 1 (January 1).

CASM_{OC} population	Initial biomass (g C/m²)
Phytoplankton	
Diatoms	0.001
Chlorophytes	0.001
Cyanophytes	0.001
Cryptophytes	0.001
Euglenoids	0.001
Periphyton	
Diatoms	0.0033
Chlorophytes	0.0033
Cyanophytes	0.0033
Macrophytes	
<i>Elodea</i>	0.228
<i>Potamogeton</i>	0.560
Zooplankton	
Copepods	0.00588
Cladocerans	0.00693
Rotifers	0.00741
Microzooplankton	0.00482
Ostracods	0.00512
Pelagic fish	
Red shiner	1.86
Fathead minnow	3.51
Johnny darter	0.0207
Topeka shiner (juvenile)	0
Topeka shiner (adult)	0.185
Pelagic fish	

CASM_{oc} population	Initial biomass (g C/m²)
Rock bass	0.351
Orangespotted sunfish	0.0394
Brassy minnow	0.0675
Common shiner	0.0884
Cirixids	0.000383
Pelagic bacteria	
Bacterioplankton	0.626
Benthic macroinvertebrates	
Ephemeroptera	0.000657
Trichoptera	0.0188
Oligochaetes	0.104
Chironomids	0.00941
Coleopterans	0.0194
Benthic fish	
Creek chub	11.7
Black bullhead	9.58
Common carp	169.
Golden redhorse	13.8
Sand shiner	0.0152
Benthic fish	
Largemouth bass	0
Bluntnose minnow	0.748
Central stoneroller	2.10
White sucker	169.
Sediment bacteria	
Benthic bacteria	0.0638

For simulations exceeding one modeled year, biomass values for each day 1 (January 1) are reset to the initial values for aquatic plants, zooplankton, and benthic invertebrates. The observed high year-to-year variability in biomass production, combined with important life-history traits (e.g., phylogenies, dormant or resting stages) that are not readily described by bioenergetics and coupled differential equations, have thus far discouraged longer-term “spin up” simulations of lower trophic level populations with previous versions of the CASM and the CASM_{OC}. Substantial time and resources could be expended in removing transient behavior from lower trophic level populations, particularly when generating dynamic steady-state conditions for lower trophic level populations that are consistent with corresponding patterns of biomass production by a diverse fish community, for which there are at least some data.

Additionally, in current applications of the CASM_{OC}, the daily environmental input data that influence the bioenergetics of population growth are simply repeated each year. Thus, any reference simulation defined by the dynamic steady-state resulting from the spin-up simulations depends directly on the repeated environmental conditions defined by the input data. Changing the environmental context of the reference simulation would require repeating the spin-up/calibration process. Finally, explorations of the impact of environmental stressors, mainly water temperature and pesticides, have focused on comparing 1-year reference and treatment simulations. Any bias introduced by the initial conditions in the 1-y reference simulation are also included in the treatment simulation: comparisons of the two model results are valid within the context of the single model year. In fact, exploration and comparison of multiple-year simulations of reference and treatment conditions are likely confounded by the use of the same environmental input data for each modeled year.

Fish population biomass values are not reset in the CASM_{OC} and fish production continues from the year-1, day-1 initial values through the selected duration of the simulation. Simulations of 40 years were performed to examine the implications of the year-1, day-1 initial values on longer-term model performance, particularly for modeled fish populations.

1.3.2. Input data

Parameters defining functional responses, bioenergetics and other growth parameters for the populations of aquatic plants, invertebrates, and fish are provided to the CASM_{OC} in a parameter input file.

In addition to the population-specific growth parameters, the other key baseline (reference) model inputs include specification of trophic (i.e., grazing, predation) interactions among the modeled populations and environmental data that determine the expression of bioenergetics-based growth and trophic dynamics of the CASM_{OC}. Table 2 lists the environmental input and sources used in developing the CASM_{OC}.

Table 2. The sources of the environmental input data used in developing the baseline CASM_{OC} simulation.

Environmental factor	Description	Source
Surface irradiance	Daily surface light intensity (watts/m ²) data from the Des Moines, IA airport	National Solar Radiation Database https://rredc.nrel.gov/solar/old_data/nsrdb
Water temperature	Daily 2 nd -order Iowa stream water temperatures (°C)	Analysis of Iowa USGS stations similar in flow to White Fox Creek, Iowa (N. Green, personal communication)
Water depth	Daily depth (m) values scaled from reconstructed Iowa oxbow	Schilling et al. (2018)
Current velocity	Assume no significant water current velocities in oxbow	Schilling et al. (2018)
Wind velocity	Daily values (m/s) scaled from Midwest 2 nd -order stream	Bartell et al. (2013)
Dissolved inorganic N	Daily values (mg/L) interpolated from the Smeltzer oxbow in Lyons Creek watershed, Iowa	Kalkhoff et al. 2016
Dissolved inorganic P	Daily values (mg/L) interpolated from the Smeltzer oxbow in Lyons Creek watershed, Iowa	Kalkhoff et al. 2016
Dissolved silica	Daily values (mg/L) scaled from Iowa headwater pool	Bartell et al. (2019)
Particulate organic carbon	Daily values (mg/L) scaled from Iowa headwater pool	Bartell et al. (2019)
Inorganic sediments	Daily values (mg/L) scaled from Iowa headwater pool	Analysis of Iowa USGS stations similar in flow to White Fox Creek, Iowa (N. Green, personal communication)

For CASM_{OC} applications in pesticide ecological risk assessment, two additional input data files are provided. One file defines the toxicity benchmarks (e.g., LC₅₀s, EC₅₀s, NOECs) developed for each modeled population. These input data are used to define the exposure-response functions for the pesticide of interest (e.g., benzovindiflupyr). The second file defines the daily concentrations of the pesticide developed for the generalized Iowa oxbow.

All of the data input files to the CASM_{OC} are formatted as ASCII text files and can be edited using standard text editing software (e.g., Notepad, Notepad).

1.4. Submodels

The key submodels in the CASM_{OC} compute the bioenergetics-based growth dynamics of the modeled populations of aquatic plants and consumers.

1.4.1. Aquatic plants and consumers modeled in the CASM_{OC}

Aquatic plants

The CASM_{OC} includes multiple populations of phytoplankton, periphyton (attached algae), and submerged aquatic vascular plants representative of an Iowa oxbow. Biomass production for primary producer populations is governed by a bioenergetics-based equation that describes changes in plant biomass (carbon) as a function of photosynthesis minus losses to catabolic processes (e.g., photorespiration, respiration, non-grazing or ‘natural’ mortality) and grazing. In the CASM_{OC}, photosynthesis is a nonlinear function of light, temperature, and nutrient (nitrogen, phosphorous, silica) availability. Growth is additionally modified by habitat factors, including accumulated degree days, water depth, and current velocity. Daily biomass (g-C/m²) for each modeled aquatic plant population (B_i) is determined by the following equation:

$$(1) \quad dB_i/B_i dt = [Pmax_i \{h(T), f(I), g(N), hmod\} (1 - presp_i) - dresp_i h(T) - (s_i + m_i) - \sum [h(T) B_j C_{ij} w_{ij} a_{ij} h_{ij} B_i] / (B_j + \sum w_{ij} a_{ij} h_{ij} B_i)]$$

where, for population i,

B_i	biomass of plant population i	gC/m ²
B_j	biomass of grazer population j	gC/m ²
$Pmax_i$	maximum photosynthetic rate of growth	1/d
$h(T)$	temperature dependence of photosynthesis	unitless
$f(I)$	light dependence of photosynthesis	unitless
$g(N)$	nutrient dependence of photosynthesis	unitless
$hmod$	habitat quality modifier of growth	unitless
$presp_i$	photorespiration rate	unitless
$dresp_i$	dark respiration rate	1/d
s_i	sinking rate (phytoplankton only)	1/d
m_i	mortality rate	1/d
C_{ij}	rate of consumption by grazer j	gC/m ² /d
w_{ij}	preference of consumer j for prey i	unitless
a_{ij}	assimilation of producer i by consumer j	unitless
h_{ij}	handling efficiency	unitless

Table 3 lists the values of the plant growth parameters. These values were developed based on the previous modeling of lower-order Midwestern streams (Nair et al. 2015, Bartell et al. 2013) and a generic Iowa headwater pool (Bartell et al. 2019).

Aquatic consumers

Biomass production for consumer populations modeled in the CASM_{OC} is a function of consumption (ingestion and assimilation of food or prey) minus losses to respiration, excretion, natural mortality, and predation. These processes are nonlinear functions of temperature (respiration) and food availability (consumption, predation). Modeled consumer populations are distinguished by population-specific rates of feeding, respiration, excretion, locomotion costs, prey preferences, prey assimilation, and temperatures for maximum feeding and respiration. The daily value of biomass (g-C/m²) for each modeled population (B_i) of zooplankton, aquatic insects, benthic invertebrates, and fish is determined by the following equation:

$$(2) \quad dB_i/B_i dt = \begin{aligned} & \Sigma[(Cm_i h(T) w_{ij} a_{ij} h_{ij} B_j)/(B_i + \Sigma w_{ij} a_{ij} h_{ij} B_j) - (u_i + f_i + rsda_i)] \\ & - r_i h(T) - m_i \\ & - \Sigma[(Cm_j h(T) w_{ij} a_{ij} h_{ij} B_j)/(B_j + \Sigma w_{ij} a_{ij} h_{ij} B_i)] \end{aligned}$$

where, for population i

B_i	predator biomass	gC/m ²
B_j	prey biomass	gC/m ²
Cm_i	maximum consumption rate	1/d
$h(T)$	temperature dependence of consumption	unitless
w_{ij}	preference of consumer i for prey j	unitless
a_{ij}	assimilation efficiency for consumer i and prey j	unitless
h_{ij}	handling efficiency	unitless
r_i	standard respiration rate	1/d
u_i	excretion rate	1/d
f_i	egestion rate	unitless
m_i	natural mortality rate	1/d
$rsda_i$	specific dynamic action (fish only)	unitless

The CASM_{OC} requires specification of an average individual size (length) for modeled fish populations. These data have been collated mainly from the FishBase data (www.fishbase.org), which also provide the best available allometric relationships for translating length to weight using Equation 3.

$$(3) \quad \log_{10}(W) = b \log_{10}(TL) + a$$

where,

TL: total fish length in mm

W: fish wet weight (g)

b: slope

a: intercept

Table 4 lists the values and sources used to allometrically scale fish length to weight for the populations modeled in the CASM_{OC}.

Rates of C_{\max} , specific maximum consumption (g/g/d), for the fish populations were estimated using population-specific parameters wherever possible and the Wisconsin Fish Bioenergetics model (Deslauriers et al. 2017, Hansen et al. 1977) according to

$$(4) \quad C_{\max} = CA \cdot W^{CB}$$

where,

CA: intercept of the allometric mass function

CB: slope of the allometric mass function

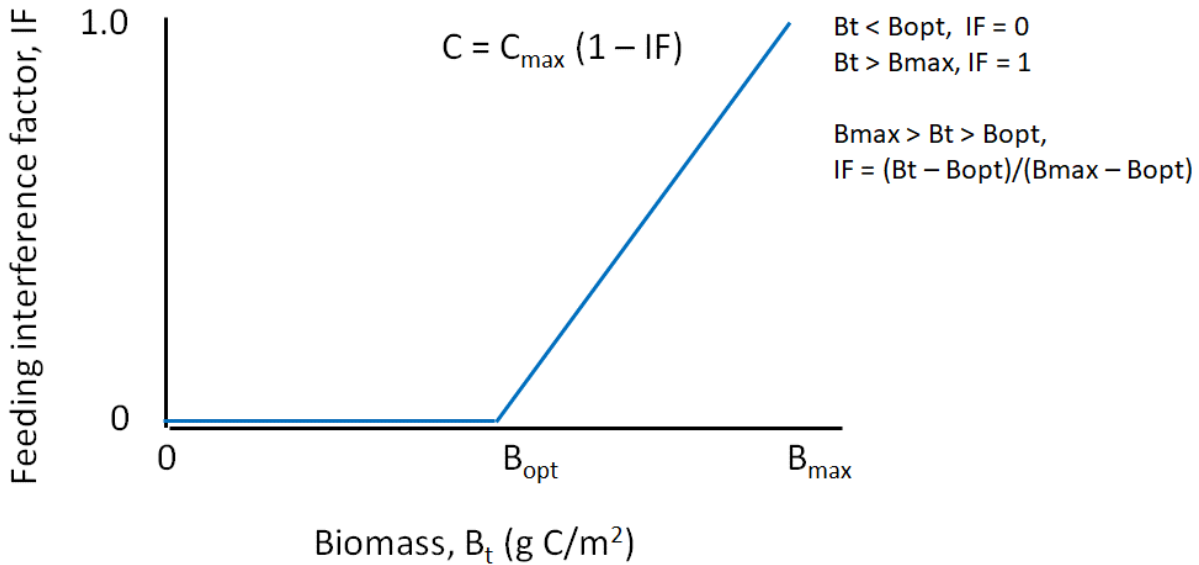
W: dry mass of individual

Table 5 lists the values and sources used to estimate consumption and respiration parameters for the fish populations modeled in the CASM_{OC}.

1.4.2. Density dependence

Density-dependence is implemented for modeled fish species in the CASM_{OC} food web (Post et al 1998). Density-dependent growth in the CASM_{OC} is implemented by adjusting rates of consumption as a function of fish biomass potentially competing for food (Figure 2). The algorithm is identical to that used in the CASM_{TS}.

Values of an optimal biomass (B_{opt}) were estimated using data reported by Bakevich et al. (2013). Maximum (B_{max}) population biomass was simply estimated as twice the value of B_{opt}. The specific target values of fish population biomass are presented in their respective sections that follow (Section 5).



Based on Post et al. 1998

Figure 2. Illustration of feeding interference factor (IF) in relation to optimum (B_{opt}) and maximum population (B_{\max}) population biomass used to define density-dependent consumption in the CASM_{OC}.

1.4.3. Predation

Predation in the CASM_{OC} is modeled as a Holling type II formulation, where predation is determined by the abundance of the predator and the prey. The formulation is the consumption term in Equation 2 above:

$$(5) \quad C_i = C_{\max} B_j \frac{pref_i ass_i h_i B_i}{\sum pref_i ass_i h_i B_i}$$

where,

C_i : consumption rate of the predator (g C/m²/d)

C_{\max} : maximum consumption rate (g/g/d)

B_j : biomass of the predator (g C/m²)

$pref_i$: preference of the predator for prey type i

ass_i : assimilation efficiency for prey i

h_i : handling efficiency for prey i (initially set to 1 for all prey guilds)

B_i : biomass of prey i (in g C/m²)

The C_{\max} parameter values applied in CASM_{OC} for the consumer populations are listed in the model parameter Table 5.

1.4.4. CASM_{OC} consumer population diet preferences

The w_{ij} values in Equation 5 specify the relative preference of predator i for prey j in the CASM_{OC}. The greater the value of w_{ij} , the greater the feeding preference for prey j by predator i . The absolute magnitudes of the w_{ij} values are not important as long as they are consistent in their derivation because each w_{ij} is normalized across all prey populations for each predator. However, fractional values are convenient scalars that can also be interpreted as the fraction of the prey population available to the predator. Prey preferences estimated from stomach contents data are desirable, but not available for all modeled species. Literature descriptions of feeding ecology and prey preferences are used in combination with diet data to estimate w_{ij} values (e.g., Table 4).

1.4.5. Bioenergetics

The Wisconsin fish bioenergetics model (Deslauriers et al. 2017, Hansen et al. 1997) is used to guide the implementation of consumer population growth (Eq.2).

Consumption

The rate of consumption for consumer populations in the CASM_{OC} is determined by a maximum rate (C_{\max}) that is estimated for an average sized organism defined for each population. The C_{\max} value is the biomass equivalent of the specific rate of consumption (g/g/d) derived from bioenergetics (Deslauriers et al. 2017, Hansen et al. 1997). Tables 4 and 5 list the values of C_{\max} estimated from the technical literature for modeled populations of zooplankton, macroinvertebrates, and fish.

The temperature dependence of consumption is modeled using the equation from Fish Bioenergetics for cool- and cold-water species (Thornton and Lessem 1978). References for fish populations identified by superscripts in Table 5 are the sources used to inform the estimation of the temperature-dependence of consumption.

Metabolism

The consumer populations use energy (biomass) for metabolism including respiration R and specific dynamic action – the energetic cost of digestion. Specific dynamic action is a constant fraction of consumption (Table 5).

Accordingly, metabolic expenses can be calculated applying:

$$(6) \quad M(T) = R(T) + SDA(C - F)$$

where,

SDA : specific dynamic action (unitless)

C : consumption (g/g/d)

F : egestion (unitless)

Respiration $R(T)$ is defined as follows:

$$(7) \quad R = RA W^{RB}$$

where,

R : specific rate of respiration (g/g/d)

W : fish wet weight (g)

RA : intercept of the allometric mass function

RB : slope of the allometric mass function

The temperature dependence function for respiration used for standard respiration is model 2 from Fish Bioenergetics 4.0 (Kitchell et al. 1977).

$$(8) \quad f_R(T) = V^X e^{X(1-V)}$$

where,

$$V = (RTM - T)/(RTM - RTO)$$

$$X = (Z^2(1 + (1 + 40/Y)^{0.5})^2)/400$$

$$Z = \ln(RQ)(RTM - RTO)$$

$$Y = \ln(RQ)(RTM - RTO + 2)$$

In these equations, RTO is the optimal respiration temperature (°C); RTM is the maximal lethal water temperature; RQ approximates the Q_{10} (the rate at which the function increases over relatively low water temperatures).

Egestion and excretion

Egestion and excretion are modeled as constant proportions of consumed energy (Table 5). Here egestion (F) represents food lost during the process of ingestion and excretion (U) represents energy lost in nitrogenous waste (i.e., urination).

$$(9) \quad E(C) = F(C) + U(C)$$

where,

$$F = FA \times C$$

$$U = UA(C - F)$$

FA : constant proportion of consumption (unitless)

UA : constant proportion of assimilated energy (unitless)

1.5. Model parameters

Table 3. Bioenergetics-based growth parameters for aquatic plant populations in the CASM_{OC}.

CASM _{OC}	Psmax	Te1	Te2	Te3	Te4	kP	kN	kS	Mortality	Respiration
Population	(1/d)	(°C)	(°C)	(°C)	(°C)	(mg/L)	(mg/L)	(mg/L)	(1/d)	(1/d)
Phytoplankton										
Diatoms	1.05	4	11	20	22	0.010	0.150	0.60	0.040	0.080
Chlorophytes	1.10	6	16	24	28	0.008	0.120	n/a	0.030	0.080
Cyanophytes	1.25	8	20	32	36	0.012	0.260	n/a	0.050	0.080
Cryptophytes	0.95	8	20	32	36	0.008	0.180	n/a	0.030	0.080
Euglenoids	0.80	6	22	30	34	0.006	0.140	n/a	0.050	0.080
Periphyton										
Diatoms	1.20	4	11	20	22	0.010	0.150	0.60	0.040	0.080
Chlorophytes	1.10	6	16	24	28	0.008	0.120	n/a	0.030	0.080
Cyanophytes	1.10	8	20	32	236	0.012	0.260	n/a	0.050	0.070
Macrophytes										
Elodea	0.08	8	16	28	32	n/a	n/a	n/a	0.006	0.026
Potamogeton	0.06	10	18	30	34	n/a	n/a	n/a	0.005	0.020

Psmax maximum daily photosynthetic rate
 Te1, Te4 upper and lower tolerances used in temperature dependence of photosynthesis (Thornton and Lessem 1978)
 Te2, Te3 temperatures that define the range of maximum photosynthesis (Thornton and Lessem 1978)
 kP, kN, kS half-saturation constants for phosphorus, nitrogen, and silica (diatoms only).

Table 4. Parameter values used in estimating fish maximum specific consumption (C_{max}) and standard respiration (R_{max}) rates.

CASM _{oc}	Length	Length:weight ^a		Weight	Consumption			Respiration			Source
Common name	mm	a	b	g	CA	CB	C _{max}	RA	RB	R _{max}	
Red shiner	57	-5.4597	3.47	4.30	0.350	-0.300	0.23	0.0007	-0.271	0.00047	Yildirim and Peters 2006, Hansen et al. 1997
Fathead minnow	73	-5.0334	3.07	5.00	0.149	-0.242	0.10	0.0096	-0.041	0.00689	Duffy 1998
Johnny darter	39	-5.4040	3.20	0.50	0.250	-0.270	0.30	0.0108	-0.200	0.01241	Schneider 2000
Topeka shiner - juv	1	n/a	n/a	0.01 ^b	0.149	-0.242	0.45	0.0096	-0.041	0.02914	Duffy 1998 ^c
Topeka shiner - adt	45	n/a	n/a	1.30 ^b	0.149	-0.242	0.14	0.0096	-0.041	0.00901	Duffy 1998 ^c
Rock bass	154	-4.8121	3.05	74.00	0.250	-0.270	0.08	0.0108	-0.200	0.00457	Schneider et al 2000
Orange-spotted sunfish	74	-5.0400	3.16	7.40	0.182	-0.274	0.11	0.1540	-0.200	0.10320	Schneider et al 2000
Brassy minnow	76	-5.7089	3.39	4.60	0.149	-0.242	0.10	0.0096	-0.041	0.00902	Schneider et al 2000
Common shiner	86	-5.6124	3.32	6.50	0.350	-0.300	0.20	0.0007	-0.271	0.00042	Schneider et al 2000
Creek chub	191	-4.8481	2.92	66.60	0.350	-0.300	0.10	0.0018	-0.120	0.00109	Rudstam et al. 1994
Black bullhead	266	-4.9740	3.09	321.2	0.120	-0.225	0.03	0.0007	-0.271	0.00015	Hartman et al. 2017
Common carp	310	-4.6390	2.92	432.3	0.150	-0.300	0.02	0.0007	-0.271	0.00014	Hartman et al. 2017
Golden redhorse	288	-4.7690	2.91	241.5	0.149	-0.242	0.04	0.0096	-0.041	0.00767	Schneider et al. 2000
Sand shiner	44	-5.0336	2.99	0.80	0.149	-0.242	0.16	0.0096	-0.041	0.00969	Schneider et al. 2000

CASM _{OC}	Length	Length:weight ^a		Weight	Consumption			Respiration			Source
Common name	mm	a	b	g	CA	CB	Cmax	RA	RB	Rmax	
Largemouth bass	400	-5.1689	3.13	930.5	0.330	-0.325	0.03	0.0028	-0.355	0.00025	Rice et al. 1983
Blunt-nosed minnow	65	-5.7089	3.39	2.70	0.149	-0.242	0.12	0.0096	-0.041	0.00922	Schneider et al. 2000
Central stoneroller	109	-5.2702	3.17	15.4	0.149	-0.242	0.08	0.0096	-0.041	0.00858	Schneider et al. 2000
White sucker	407	-4.755	2.94	826.4	0.149	-0.242	0.03	0.0006	-0.041	0.00044	Bister 2000

^aLength:weight parameters taken from www.fishbase.org

^b $\log_{10}(W) = 3.3798 (L) - 5.3722$ (Derived from data in Kerns and Bonneau (2002) and Dahle (2001))

^cConsumption (Duffy 1998) and respiration (Deslauriers et al. 2017) parameters assumed using fathead minnow as surrogate for Topeka shiner; the TS-IBM consumption parameters for the fathead minnow were used in calibrating Topeka shiner consumption values and differ from the values used in the CASM_{OC}

Table 5. Bioenergetics-based growth parameters for consumer populations in the CASM_{oc}.

CASM_{oc}	Cmax	Te1	Te2	Te3	Te4	SDA	Rmax	Egestion	Excretion	Mortality
Population	(1/d)	(°C)	(°C)	(°C)	(°C)	(unitless)	(1/d)	(unitless)	(unitless)	(1/d)
Zooplankton										
Copepods	0.37	4	18	26	40	n/a	0.012	0	0.02	0.010
Cladocerans	0.22	5	20	28	34	n/a	0.014	0	0.03	0.040
Rotifers	0.21	5	14	27	35	n/a	0.016	0	0.03	0.040
Microzooplankton	0.22	5	16	24	35	n/a	0.035	0	0.03	0.050
Ostracods	0.08	4	20	28	34	n/a	0.014	0	0.03	0.020
Pelagic fishes										
Red shiner	0.04	3	16	25	36 ^a	0.172	0.00370	0.15	0.10	0.0050
Fathead minnow	0.07	4	21	27	30 ^b	0.172	0.00899	0.10	0.10	0.0050
Johnny darter	0.39	5	18	28	31 ^c	0.150	0.01241	0.15	0.10	0.0050
Topeka shiner-juv	0.22	10	26	28	33	0.172	0.01808	0.10	0.10	0.0050
Topeka shiner-adt	0.11	10	26	28	35 ^d	0.172	0.00791	0.10	0.10	0.0050
Pelagic fish										
Rock bass	0.06	3	16	24	30 ^e	0.170	0.00457	0.146	0.088	0.0040
Orange-spotted sunfish	0.14	11	24	30	36 ^f	0.172	0.10320	0.158	0.025	0.0040
Brassy minnow	0.04	5	12	20	26 ^g	0.172	0.00090	0.100	0.100	0.005
Common shiner	0.05	5	15	20	26 ^h	0.170	0.00042	0.100	0.100	0.005
Corixids	0.11	6	12	22	30	n/a	0.010	0.010	0.002	0.007
Benthic invertebrates										
Ephemeroptera	0.65	6	12	22	28	n/a	0.005	0.005	0.003	0.001
Trichoptera	0.75	8	14	17	20	n/a	0.005	0.005	0.002	0.002
Oligochaetes	0.95	4	16	25	32	n/a	0.005	0.005	0.006	0.001
Chironomids	1.45	8	18	26	32	n/a	0.002	0.004	0.004	0.0003
Coleopterans	0.52	8	14	26	30	n/a	0.020	0.010	0.002	0.008
Benthic fishes										
Creek chub	0.35	3	16	24	32 ⁱ	0.160	0.00010	0.150	0.100	0.00020
Black bullhead	0.46	11	24	26	30 ^j	0.135	0.00008	0.150	0.100	0.00020
Common carp	0.20	7	20	25	30 ^k	0.145	0.00010	0.150	0.100	0.00050

CASM _{oc}	C _{max}	Te ₁	Te ₂	Te ₃	Te ₄	SDA	R _{max}	Egestion	Excretion	Mortality
Population	(1/d)	(°C)	(°C)	(°C)	(°C)	(unitless)	(1/d)	(unitless)	(unitless)	(1/d)
Golden redhorse	0.06	4	17	24	30 ^l	0.172	0.00767	0.100	0.100	0.0050
Sand shiner	0.08	8	21	37	42 ^m	0.172	0.00969	0.150	0.100	0.0075
Largemouth bass	0.04	8	27	32	37 ⁿ	0.158	0.00025	0.104	0.068	0.001
Blunt-nosed minnow	0.05	5	18	24	30 ^o	0.172	0.00922	0.100	0.100	0.005
Central stoneroller	0.05	5	18	24	30 ^p	0.172	0.00858	0.100	0.100	0.005
White sucker	0.14	5	14	21	25 ^q	0.172	0.00044	0.100	0.100	0.005

C_{max} maximum daily consumption rate (g/g/d)

Te₁, Te₄ upper and lower tolerances used in temperature dependence of consumption (Thornton and Lessem 1978)

Te₂, Te₃ temperatures that define the range of maximum consumption (Thornton and Lessem 1978)

SDA specific dynamic action (metabolic cost of digestion)

R_{max} maximum daily respiration rate (g/g/d)

^aMessad et al. 2000, Yildirim and Peters 2006

^bDuffy 1998

^cIngersoll and Claussen 1984

^dKoehle 2006

^eRoell and Orth 1993

^fKitchell et al. 1974 (bluegill sunfish)

^gScheirer and Fausch 2002

^hTrial et al. 1983, MacNaughton et al. 2019

ⁱCaterina and Tome 2013

^jWisner and Christie 1987

^kAnonymous 2016 report

^lOhio DNR report

^mMontana field guide

ⁿRice et al. 1983

^oWisner and Christie 1987

^pBartell et al. 2013

^qEldridge et al. 2015

Table 6. Prey preferences (w_{ij}) for juvenile and adult Topeka shiner in the CASM_{OC}. Periphyton includes three populations simulated separately in the model. Values from Schmolke et al. (2019).

Prey population	Juvenile TS	Adult TS	Remarks
Microzooplankton	0.25		
Rotifera	0.25		
Copepoda	0.25	0.04	
Cladocera	0.25	0.26	
Chironomidae		0.28	Population representative of all Diptera eaten by TS
Ephemeroptera (mayflies)		0.01	
Trichoptera (caddisflies)		0.06	Diet guild representative of all insects other than Diptera and Ephmeroptera, and Hydrocarina eaten by TS
Periphyton		0.16	Guild included in Periphyton: Diatom 3-5; Chlorophyte 5-7; Cryptophyte 1; Cyanophyte 5-6; Euglenoid 1; Elodea; Potamogeton
Detritus		0.17	Sediment POC in the CASM _{OC}

2. DATA EVALUATION FOR MODEL CONCEPTUALIZATION AND PARAMETERIZATION

2.1. Factors regulating photosynthesis

2.1.1. Light saturation

The effects of light availability and light saturation on photosynthesis are modeled using a formulation derived by Thomann and Mueller (1987).

$$(10) \quad f_l(I) = I / I_s \cdot \exp \left(- (I / I_s) + 1.0 \right)$$

where,

$$\begin{array}{lll} I & = & \text{light intensity} \quad \text{eins/m}^2/\text{d} \\ I_s & = & \text{light saturation intensity} \quad \text{eins/m}^2/\text{d} \end{array}$$

Population-specific values of I_s define the relationship between light intensity and the value of $f_l(I)$ for the modeled plant populations. Daily values of $f_l(I)$ range between zero and 1.0 for each modeled population. For all modeled plant populations, the value of I is attenuated surface light intensity, I_0 .

In the field, the following factors play a role in producing complex underwater light regimes:

- 1) Variations in surface light intensity.
- 2) Wavelength-specific reflectance.
- 3) Attenuation of direct and diffuse light by water.
- 4) Absorption and reflectance of light by both dissolved and particulate organic and inorganic compounds.

In CASM, daily values of I_0 are attenuated by water color, suspended particulate organic carbon, phytoplankton biomass, and suspended inorganic matter. Constant attenuation coefficients (m^{-1} per mg/L) are defined for each of these particulates. A separate coefficient (m^{-1}) is defined for water color. The sum of these coefficients is used to attenuate surface light with increasing depth using a negative exponential function (i.e., Beer's Law). Light attenuation varies in relation to changing concentrations of phytoplankton, particulate organic carbon, and inorganic sediments.

Values of light saturation were derived for the modeled phytoplankton populations based on Robarts (1987) and Lehman et al. (1975). Light saturation intensities ranging from 1.0 to 3.36 Einsteins/ m^2/d were previously used in a model of periphyton production by Son and Fujino

(2003). Robarts and Zohary (1987) estimated light saturation values that ranged from 1.5 to 21.6 Einsteins/m²/d (mean = 5.2 Einsteins/m²/d) for several species of blue-green algae. Bothwell (1988) observed maximum growth rates of benthic diatoms from 2.5 to 5.0 Einsteins/m²/d. Kelly et al. (1983) and Nielsen and Sand-Jensen (1989) estimated light saturation values for macrophytes ranging from 1.7 to 19.4 Einsteins/m²/d and 10 to 14 Einsteins/m²/d respectively. Table 7 lists the calibrated values of the light saturation constants for populations of aquatic plants included in the CASM_{OC}.

Table 7. Light saturation (I_s) values derived for CASM_{OC} aquatic plant populations.

CASM _{OC} population	I_s (einsteins/m ² /d)
Phytoplankton	
Diatoms	10
Chlorophytes	8
Cyanophytes	8
Cryptophytes	8
Euglenoids	6
Periphyton	
Diatoms	10
Chlorophytes	8
Cyanophytes	8
Macrophytes	
<i>Elodea</i>	6
<i>Potamogeton</i>	8

2.1.2. Nutrient limitation

CASM addresses the effects of nutrient availability on photosynthesis. The model includes effects of nitrate, phosphate, and silica (diatoms only). A multiplier of photosynthesis (0-1) is calculated using a simple Monod expression for each potentially limiting nutrient:

$$(11) \quad f_{NO_3} = NO_3 / (k_N + NO_3)$$

$$(12) \quad f_{PO_4} = PO_4 / (k_P + PO_4)$$

$$(13) \quad f_S = Si/(k_S + Si)$$

The values of NO₃, PO₄, and Si are the dissolved concentrations (mg/L) of nitrate, phosphate, and silica respectively. The k_N, k_P, and k_S values define the Monod (or ‘half-saturation’) constants, where f_{NO3}, f_{PO4}, and f_{Si} are equal to 0.5.

The overall effect of nutrient limitation is defined using a Liebig minimum approach:

$$(14) \quad f_N = \min(f_{NO3}, f_{PO4}, f_{Si})$$

Nutrient limitation is assumed to only affect photosynthesis rates of phytoplankton and periphyton. Population-specific values of k_N (algae and diatoms), k_P (algae and diatoms), and k_S (diatoms only) are required as input parameters to CASM_{OC}. It is assumed that submerged aquatic and emergent vegetation derive nutrients from sediments and that these plants are seldom nutrient-limited; therefore, half-saturation constants are not required as input parameters for macrophyte or emergent plant populations modeled in the CASM.

CASM does not directly simulate accumulation of dissolved nutrients by modeled producers. Rather, the summed products of population-specific gross photosynthetic rates (gC/m²/d) are converted to equivalent nutrient concentrations using a constant C:N:P stoichiometry (140:16:1) in order to derive the necessary conversions. It is recognized that *in situ* plant N:P ratios can vary in relation growth and nutrient availability, but the model does not currently address these variations. Decomposition and nutrient remineralization by consumers are similarly governed by this assumed stoichiometry, with the understanding that variations in these ratios occur in aquatic ecosystems (e.g., Cross et al. 2005). These conversions to nutrient equivalents are used in calculating changes in available nutrients and preserving the mass-balance of NO₃, PO₄, and dissolved Si during model simulations.

Values of half-saturation (Monod) constants were assigned to model algae populations based on reported values for silica (Paasche, 1973), nitrogen (Son and Fujino, 2003; Reuter et al. 1986; Lehman et al. 1975; Carpenter and Guillard, 1971), and phosphorus (Son and Fujino, 2003; Bothwell, 1985; Bothwell, 1988; Buzzelli et al. 2000; Lehman et al. 1975). Populations of macrophytes and emergent aquatic plants were assumed to derive their nutrients from sediments and half-saturation constants do not apply to the growth dynamics of these plant populations. Table 3 lists the values of the half-saturation constants used in the calibration of the CASM_{OC} to the generalized Iowa oxbow.

2.1.3. Photorespiration and dark respiration

Photorespiration

Photorespiration occurs in the presence of light, resulting in excretion of dissolved organic matter (carbon) and release of carbon dioxide. Photorespiration applies to modeled populations of phytoplankton, periphyton, and submerged aquatic plants in CASM. Photorespiration is modeled as a complement to light limitation of photosynthesis (Park et al. 2004) and is expressed as a population-specific fraction of photosynthesis:

$$(15) \quad \text{photorespiration} = \text{presp}_i \cdot \text{Ps}_i$$

where,

presp_i is the photorespiration coefficient for population i (unitless).

Carbon excreted via photorespiration is added to the dissolved organic carbon pool.

Birmingham et al. (1982) provided estimates of photorespiration for diatoms, green algae, blue-green algae, and other algae. Their estimates ranged from 1.3 to 8.7% of gross photosynthesis. Photorespiration values ranging from 3.5 – 5.5% were determined to provide the best agreement between modeled and measured phytoplankton biomass in the calibration of the models to available data for lower-order streams. These values were adjusted to a range of 2.0 – 4.0% in calibrating the CASM_{OC} for the generalized Iowa oxbow (Table 3). These values were well within the range reported by Birmingham et al. (1982).

Dark Respiration

Dark respiration requires oxygen for the production of maintenance energy, a catabolic process that releases carbon dioxide. The biomass-equivalent of respiration is modeled within the CASM_{OC} as a constant fraction of gross photosynthesis:

$$(16) \quad \text{dark respiration} = \text{dresp}_i \text{ bp}_i$$

where,

$$\begin{array}{ll} \text{dresp}_i & = \text{dark respiration rate} & 1/\text{d} \\ \text{bp}_i & = \text{biomass of producer} & \text{g-C/m}^2 \end{array}$$

Buzzelli *et al.* (2000) used basal (dark) respiration rate of 0.1/d in a model of algal production in the Florida Everglades. Burris (1977) measured somewhat higher rates of dark respiration of 0.11/d to 0.42/d of gross photosynthesis for several marine algae. Values of 0.07 – 0.08 d⁻¹ were assigned to modeled populations to calibrate phytoplankton and periphyton in the generic oxbow model. Values ranging from 0.06 – 0.12 d⁻¹ were used in calibrating rooted aquatic plant production for the generalized Iowa oxbow (Table 3).

2.1.4 Photosynthetic rates

Maximum photosynthetic (growth) rates vary widely among phytoplankton, although values within a range of $\sim 1\text{--}3\text{ d}^{-1}$ are commonly reported (e.g., Saravia *et al.* 1998, Roberts 1987, Lehman *et al.* 1975, Goldman and Carpenter 1974, Sorokin and Kraus, 1958). Estimation of parameter values for periphyton and macrophyte populations was supported by the technical literature and other modeling studies. For example, Goldman and Carpenter (1974) reported growth rates ($1/\text{d}$) for several green algae ranging from 1.36/d to 4.32/d for temperatures relevant to the CASM_{OC}. Based on a different study, diatom growth rates ranged from 1.3/d to 4.0/d (Paasche 1973). Saravia *et al.* (1988) derived periphyton growth rates ranging from 1.06/d to 3.69/d. Nielsen and Sand-Jensen (1989) measured rates of photosynthesis for 14 aquatic vascular plants, with results ranging from 0.05/d to 1.06/d and a mean value of 0.53/d ($\text{SD}=0.29/\text{d}$). Calibration of the CASM_{OC} phytoplankton biomass production required values that ranged from $0.80\text{--}1.25\text{ d}^{-1}$ (Table 3). Corresponding value for CASM_{OC} periphyton photosynthesis ranged from $1.10\text{--}1.20\text{ d}^{-1}$. Macrophyte maximum photosynthesis rates were 0.10 and 0.08 d^{-1} for *Potamogeton* and *Elodea*, respectively.

Absent data describing the productivity and biomass of aquatic plants for an Iowa oxbow, the calibration strategy was simply to derive parameters consistent with the technical literature that also supported the range of biomass production of higher trophic levels for which calibration data were available (e.g., fish populations described by Bakevich *et al.* 2013).

2.2. Factors regulating consumer populations

Given the complexity of the CASM_{OC} food web, the general strategy adopted for parameter estimation focused on species-specific values whenever available, augmented by values adapted from ecologically similar (surrogate) species, and the more generalized bioenergetics literature for remaining species (e.g., Deslauriers *et al.* 2017, Hansen *et al.* 1997).

2.2.1 Consumption

The formulation for consumption (equation 5) calculates grazing or predation as a normalized product of predator and prey biomass. Predator and prey biomass are modified by the preference of predator i for prey j (w_{ij}), the assimilation of prey j by predator i (a_{ij}), and a handling efficiency for predator i consuming prey j (h_{ij}) (DeAngelis *et al.* 1975; DeAngelis *et al.* 1989). The nature of the trophic interactions defined in the CASM_{OC} and the absence of data for populations of the generalized headwater pool caused handling efficiencies to be defined as 1.0 for all trophic interactions in the initial development and application of the CASM_{OC}. The food consumed by each population is either assimilated, excreted, or egested. The egested (or unused food) fraction is remineralized by a temperature-dependent decomposition process. Recycled

nutrients are added to the dissolved nutrient pools by assuming a constant C:N:P stoichiometry for plant and animal organic matter.

The mathematical nature of the consumption term introduces a density dependence in the overall production of consumer populations in the CASM_{OC} (DeAngelis et al. 1975). At low predator abundances, the biomass of the available predator determines the flux of ingested material into the predator populations. As the predator biomass increases, the flux becomes increasingly determined by the biomass of the prey. Such density dependence can influence the growth of individual populations and structure of complex food webs in the CASM_{OC}.

Zooplankton feeding rates were derived primarily from Peters and Downing (1984), Schindler (1968), and Richman and Dodson (1983). Ostracod feeding rates were developed from Buffan-Dubau and Carman (2000). Consumption rates for benthic invertebrates were based on the technical literature (e.g., Cummins 1973) or based on allometric interpolations of zooplankton feeding rates (Methot et al. 2012, Ricciardi and Bourget 1998, Wetzel et al. 2005). Feeding rates for corixids were estimated based on Pajunen (1990).

Maximum consumption rates for modeled populations of fishes were derived either from species-specific data or from ecologically similar species. Species-specific data are used to define length-weight relationships (www.fishbase.org) and weight-consumption relationships (e.g., Deslauriers et al. 2017, Hanson et al. 1997). When species-specific data are lacking, functional similarity was used to estimate maximum consumption from available species data (Table 5).

2.2.2 Respiration

Respiration rates for zooplankton were derived using results from Schneider (1992) and Schindler (1968). Benthic invertebrate respiration rates were estimated based on Hamburger and Dall (1990), Brinkhurst et al. 1983, and Methot et al. 2012. Standard respiration rates for modeled freshwater fish were estimated using data reported by Hanson *et al.* (1997). Table 5 lists the values for maximum daily respiration (R_{max}) estimated for consumer populations in the CASM_{OC}.

2.2.3 Specific dynamic action

Values of specific dynamic action for modeled fish populations were estimated using data reported by Hanson et al. (1997). The previously identified studies used to estimate maximum rates of consumption and respiration for the modeled fish populations in the CASM_{OC} applications were also used to estimate rates of specific dynamic action for these same populations (Table 5).

2.2.4 Egestion rates

Estimates of egestion rates for modeled fish populations were derived using data reported by Hanson et al. (1997). The previously identified studies used to estimate maximum rates of consumption and respiration for the modeled fish populations in the CASM_{OC} were also used to estimate egestion rates of for these same populations (Table 5).

2.2.5 Excretion rates

Zooplankton excretion rates were estimated using the results of Mayzaud (1976), Hargrave and Geen (1968), and Wen and Peters (1994). Excretion rates for modeled fish populations were estimated using data reported by Hanson et al. (1997). Excretion by benthic invertebrates was interpolated using the rates obtained for zooplankton. The previously identified studies used to estimate maximum rates of consumption and respiration for the modeled fish populations in the CASM_{OC} were also used to estimate excretion rates for these same populations (Table 5).

2.2.6 Mortality rates

Zooplankton mortality rates were based on studies by Eiane et al. (2002) and Ohman and Hirche (2001). Benthic invertebrate mortality rates were extrapolated from zooplankton mortality rates. Survival rates for corixids were derived using Cespedes et al. (2019). Mortality rates for modeled fish populations were based on estimates for 30 lotic and lentic fish species used for modeling effects of commercial navigation on fish entrainment (Bartell and Campbell, 2000). Table 5 lists the mortality rates for consumer populations used in the CASM_{OC}.

2.2.7 Diet and assimilation values

The CASM_{OC} permits specification of grazing and predator-prey interaction among the modeled populations of aquatic producers and consumers (DeAngelis et al. 1989). A non-zero prey preference value, w_{ij} , is specified for each trophic interaction between prey i and consumer j . The magnitudes of the w_{ij} values is somewhat arbitrary, because the calculation of each trophic interaction involves a normalization across all prey items consumed by a grazer or predator. However, in practice, values of w_{ij} range from 0 to 1, with higher values indicating increased preference. If available, diet composition data can be used to derive w_{ij} values. Qualitative descriptions of diet preferences can be used with professional judgment to develop these input parameters as well. Current versions of the CASM_{OC} assume that specified prey preferences are constant; ontogenetic shifts in diet are not included, unless different life stages of consumers are modeled explicitly.

The CASM_{OC} also permits specification of assimilation efficiency for each grazing or predator-prey interaction. The a_{ij} parameters are analogous to the prey preference parameters, except these parameters quantify the fraction of consumer prey converted to new consumer biomass. In the

CASM_{OC}, the assimilation efficiency multiplies the calculated amount of food ingested minus losses to egestion. The a_{ij} parameters characterize food quality derived from published values (Richman and Dodson 1983; Lampert 1987). The a_{ij} parameters are constant during a CASM_{OC} simulation.

The CASM_{OC} also permits specification of a prey handling efficiency for each grazing or predator-prey interaction. In the CASM_{OC}, the assimilation efficiency multiplies the calculated amount of food ingested. The h_{ij} parameters are analogous to the prey preference parameters, except these parameters quantify the fraction of prey not ingested as a result of behavioral or mechanical inefficiencies that make the prey more difficult to ingest. Values of h_{ij} were defined as 1.0 for all trophic interactions in the CASM_{OC}.

The technical literature (e.g., Muhlfield et al. 2008, Bajer et al. 2004, Rice and Cochran 1984, Kitchell et al. 1977, 1974), including previously developed versions of the CASM, was used to derive values for the diet matrix that defines the grazing and predator-prey interactions in the CASM_{OC} (e.g., Bartell et al. 2013, 2000; Naito et al. 2002, 2003). Similarly, values of assimilation efficiencies for grazer and predator-prey interactions were obtained from the literature and previous versions of the model.

2.3. Environmental input data

In the CASM_{OC}, the expression of bioenergetics-based population growth is influenced by physical-chemical characteristics of the particular environments defined for model applications. The following sections briefly describe these characteristics for the off-channel oxbow habitat simulated by the CASM_{OC}.

2.3.1 Surface light intensity

Photosynthetically active incident solar radiation (PAR) drives plant growth in all versions of the CASM. The model for the generalized Iowa oxbow uses average values of daily incident PAR calculated from solar radiation data reported for Des Moines, IA for year 2010 (Figure 3). The CASM_{OC} uses the same incident solar radiation values as the CASM_{TS} (Bartell et al. 2019).

Values of surface light intensity are attenuated as a function of depth and daily values of water column constituents (e.g., phytoplankton biomass, suspended POC, suspended inorganic sediments) as described in Section 2.1.1.

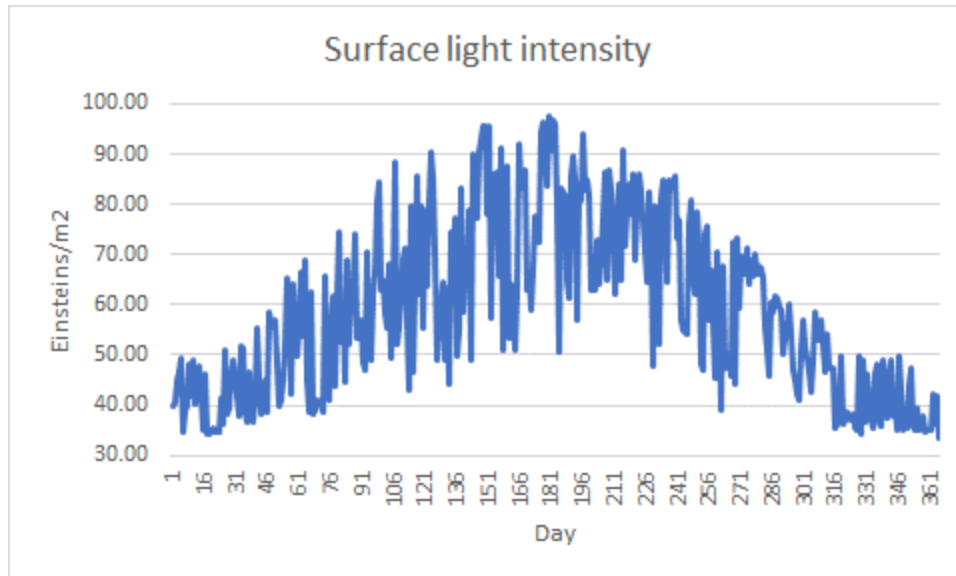


Figure 3. Daily irradiance data for 2010 obtained for Des Moines, IA. Source: National Solar Radiation Data Base.

2.3.2 Water temperature

The following water quality data description and development were adapted from Nicholas Green (Waterborne Environmental Incorporated). Water quality and streamflow data were obtained for all active USGS stations in Iowa since 1988. Water quality variables queried included water temperature (°C), dissolved oxygen (DO; mg/L), and suspended sediment (mg/L). Locations with at least one of these variables were screened to identify those with streamflow distributions similar to that of White Fox Creek near Clarion, IA (USGS 05480930). White Fox Creek was chosen because it is the stream connected to the restored oxbow studied by Schilling et al. (2017, 2018).

Four gages had streamflow distributions statistically similar to White Fox Creek: Moquotketa River at Manchester (USGS 05416900), Boone River near Webster City (05481000), North Raccoon River near Sac City (USGS 05482300), and Nodaway River at Clarinda (USGS 06817000). Moquotketa River and Nodaway River had sediment data, while Boone River and North Raccoon River had temperature data.

Daily temperature values were developed for the Iowa oxbow as the average of data across the Iowa stream stations for available sampling years (Figure 4). The modeled oxbow does not freeze entirely, although water temperatures <3°C are assumed to be associated with some ice and snow cover. Under these conditions, the model reduces daily surface light intensity by 33%.

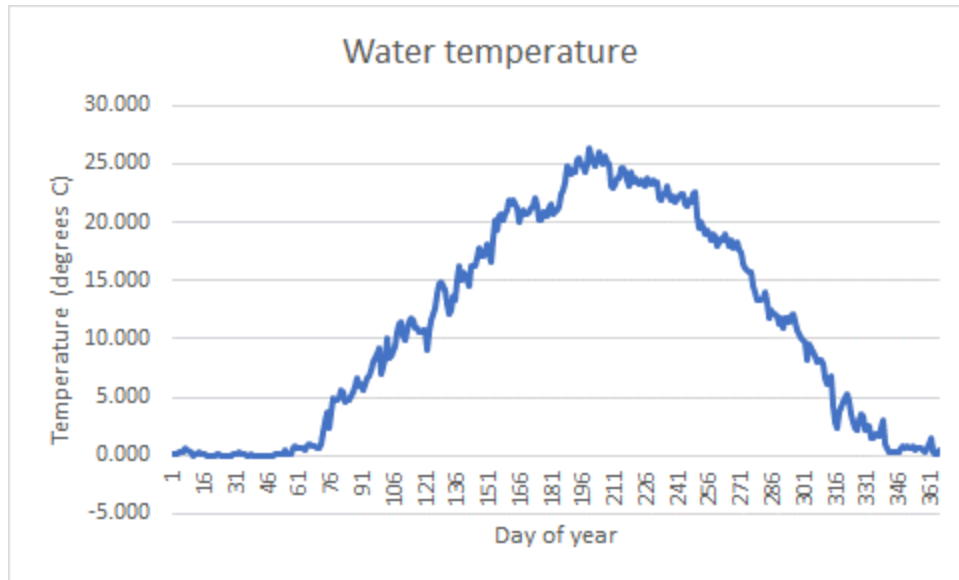


Figure 4. Daily water temperature values used in the CASM_{OC}.

2.3.3 Water depth

Daily values of water depth for the modeled Iowa oxbow were defined as a constant 1.2 m, based on depths reported by Schilling et al. (2017, 2018) for reconstructed oxbows in Iowa. Surface light intensity attenuates as a function of depth in the CASM_{OC}. Depth is also an important habitat component of the modeled populations of primary producers and consumers.

While depth is constant in current simulations, the model provides opportunities to examine the implications of changes in depth (e.g., flooding, drought) on oxbow structure and function.

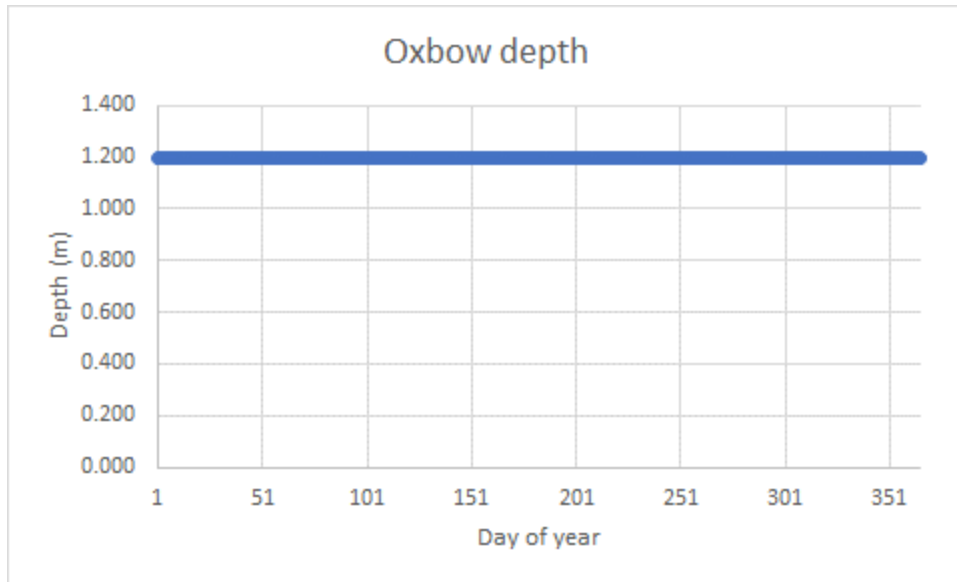


Figure 5. Constant daily values of water depth for the Iowa oxbow off-channel habitat.

2.3.4 Current velocity

Daily values of current velocity for the Iowa oxbow are assumed to be zero (Figure 6). Velocity determines habitat quality for periphyton and macrophytes. While velocity is assumed unimportant in the current model applications, the structure of the CASM_{OC} provides the capability to examine the implications of current velocities imposed on the ecological production dynamics of the simulated Iowa oxbow.

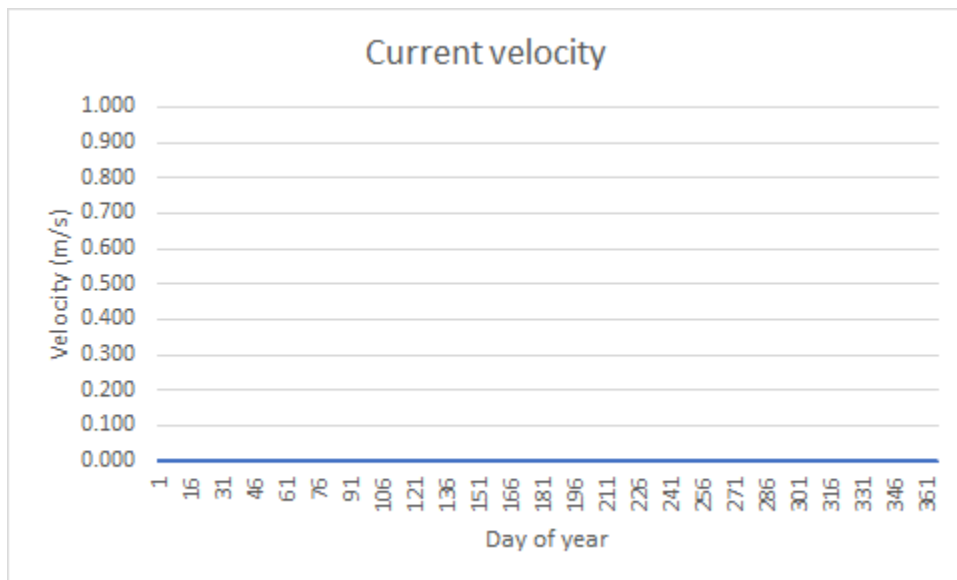


Figure 6. Daily values of water current velocity defined for the generalized Iowa oxbow.

2.3.5 Dissolved inorganic nitrogen

Data describing the seasonal concentrations of dissolved inorganic N for the Smeltzer oxbow in the Lyons Creek watershed, Iowa were used to construct daily values of DIN for the CASM_{OC} (Figure 7). Concentrations were reported for samples collected at the inlet and outlet of this Iowa oxbow (Kalkhoff et al. 2016). A third-order polynomial function was fit to the data reported for the inlet ($R=0.53$) and outlet ($R=0.66$). Daily concentrations of DIN used by the CASM_{OC} were calculated as the average between the daily inlet and outlet values produced using the polynomial functions.

The autumn peak in DIN values seems unusually high and might reflect runoff from autumn precipitation. The peak might also be influenced by extrapolating limited data across days 300-365; sample were not collected from the Smeltzer oxbow beyond day of year 300. Nutrient data for Iowa oxbows were largely unavailable and the Kalkhoff et al. (2016) study provided the most comprehensive seasonal characterization of macronutrients, including DIN.

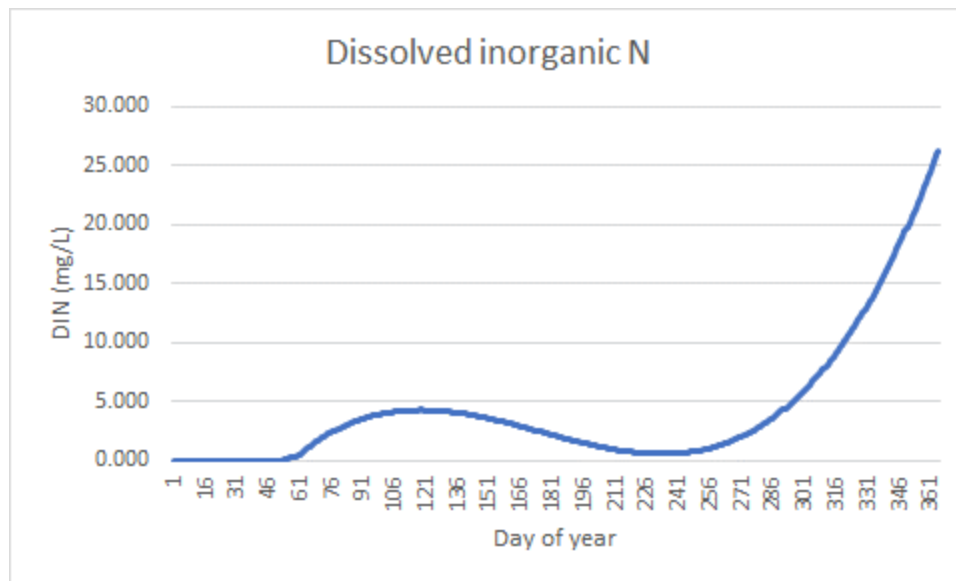


Figure 7. Daily values of DIN derived for the generalized Iowa oxbow.

2.3.6 Dissolved inorganic phosphorus

Kalkhoff et al. (2016) also reported data for inorganic P collected from the Smeltzer oxbow. The data were similarly fit to second-order polynomial functions for both the inlet ($R=0.74$) and outlet ($R=0.88$). The daily concentrations of DIP used by the CASM_{OC} were computed as the average of the daily values for the inlet and outlet produced by the functions (Figure 8).

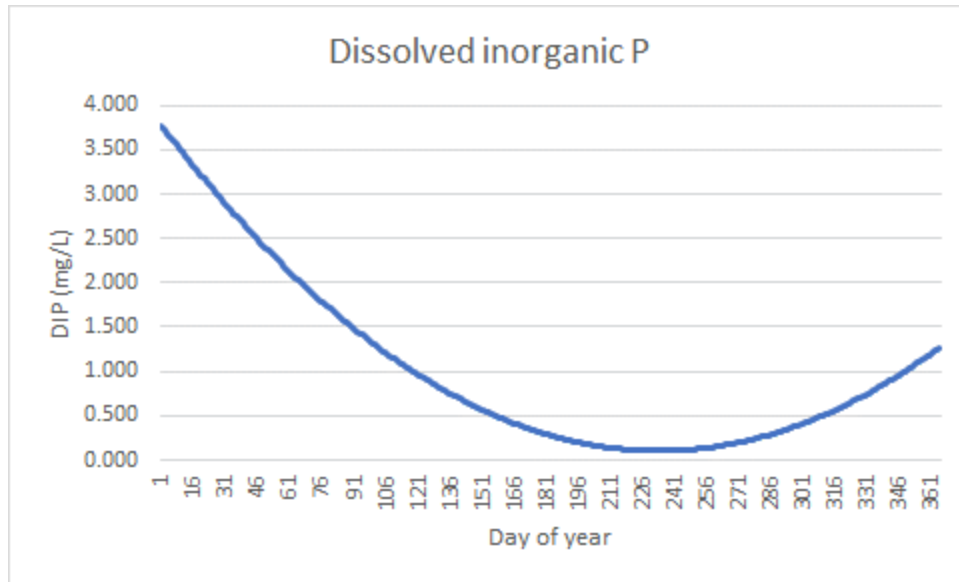


Figure 8. Daily values of DIP defined for the generalized Iowa oxbow.

2.3.7 Dissolved silica

Daily concentrations of dissolved silica influence the growth of diatoms populations that are specified in the phytoplankton and periphyton communities in applications of the CASM_{OC} (Figure 9) Silica data were not identified for off-channel habitats in Iowa. Values for the Iowa oxbow CASM_{OC} were computed as the averages of data reported from Upper Honey Creek (e.g., Bartell et al. 2013) and are the same values used in developing the CASM_{TS} (Bartell et al. 2019). The basic assumption was that diatoms are seldom limited by the availability of dissolved silica in this generic oxbow application of the CASM_{OC}. While not limiting in current applications of the CASM_{OC}, future scenarios might be constructed where silica availability constrains diatom productivity in the modeled Iowa oxbow.

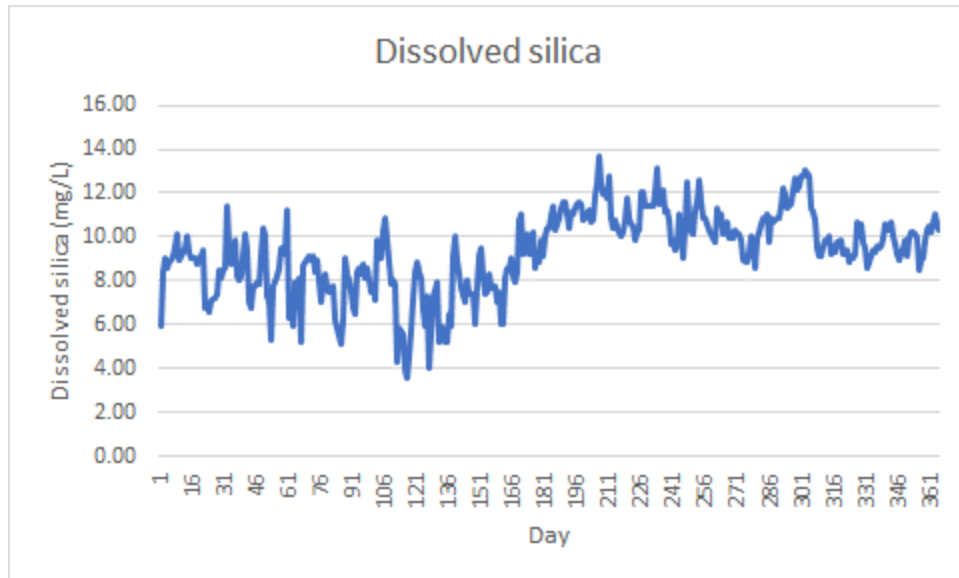


Figure 9. Daily concentrations of dissolved silica developed for the generalized Iowa oxbow.

2.3.8 Total inorganic solids

Inorganic sediment data were developed in parallel with the derivation of water temperature data (personal communication, N. Green, WEI). Two Iowa sampling stations had streamflow distributions statistically similar to White Fox Creek and measures of inorganic sediments: Moquotketa River at Manchester (USGS 05416900) and Nodaway River at Clarinda (USGS 06817000).

Daily values of suspended sediment concentrations were developed for the Iowa oxbow as the average of data across the Iowa stream stations for available sampling years (Figure 10).

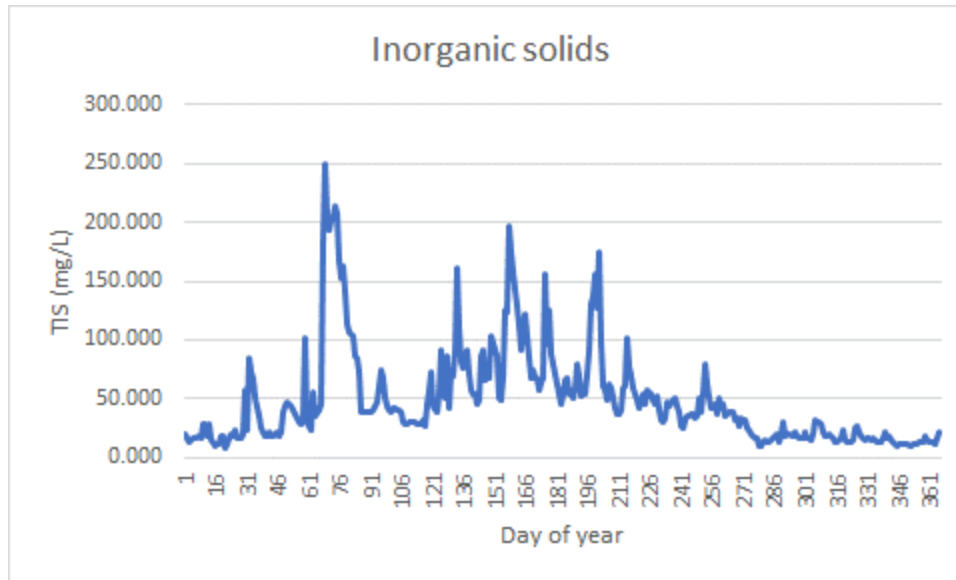


Figure 10. Daily concentrations of suspended inorganic solids developed for the generalized Iowa oxbow.

2.3.9 Particulate organic carbon

Particulate organic carbon data were not identified for Iowa oxbow habitats. As a result, the allochthonous input of suspended particulate organic carbon (POC) values were the same as used in the Iowa headwater pool (Bartell et al. 2019) (Figure 11).

The overall CASM_{OC} modeling approach includes biogenic sources of POC generated during model simulation as the result of egestion by consumers and plankton mortality. Particulate organic carbon serves as a food source for certain consumer populations in these CASM_{OC} applications. Suspended POC also contributes to the attenuation of surface light intensity in the CASM_{OC}. Suspended and sedimented POC are subject to decomposition by modeled planktonic and sediment bacteria populations.

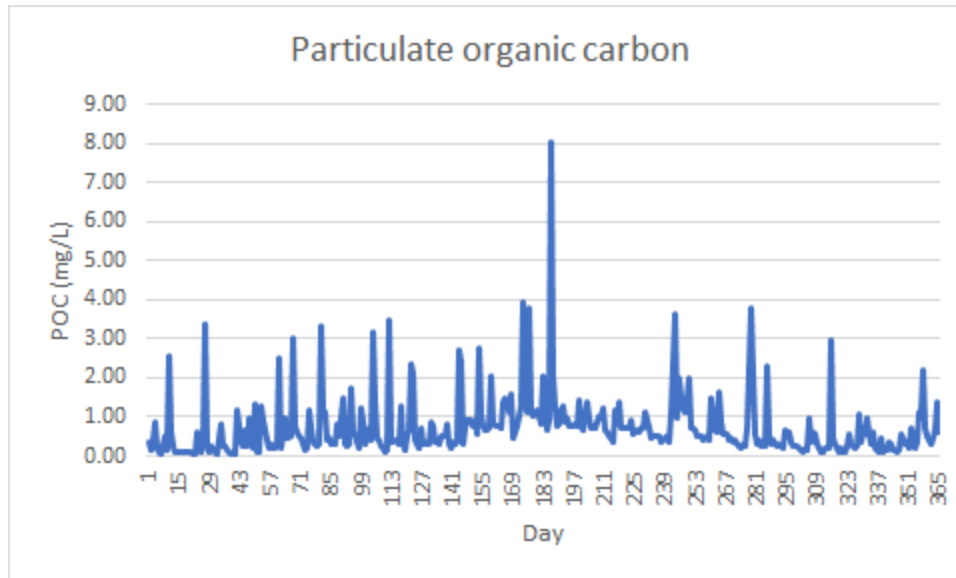


Figure 11. Daily input concentrations of suspended particulate organic carbon for the generalized Iowa headwater stream.

2.3.10 Surface wind velocity

Daily values of wind velocity (m/s) are used to estimate re-aeration of oxygen at the modeled air:water surface interface in the CASM_{OC} during each model time step using the equation reported by Park and Clough (2014):

$$(17) \quad k_r = 3.93 (v^{0.50}) (d^{-1.50}) (1.024)^{(t-20)}$$

where,

v is wind velocity (m/s)

d is depth (m)

t is water temperature (deg C), and

k_r is reaeration coefficient (1/d)

Input wind velocities are derived from system-specific measures, relevant weather station data, or results of other models. The CASM_{OC} uses the same wind data as the CASM_{TS} (Bartell et al. 2019), which were derived from the Des Moines, Iowa airport data (Figure 12). Each daily wind velocity uniformly determines the reaeration of oxygen across the surface:water interface over the physical area being modeled. Concentrations of dissolved oxygen determine habitat quality and mortality of modeled populations of aquatic invertebrates and fish.

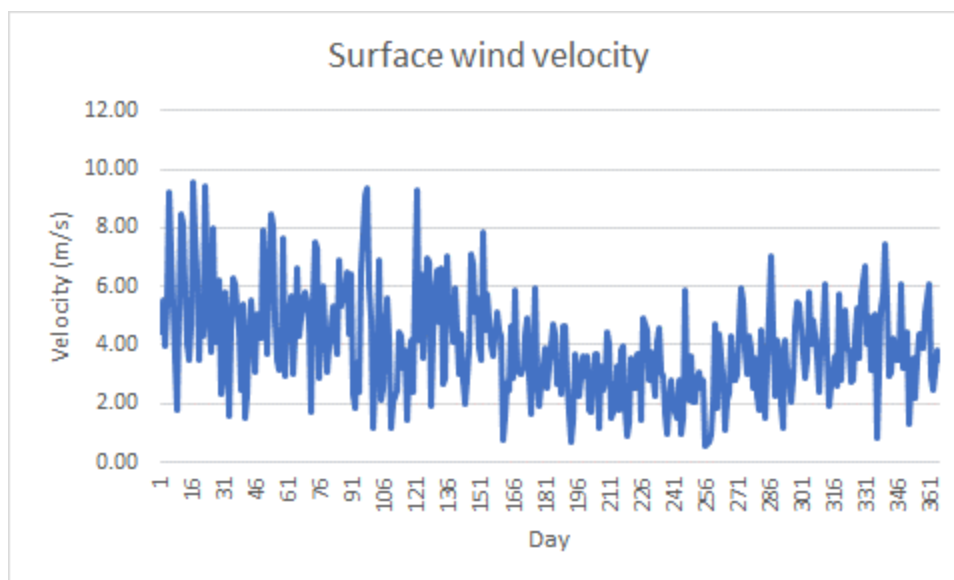


Figure 12. Daily wind velocities developed for the generalized Iowa oxbow.

3 MODEL LINKING BETWEEN THE TS-IBM AND THE CASM_{OC}

The hybrid TS-IBM/CASM_{OC} was developed as two stand-alone models (CASM_{OC} and TS-IBM). The two models can be run independently and in combination (Figure 13). If run independently, the CASM_{OC} can include the simulation of Topeka shiner populations as guilds (juvenile and adults separately) in the food web. Alternatively, the CASM_{OC} can simulate the Iowa oxbow food web dynamics in the absence of Topeka shiners. The TS-IBM requires daily biomass values of its defined prey, including detritus (i.e., POC) (Schmolke et al. 2019). These values are provided by the stand-alone CASM_{OC}.

When run in combination, the two models exchange information on a daily basis according to the algorithm developed for the CASM_{TS} and TS-IBM hybrid model (Bartell et al. 2019, Schmolke et al. 2019). Topeka shiner biomass values are not changed within CASM_{OC} in the hybrid model. The biomass of Topeka shiner handed over from TS-IBM is used in the linked CASM_{OC} version to calculate the food web effects using the CASM_{OC}. The models also transfer the biomass of adult Topeka shiner consumed by largemouth bass in the time step, if largemouth bass is included in the simulations. Topeka shiner biomass consumed by the bass is passed back to the TS-IBM to determine the corresponding Topeka shiner mortality.

Initial biomass values in the food web are defined by an input file stating the biomass values (in g C) of each guild included in the food web. TS-IBM reads the relevant values from the initial biomass of prey guilds and the initial Topeka shiner biomass. These biomass values are changed in the TS-IBM in each daily time step and recorded at the end of the time step. The linking script inserts these biomass values in a transfer file that contains the biomass values of all prey guilds simulated in CASM_{OC}. The CASM_{OC} reads the transfer file and calculates the subsequent biomass values of all food web populations other than Topeka shiner for one day. The resulting output file from CASM_{OC} is the used as input file for the TS-IBM.

Depending on whether the hybrid simulation is for baseline conditions or for selected pesticide exposure scenarios, the daily biomass values are stored in corresponding output files for subsequent analysis and presentation.

IBM - CASM daily interaction

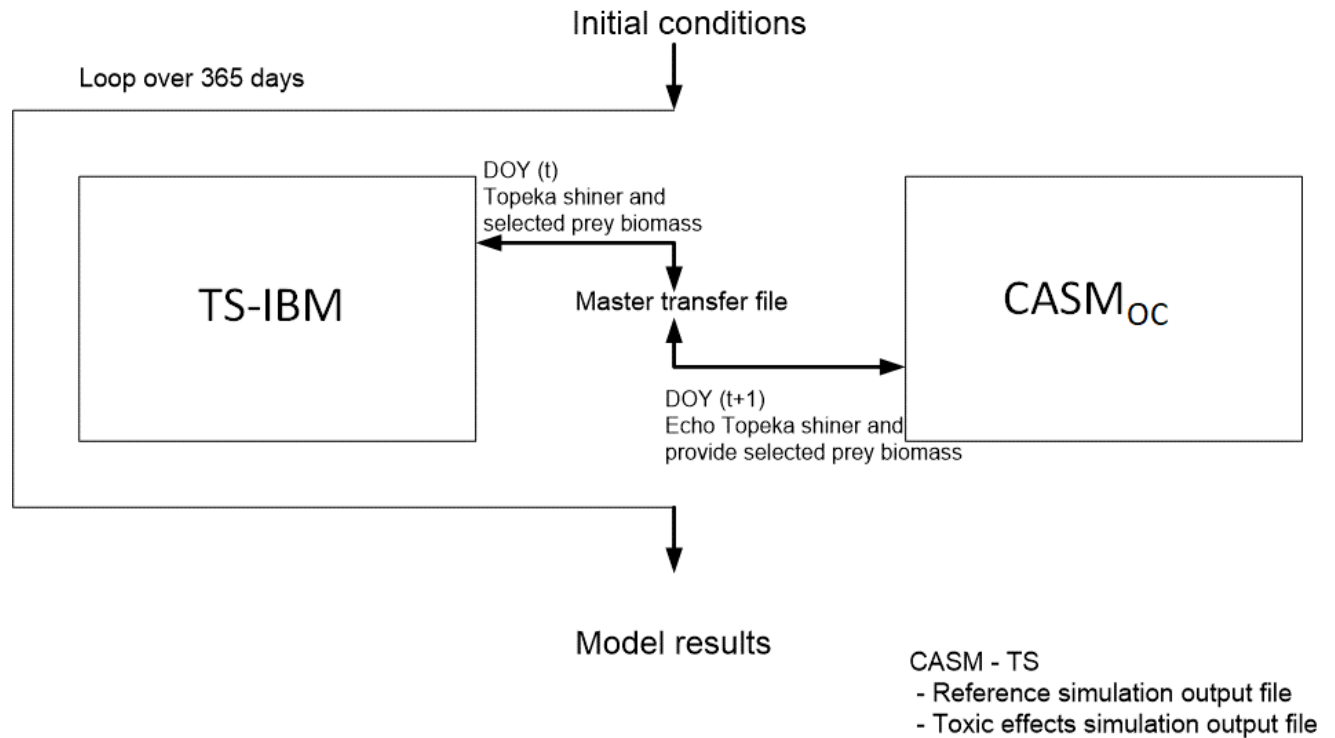


Figure 13. Schematic illustration of data transfers in the hybrid TS-IBM and CASM_{OC} hybrid model implementation.

4. IMPLEMENTATION AND VERIFICATION

The CASM_{OC} was adapted from the CASM_{TS}, which is programmed in Fortran (Bartell et al. 2019). Individual subroutines and functions in the CASM_{TS} were implemented in spreadsheets or independent Fortran codes to verify them separately from the overall CASM_{TS} code.

Calculations verified include the nonlinear functions for the influence of light intensity on photosynthesis, and the effects of water temperature on consumption and respiration. The subroutines and functions are the same in each model. Therefore, the verification was not repeated for the CASM_{OC}. These relationships have been identified as highly sensitive in determining the overall model results (Bartell et al. 1988, 1986).

The CASM_{OC} is also self-diagnostic in the sense that all input values are echoed to output files that can be easily inspected to identify any incorrect formatting of model inputs. Incorrect filename specifications routinely cause the code to terminate as part of the overall Fortran environment.

Model executable files have been executed on different computers and cross-checked for accuracy and reproducibility.

5. MODEL OUTPUT VERIFICATION

5.1. Calibration

Calibration of the CASM_{OC} followed the same overall strategy as calibration of the CASM_{TS} (Bartell et al. 2019). The CASM_{OC} calibration was based on : 1) derivation of initial fish biomass values and adjustment of fish bioenergetics parameters to achieve reported fish population biomass values for Iowa oxbows, 2) implementation of density-dependent fish growth and resetting initial biomass values for aquatic plants and invertebrates to produce stable population sizes across multiple years throughout the CASM_{OC} food web, and 3) adjustments to bioenergetics parameters for phytoplankton, periphyton, zooplankton, and benthic invertebrates to generate biomass values for these guilds that were consistent with supporting modeled fish biomass.

The calibration was guided in part by data provided in Bakevich et al. (2013) for fish, as well as estimates for zooplankton and benthic macroinvertebrate abundances based on numbers commonly encountered in freshwater systems (Table 8). The CASM_{OC} performs its calculations using units of carbon for the biomass state variables. However, the TS-IBM uses numbers of individuals in its computations with inputs from the CASM_{OC}. Accordingly, the target values for calibration are presented in both units of carbon and abundance (individuals/m²) in Table 8. Conversion from carbon to numbers of individuals was based on the assumption of homogeneous distribution throughout a well-mixed 1.2-m deep water column. The plots of calibration results (except for phytoplankton and periphyton) are presented using abundances simulated by the CASM_{OC}.

Table 8. Calibration targets for the CASM_{OC} derived from Bakevich et al. (2013) data.

CASM_{OC} population	g C/Individual	Target biomass g C/m²	Target abundance Individuals/m²
Copepods	2.9 (µg C/ind)	0.17	60,000
Cladocerans	0.8 (µg C/ind)	0.02	30,000
Rotifers	0.7 (µg C/ind)	0.06	90,000
Microzooplankton	1.0 (µg C/ind)	0.12	120,000
Ostracods	1.0 (µg C/ind)	0.12	24,000
Red shiner	1.090	2.18	2.0
Fathead minnow	0.790	2.203	2.78
Johnny darter	0.500	0.00057	0.0011
Topeka shiner (juv)	0.001	0	0
Topeka shiner (adult)	0.149	0.195	1.31
Rock bass	8.46	0.0051	0.0006
Orange-spotted sunfish	0.850	1.158	1.36
Brassy minnow	0.530	0.0532	0.1004
Common shiner	0.740	0.1616	0.218
Corixids	0.000166	0.008	50
Ephemeroptera	0.000015	0.0007	50
Trichoptera	0.000166	0.02	100
Oligochaetes	0.000534	0.11	200
Chironomids	0.000149	0.01	100
Coleopterans	0.000166	0.02	100
Creek chub	20.87	0.2077	0.01
Black bullhead	58.33	67.68	1.160
Common carp	109.85	29.92	0.272
Largemouth bass	201.66	46.43	0.230
Blunt-nose minnow	0.31	0.0141	0.045
Central stoneroller	1.76	No data	-
White sucker	94.95	13.26	0.140

Calibrations were based on the results of repeated 40-year simulations using the CASM_{OC}. This model duration proved sufficient to remove year-to-year transient behavior associated with the initial model biomass and parameter values for fish populations included in the CASM_{OC} food web. Transient dynamics in fish biomass dampened to repeated cyclic biomass patterns after 20 model years for fish populations. To error on the side of conservatism, the biomass values at the end of day 365 for model year 39 were used to define initial conditions for applications of the CASM_{OC} to examine the impacts of temperature and benzovindiflupyr exposures.

5.1.1. Calibration of Topeka shiner population biomass

The initial biomass value for Topeka shiner of 0.00149 g C/m² and the growth parameters of the fish bioenergetics model implemented for Topeka shiner (Table 4) were used to calibrate the CASM_{OC} to produce seasonal biomass values on the order of 0.2 g C/m² by simulated year 40 based on values derived from Bakevich et al. (2013). The calibration also reflects the density-dependent growth implemented for all CASM_{OC} fish populations.

Figure 14 illustrates the year 40 biomass values for adult Topeka shiner produced by the CASM_{OC}. Year 40 values are illustrated because the day 1 values for year six of CASM_{OC} populations are used as initial inputs of the TS-IBM.

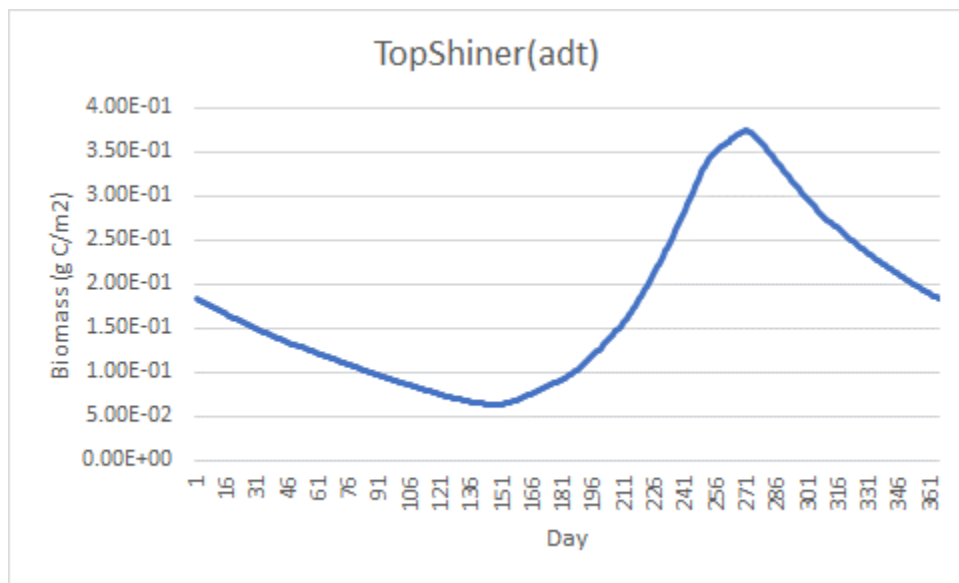


Figure 14. CASM_{OC} simulated biomass values for adult Topeka shiner

Figure 15 illustrates the stable limit cycle of the calibrated CASM_{OC} for adult Topeka shiner biomass. The density-dependent growth largely determines the nature of the limit cycle which is evident after year one in the 5-y simulation illustrated in Figure 15.

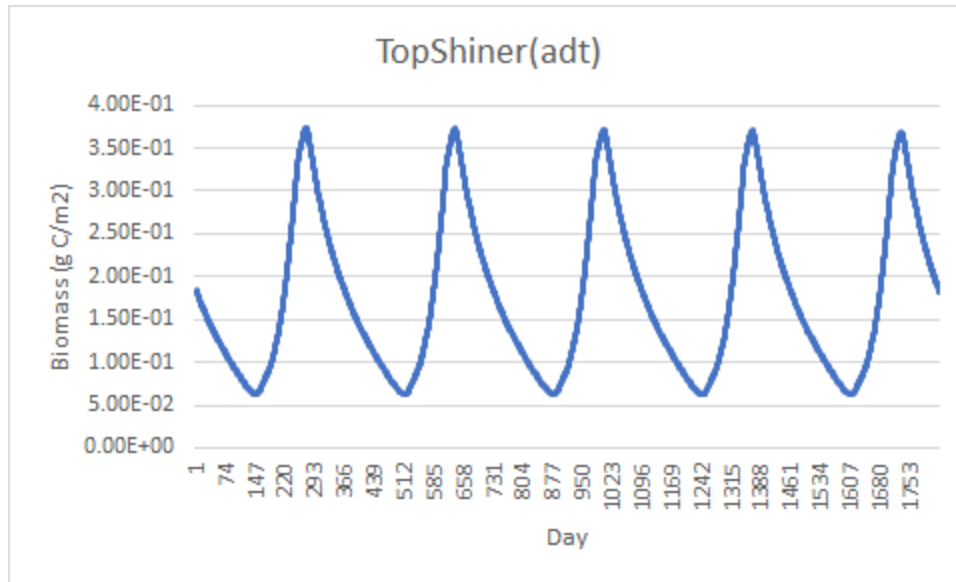


Figure 15. CASM_{OC} 5-year simulation showing stable limit cycle for adult Topeka shiner.

5.1.2. Calibration of stable populations of aquatic plants, invertebrates, and fish

The calibration of the CASM_{OC} to produce population biomass results consistent with the available Topeka shiner and other fish data correspondingly generated seasonal patterns of biomass for modeled populations of aquatic plants, invertebrates and fish for which data were largely unavailable. The following CASM_{OC} baseline simulations show results for year 40 (used by the TS-IBM).

To reduce the potential artifactual effects of initial biomass values on overall model behavior, day 1 biomass values for phytoplankton, periphyton, macrophytes, and macroinvertebrates were reset each model year to their defined initial biomass. Fish population dynamics, with the exception of largemouth bass, included density-dependent growth constraints that similarly reduced the effects of initial biomass estimates for the baseline CASM_{OC}. The effects of initial conditions on fish population biomass values were largely stabilized by modeled year two. To ensure that stable baseline population dynamics were used as inputs to the TS-IBM, the results of modeled year 40 were arbitrarily selected for comparison of the models and for evaluating the potential impacts of food availability and predation on the population dynamics of the Topeka shiner. For multiple year simulations with CASM_{OC}, the same input file for environmental conditions was used for each simulated year.

Figure 16 presents the seasonal biomass values of the five populations of phytoplankton defined in the generic Iowa oxbow food web. Lacking phytoplankton data for this aquatic system, the CASM_{OC} was calibrated to produce a seasonal progression of phytoplankton populations that characterizes typical temperate freshwater aquatic systems. The calibration indicates minimal

phytoplankton productivity during the winter and early spring, followed by a spring pulse of diatoms. The assemblage progresses through chlorophytes, cryptophytes, and blue-green algae through the remainder of the modeled year. Modeled euglenoid algae are minimally abundant in the generic oxbow. Although necessarily speculative, the assemblage does provide sufficient productivity to sustain zooplankton and modeled planktivorous fish (e.g., red shiner, fathead minnow, and Topeka shiner), for which limited calibration data are available (e.g., Bakevich et al. 2103). That is, the phytoplankton assemblage is bioenergetically consistent with the calibrated production dynamics of higher trophic levels that depend in part on phytoplankton as a food source.

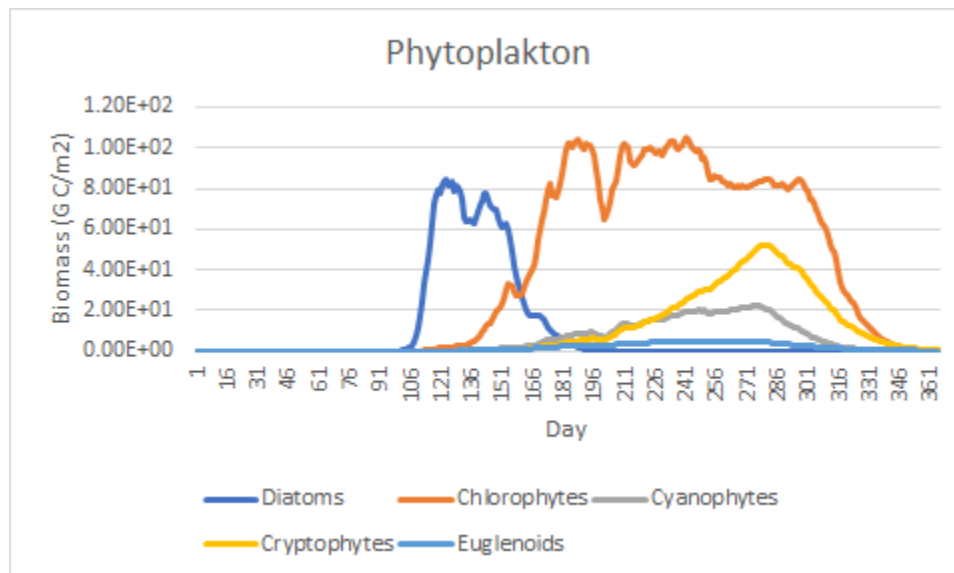


Figure 16. CASM_{OC} simulated phytoplankton biomass.

Lacking longer-term data for phytoplankton productivity in an Iowa oxbow, the CASM_{OC} begins each model year (i.e., January 1) with the same initial biomass values for modeled phytoplankton populations. This approach results in the same pattern of population production over the 40-y modeling duration, given that the 365-days of environmental input data that influence phytoplankton productivity are currently repeated for each year.

The CASM_{OC} calibration resulted in two seasonal peaks of periphyton (attached algae) biomass (Figure 17). The modeled periphyton community is dominated by diatoms and chlorophytes. The same strategy used to calibrate modeled phytoplankton was used for periphyton. Absent periphyton productivity data, the model was calibrated to provide sufficient periphyton biomass to sustain macroinvertebrates, which graze on periphyton, and thus provide sufficient prey biomass to support modeled fishes that consume macroinvertebrates, including the Topeka shiner. The initial biomass values of periphyton are used in all modeled years, which produces a repeating pattern of periphyton seasonal biomass values.

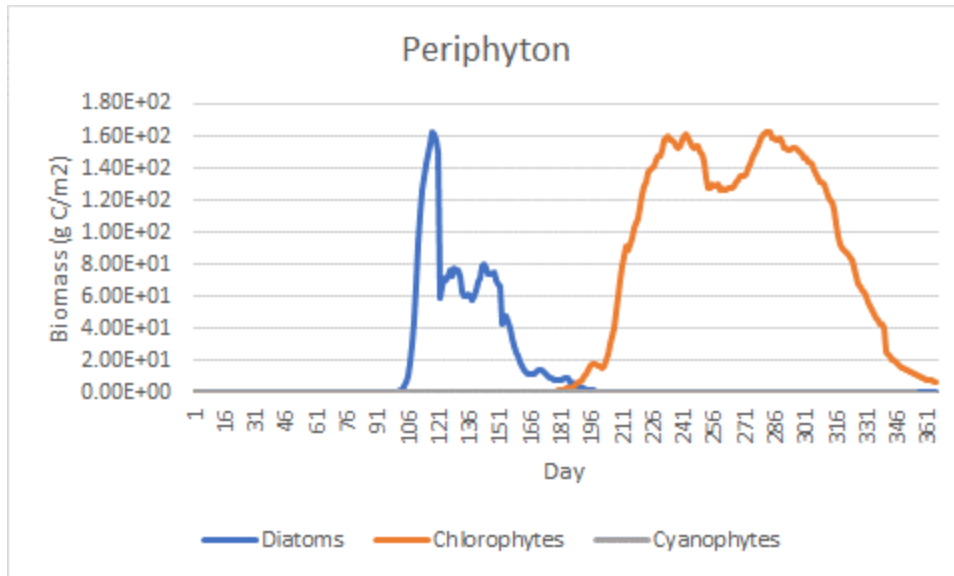


Figure 17. CASM_{OC} simulated periphyton biomass values.

The CASM_{OC} modeled zooplankton spring assemblage for the generalized Iowa oxbow is dominated by copepods, followed by rotifers, and cladocerans (Figure 18). The spring peak in zooplankton biomass follows the peak production of modeled phytoplankton. A secondary pulse of zooplankton production in the fall is dominated by rotifers, microzooplankton, and cladocerans.

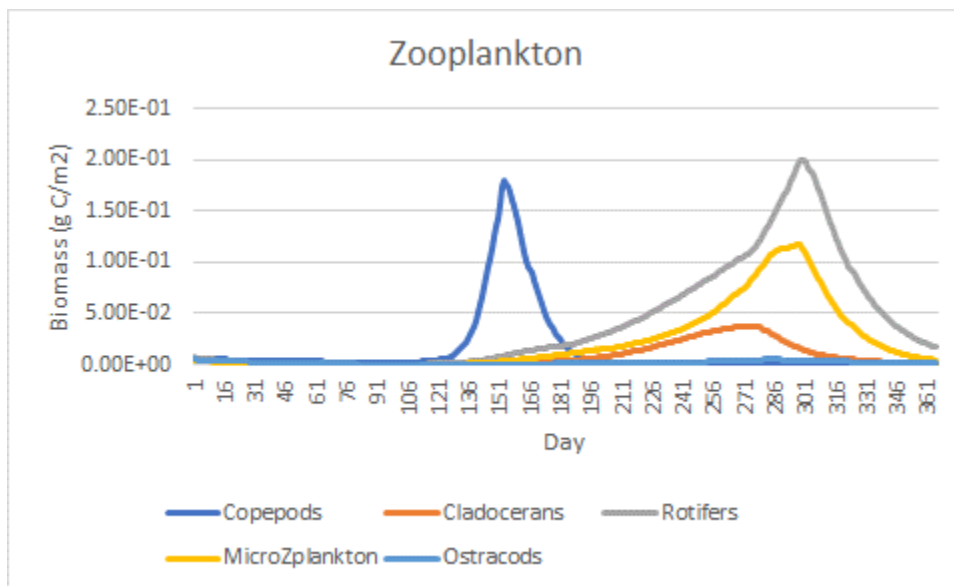


Figure 18. CASM_{OC} simulated zooplankton biomass.

Zooplankton population initial biomass values are set to the same day 1 values for each simulated year. This approach parallels that used for phytoplankton and periphyton and produces identical seasonal patterns of zooplankton biomass across all modeled years.

Figure 19 shows the modeled values for total zooplankton abundance, which are used as inputs to the TS-IBM. The numbers are lower than the target values (Table 8) and result from intense predation pressure by the modeled fish assemblage, which contains many populations that preferentially feed on zooplankton (e.g., Topeka shiner).



Figure 19. CASM_{OC} simulated total zooplankton abundance.

The CASM_{OC} modeled benthic macroinvertebrate assemblage is dominated by oligochaetes, ephemeropterans (mayflies), and trichopterans (caddisflies) in the spring production peak (Figure 20). Chironomids dominate the assemblage in the late summer and fall. Modeled caddisflies and mayflies are important components of the fall assemblage. Modeled values on the order of 100 individuals/m² are consistent with the target values developed in Table 8 for the microbenthic invertebrates. The depressed biomass values during the summer months result from intense predation by the modeled fish assemblage.

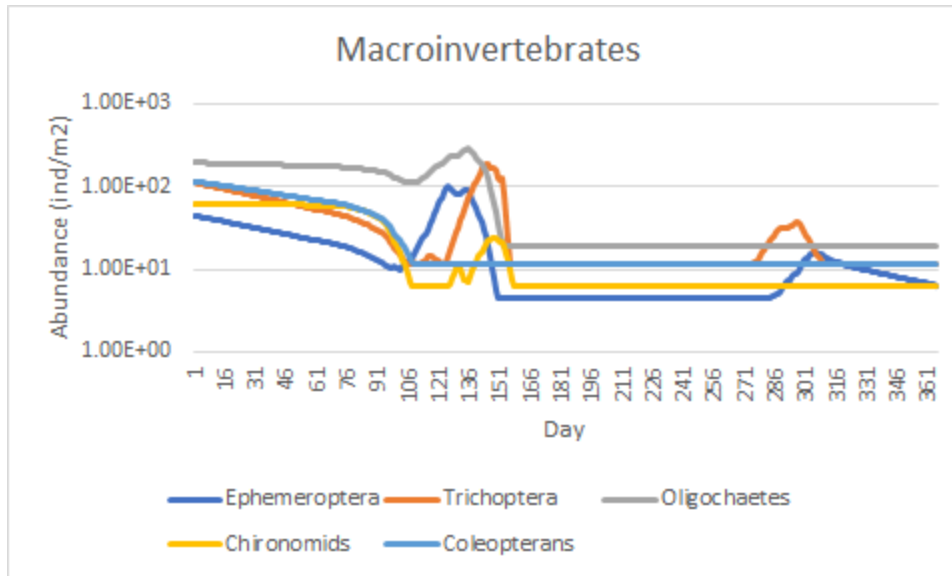


Figure 20. CASM_{OC} simulated abundance values for benthic macroinvertebrates.

The same approach for initializing zooplankton population biomass is applied to the macroinvertebrate populations. The seasonal pattern of macroinvertebrate population biomass repeats across all modeled years.

Figure 21 illustrates the year 40 daily abundance values for red shiner, fathead minnows, and Johnny darter produced by the calibrated baseline CASM_{OC}. The target abundance values of ~2-3 ind/m² for red shiners and fathead minnow derive from Bakevich et al. (2013) data (Table 8). The reference calibration suggests that the model somewhat over-estimates fathead minnow abundance, while similarly under-estimating red shiner abundance. Results for the Johnny darter are consistent with the low target abundance values based on available data (Table 8).

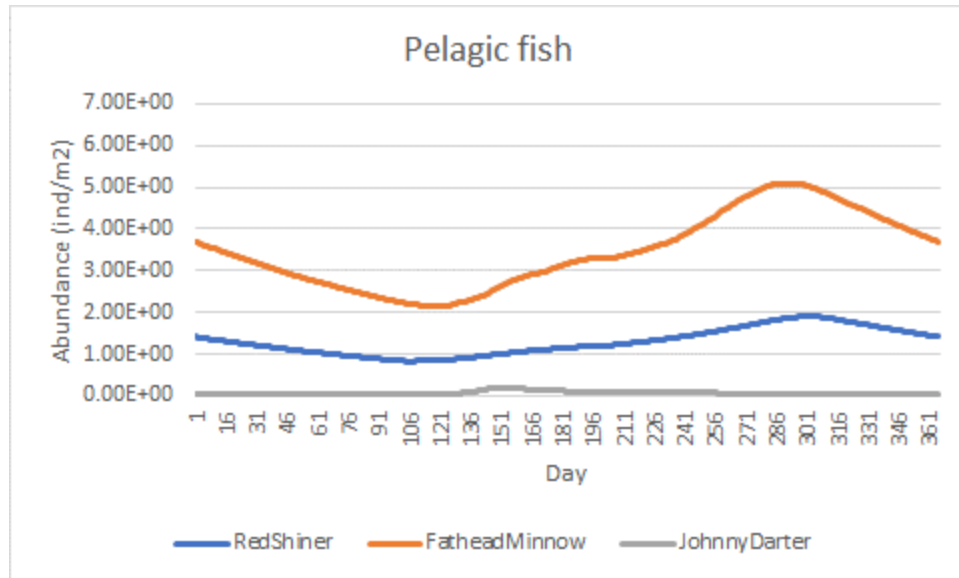


Figure 21. CASM_{OC} simulated pelagic fish abundance.

The calibrated year 40 abundance values for rock bass, orange-spotted sunfish, brassy minnow, and the common shiner are shown in Figure 22. The target abundance values ranged from 0.0006 (rock bass) to 1.4 (orange-spotted sunfish) individuals/m² with brassy minnow (0.10) and common shiner (0.218) (Table 8). The calibrated reference underestimates these target values, but modeled values are generally in the same order of magnitude with brassy minnow and common shiner ranging from ~ 0.75 to 0.15 individuals/m².

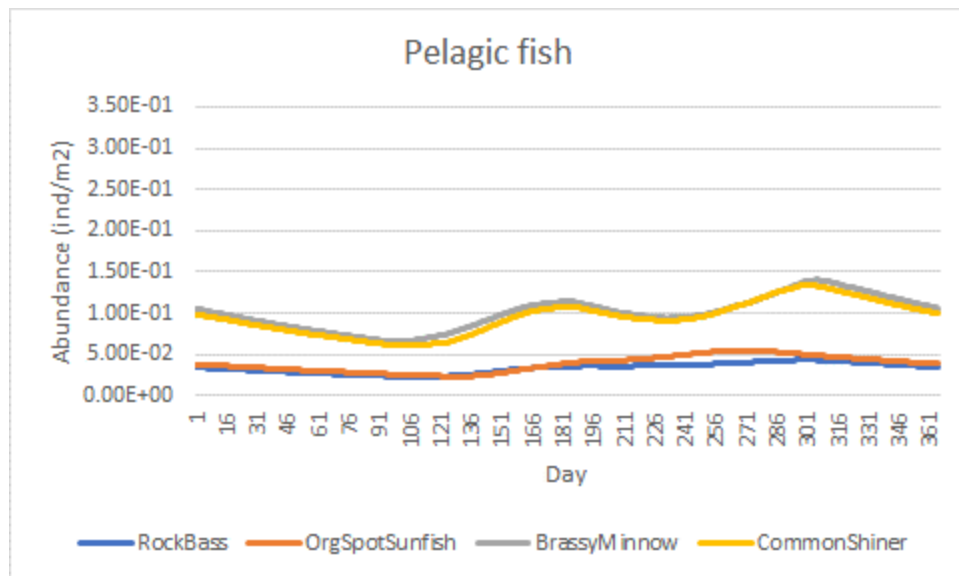


Figure 22. CASM_{OC} simulated pelagic fish abundance.

Year 40 abundance values calibrated for the baseline populations of creek chubs, black bullheads, common carp, golden redhorse, and sand shiner are shown in Figure 23. Target values ranged from 0.003 (golden redhorse) to 1.16 (black bullhead) individuals/m² (Table 8). The reference calibration overestimates the abundance of sand shiner and common carp, while underestimating numbers of black bullheads. Simulated creek chub average about 0.05 individuals/m², compared to the target value of 0.01. Golden redhorse are relatively rare in the reference simulation, consistent with their low target value.

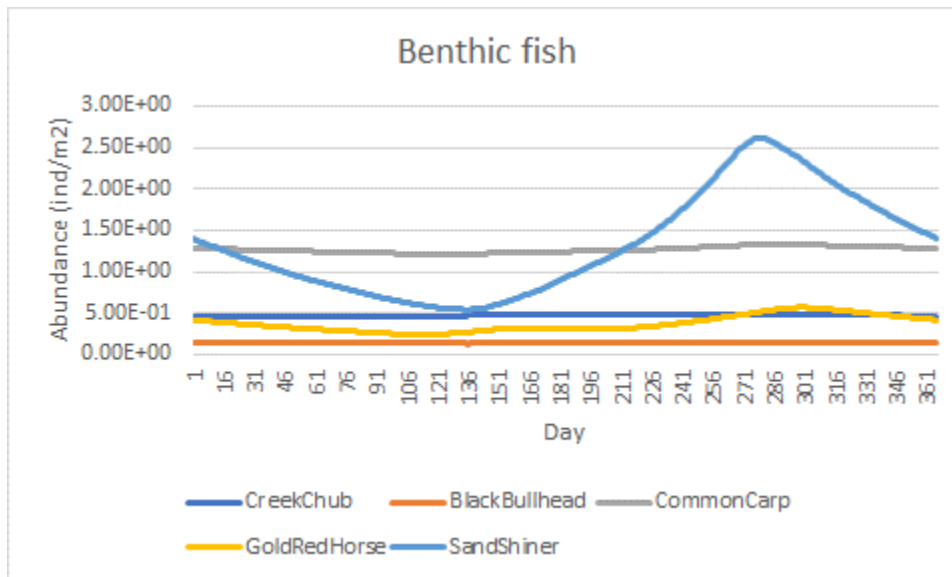


Figure 23. CASM_{OC} simulated benthic fish abundance in Iowa oxbow.

The calibrated reference simulation overestimates the abundances of the benthic oriented fish guild comprising blunt-nosed minnow and white suckers compared to the Table 8 target values (Figure 24). Data were not available for the central stoneroller in Bakevich et al. (2013).

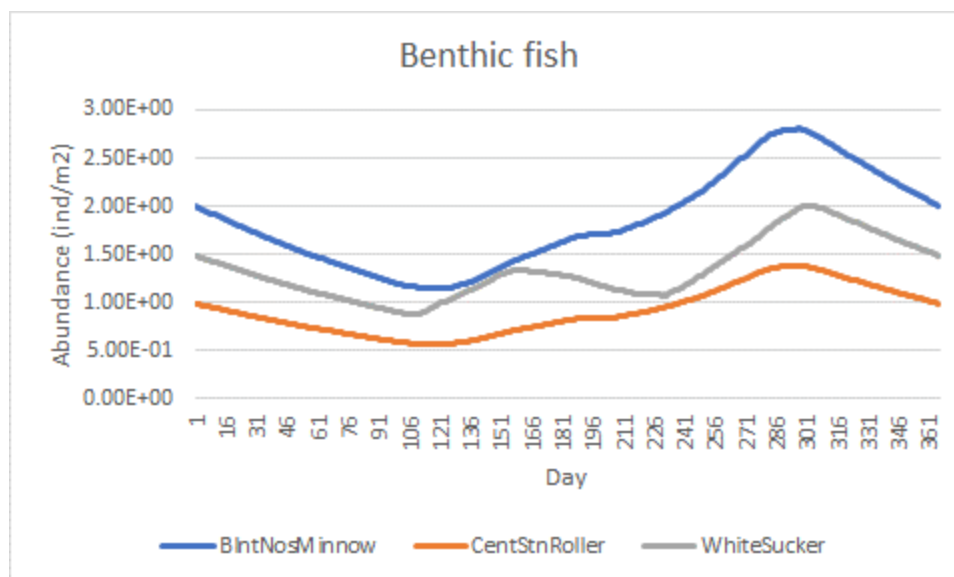


Figure 24. CASM_{OC} simulated benthic fish abundance in Iowa oxbow.

6. MODEL ANALYSIS

6.1. Sensitivity analysis

The CASM_{OC} has not directly been the subject of detailed model analysis. However, other versions of the CASM have been analyzed in detail (e.g., Bartell et al. 2013). In addition, the sensitivities of the basic fish bioenergetics model formulations to parameter uncertainty have been characterized (e.g., Bartell et al. 1992, 1988, 1986). The following sections briefly summarize the previous findings that can be used to inform additional model sensitivity analysis that might be warranted.

6.1.1. Fish bioenergetics model sensitivities

Bartell et al. (1986) compared the results of individual parameter perturbation (e.g., +/- 10%) and quantitative error analysis in describing the sensitivity of three fish bioenergetics models, including largemouth bass. Error analysis was performed using Monte Carlo simulations that sampled distributions of model parameter values and used statistical measures (e.g., relative partial sums of squares) to quantify model sensitivity to uncertain parameter estimates. Figure 25 identifies the key model parameters that influence model results; Table 9 identifies and defines the parameters. The pattern of parameter sensitivity differs with model usage: simulating fish growth with parameter estimates shows somewhat different sensitivity than fitting the model to observed fish growth by estimating consumption.

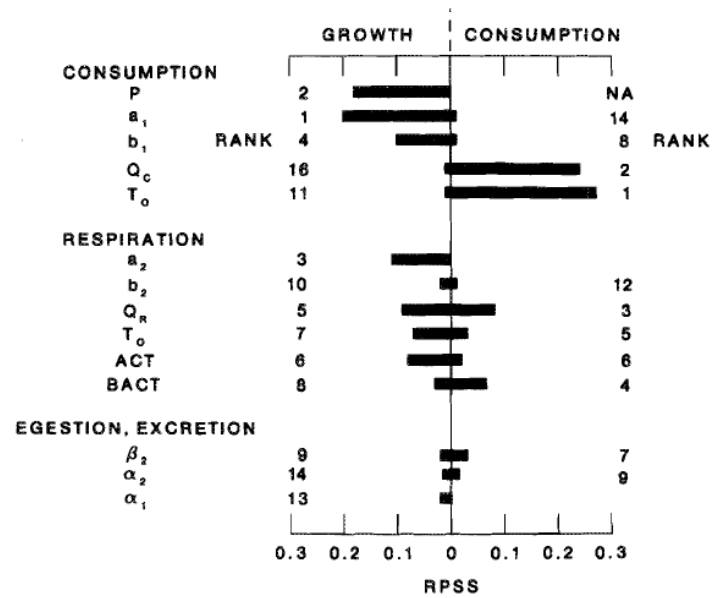


Figure 25. Sensitivity of fish bioenergetics model to parameter uncertainty based on quantitative error analysis (adapted from Bartell et al. 1986).

Table 9. Bioenergetics parameters identified as sensitive by Bartell et al. (1986).

Parameter	Parameter definition
Consumption	
P	Proportion of C _{max} expressed (not used in the CASM _{TS} or CASM _{OC})
a ₁	Scalar of allometric function relating consumption to fish body weight
b ₁	Exponent of function relating consumption to fish body weight
Q _C	Slope of Q-10 function relating consumption to water temperature
T _O	Temperature where consumption is at C _{max}
Respiration	
a ₂	Scalar of allometric function relating respiration to fish body weight
b ₂	Exponent of function relating respiration to fish body weight
Q _R	Slope of Q-10 function relating respiration to water temperature
T _O	Temperature where respiration is at R _{max}
ACT	Specific dynamic action, the metabolic cost of digestion
BACT	Respiration associated with swimming activity
Egestion, excretion	
β ₂	Exponent of function relating excretion to water temperature
α ₂	Scalar in the function relating excretion to water temperature
α ₁	Scalar in the function relating egestion to water temperature

The CASM_{OC} is used to simulate fish growth from initial estimates of biomass and associated growth parameters for the species included in the Iowa oxbow food web. The results of Bartell et al. (1986) point to the importance of the allometric parameters a₁ and b₁ in defining fish specific consumption rates. (P is not included in the fish bioenergetics formulations in the CASM_{OC}.) The allometric respiration value of a₂ and the temperature dependence (Q_R, T_O) of respiration are also sensitive model parameters for estimating fish growth. The corresponding parameters that relate organism size to consumption and respiration, as well as parameters that define the temperature dependence of consumption and respiration will be key parameters in determining the results of the CASM_{OC}. However, the parameters related to consumption will diminish in importance for conditions where the density-dependence of consumption limits fish growth in the CASM_{OC}.

6.1.2. Aquatic food web model sensitivities

Bartell et al. (1992, 1988) performed a detailed analysis of the daily sensitivity of modeled aquatic populations of producers and consumers in a pelagic food web model. These analyses

underscored the scale-dependence of sensitivity analysis of bioenergetics-based models of aquatic food webs. The analysis identified parameters associated with the environmental influences on population growth (i.e., “bottom-up” factors such as light, temperature, and nutrient parameters) as important controlling factors during the onset of growth during the spring months. Key parameters shifted to those associated with “top-down” control of biomass production (e.g., maximum feeding and respiration rates of consumer populations) during the summer and fall months. These results emphasized the importance of precisely specifying the focus of a sensitivity analysis of dynamic models in relation to overall modeling objectives. There is no single answer to the sensitivity question for dynamic bioenergetics-based models of aquatic food webs.

7. TOXICITY BENCHMARKS

Benzovindiflupyr is a pyrrole-carboxamide fungicide that is effective against a broad range of fungal diseases (Rothman and Sinclair 2015). This pesticide persists in soils and surface waters and may pose risks to non-target aquatic organisms. Benzovindiflupyr inhibits energy production within the mitochondria of eukaryotic cells.

Preliminary toxicity benchmark values (LC50s/EC50s/NOECs) for the pesticide benzovindiflupyr were derived for the populations of aquatic producers and consumers included in the CASM_{OC} Iowa oxbow food web. The CASM_{OC} uses the benchmark values to simulate the ecological effects of measured and modeled time-varying exposure concentrations of benzovindiflupyr on aquatic populations in a generalized Iowa oxbow.

The following describes the derivation of the preliminary benzovindiflupyr benchmark values for the CASM_{OC}.

7.1. Methods

The USEPA ecological risk assessment for benzovindiflupyr (e.g., Rothman and Sinclair 2015) and the USEPA interspecies correlation estimation tool (Web-ICE) were used to estimate preliminary values of toxicity benchmarks for the populations of producers and consumers included in the CASM_{OC} Iowa oxbow food web. Relevant data were directly available for *Chlorella*, *Daphnia*, chironomid larvae, the fathead minnow (FHM), and the common carp (Rothman and Sinclair 2015). These data were either (1) assigned to other similar modeled populations, (2) averaged over similar populations and assigned to modeled populations, or (3) extrapolated to modeled populations using the web-ICE (Raimando et al. 2013).

Extrapolations using the ICE focused on the mean LC50 produced by the regression equations that constitute the methodology. Upper and lower 95% confidence limits were computed by the web-ICE, but these values, while recorded, were not used in the estimation of the preliminary benchmark values.

The CASM_{OC} builds population-specific exposure-response functions based on the LC50, EC50, and NOEC values for the modeled consumer populations. Absent population-specific NOEC values, the probit (sigmoidal) function implemented in the CASM_{OC} uses a default NOEC of 0.1 µg/L to avoid taking the logarithm of zero in computing exposure-response relationships for the modeled populations.

7.2. Results

Table 10 lists the preliminary EC50 values estimated for modeled populations of phytoplankton, periphyton, and macrophytes (rooted aquatic plants) included in the CASM_{OC} community of primary producers.

Table 10. Benzovindiflupyr toxicity benchmark values derived for CASM_{OC} aquatic plants.

Population	EC50 (µg/L)	Comments
Phytoplankton		
Diatoms	240.0	Based on USEPA risk assessment ^a
Chlorophytes	890.0	Based on USEPA risk assessment
Cyanophytes	500.8	ICE ^b extrapolation of <i>Chlorella</i> to <i>Anabaena</i>
Cryptophytes	474.7	Geometric mean of diatoms, chlorophytes, and cyanophytes
Euglenoids	474.7	Geometric mean of diatoms, chlorophytes, and cyanophytes
Periphyton		
Diatoms	240.0	Same as phytoplankton diatoms
Chlorophytes	890.0	Same as phytoplankton chlorophytes
Cyanophytes	500.8	Same as phytoplankton cyanophytes
Macrophytes		
<i>Elodea</i>	880.0	Based on USEPA risk assessment (<i>Lemna</i>)
<i>Potamogeton</i>	880.0	Based on USEPA risk assessment (<i>Lemna</i>)

^aRothman and Sinclair (2015)

^bICE, web-based interspecies correlation estimation <http://www.epa.gov/ceampubl/fchain/webice>

Rothman and Sinclair (2015) provide benchmark values for diatoms and chlorophytes (*Chlorella*), which were assigned to the corresponding CASM_{OC} populations of phytoplankton and periphyton. An EC50 for cyanophytes was derived using an ICE extrapolation of *Chlorella* to *Anabaena*, a common blue-green algae. As an initial assumption, EC50 values for cryptophytes and euglenoids were estimated simply as the geometric mean value for diatoms, chlorophytes, and cyanophytes. The USEPA EC50 value for *Lemna* was assigned directly to the modeled macrophyte populations of *Elodea* and *Potamogeton*.

Available data (Rothman and Sinclair 2015), data averaging, and ICE extrapolation produced the preliminary LC50 values for zooplankton and macroinvertebrates included in the CASM_{OC} food web (Table 2). LC50 values ranged from 85 – 3,354.7 µg/L across the populations of aquatic invertebrates, with zooplankton being relatively more sensitive (based on the single value for *Daphnia*).

A NOEC value was reported for *Daphnia* (Rothman and Sinclair 2015) and this value (5.6 µg/L) was assigned to all modeled zooplankton populations. A value of 2.8 µg/L was reported for chironomids. All other invertebrates were assigned the CASM_{OC} default NOEC value of 0.1 µg/L (Table 11). Rothman and Sinclair (2015) provided a benchmark value for chironomids. An ICE extrapolation from *Daphnia* to *Tubifex* provided a benchmark value assigned to modeled oligochaetes. The remaining macroinvertebrates were assigned the geometric mean value of the chironomid and oligochaete benchmarks.

Table 11. Benzovindiflupyr toxicity benchmark values derived for CASM_{OC} aquatic invertebrates.

Population	EC50/LC50 (µg/L)	NOEC (µg/L)	Comments
Zooplankton			
Copepods	85.0	5.6	Same as cladocerans
Cladocerans	85.0	5.6	Based on USEPA risk assessment
Rotifers	85.0	5.6	Same as cladocerans
Microzooplankton	85.0	5.6	Same as cladocerans
Ostracods	85.0	5.6	Same as cladocerans
Macroinvertebrates			
Ephemeroptera	1,686.0	0.1	Geometric mean of chironomid and oligochaete values; CASM NOEC default value
Trichoptera	1,686.0	0.1	Geometric mean of chironomid and oligochaete values; CASM NOEC default value
Oligochaetes	3,354.7	0.1	ICE extrapolation of <i>D. pulex</i> to <i>Tubifex</i> , CASM NOEC default value
Chironomids	848.0	2.8	NOEC based on USEPA risk assessment
Coleoptera	1,686.0	0.1	Geometric mean of chironomid and oligochaete values; CASM NOEC default value
Corixids	1,686.0	0.1	Geometric mean of chironomid and oligochaete values; CASM NOEC default value

Available data (Rothman and Sinclair 2015), data averaging, and ICE extrapolation also produced the preliminary LC50 values for fish populations included in the CASM_{OC} food web (Table 12). LC50 values were reported for only two of the modeled populations, fathead minnow (4.7 µg/L) and common carp (3.5 µg/L) (Rothman and Sinclair 2015). The FHM value was assigned to the Topeka shiner age classes, and bluntnose minnow (Table 12). The common carp value was assigned to brassy minnow, common shiner, and the central stoneroller – all members

of the Cyprinidae. Derivation of LC50 values for the remaining populations were based on ICE extrapolations of the reported fathead minnow LC50. ICE provided extrapolations from FHM directly to black bullhead, largemouth bass, and white sucker populations. Absent direct extrapolations to modeled fish populations, ICE was used to estimate benchmark values for taxonomically similar species. For example, an ICE extrapolation from FHM to green sunfish was used as a proxy for modeled orange-spotted sunfish. The ICE FHM to yellow perch extrapolation was used for the Johnny darter, a fellow member of the Percidae. The FHM to sheepshead minnow extrapolated benchmark was assigned to modeled red shiners and creek chubs; all four species are cyprinids. The only shiner (Cape Fear) in the ICE database was used to estimate the benchmark value for the modeled sand shiner. The FHM to yellow perch extrapolation was used to derive a benchmark for rock bass, also known as rock perch. The white sucker estimated benchmark was assigned to the modeled golden redhorse (both are members of the Catostomidae).

Table 12. Benzovindiflupyr toxicity benchmark values derived for CASM_{OC} fish populations.

Population	LC50 (µg/L)	NOEC (µg/L)	Comments
Red shiner	28.5	0.1	ICE fathead minnow (FHM) to sheepshead
Fathead minnow	4.7	0.95	Based on USEPA risk assessment
Johnny darter	1.9	0.1	ICE FHM to yellow perch
Topeka shiner (juv)	4.7	0.1	Use USEPA FHM values
Topeka shiner (adult)	4.7	0.1	Use USEPA FHM values
Rock bass	1.9	0.1	ICE FHM to yellow perch
Orange-spotted sunfish	2.8	0.1	ICE FHM to green sunfish
Brassy minnow	3.5	0.1	Use USEPA common carp values
Common shiner	3.5	0.1	Use USEPA common carp values
Creek chub	28.5	0.1	ICE FHM to sheepshead minnow
Black bullhead	3.9	0.1	ICE FHM to black bullhead
Common carp	3.5	0.1	Based on USEPA risk assessment
Golden redhorse	3.6	0.1	ICE FHM to white sucker
Sand shiner	2.1	0.1	ICE FHM to Cape Fear shiner
Largemouth bass	2.3	0.1	ICE FHM to largemouth bass
Bluntnose minnow	4.7	0.1	Use USEPA values for FHM
Central stoneroller	3.5	0.1	Use USEPA values for common carp
White sucker	3.6	0.1	ICE FHM to white sucker

A single value of the NOEC was reported for the fathead minnow (Rothman and Sinclair 2015). All other fish populations were assigned the CASM_{OC} default value of 0.1 µg/L.

7.3 Discussion

The results demonstrate that it was possible to derive preliminary benzovindiflupyr toxicity benchmark values for the populations of aquatic organisms included in the CASM_{OC} food web for the generalized Iowa oxbow (Tables 10-12). The resulting values suggested that macroinvertebrates were less sensitive to benzovindiflupyr followed by increasing sensitivity of aquatic plants, and zooplankton with fish being the most sensitive populations.

ICE extrapolations were used substantially in estimating benzovindiflupyr benchmarks for several fish populations, as well as oligochaetes and bluegreen algae. Depending on the particular combination of species and data underlying the extrapolation, ICE can produce large confidence intervals associated with estimation of LC50 values (Table 13).

Table 13. Mean values and 95% confidence intervals for ICE extrapolations

Extrapolation	Mean LC50 (µg/L)	Lower limit (µg/L)	Upper limit (µg/L)
<i>Chlorella</i> to <i>Anabaena</i>	500.80	4.94	50,719.86
FHM to <i>Tubifex</i>	1.88	0.013	272.27
FHM to sheepshead	28.54	9.51	85.67
FHM to black bullhead	3.91	0.13	117.85
FHM to white sucker	3.62	0.0976	134.59
FHM to yellow perch	1.92	0.334	11.08
FHM to largemouth bass	2.27	0.330	15.71
FHM to Cape Fear shiner	2.12	0.0374	121.10

The preliminary toxicity benchmarks for benzovindiflupyr (Tables 10-12) should be interpreted as a point of departure for initial simulations of ecological risks posed by this pesticide.

Additional scenarios could be developed that begin to address the uncertainties associated with estimating benchmarks for this compound. For example, scenarios could be constructed using all upper or lower limits suggested by the ICE extrapolations (Table 13). Other percentile values of the ICE extrapolations could be similarly explored in scenario development. Relatedly, O'Neill et al. (1983) have addressed the use of the geometric mean as a useful approach for developing toxicity benchmarks in the absence of species-specific toxicity assay results.

Benchmark scenario development can be additionally informed by realistic exposure profiles measured or modeled for Iowa oxbows and other off-channel habitats important to the Topeka shiner and associated species. Time series of benzovindiflupyr concentrations can be simply inspected to identify toxicity benchmark values (or ranges of values) that would likely produce direct toxic effects on modeled populations.

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