

# Explaining and Predicting Recruitment of Yellow Perch in North American Inland Lakes

**Abstract:** Managing sustainable fisheries populations relies on an understanding of the interplay between recruitment, growth, and mortality. Recruitment is frequently noted as the most influential parameter of these three dynamic rate functions. The erratic recruitment dynamics of yellow perch (*Perca flavescens*) often confound fisheries scientists, managers, and regulators of inland lakes. Yellow perch populations provide many recreationally important fisheries directly or supports fisheries for other species. Additionally, recruitment patterns of yellow perch are expected to become more erratic under changing environmental conditions such as climate change. Traditional fisheries modeling approaches often fail to capture the dynamics and complexities of recruitment. In this paper, we describe the initial stages of building an SD model of yellow perch recruitment for inland lakes. We compare this approach to traditional fisheries recruitment modeling approaches and describe the next steps in model development and use. Initial model sensitivity testing shows promise in our model to date and is congruent with ecological information. We believe that our final SD model will benefit fisheries scientists, managers, and regulators in anticipating and potentially mitigating recruitment variation to provide sustainable recreational fisheries in inland lakes across the geographic range of yellow perch.

## Introduction:

Populations of wild animals are affected by three dynamic rate functions:

- recruitment – the number of individuals that are hatched in a year or the number of individuals that survive to a specific size or life stage on an annual basis;
- growth – the amount of weight or length gained by an individual annually; and
- mortality – the percentage of a population that dies, either naturally or by harvest, in a given year.

These three functions interact to determine the nature (e.g., abundance, size structure) of a population (Figure 1). For example, recruitment add individuals to a population; growth in body length or weight adds biomass to a population; and mortality reduces both the number of individuals in a population and the population's biomass (Willis *et al.*, 2008).

Managing sustainable fisheries populations relies on an understanding of the interplay between recruitment, growth, and mortality. But recruitment is frequently noted as the most influential parameter of the three (Ricker, 1975). Seemingly minor fluctuations in recruitment may contribute to substantial changes in other parameters (e.g., Carline *et al.*, 1984). For example, a higher number of recruits may lead to reduced growth rates via intraspecific competition (i.e., competition for food, habitat, or other resources within a population). Conversely, years of lower or failed recruitment may reduce competition for such resources and lead to higher growth rates within the population (Anderson, 1988).

Most research of recreational fisheries indicates that recruitment from egg to adult in fishes is established early in life after a point at which natural mortality stabilizes and before a cohort is large enough to be harvested (e.g., Ludsin and Devries, 1997; Isermann and Willis, 2008). Both biotic (i.e., density dependent) and abiotic (i.e., density independent) factors influence recruitment from one successive life stage (e.g., egg, larvae, juvenile, adult) to the next. Biotic factors may include prey availability, competition, and predation, to name a few. Abiotic factors may include climate, habitat, environmental stochasticity, etc. The relative influence of these biotic and abiotic factors may depend on the species of interest and the life stage being studied.

Recruitment dynamics have been studied for many recreationally important fishes, including yellow perch (*Perca flavescens*). Yellow perch support many recreationally important fisheries across North American from the Atlantic to the Pacific Coasts (e.g., Mayer *et al.*, 2000, Wilberg *et al.*, 2005; Isermann and Willis, 2008) but are also an important prey species for other recreational fisheries such as walleye (*Sander vitreus*), northern pike (*Esox lucius*), and smallmouth bass (*Micropterus dolomieu*; Hansen *et al.*, 1998; Blackwell *et al.*, 1999). Erratic recruitment patterns (i.e., strong year classes followed by weak or missing year classes) have been noted in many yellow perch populations (Forney, 1971; Kallemeyn, 1987; Sanderson *et al.*, 1999; Isermann and Willis, 2008), and recruitment patterns are expected to become more erratic under changing environmental conditions such as climate change (Farmer *et al.*, 2015). Managing such varying yellow perch populations as prey and for human consumption will be challenging.

Indeed, much research has been focused on identifying the particular life stage or stages where yellow perch year class strength is established and the abiotic and biotic factors that influence recruitment from one life stage to the next. Most work focused on early life stages (i.e., egg, larvae, and juvenile). Density-independent factors that have been identified as important influences on yellow perch recruitment at this stage include lake morphology characteristics (Isermann, 2003), climatological variables (Ward *et al.*, 2004; Jensen, 2008; Redman *et al.*, 2011; Weber *et al.*, 2011), fluctuations in water levels (Kallemeyn, 1987; Dembkowski *et al.*, 2014), and environmental variability (Clady and Hutchinson, 1975). Potentially important density-dependent factors include prey density (Jolley *et al.*, 2010; Redman *et al.*, 2011), prey size (Fisher and Willis, 1997), prey community composition (Whiteside *et al.*, 1985), spawning stock characteristics (Sanderson *et al.*, 1999; Tyson and Knight, 2001; Wilberg *et al.*, 2005), competition (Shroyer and McComish, 2000), and predation (Forney, 1974). Abiotic factors appear to be more influential on recruitment between the earliest life stages (e.g., egg to larvae;

e.g., Kallemeyen, 1987; Ward *et al.*, 2004; Weber *et al.*, 2011), whereas biotic factors appear to be more important in determining recruitment between later life stages (e.g., juvenile to adult; Dembkowski, 2014).

Most studies of yellow perch recruitment focus on one or two particular life stages and tend to follow traditional statistical approaches (see Discussion below). To our knowledge, only one study has examined yellow perch recruitment between successive life stages (Wilberg *et al.*, 2005), but this work focused solely on the Lake Michigan population. Overfishing has occurred in many Great Lakes, but there have been no such documented cases in inland lakes to our knowledge. Recruitment of yellow perch populations in inland lakes is likely regulated by different factors than those in the Great Lakes, and most recreational perch fisheries in the United States now occur on inland lakes.

To date, no study has employed a System Dynamics (SD) simulation approach to model recruitment of yellow perch populations in inland lakes. Using SD has distinct advantages compared to other traditional approaches to studying fish recruitment. First, SD allows for modeling recruitment to successive life stages that reflects natural processes (e.g., adults deposit eggs; eggs hatch; larvae grow to become juveniles; juveniles grow to adults; and the cycle repeats). Second, SD models can handle complex feedback processes endogenously while also incorporating exogenous factors that promote or inhibit recruitment at each life stage simultaneously. Finally, SD models can be used to test various scenarios that may support or reduce recruitment so that fisheries managers may take proactive steps as needed. The goal of this paper is to describe the initial stages of building an SD model of yellow perch recruitment for inland lakes. We will compare and contrast this approach to traditional fisheries recruitment modeling approaches and describe the next steps in model development and use.

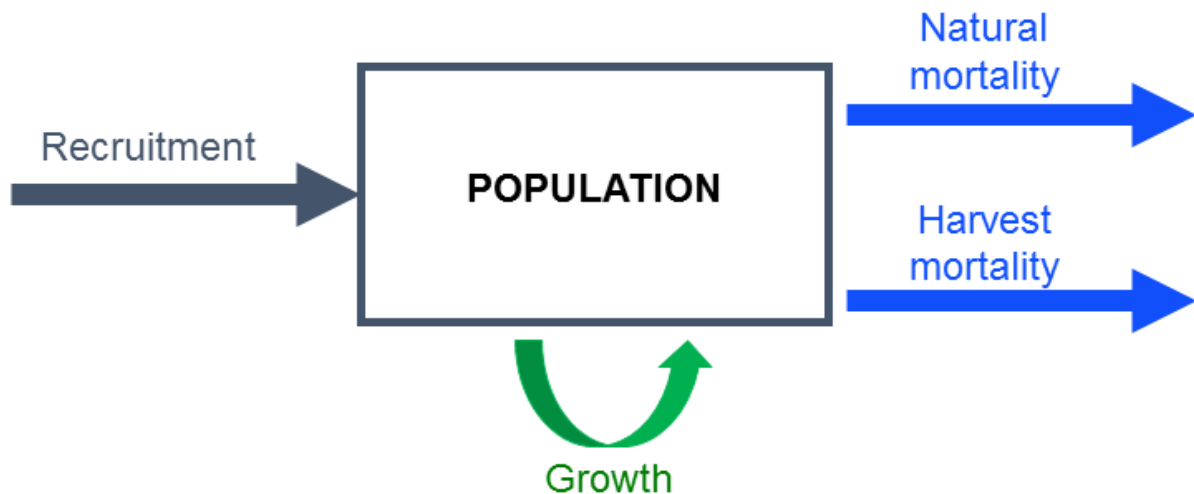


Figure 1. The three dynamic rate functions (recruitment, growth, and mortality) that interact to determine the nature of wild animal populations (adapted from Willis *et al.*, 2008)

## **Model Overview:**

The model is based on a typical aging chain dynamic of disaggregated stocks and flows representing specific stages relevant to the population of interest (Sterman 2000; Ford, 2010), in this case yellow perch (Figure 2). The model was created in Vensim™ (Ventana Systems, Harvard, MA) modeling environment. The time unit used for simulation was 1 month, with a time-step of 0.0625 and simulation horizon of 240 months (or 20 years). Currently, climatic forcing functions are not well parameterized or non-existent in the model. However, these are actively being refined since they are the key exogenous components for this model. The key endogenous components are the stock-and-flow linkages between various life stages of a typical perch population. The main strength of using the SD platform was the ease of use handling the core feedback mechanisms for the population and a rapid simulation time. The main contributions of the model were the inclusion of all relevant life stages that typically are not included in traditional fish population models (see Discussion section below). In the sections that follow, we describe the scientific foundations that inform each of the stock-and-flow components of the model and the basic equations used for the early (immature) versus mature life stages. For a full list of variable names and equations used, see Tables A and B Supplementary Material.

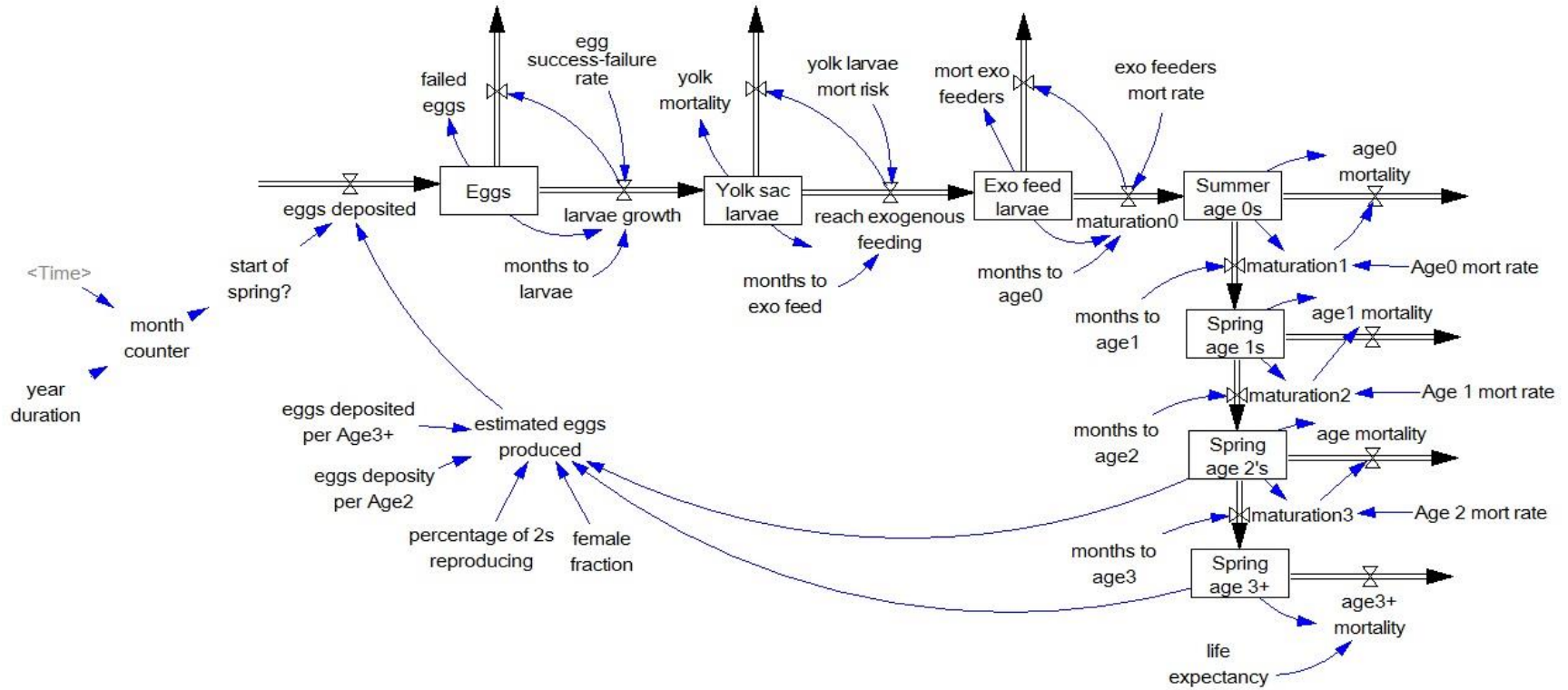
## **Description of Endogenous Model Dynamics:**

This model begins at the egg deposition phase (initial stock) and progress through successive life stages until yellow perch reach sexual maturity and, thus, can produce eggs (final stock; Figure 2). Each life stage in the model is considered important to understanding recruitment of yellow perch as demonstrated or hypothesized in scientific literature (Table 1). As each life stage progresses to the next, some individuals are removed from the population through mortality, which may occur due to natural phenomena (e.g., starvation, predation, weather events) or anthropogenic effects (namely, harvest of adults of a legally defined body length). Mortality may be *density-dependent* (i.e., the rate of mortality is based on the density of the population; for example, starvation; endogenous factors) or *density-independent* (i.e., the rate of mortality is unrelated to population density; for example, harvest; weather events; exogenous forces). Mortality at the earliest life stages of yellow perch is hypothesized to be driven by both density-dependent and -independent factors (Table 1). Those individuals that survive move on to the next life stage.

Individual yellow perch survive and grow until they reach sexual maturity. The timing of sexual maturity in yellow perch differs by sex and population. In most populations, male yellow perch reach sexual maturity during their second year of life (age-2) while females may be at least 3 years old before becoming sexually mature (age-3; see Jansen, 1996). However, yellow perch populations that grow slower may mature earlier (age-1 in males and age-2 in females; Jansen, 1996). Interestingly, sexual maturity is often reached before yellow perch reach harvestable sizes (Jansen, 1996).

Growth in body length and weight is also intimately related to mortality and survival. High density fish populations tend to grow slower than low density- populations as relative influence of density-dependent factors on mortality decreases (Ware, 1975; Anderson, 1988). Fish that

Figure 2. Basic structure of the SD model proposed to explain and predict yellow perch recruitment in inland North American lakes.



grow faster may also survive at higher rates, either by avoiding predation or by having enough energy reserves to survive starvation and harsh winters. Thus, many of the factors that influence mortality and survival may also influence growth and vice versa (e.g., Weber *et al.*, 2011).

Fecundity, or the number of eggs produced by a female yellow perch, may be related to age where younger perch tend to produce more eggs than older individuals (Jansen, 1996). Fecundity may also be related to environmental conditions whereby female yellow perch can reduce or increase the number of eggs produced annually based on whether environmental conditions are favorable or not (see Jansen, 1996).

Overall, survival, mortality, growth, and fecundity are influenced by environmental conditions that vary intra- and interannually, and tradeoffs may occur to increase survival at the expense of other dynamics. For example, if water temperatures are too warm and create a metabolic demand on fish, then fecundity and growth may be reduced to conserve energy that will be used to enhance survival and reduce mortality (Jansen, 1996). Other factors that reduce survival such as harvest, may vary by year, season, and sex. For example, female yellow perch may be harvested at higher rates than males by anglers, especially during the winter (Clady, 1977; Weber and Les, 1982; Purchase *et al.*, 2005; Isermann *et al.*, 2007). The SD model for this study will include the influences of these factors on survival, mortality, growth, and fecundity.

### **Description of Quantitative Model and Preliminary Testing:**

The quantitative model is represented by seven stocks representing distinct ages and seasons between the egg stage through Spring age 3+ (i.e., yellow perch that are at least 3 years old; Figure 2). These ages and seasons were hypothesized to be either significant stages after potentially catastrophic mortality periods (e.g., after switching to exogenous feeding; the first overwinter period) or of sexual maturity. Two different formulations were used to represent the flows from one age class stock to another due to the differing time delays associated with younger versus mature fish in the model. The first half of the aging chain (eggs to Summer age 0s) happens within about a three-month period (April through June). Eggs are produced and hatched in the spring, and larvae survive and grow rapidly and in a batched-like process (i.e., individual eggs and larvae are less likely to be accounted for over time until they reach maturity). Therefore, the flows were characterized with a smoothed delay such that the maturation outflows were equal to:

$$\frac{\text{stock level} * \text{percentage of fish aging onward}}{\text{average time in stock}},$$

and the mortality outflows were equal to the remaining fish not aging forward. The second half of the aging chain (Summer age 0s to Spring age 3+) represent aggregated stocks by age in years, where it would be less realistic to formulate the maturation flow based on an average maturation time (i.e., climatic factors between each year age class will impact the maturation flow rates, and 2-year-old fish should not rapidly become 3-year-old fish until the correct duration of time has passed). Therefore, a fixed delay was applied to the mature fish age progression, where

maturation = fixed delay (stock level\*(1-mortality rate), 12 months, stock level\*(1-mortality rate)),

and mortality was equal to the remaining stock level. The final stock, Spring age 3+, represents the mature individuals of the population that no longer exhibit the maturation indicators seen in the younger age classes. Therefore, the mortality outflow was constructed similar to a batched process, with the outflow being smoothed over the average residence time in the stock. In this case, the average residence time, shown as life expectancy, was set equal to 48 months. Initial values for the immature stocks (eggs to Spring age 0s) were set to 0 to avoid fish maturation during months that eggs and larvae are not able to survive. The remaining initial values were set to arrive at an equilibrium population of Spring age 3+ fish.

After arriving at an equilibrium population of Spring 3+ aged fish, three preliminary tests were conducted on several of the more uncertain parameter values, including: mortality rates for Summer age-0 fish (shown as Age0 mort rate in Figure 2), mortality rates for Spring age-1 fish (shown as Age 1 mort rate in Figure 2), number of Spring age-2 fish capable of reproducing (shown as percentage of 2s reproducing in Figure 2), the eggs produced per Spring age-2 fish that is reproducing (shown as eggs deposited per Age2), and the eggs produced per Spring age-3+ fish (shown as eggs deposited per Age3+). The values used for model development (based on information in Table 1) along with the adjusted values used for sensitivity testing are provided in Table C in the Supplementary Material.

**Results:**

Dynamic equilibrium was reached between month one and fifty (i.e., delay). Both Spring age 3+ and Spring age 2 stocks remained stable with low oscillation. However, Summer age 0s and eggs oscillate widely throughout the simulation (Figure 3)

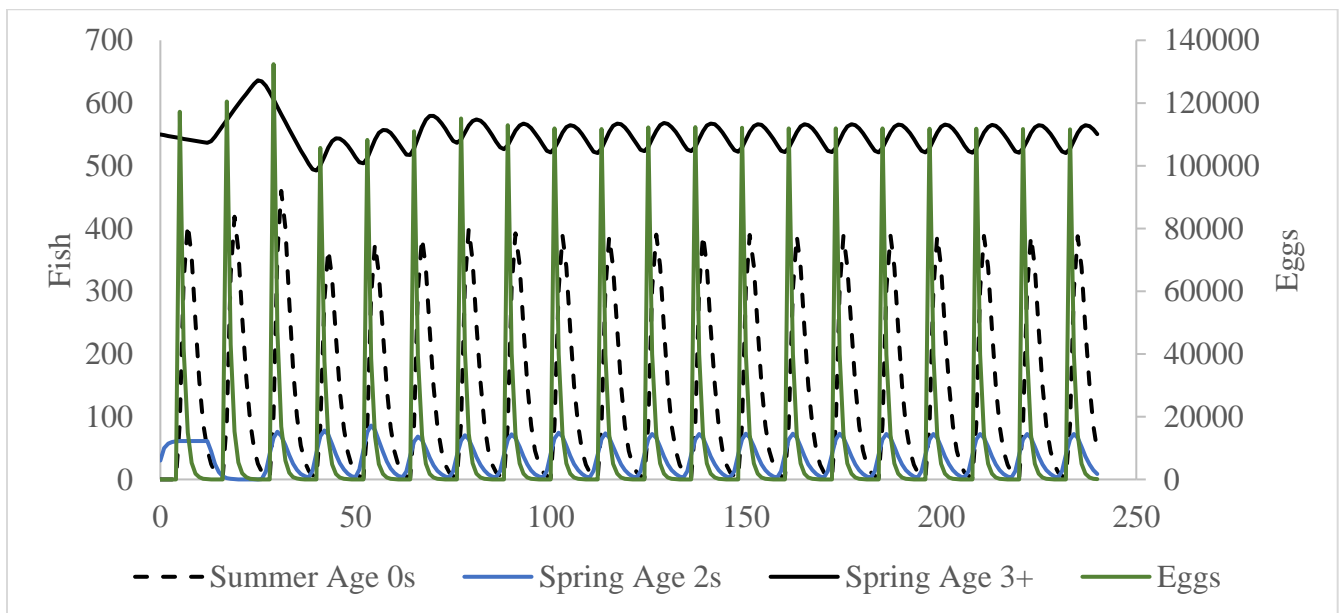


Figure 3 Egg, Summer age 0, Spring age 2, and Spring age 3+ stocks at dynamic equilibrium.

Reproductive scenarios displayed minimal variation after an initial delay for the Spring age 3+ stock in both the high and low scenarios, although a slight positive trend was observed for our high reproduction scenario (Figures 4 and 5). Spring age 1s appear to be relatively sensitive to mortality factors that act on the Summer age 0 stock. Results show a short delay in the beginning and then an exponential decrease for our high mortality scenarios (Figures 6 and 7). Similar sensitivity responses were observed for low and high mortality scenarios of Spring age 1s in relation to Spring age 2s (Figures 8 and 9). Low and high egg production by Spring age 2s appeared to have minimal impact on Exogenous feeding larvae stock, either in delays or oscillations (Figure 10 and 11). However, stocks of Exogenous feeding larvae and Yolk sac larvae appeared to be sensitive to both high and low variations in eggs produced by Spring Age3+ stocks (Figures 12 and 13). Overall, expected corresponding increases or decreases in stocks were noted for all scenarios, except Spring age 2s. We also observed the greatest oscillation in Yolk sac larvae and Summer age 0s across all simulations (Figures 14 and 15).

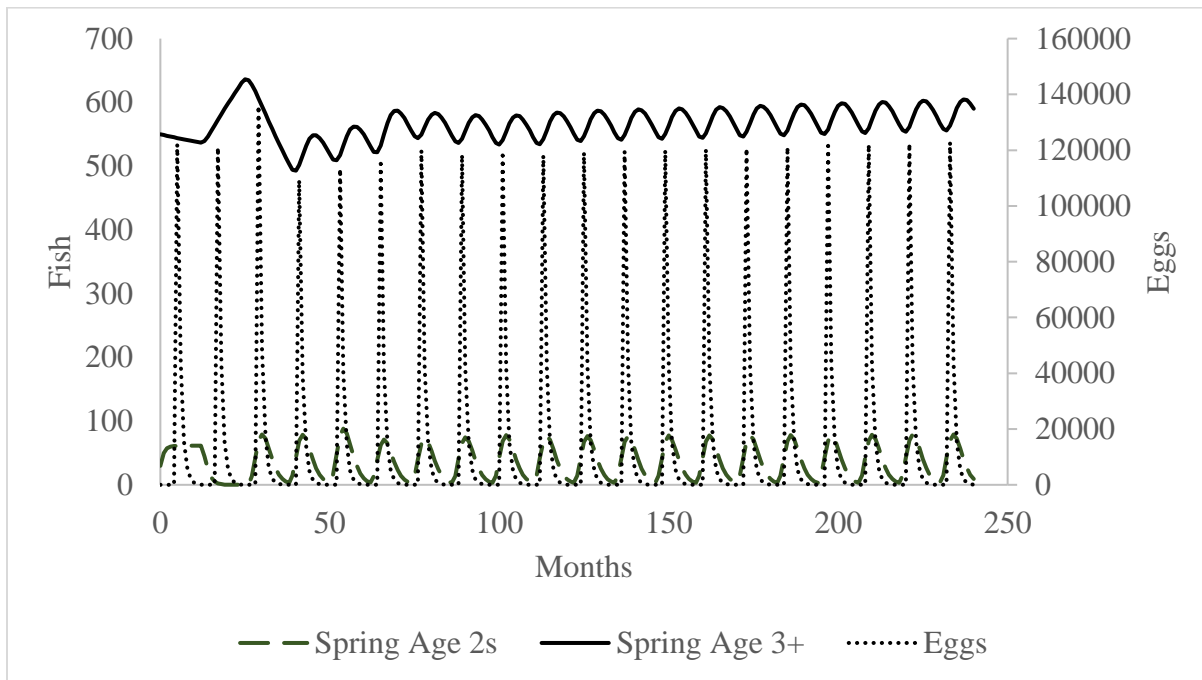


Figure 4. High reproduction scenario illustrating Spring Age 2s and Age 3+ relative to egg production.



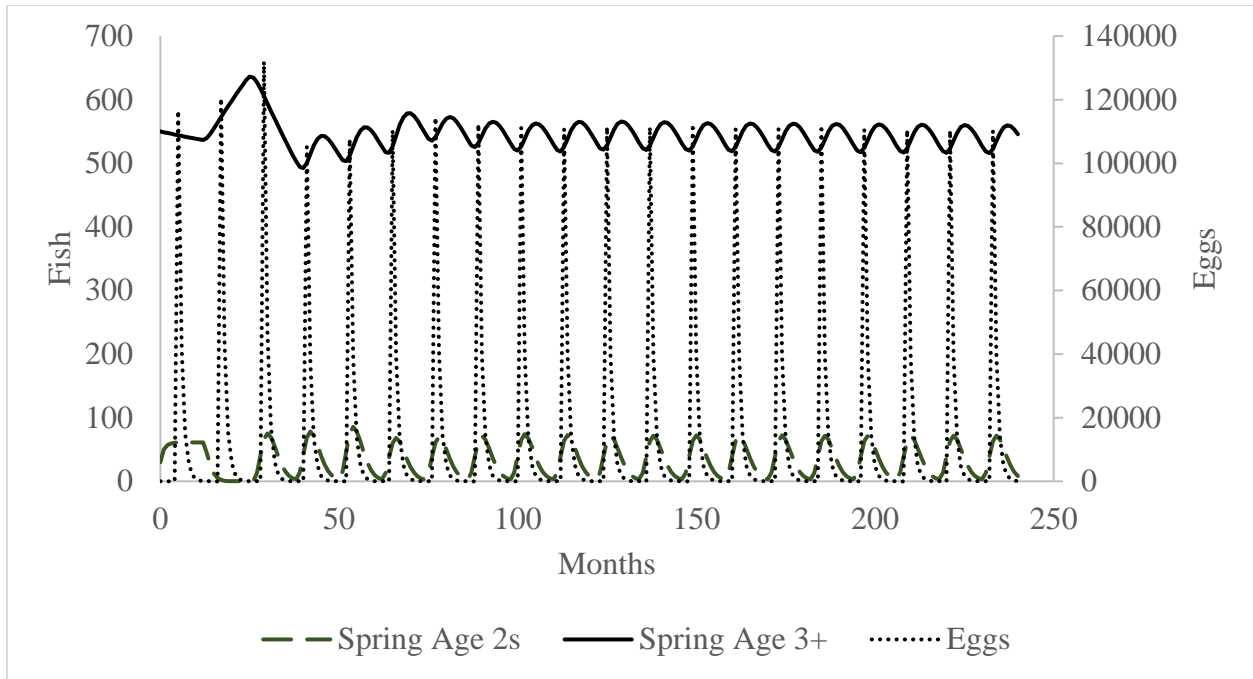


Figure 5. Low reproduction scenario illustrating Spring Age 2s and Age 3+ relative to egg production.

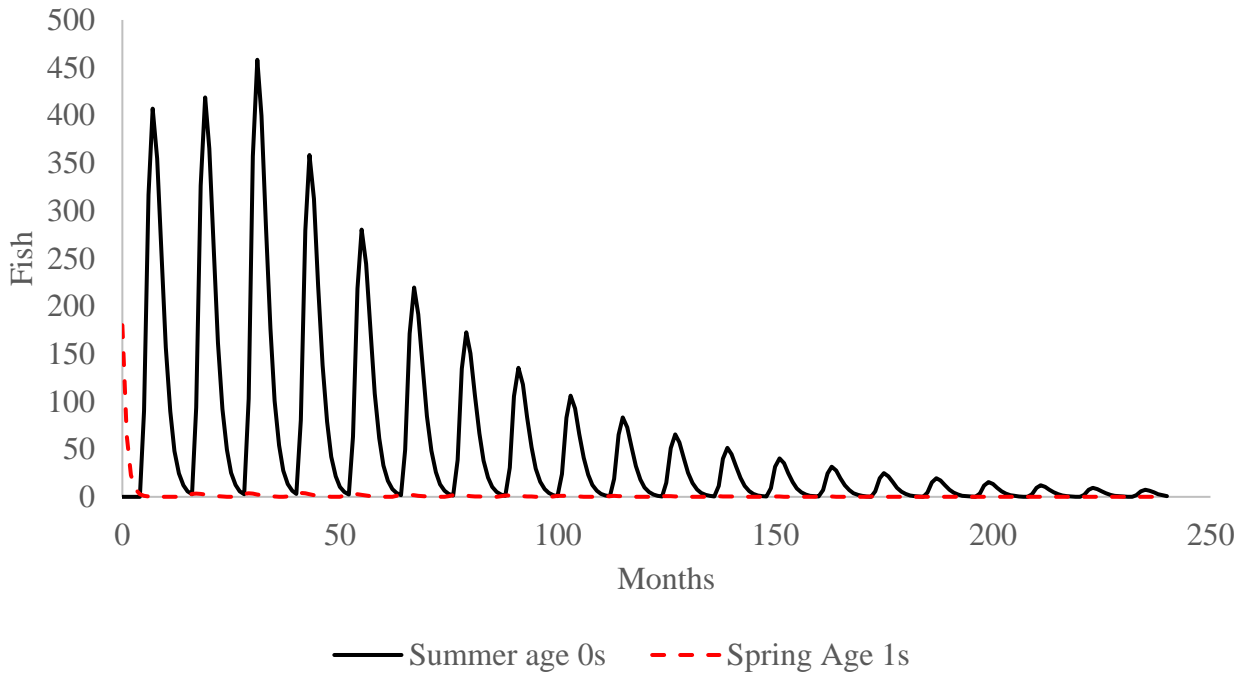


Figure 6. The impact of high mortality of Summer age 0s on Spring age 1s.

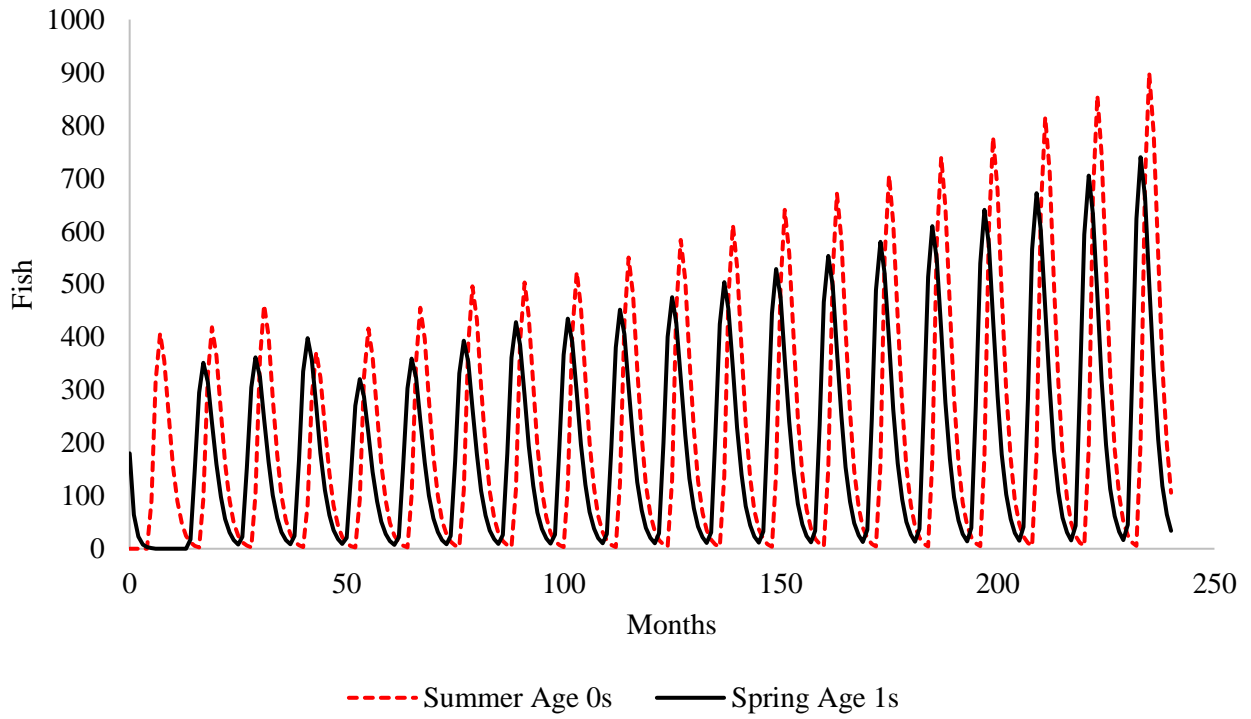


Figure 7. The impact of low mortality of Summer age 0s on Spring age 1s.

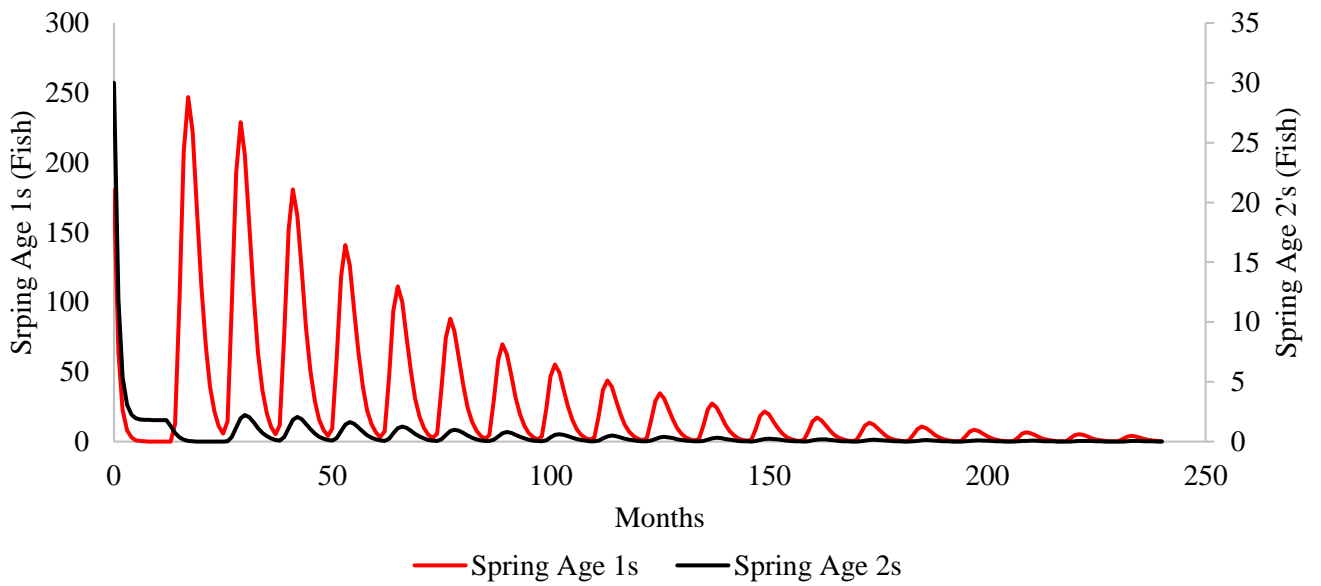


Figure 8. The impact of high mortality of Spring age 1s on Spring age 2s.

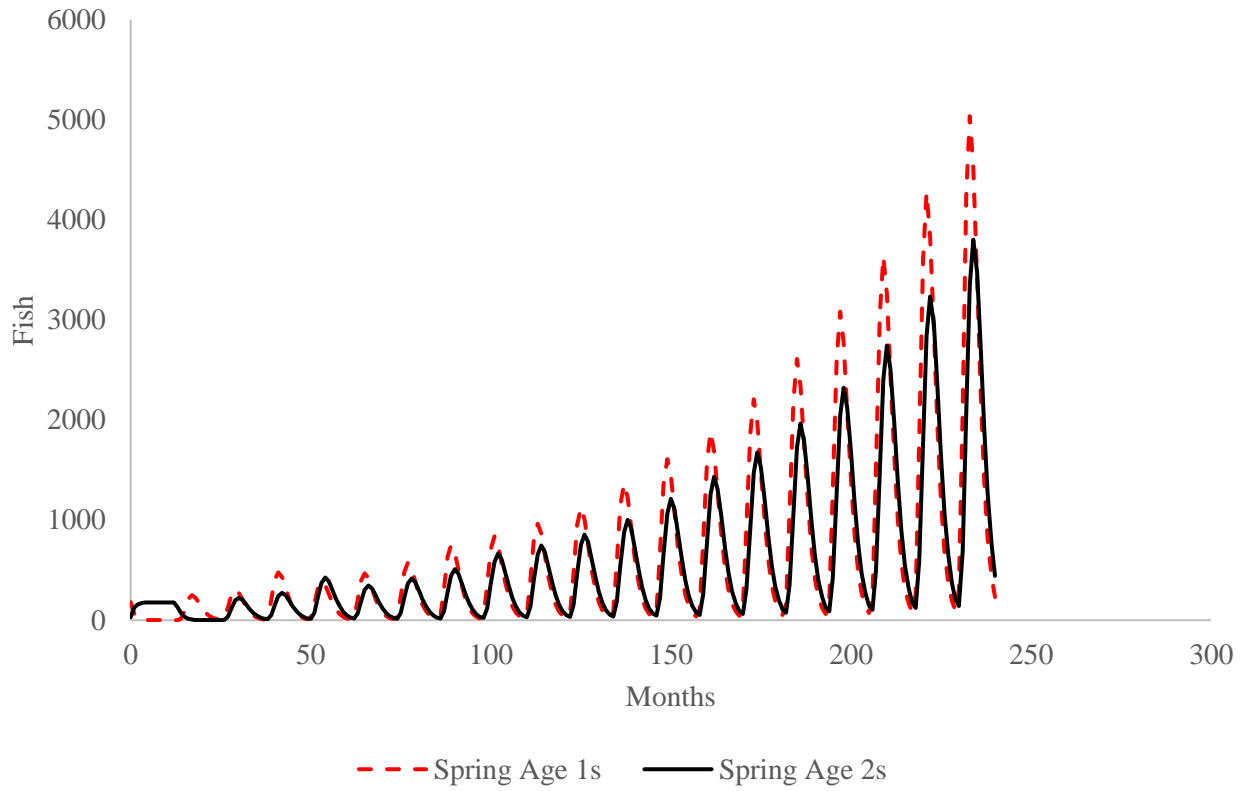


Figure 9. The impact of low mortality of Spring age 1s on Spring age 2s.

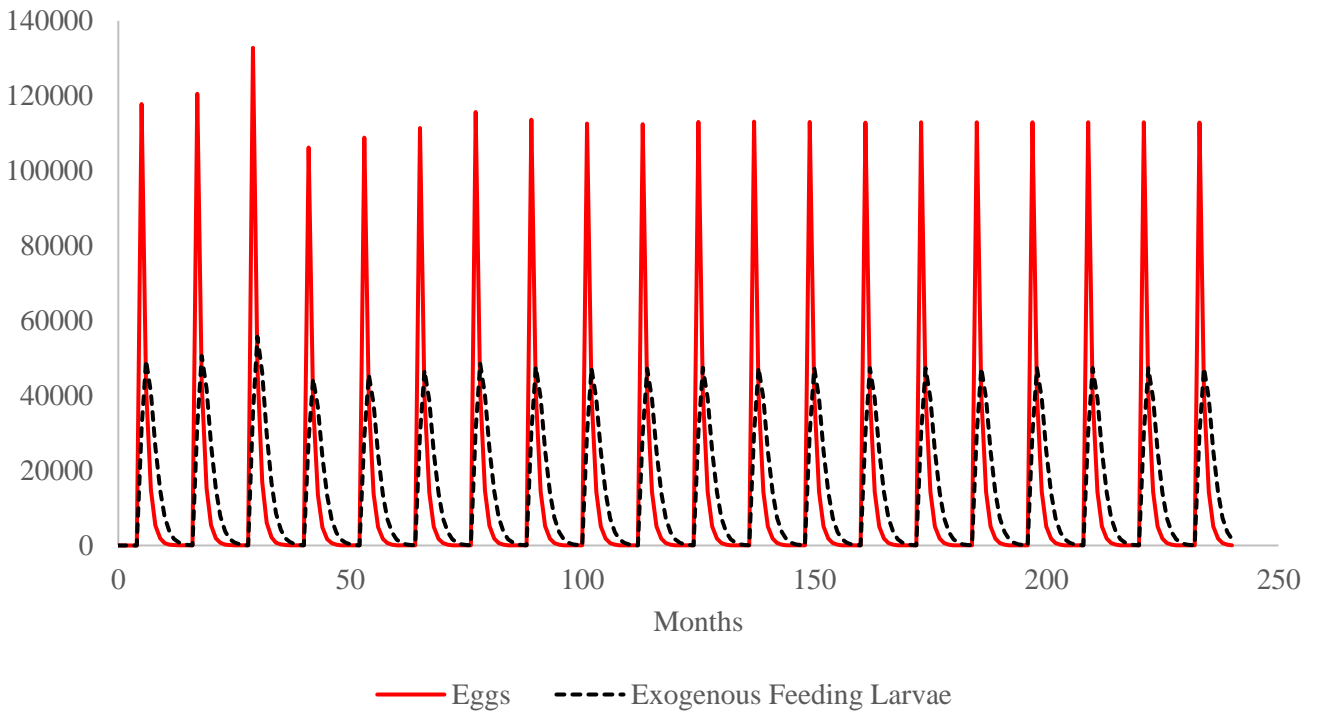


Figure 10. The influence of high egg production by Spring age 2's on Exogenous feeding larvae.

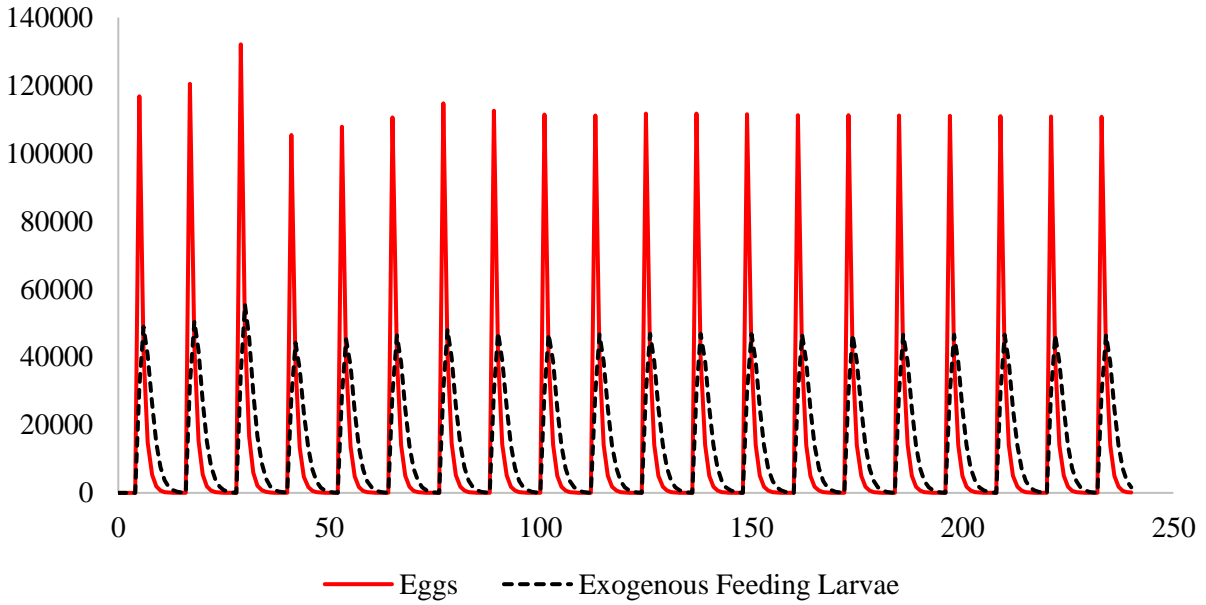


Figure 11. The influence of low egg production by Spring age 2's on Exogenous feeding larvae.

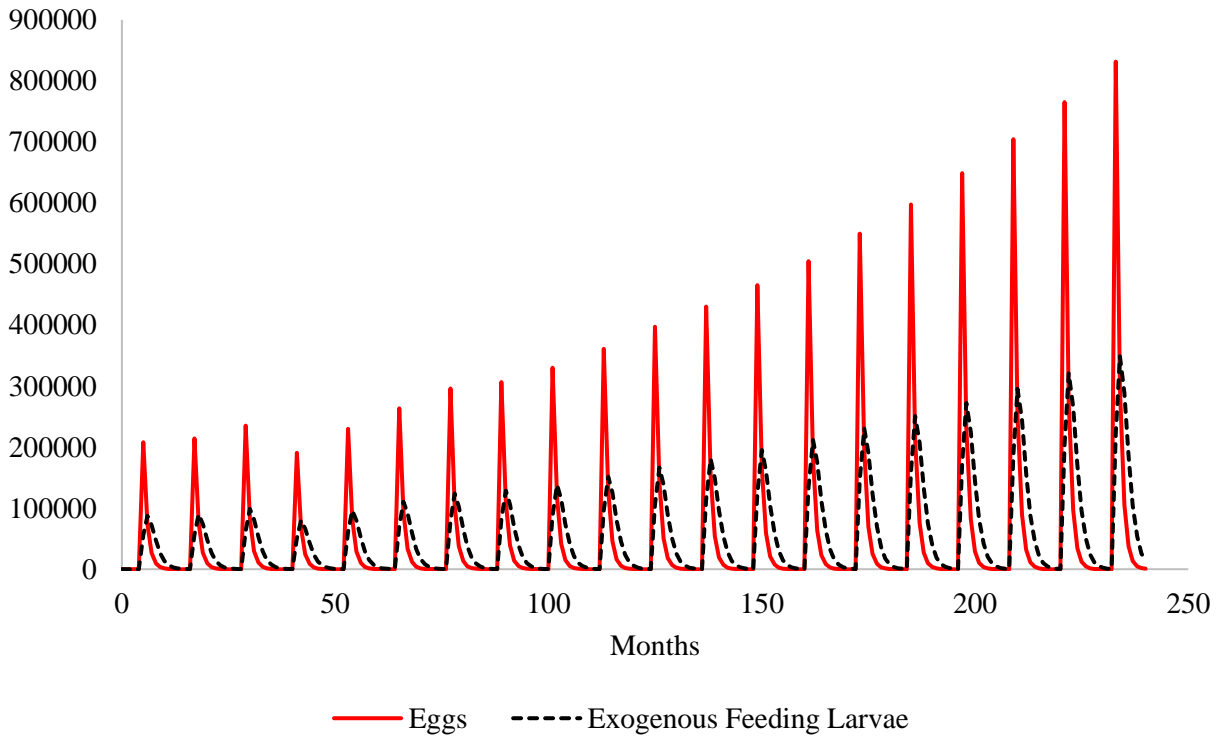


Figure 12. The influence of high egg production by Spring age 3's on Exogenous feeding larvae.

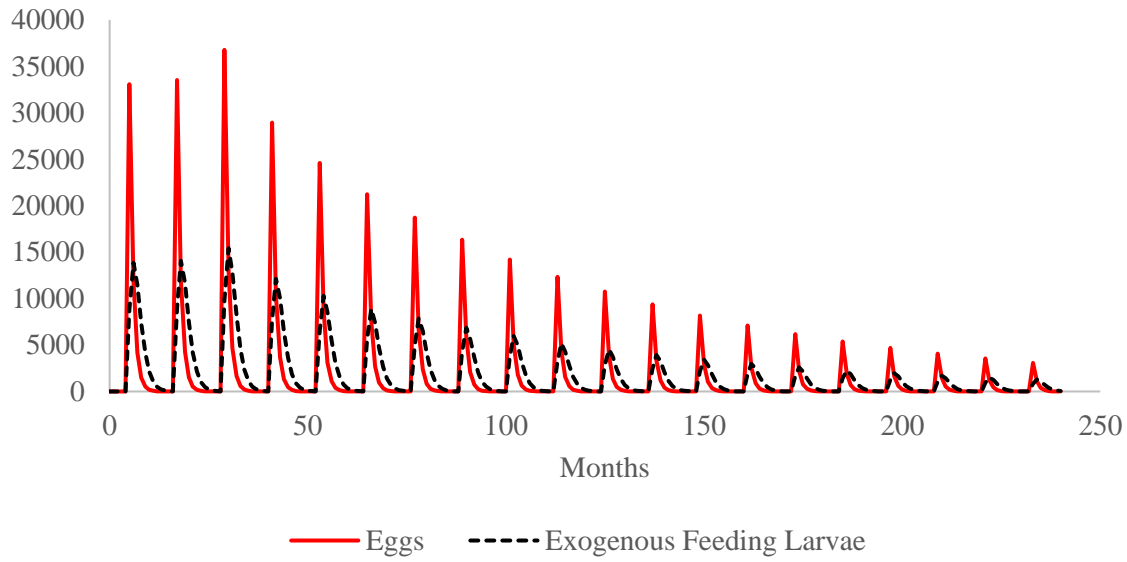


Figure 13. The influence of low egg production by Spring age 3's on Exogenous feeding larvae.

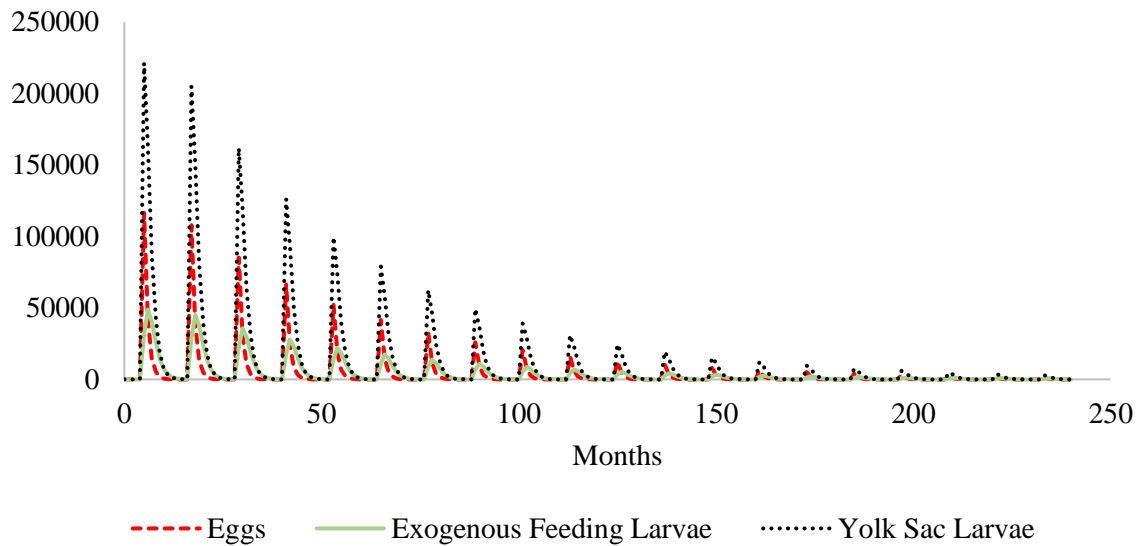


Figure 14. Influence of high mortality of eggs, Exogenous feeding larvae and Yolk sac larvae on Spring age 1s.

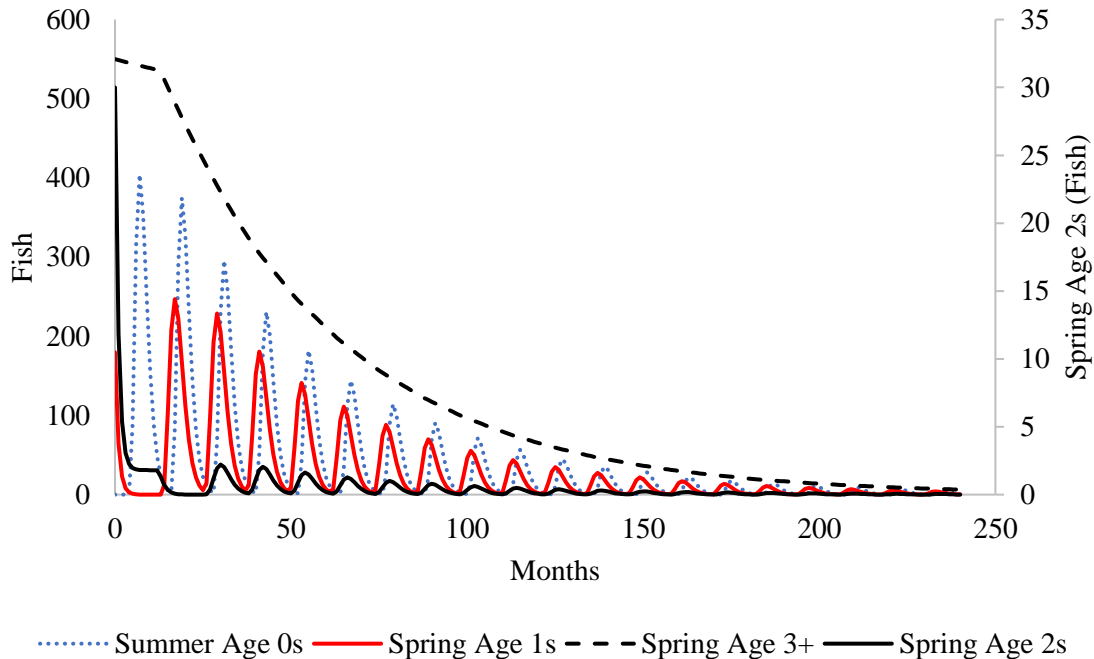


Figure 15. Influence of high mortality of Spring age 1s on Summer age 0s, Spring age 1s, Spring age 2s, and Spring age 3+.

Overall, the model was most sensitive to mortality and reproductive characteristics of Spring age 3+ but not very sensitive to Spring age 2s. These results are expected given the some of the life history characteristics of yellow perch. As previously noted, male yellow perch may reach sexual mature by the spring of their second year (Spring age 2s) but maturation of females may be delayed at least one year (Spring age 3+; Jansen 1996). Given that fecundity is a measure of reproduction by females, we would expect that the model would be more sensitive to Spring age 3+ yellow perch rather than Spring age 2s. Thus, sensitivity analyses are congruent with ecological knowledge of the species.

### Discussion:

Several traditional statistical modeling approaches have been previously developed and used to explain and predict recruitment of harvestable or sexually mature fish in general and yellow perch specifically. These approaches are generally categorized as “stock assessments,” whereby “stock” refers to the number or biomass of harvestable or sexually mature fish or their reproductive capability and “recruit” refers to the population still alive at any time after the egg stage. Three stock assessment types include stock-recruitment models, surplus production models, and statistical catch-at-age models. Each model type varies in complexity.

Stock-recruitment models are the simplest type and examine only a relationship between the stock and recruit life stage. “Stock” in this stage is a measure of the reproductive capacity of female fish such as fecundity and recruits are often defined as fish that reach the minimum size

allowed for harvest (though not always). Depending on the specific stock-recruitment equation used (e.g., Beverton and Holt, 1957; Ricker, 1975), the model may account for density-dependent survival rates. Further, density-independent environmental factors may be included within the equation in order to account for unexplained variability in the relationship between stock and recruits (Haddon, 2001). However, the equation does not account for feedback between the recruit back to the stock.

To our knowledge, only one published study has modeled yellow perch recruitment using a stock-recruitment recruitment approach. Henderson (1985) tested three hypotheses of recruitment variation in South Bay, Lake Huron, U.S.A. Results showed that recruitment was not a function of parental stock abundance or water temperature but was positively related to lake water levels. Stock-recruitment models for yellow perch populations in natural lakes in South Dakota, U.S.A. are currently under development (Dembkowski, *unpublished data*) but have not been created for other inland lakes across the geographic range of perch to our knowledge.

Surplus-production models are also simple in nature and are advantageous for modeling recruitment when limited information on the population of interest is available (Haddon, 2001). The “stock” used in this model pools recruitment, growth, and mortality into a single production function (e.g., all fish of a harvestable size) rather using a measure reproductive capacity. The only data required for this model type is an index of relative abundance of the stock and the associated catch data (e.g., fishing effort; Haddon, 2001). Surplus-production models are often used to predict how much biomass of a commercially or recreationally important fishery may be harvested or lost due to other human factors over the long term. In fact, economic data, including the cost to fish and the revenue gained may be included in models (Christy and Scott, 1965; Grafton *et al.*, 2006). However, much like stock-recruitment models, surplus production models also do not account for feedback between the recruit back to the stock.

To date, only one study has used a surplus production model to predict biomass loss of yellow perch due to the impacts of water intakes for industrial and municipal purposes and subsequent impingement of eggs, larvae, and standing stock biomass in Lake Michigan, U.S.A. (Spigarelli *et al.*, 1981). Results showed minimal impact on all three life stages of yellow perch due to impingement. However, no surplus production models for yellow perch have been developed for inland lakes in North America.

The third type of commonly used stock assessment are age-structured models. These models offer an advantage over surplus-production models by differentiating “stock” into sex, size, age, or some combination of the three (Haddon, 2001). This distinction helps to account for time delays in production (e.g., the time it takes for a juvenile recruit to reach sexual maturity; Haddon, 2001). The data required for this model type thus includes not only stock and recruit information but also the sex, size, or age of the recruits. Cohorts of fish can be followed over time, typically on an annual basis.

Age-structured models have also been developed for yellow perch populations in southwestern Lake Michigan, U.S.A. (Wilberg *et al.*, 2005). The model partitioned stock by age, size, and sex

to examine whether reproductive failure or recreational and commercial fishing led to a population collapse. Further, various management actions were evaluated in predicting potential recovery responses of the population. However, the model did not include environmental factors, provided no feedback between recruits and stocks, and was for a Great Lakes fishery rather than an inland lake fishery.

Overall, traditional fisheries stock assessments, including those for yellow perch, are useful to fisheries scientists, managers, and regulators but appear to be limited in their ability to fully capture feedbacks in the system and the complexity of factors that may influence recruitment of fishes, including both density-dependent and -independent effects. Modeling the process of recruitment with only stocks and recruits often fails because the models do not capture catastrophic mortality events that occur at different life stages and at different rates between stock and recruit. Differentiation of stock by sex, age, or length may help to a certain extent, but even these more structured models do not account for feedbacks from recruits back to the stock.

An SD modeling approach could overcome these limitations of traditional fisheries stock assessments. Critical life stages can be represented as several different stocks and flows can represent both survival and mortality. Growth rates of fish may influence those flows as the ability of fish to reach the next life stage may depend on their body size and the rate at which sizes are achieved. In this way, SD models can integrate the three dynamic rate functions (recruitment, growth, and mortality) that interact to determine the nature of fish populations (see Figure 1).

Further, SD models can integrate the various density-dependent and -independent environmental and anthropogenic factors that influence fish growth, survival, and mortality at various life stages. The inclusion of these relationships into the model can allow for the stimulation of various scenarios (see Next Steps in Model Development below) to examine the effects of environmental and anthropogenic changes on various life stages over the long term. We believe this model will be useful for fisheries scientists, managers, and regulators to identify limits to recruitment and develop management strategies to help provide more consistent and sustainable yellow perch populations for recreation and to serve as prey for other recreationally important fish in the same waterbodies.

### **Next Steps in Model Development:**

Initial model testing shows promise in developing a yellow perch recruitment model with stocks and flows between important life stages but does not yet capture the complexity of factors that may influence recruitment. First, growth of fish in terms of body length and weight has yet to be included as a subcomponent. Both length and weight influence survival and mortality at several life stages in different ways. For example, age-0 yellow perch that grow large enough in body length and at a relatively rapid rate may avoid predation and be more likely to survive, but adult perch of a certain length may become vulnerable to harvest mortality. Additionally, inclusion of growth, particularly in body weight, may also provide linkages to other factors such as food supply and fecundity.



The model must also incorporate exogenous environmental and anthropogenic factors in order to capture the complexity of recruitment. Climate, fish community characteristics, angling, and management decisions can influence survival, mortality, and growth at each life stage. Inclusion of these factors also allows for the development of various scenarios to predict yellow perch recruitment over the long term. At a minimum, we plan to test at least three scenario types that have been hypothesized to impact recruitment of yellow perch in inland lakes:

- Scenario Type #1(Climate): How might recruitment of yellow perch respond to increased water temperatures and precipitation and decreased duration in ice cover as predicted under climate change?
- Scenario Type #2 (Fish Community): How might recruitment of yellow perch respond if smallmouth bass (*Micropterus dolomieu*; a predator) and bluegill (*Lepomis microchirus*; a competitor) increased in abundance?
- Scenario Type #3 (Angling and Management): How might recruitment of yellow perch respond if bag limits (i.e., the number of allowable fish harvested by anglers) increased? How might recruitment respond if female yellow perch were harvested at a greater rate than males in the winter months?

### **Conclusion:**

This paper presented the first version of a yellow perch population dynamics model to be used for fisheries management and research relevant to North American inland lakes. The model was constructed in Vensim modeling environment. After initial model development to reach a generalized population in equilibrium state, several sensitivity tests were run on the most uncertain parameters, including: Spring age-0 mortality rate, Spring age-1 mortality rates; percentage of Spring age-2 fish that are reproducing, and the number of eggs produced per reproducing Spring age-2 and age-3+ fish. Results showed that the model behaved fairly well to the altered conditions, with corresponding and logical increases or decreases in fish population responding to the altered parameter value. Although internally consistent, the model needs improvement in auxiliary variables representing mortality (whether natural or anthropogenic) and reproduction that better represent the climate, lake, or management forces known to influence yellow perch inland lake populations across their geographic range. Additional testing and validation of the model are also needed to ensure that the boundary and structure of the model are appropriate once the auxiliary variables described above are improved. Compared to other types of the fisheries recruitment models, the SD approach is likely to improve our understanding of yellow perch population dynamics through the integration of and feedbacks between critical life stages with important environmental and anthropogenic factors hypothesized to influence populations of perch in inland lakes where these fish provide recreational fisheries as well as serve as prey to other recreationally important species in the same waterbody.

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**Supplementary Material:**

Table A. Description and rates survival and mortality at each life stage of yellow perch (both sexes) and fecundity of sexually mature female perch as described in scientific literature. Each of these factors will be used in the model identified in Figure 2.

Life stage	Variable name	Description	Rate or Relationship	Justification or Citation
Egg	Viability	Fertilized eggs with potential to hatch	95.0%	Clady (1975; in Dahlberg, 1979)
	Survival	Percent of cohort surviving from fertilized egg to hatch/swim-up larvae	1.6 – 18.4%	Clady (1976; Carlander, 1997)
Yolk-sac larvae	Survival	Percentage of cohort surviving between egg hatch to T <sub>25 days post-emergence</sub>	100.0%	No published data available. Assumed to be high given relatively short time frame.
Exogenous feeding larvae	Survival	Percentage of larvae surviving from T <sub>25 days post-emergence</sub> to time T <sub>55 days post-emergence</sub>	2.0%	Noble (1975; in Dahlberg 1979).
Summer age-0	Survival	Percentage of larvae surviving between T <sub>55 days post-emergence</sub> and the first juvenile stage (August)	100.0%	No published data available. Assumed to be high when predator abundance is low and available cover is high.
Fall age-0	Survival	Percentage of juveniles surviving between the first juvenile stage (August) to the end of the growing period (October)	100.0%	No published data available. Assumed to be high when prey resources are abundant and predator abundance is low.
Spring age-1	Annual mortality	Percentage of the cohort that leaves the population due to death during the first winter period	5.0 – 60.0%	No published data available but several studies have hypothesized that the first overwinter period may be a point of catastrophic mortality depending on winter severity and lake characteristics (see Jansen 2008 for a review).

Life stage	Variable name	Description	Rate or Relationship	Justification or Citation
Spring age-2	Annual mortality	Percentage of the cohort that leaves the population due to death	45.0 – 92.0%	Isermann (2003)
	Fecundity	Number of eggs produced by individual females of this cohort	3,630 – 14,696 eggs/female	Clady (1976); Jackson <i>et al.</i> (2008)
Spring age-3	Annual mortality	Percentage of the cohort that leaves the population due to death	45.0 – 92.0%	Isermann (2003)
	Fecundity	Number of eggs produced by individual females of this cohort	5,390 – 31,419 eggs/female	Clady (1976); Jackson <i>et al.</i> (2008)

Table B. Equations used in the yellow perch recruitment model as described in Figure 2.

Eq.#	Variable (type)	Equation	Initial value; Units
1	Age 1 mort rate (flow)	=0.66	Dmnl
2	Age 2 mort rate (flow)	=0.66	Dmnl
3	age mortality (auxillary)	= Spring age 2's/month unit-maturation3	fish/Month
4	Age0 mort rate (constant)	=0.3	Dmnl
5	age0 mortality (auxillary)	=Summer age 0s/month unit-maturation1	Fish/Month
6	age1 mortality (auxillary)	=Spring age 1s/month unit-maturation2	Fish/Month
7	"age3+ mortality" (auxillary)	=MAX("Spring age 3+"/life expectancy, 0)	fish/Month
8	"egg success-failure rate" (flow)	=0.05	Dmnl
9	Eggs (stock)	= INTEG (eggs deposited-failed eggs-larvae growth, inital eggs)	fish
10	eggs deposited (auxiliary)	=MAX(estimated eggs produced*"start of spring?", 0)	fish/Month
11	"eggs deposited per Age3+" (constant)	=18000	fish/Month
12	eggs depository per Age2 (constant)	=8000	fish/Month
13	estimated eggs produced (auxiliary)	=("Spring age 3+"/fish unit*female fraction*"eggs deposited per Age3+")+(Spring age 2's/fish unit*percentage of 2s reproducing*eggs depository per Age2*female fraction)	fish/Month
14	Exo feed larvae (stock)	= INTEG (reach exogenous feeding-maturation0-mort exo feeders, initial exo feed larvae)	fish
15	exo feeders mort rate (flow)	=0.98	Dmnl
16	failed eggs (auxiliary)	= Eggs/month unit-larvae growth	fish/Month
17	female fraction (constant)	=0.5	Dmnl
18	FINAL TIME	=240	Month



Eq.#	Variable (type)	Equation	Initial value; Units
19	fish unit (constant)	=1	fish
20	initial eggs (constant)	=0	fish
21	initial spring 1s (constant)	=180	fish
22	initial summer 0s (constant)	=0	fish
23	initial exo feed larvae (constant)	=0	fish
24	initial spring 2s (constant)	=30	fish
25	"initial spring 3+" (constant)	=550	fish
26	INITIAL TIME	=0	Month
27	initial yolk sac larvae (constant)	=0	fish
28	larvae growth (auxiliary)	=(Eggs*(1-"egg success-failure rate"))/months to larvae	Fish/month
29	life expectancy (constant)	=48	Month
30	maturation0 (auxiliary)	=(Exo feed larvae*(1-exo feeders mort rate))/months to age0	Fish/Month
31	maturation1 (auxiliary)	= DELAY FIXED (Summer age 0s*(1-Age0 mort rate)/month unit, months to age1, Summer age 0s*(1-Age0 mort rate/month unit))	fish/Month
32	maturation2 (auxiliary)	= DELAY FIXED (Spring age 1s*(1-Age 1 mort rate)/month unit, months to age2, Spring age 1s *(1-Age 1 mort rate)/month unit)	fish/Month
33	maturation3 (auxiliary)	= DELAY FIXED (Spring age 2's*(1-Age 2 mort rate)/month unit, months to age3, Spring age 2's*(1-Age 2 mort rate)/month unit)	fish/Month
34	month counter	MODULO(Time, year duration)	Month
35	month unit	=1	Month
36	months to age0 (constant)	=2	Month
37	months to age1 (constant)	=9	Month
38	months to age2 (constant)	=12	Month
39	months to age3 (constant)	=12	Month
40	months to exo feed (constant)	=0.5	Month

Eq.#	Variable (type)	Equation	Initial value; Units
41	months to larvae (constant)	=0.5	Month
41	mort exo feeders (auxiliary)	= Exo feed larvae/month unit-maturation0	Fish/Month
42	percentage of 2s reproducing (constant)	=0.125	Dmnl
43	Reach exogenous feeding (auxiliary)	=(Yolk sac larvae*(1-yolk larvae mort risk))/months to exo feed	fish/Month
44	SAVEPER	=TIME STEP	Month [0,?]
45	Spring age 1s (stock)	= INTEG (maturation1-age1 mortality-maturation2,initial spring 1s)	fish
46	Spring age 2's (stock)	= INTEG (maturation2-age mortality-maturation3,initial spring 2s)	fish
47	"Spring age 3+" (stock)	=INTEG (maturation3-"age3+ mortality","initial spring 3+")	fish
48	"start of spring?"	IF THEN ELSE(month counter=4, 1, 0)	1
49	Summer age 0s(stock)	= INTEG (maturation0-age0 mortality-maturation1,initial summer 0s)	fish
49	TIME STEP	= 0.0625	Month[0,?]
50	year duration (constant)	=12	Month
51	yolk larvae mort risk (constant)	=0.85	Dmnl
52	yolk mortality (auxiliary)	= Yolk sac larvae/month unit-reach exogenous feeding	fish/Month
53	Yolk sac larvae (stock)	= larvae growth-reach exogenous feeding-yolk mortality, initial yolk sac larvae)	fish

Table C. Numerical values arrived at after model development and used for preliminary sensitivity testing for three uncertain model parameters.

Model parameter	Value at model equilibrium	Adjusted values (low, high)
Age 0 mort rate	0.30	0.01, 0.99
Age 1 mort rate	0.66	0.01, 0.99
percentage of Age 2's reproducing	0.125	0.01, 0.99
eggs deposited per Age 2	8,000	3,500, 14,500
eggs deposited per Age 3+	18,000	5,000, 32,000