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Modeling Yellow Perch (*Perca flavescens*) Abundance in Inner Saginaw Bay, Lake Huron, 1971-2001: The Importance of Density Independent and Density Dependent Processes

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MODELING YELLOW PERCH (*PERCA FLAVESCENS*) ABUNDANCE IN INNER SAGINAW BAY, LAKE HURON, 1971-2001: THE IMPORTANCE OF DENSITY INDEPENDENT AND DENSITY DEPENDENT PROCESSES

By

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ABSTRACT

MODELING YELLOW PERCH (*PERCA FLAVESCENS*) ABUNDANCE IN INNER SAGINAW BAY, LAKE HURON, 1971-2001: THE IMPORTANCE OF DENSITY INDEPENDENT AND DENSITY DEPENDENT PROCESSES

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Yellow perch (*Perca flavescens*) in Inner Saginaw Bay, Lake Huron, have exhibited wide variations in total abundance over the last thirty years. Abundance was low in the 1970s, high in the 1980s, and low in the 1990s. Abundance increased gradually from the late 1970s to the early 1980s, but decreased abruptly at the end of the 1980s. Fifteen competing hypotheses involving density independent survival, density dependent survival, and/or density dependent growth from age 0 through age 5 were modeled and evaluated using a method that minimized residual summed squares between observed and modeled catch per unit effort at age, 1971-2001. Model strength was measured using Akaike Information Criteria and Akaike weights. The top-ranking models showed the following processes to be important in determining the abundance of this yellow perch population: (1) compensatory survival at age 2-4, (2) compensatory survival at age 0, and (3) compensatory survival at age 1; however, a model with constant survival and growth rates ranked the highest. Compensatory survival at age 2-4 ranked second and is supported by other studies; however, compensatory survival at age 1 is best supported by auxiliary data in this study. In addition, the modeling process itself indicated that the dramatic drop in abundance in 1991 could only be accurately simulated if all age groups experienced a significant reduction in survival, suggesting the shift in abundance at this time was caused by a mortality event that affected all age groups. The

top four models also predict total abundance to gradually increase in the future, an increase that could be hastened with a reduction in fishing mortality.

This work is dedicated to Robert C. Haas, fisheries research biologist at the Michigan Department of Natural Resources Lake St. Clair Great Lakes Fisheries Research Station, who has devoted a large part of his career and life to studying yellow perch in Inner Saginaw Bay.

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INTRODUCTION

Fisheries management seeks to produce sustainable, optimal yields of fish (Roedel 1975, Levin 1993). To do this, it is often necessary to understand how changes in birth, survival, and individual growth rates lead to observed fish abundance. Birth, survival, and growth rates affect fish abundance by changing how many fish are born each year, how many survive, and how well they grow (which affect birth and/or survival rates). These rates may or may not be affected by fish density. Rate changes are *independent* of fish density if they are caused by mechanisms such as weather and physical lake processes that are not casually related to fish density. In this case, the rates may change randomly within some upper and lower bounds. Rate changes are *dependent* on fish density if they are caused by mechanisms such as competition, predation, and mating success, to name a few (Goodyear 1980, Hilborn and Walters 1992, Rose et al. 2001) that vary predictably with fish density. These are the types of mechanisms that are thought to "regulate" a population around some "equilibrium density", thus preventing fish density from growing without an upper bound or inevitably declining to zero. Birth, survival and growth rates can be *compensatory* (e.g., survival rate increases as density decreases) or *depensatory* (e.g., survival rate increases as density increases) (Goodyear 1980, Hilborn and Walters 1992, Rose et al. 2001). Compensatory rates change according to fish density by either causing the population to grow or shrink towards some upper and lower bounds. Recognition of how changes in density independent and density dependent rates can impact population size can help fisheries managers determine the ways in which a fish population can be enhanced, as well as make better predictions of future yield.

In general, most animal populations are influenced by both density independent and density dependent processes (Milne 1962, Wolda 1989); therefore it is difficult to separate the relative impacts that they have on population size (Murdoch 1994). In addition, density dependent processes can occur among separate age classes. One way to evaluate the relative importance of these processes is to test them within separate hypotheses, or models (Franklin et al. 2001). This approach, however, presents some challenges. First, these separate models, individually, may not be representative of the real world, where it is unlikely that only one or two rates will vary, while all other rates remain constant. However, the results of these separate models are still useful because the effect of a single rate change on population abundance can still be indicative of its influence on population size, particularly if the impact is large. Second, the separate models represent a single hypotheses; therefore, this type of testing does not fit the traditional "Frequentist" framework of testing a single null and a single alternative hypothesis (Royall 1997). An alternative approach to null hypothesis testing is that of "statistical model selection" in which competing hypotheses (models) are tested relative to one another. A discussion of this approach can be found in Franklin et al. (2001).

Yellow perch in Inner Saginaw Bay, Lake Huron, have exhibited wide fluctuations in abundance during the 20th century (Hile and Jobes 1941, El-Zarka 1959, Eschenroder 1977, Haas and Schaeffer 1992). Some studies suggest compensatory growth has been an important factor regulating population size (El-Zarka 1959, Diana and Salz 1991, Haas and Schaeffer 1992, Schaeffer et al. 2000), while others suggest density independent influences, such as spring water temperatures (Eshenroder 1977), are important. El-Zarka (1959) reported increased abundance through 1955, accompanied by slow individual growth rates. In the 1980s, yellow perch abundance increased and growth rates decreased, and this has been hypothesized to be due to the density dependent impacts of food limitation (Diana and Salz 1991, Haas and Schaeffer 1992).

There are multiple hypotheses about the density independent and density dependent mechanisms that affect yellow perch population size in Inner Saginaw Bay. For example, recruitment may be influenced by weather-related events (density independent mechanisms), or young-of-the-year competition for food (density dependent mechanisms). Furthermore, these multiple hypotheses are not limited to age 0 yellow perch (i.e., recruitment). Evidence in Haas and Schaeffer (1992) and Diana and Salz (1991) suggest the Saginaw Bay yellow perch population may be regulated at older ages (e.g. age 2-4) due to food limitation. The goal of this study, therefore, was to determine the importance of density independent and density dependent rates (birth, survival and growth) in influencing the abundance of yellow perch in Inner Saginaw Bay, Lake Huron. My primary objectives were to determine the likelihood of various models that describe how the abundance of yellow perch has changed. This was done by (1) compiling a dataset of observed abundance and growth of yellow perch, (2) developing a population modeling framework capable of representing competing hypotheses, (3) determining which hypothesis(es) are most consistent with changes in yellow perch abundance, and (4) using auxiliary data to lend further evidence to top ranking models.

METHODS

Observed data

Observed data were used to model abundance of yellow perch in the Inner portion of Saginaw Bay, and to calculate survival and growth increments that could be compared to model output. Observed data were based on yellow perch trawl survey catch statistics gathered by the Michigan Department of Natural Resources (MDNR) Fisheries Division from Inner Saginaw Bay, Lake Michigan. Detailed descriptions of these methods can be found in Haas and Schaeffer (1992) and Thomas and Haas (1994). The Inner Bay is separated from the Outer Bay by a shallow area that extends from Point Lookout in the Northwest to Sand Point in the Southeast (Figure 1). Yellow perch were collected with bottom trawls from a variety of index sites in September or October of each year, 1971-2001, except data from 1985 were unavailable. Data from individual sites were usually collected from three consecutive ten-minute tows. In the 1990s, randomly selected sites were added to the index site design.

Catch statistics were used to calculate age specific relative abundance and size composition. Catch-per-unit-effort (CPUE) at age was used as an index of abundance, and mean total length at age represented size at age. CPUE was equivalent to actual abundance and gear selectivity; however, selectivity was not parameterized in these models because (1) this would have introduced too many parameters into some of the models, therefore making it difficult to estimate survival and growth rate parameters, and (2) it was not necessary to determine absolute abundance for this study since relative comparisons among models could be made. It was, however, assumed that catchability at

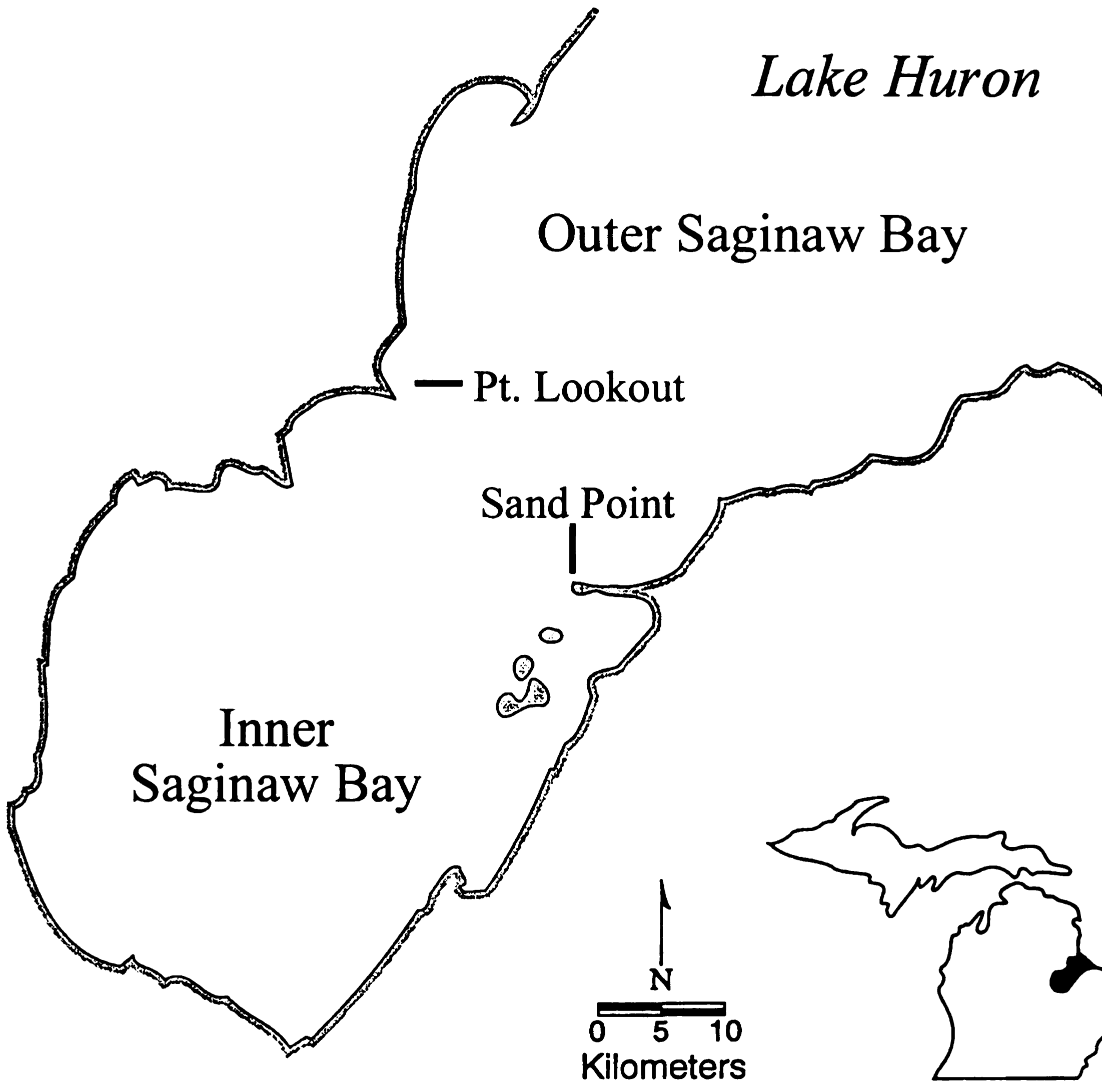

Figure 1. Inner and Outer Saginaw Bay, Lake Huron, separated by an imaginary line between Point Lookout and Sand Point.

age remained constant over time. Calculations of CPUE, with and without random sites, indicated that the addition of random sites did not significantly change CPUE or length values, but added greater precision to measures of relative abundance. There were no data for 1985. To ensure a continuous time series, CPUE and mean length for this year were interpolated from the CPUE (or mean length) of the previous age group in the previous year and the CPUE (or mean length) of the following age group in the following year. The interpolation assumed CPUE decreased exponentially, and length at age increased exponentially.

The CPUE for each age group, age 1-8, for every year, 1971-2001, was used to fit the models. I assumed no change in abundance or growth from October to April, the following year, and applied all data from fall collections to the spring of the following year. This adjustment was needed to simulate changes in abundance within the population models, which apply birth rates in the spring. For example, young-of-the-year yellow perch collected in the fall were assumed to be age 1 yellow perch in April of the following year. This increased the "assigned" ages of observed fish by one year, and changed the dataset years to 1971-2001. In the models, age 0 yellow perch were assumed to be egg number, rather than young-of-the-year. Observed data consisted of data on females only, because the population model included fecundity rates that only involved females. Age 1 yellow perch were not separated by sex in the observed datasets; therefore, female CPUE of this age group was calculated as one half the CPUE of both sexes, assuming there was a 1:1 ratio of females to males.

Hypothesis formulation

The hypotheses in this study (Table 1) were related to population processes (survival, growth, and fecundity), rather than specific mechanisms (e.g., water temperature, predators, food) that affect the population processes. Hypothesis formulation was based on (1) the biological likelihood of the hypothesis, (2) the limitations of the population model (e.g., the models used could not simultaneously test density independent and density dependent rates within the same age group), and (3) the number of parameters (i.e., some hypotheses were overparameterized). Age 2-4 yellow perch were grouped together because they represented the benthivorous feeding stage of yellow perch in Inner Saginaw Bay (Tharratt 1959, Haas and Schaeffer 1992, Synnestvedt 1996). Hypotheses based on compensatory rates at age 5+ were not included in this study because preliminary model testing showed these rates had very weak relationships with abundance. Compensatory growth impacts on fecundity were hypothesized for all age groups, including immature yellow perch. Immature fish do not produce eggs; however, it was assumed that their growth would influence their size and fecundity when they became mature.

HYPOTHESES	MODEL NO.
Null Hypothesis	
1. Constant survival and growth rates at all ages	1,4
Age 0 (recruitment) Hypotheses	
2. Density independent survival rates at age 0	2,3
3. Compensatory survival rates at age 0	5,6,7,8
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Table 1. Alternative hypotheses, by age, of the processes that may have impacted overall abundance of yellow perch in Inner Saginaw Bay, Lake Huron, 1971-2001. Each hypothesis is incorporated into one or more models, indicated by model number.

Population model and parameter estimation

The population model

Observed changes in abundance of yellow perch were simulated with the following population model:

Population abundance at age "a" and time "t" = $N_{a,t}$

$$N_{0,t} = \sum_{a=1}^{8} N_{a,t-1} * m_{a,t-1} * f_{a,t-1} * p \text{, where}$$

m = percent mature, f = fecundity, and p = sex ratio = 0.5.

$$N_{(a>0,t)} = N_{(a-1,t-1)} * S_{(a-1,t-1)} \text{, where}$$

$S_{(a-1,t-1)}$ = survival from a-1,t-1 to a,t.

Modeled $N_{a,t}$ was fit to observed $N_{a,t}$ through an optimization process that minimized the residual sum of squares (RSS) between the modeled and observed N. Model predictions of N, at every age, (a = 1-8), in every year (t = 1971-2001), were compared to observed N, at every age and year. The differences between them were squared and summed, so as to produce a RSS. Parameters contained within components of the model were selected based on the values that minimized the RSS. $N_{(0,t)}$ was not included in the minimization; but was needed to calculate $N_{(1,t)}$, and to model those hypotheses that involved age 0 survival or growth rates. It was not included in the minimization because there were no observed measures of egg number. The ability of the model to fit observed data was assessed by the value of the RSS (i.e., a lower RSS indicates a better fit), as well as through the model selection process described in the following section. All models were tested with different parameter starting values to increase the likelihood that all global minima would be found. Those starting values that produced the most realistic model with the lowest RSS were used.

Parameters within the population models were estimated based on the closest fit of modeled abundance to observed abundance as described above. Estimated parameters were either representative of a rate (e.g., density independent age 0 survival rate), or they were contained within a function that represented a rate (e.g., density dependent age 0 survival rate = a – (b*density), where a and b are the parameters). Parameters were automatically scaled during the optimization procedure because they often differed in magnitude. Models were always evaluated to determine if survival and growth rates were realistic. “Realistic” rates were considered to be those growth and survival rates that fell within a range of values found in other studies that measured growth or mortality of yellow perch (Schneider 1973, Brazo et al. 1975, Ney and Smith 1975, Weber and Les 1982, Pycha and Smith 1984, Henderson 1985, Henderson and Nepszy 1989, Hayes 1990, Haas and Schaeffer 1992). I used constraints when the model output was not realistic, but only after many attempts at searching for the parameters that minimized the sum of squared deviations. All models presented in the results have realistic survival and growth rates. Growth and survival rates remained constant when they were not parameterized within a model.

In models where survival rates remained constant, they were based on a mean survival rate (S), at age (a), averaged across years (t) (Table 2). These survival rates were actually "relative" survival rates because they were not adjusted for catchability. They were calculated from observed data as:

$$S_a = \frac{\sum N_{a,t}}{\sum N_{a-1,t-1}}$$

Age 0 survival rate was not known; therefore it was estimated in every model, except where noted.

In models where length remained constant, length was based on the mean length at age of yellow perch, summed and averaged across all years, 1971-2001 (Table 2).

Age	Survival Rate	Mean Length at Age (mm)	Percent Mature	Fecundity (eggs/female)
0	Estimated	0	0.000	0
1	0.653	81	0.000	0
2	0.571	134	0.384	2,138
3	0.388	165	0.890	9,482
4	0.302	187	0.980	15,600
5	0.302	205	0.997	21,246
6	0.401	229	1.000	30,558
7	0.450	251	1.000	40,573
8	0.000	260	1.000	45,732

Table 2. Constant values used in models, as calculated from observed female yellow perch data, 1971-2001.

Percent maturity was determined from the mean maturity of all yellow perch in the observed dataset, 1971-2001 (Table 2). Fecundity was calculated using an equation for yellow perch in Lake Erie from Henderson and Nepszy (1989):

$$\text{Log (fecundity)} = 3.1795 * \log(\text{length}) - 3.0202$$

Survival rate parameter estimates

In models based on hypotheses of density independent and compensatory survival, the survival rate involved parameter estimates. The parameter estimates were equivalent to the survival rates themselves in density independent models. One parameter was estimated in density independent models with a constant survival rate over time. Thirty parameters were estimated in density independent models with variable survival rates over time, one for each year. Density independent models were actually considered to be "free-fitting" models because the survival rate estimates were selected independently, but were not necessarily unrelated to density. To determine if they were related to density, I used linear regression to compare modeled survival rates with log-transformed modeled density, and based the significance of this relationship on analysis of variance.

In models based on hypotheses of density dependent "compensatory" survival, survival rate for each year was based on the relationship the instantaneous mortality rate (Z) had with the density of fish; therefore, the parameter estimates were contained within this relationship. The mathematical relationship was derived from a Ricker function (Ricker 1954, 1975), and parameter estimates were contained within the solution for Z:

$$Z_{age} = a + b(N_{age}), \text{ where a and b = parameter estimates}$$

Z_{age} was converted to S_{age} because an annual survival rate was needed in the population model:

$$S_{age} = e^{Zage}$$

Age 0 and age 1 instantaneous mortality rates were dependent on the density of one age group (i.e., age 0 or age 1). In contrast, I modeled one instantaneous mortality rate per year for age 2-4 yellow perch because hypotheses were based on a combination of these age groups. This single mortality rate was dependent on the combined density of all three age groups in the current year and was applied to each of the three age groups in the model. All survival rates were constrained to be greater than 0.0 and less than 1.0.

Some of the density dependent compensatory survival rate models included a time delay, in which survival rate of an age group was based on the density of that age group from a number of previous years (three, five or seven), thus simulating the time delayed effect that a previous population had on the current population:

$$S_{a,t} = a + (b * \sum_{x=1}^{3,5,or7} N_{a,t-x})$$

Time delays were used in age 1 and age 2-4 models because I hypothesized that these age groups may have been impacted by the abundance of the same age group from many previous years, rather than just the current year. This could occur if prey required more than a year to rebound from heavy predation by yellow perch. For example, a dense population of age 1 (or age 2-4) yellow perch can reduce their food base for many years if the invertebrates take many years to recover, thereby having a potential impact on age 1 (or age 2-4) yellow perch a few years later.

In all of the above density dependent models, variation in survival rates was explored in two ways: (1) based on the modeled abundance (one version of the same model), and (2) based on the observed abundance (another version of the same model). Models based on observed abundance were developed because a density dependent model that incorporates deterministic feedback based on its own egg production may be incapable of simulating the stochastic population variability that occurs in nature.

In density dependent "depensatory" models, survival rate was based on a depensatory relationship from Liermann and Hilborn (2001) that assumes depensation occurs as a result of predator satiation. When yellow perch are at low abundance, their survival rate is very low (predators are not satiated) relative to higher abundance (predators become satiated), although they eventually become abundant enough so that food limitation occurs, leading to compensatory survival rates (lower survival rates at very high abundance).

Unlike the above models, in which parameters were contained within the solution for the survival rate, parameters in these models were contained within the solution for $N_{(a)}$, for which a = 0 (Model 12 and 13) or a = 1 (Model 24):

$$N_{(a)} = pS \exp\left(\frac{S}{g} * \frac{mS}{h^2 + S^2} \right)$$

In the above equation, p = productivity, S = spawning stock, m = maximum level of predation, g = maximum spawner-recruit curve in the absence of predation, and h = number of spawners at which predation = ½ the maximum level of predation (m). I assumed S = egg number. All depensatory models were based on observed density of age 0 yellow perch because models based on modeled density had the potential to continuously increase or lower yellow perch density rather than simulate variability in the production of eggs.

Growth rate parameter estimates

In models that did not parameterize growth, fish length for every year was based on an overall mean length at age calculated from the observed data (Table 2). In contrast, models based on hypotheses of compensatory growth (as it impacts fecundity), fish lengths were based on the following equations:

$Length_{(a,t)} = length_{(a-1,t-1)}$ + length increment

Length increment = intercept - [slope*$length_{(a-1,t-1)}$], where

the slope = a parameter estimate and 0.4<=slope>=0.1.

$Length_{(a,t)}$ was based on the length of a fish from the previous age and year, plus a length increment. Rather than arbitrarily estimating the length increment, it was estimated from the linear relationship it had with length from the previous year and age; therefore accommodating the prior growth history of the fish. A negative linear relationship was used because increments were assumed to linearly decrease as fish length increased, which parallels how length changes in a von Bertalanffy growth equation (von Bertalanffy 1938). I had the option to incorporate a density impact on the intercept or the slope of the increment equation. In addition, the relationship between density and the intercept (or slope) could be based on a multitude of equations. I tested several types of equations for the intercept and slope, and found a modified inverse equation to be the best:

$$\text{Intercept} = \frac{a}{b + N_{(a-1,t-1)}}, \text{ where}$$

a and b = parameter estimates, a >=15000 and 40<=b<=200.

When other equations were used, fish length was often too low or equal to zero when fish density was high. The modified inverse equation prevented these unrealistic low values from occurring because it forced the length increment to be greater than zero. The equation worked equally well for the intercept or the slope, so I also applied the equation to the intercept of the length increment equation. The constraints were needed in order to obtain realistic fish lengths. As with survival parameterization, growth increments could be dependent on modeled abundance or observed abundance; therefore both types of formulations were tested. Time delays were not included in these models because preliminary model testing indicated growth models fit the observed data worse when time delays were included.

In models that did *not* parameterize growth, fish lengths for every age were equivalent to the mean lengths in Table 2. In the growth models, growth was parameterized for one age group as described above. The mean lengths in Table 2 were applied to age groups younger than the parameterized age group; however, length-at-age of fish that were older than the parameterized age group were based the length of the fish that were parameterized using the following equation:

$\text{Length}_{(a,t)} = a - [b*\text{length}_{(a-1,t-1)}]$, where

a and b = parameter estimates, a = 75 mm, and $0.4<=b<=0.1$

As with the younger fish in these growth models, it was also necessary to constrain the intercept and slope to obtain realistic lengths for older fish. Finally, it was necessary to set age 0 survival at a rate of 0.0002, rather than parameterize this rate. The value of this rate was estimated using a method by Vaughan and Salia (1976) that uses a Leslie matrix population model (Leslie 1945) to determine the rate based on an observed age distribution of fish. When age 0 survival rate was parameterized in these models, it was not possible to obtain realistic growth rates because the age 0 survival rate would be estimated at a value that accounted for changes in abundance regardless of fish growth. Fish would grow poorly, and produce fewer eggs, but good survival at age 0 would compensate for the reduced fecundity.

Model selection

In addition to RSS, models were also evaluated with Akaike's Information Criterion (AIC) (Akaike 1973):

$$\text{AIC} = -2\log_e \mathcal{L}(\text{parameters} \mid \text{data}) + 2(\text{number of parameters})$$

AIC is another measure of model fit. It is different from RSS because it penalizes models for the number of parameters, thus incorporating the principle of parsimony (Burnham and Anderson 1992). AIC is an estimate for samples in which $n/K >= 40$, where n = sample size, and K = number of parameters. Even though each year of the data used in these models was based on CPUE of several age groups from several collections and index sites per year, sample size was set at 31 because measures of CPUE were “nested” within each year. This required the use of a modified AIC (Hurvich and Tsai 1989):

$$AICc = AIC + \frac{[2K(K+1)]}{n-K-1}, \text{ where}$$

K = parameter number and n = sample size

Inspection of the residuals between modeled and observed CPUE from several models indicated most models were normally distributed; therefore the likelihood equation could be based on the residual summed squares (RSS) obtained from the optimization methods described above. I used the following equation adopted from Seber and Wild (1989) to calculate log likelihood:

$$\log_e L(parameters|data) = -\left(\frac{n}{2}\right) * \log_e(RSS)$$

I did not include any of the constant values often found within the above likelihood equation because they do not affect the equation outcome (Seber and Wild 1989). The value of AICc was used to rank the models, with the best-ranking model equivalent to the lowest AICc. Neither RSS or AIC provided measures of the relative importance of each model; therefore, Akaike weights (Buckland et al. 1997) were used to compare the models with each other:

$$w_i = \frac{\exp\left(-\frac{\Delta i}{2}\right)}{\sum_{m}^{M} \exp\left(-\frac{\Delta i}{2}\right)}, \text{ where}$$

M = total number of models, and Δi = difference in AICc of an individual model compared to the best model.

Auxiliary data

Several types of auxiliary data were used to support or refute the top-ranking models. First, age-specific survival and growth rates were estimated for each year *directly* from the observed data. This estimation process differed from model estimation, which estimated survival and growth parameters using an optimization process that minimized the sum of squared deviations between the observed and modeled abundance for each age and year. The observed data estimates were compared to fish density each year to determine if density dependent survival and growth occurred. Linear regression was used to compare the relationship between observed female survival (or growth increment) and observed female fish density, and significance was determined from ANOVA.

Observed survival rates were determined by:

$$S_a = \frac{\log_e\left(N_{a+1}\right)}{\log_e\left(N_a\right)}$$

Observed growth was evaluated from length increments. Length increments were calculated as:

$$Increment_{a \rightarrow a+1} = L_{a+1} - L_a \text{, where}$$

L = mean length-at-age obtained from the observed data

Growth rate evaluations from observed data served as auxiliary evidence for (1) compensatory growth, as it impacts fecundity, and (2) compensatory survival models, since compensatory growth can act as a mechanism of compensatory survival.

Additional auxiliary data were obtained by comparing observed temporal trends in growth increments (based on the above estimates) to temporal trends in abundance, 1971-2001. Furthermore, temporal changes in growth increments were examined for the entire 20th Century using data from Hile and Jobes (1941), El-Zarka (1959), Eschenroder (1977), and data from this study.

RESULTS AND DISCUSSION

Observed abundance

Although highly variable, estimated yellow perch abundance (CPUE) in Inner Saginaw Bay generally was low in the early 1970s, high in the 1980s, and low again in the 1990s (Figure 2A). Overall abundance appeared to have declined abruptly in 1983 and 1991, although it remained consistently low after 1991. Total abundance appeared to be most variable in the 1980s. Similar to total abundance, age 1 yellow perch were most abundant in the 1980s (Figure 2B). Age 2-4 yellow perch were most abundant from the late 1970s through the mid 1980s (Figure 3A-C). By age 5, yellow perch became less abundant, likely due to a combination of (1) lower vulnerability to gear and (2) lower survivorship at older ages. Age 5 yellow perch were most abundant from the late 1970s through the mid 1990s (Figure 4A). Age 6 yellow perch began to show more distinct peaks in the late 1970s and late 1980s (Figure 4B). Age 7 and 8 yellow perch were most abundant in the 1990s (Figure 5A and B). CPUE of a cohort could be easily tracked through subsequent year and age groups, implying CPUE measures were reasonably precise.

Overall abundance declined abruptly in 1991. This event, however, was actually *observed* in the previous year. This discrepancy occurs because observed data were applied to spring of the following year, when reproduction occurs. To avoid any confusion over the actual timing of the change, the change will always be called "the change in 1991" (later referred to as "the perturbation in 1991"); however, it still represents the change that occurred between Fall, 1989, and Fall, 1990, rather than between 1990 and 1991. Graphical representations of the data will also show this abrupt change occurring in 1991, rather than 1990. It is important to be aware of this because the mechanism that may have caused the abrupt change in yellow perch abundance would have occurred between Fall, 1989, and Fall, 1990, rather than between 1990 and 1991.

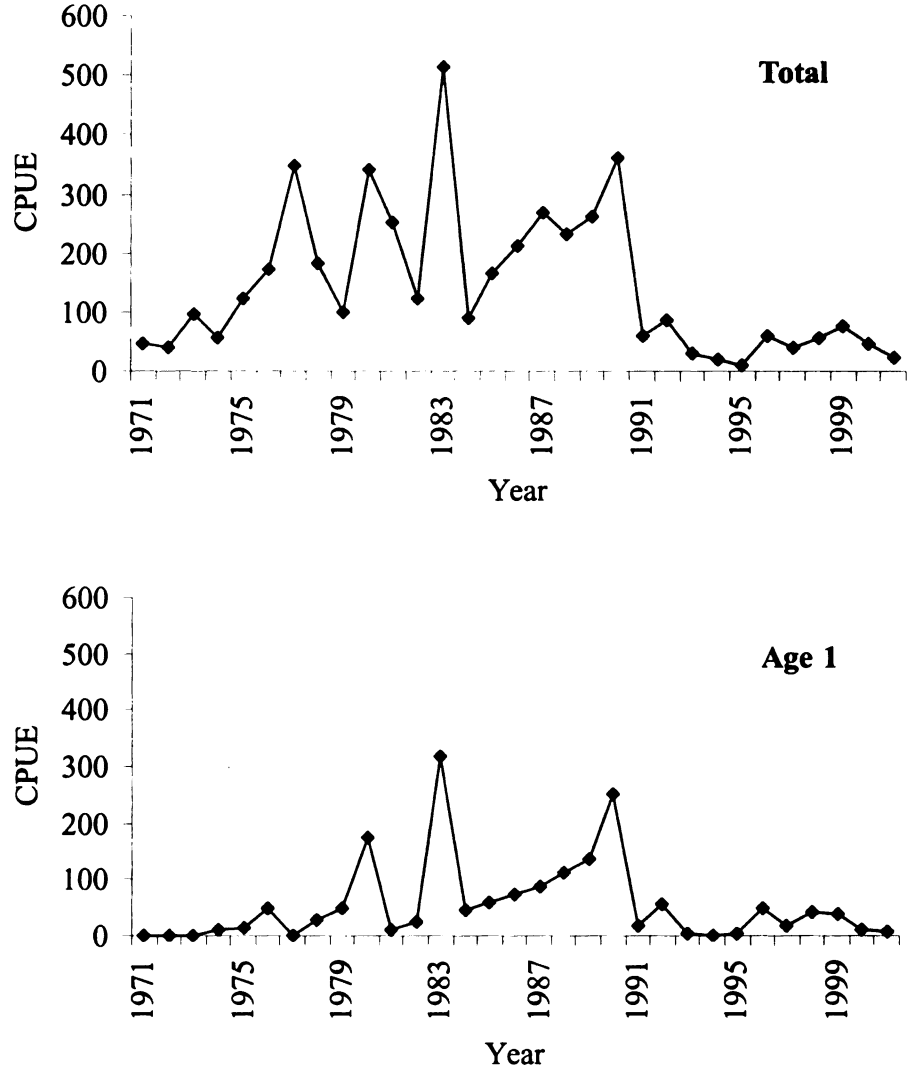


Figure 2. Temporal changes in total CPUE and age 1 yellow perch in Inner Saginaw Bay, Lake Huron.

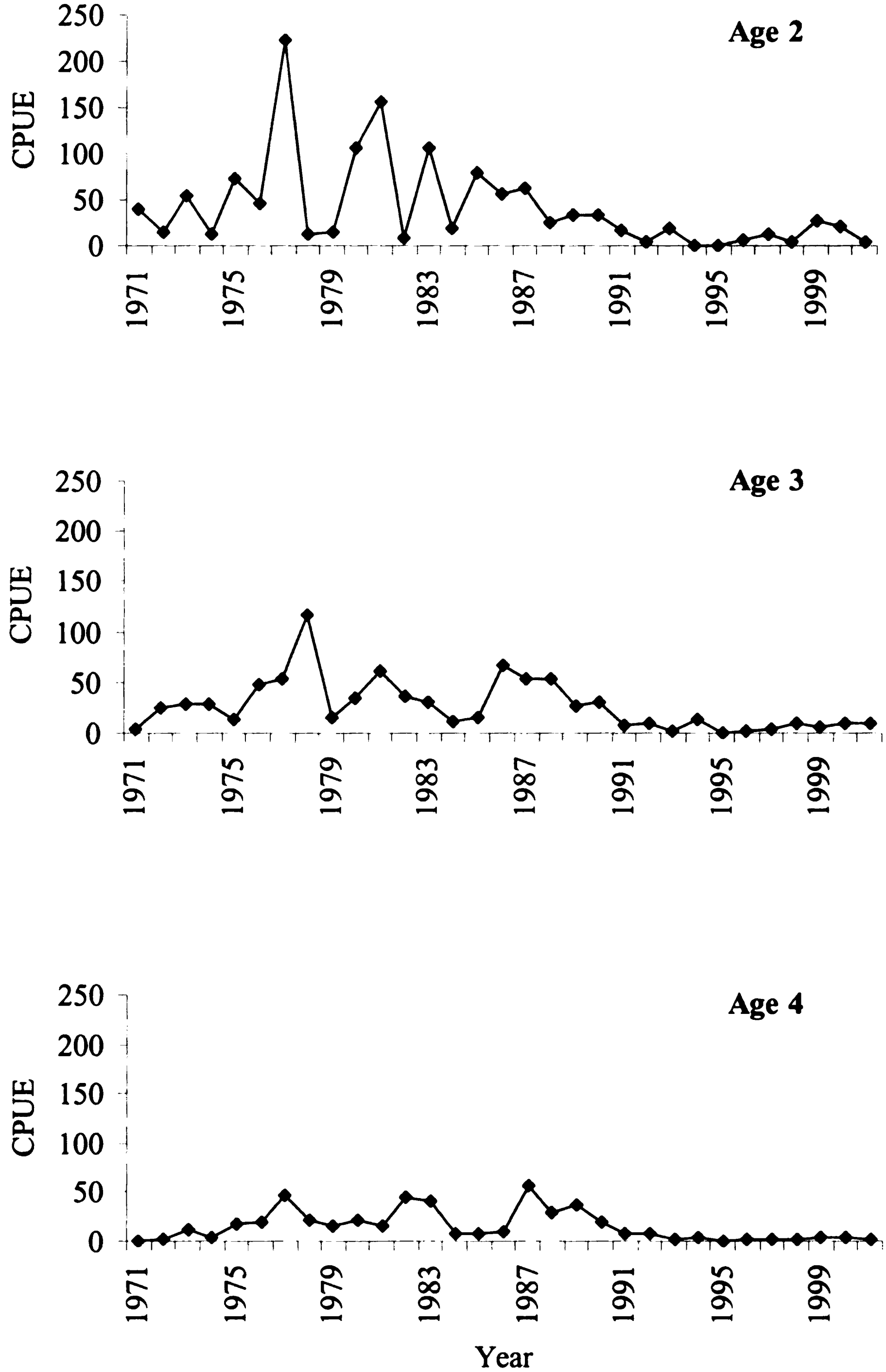
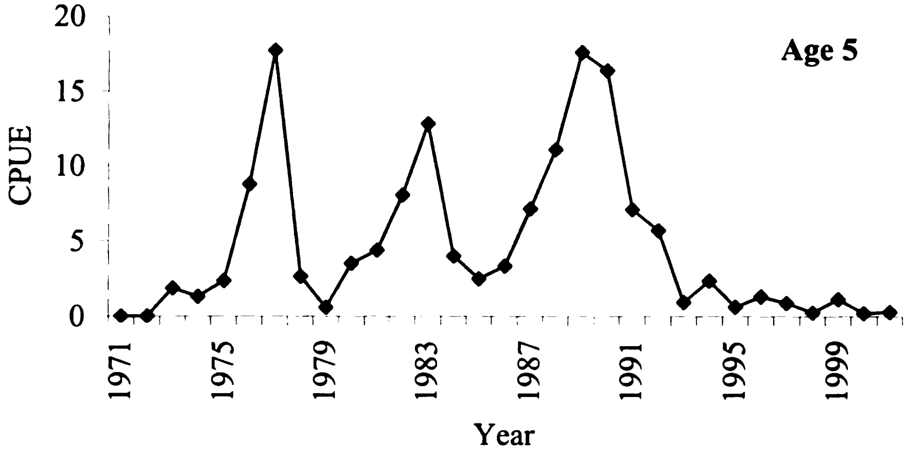


Figure 3. Temporal changes in CPUE of age 2, age 3 and age 4 yellow perch in Inner Saginaw Bay, Lake Huron.



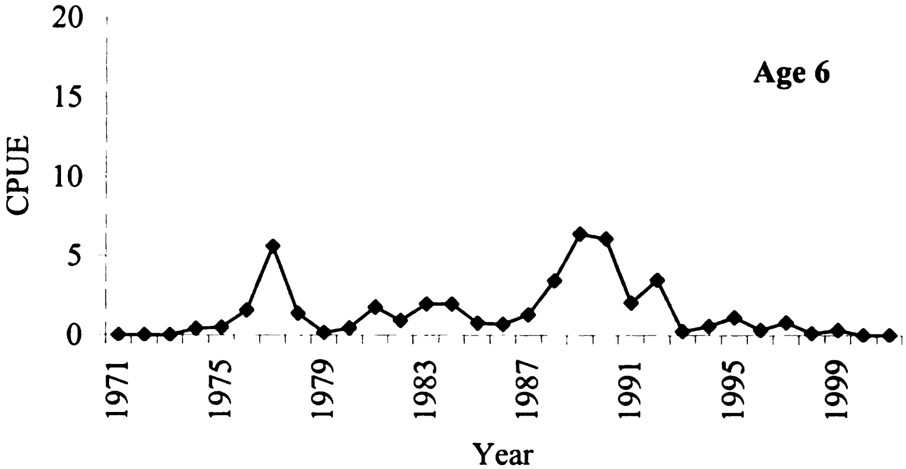
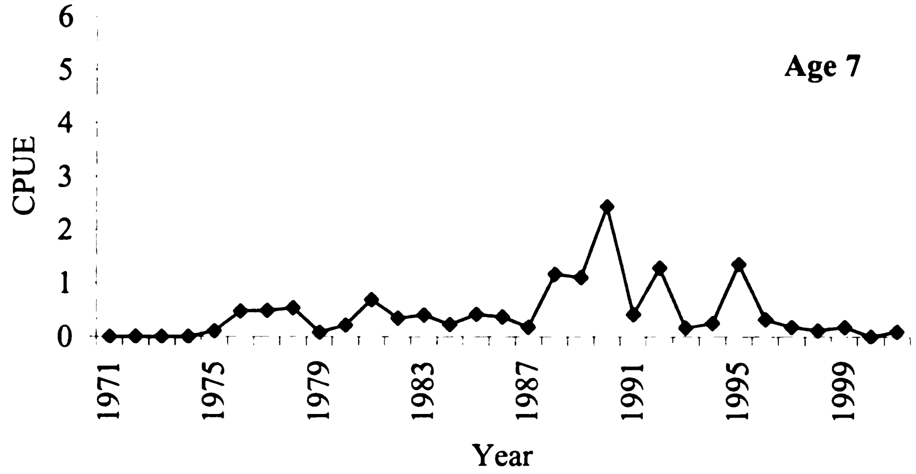


Figure 4. Temporal changes in CPUE of age 5 and age 6 yellow perch in Inner Saginaw Bay, Lake Huron.



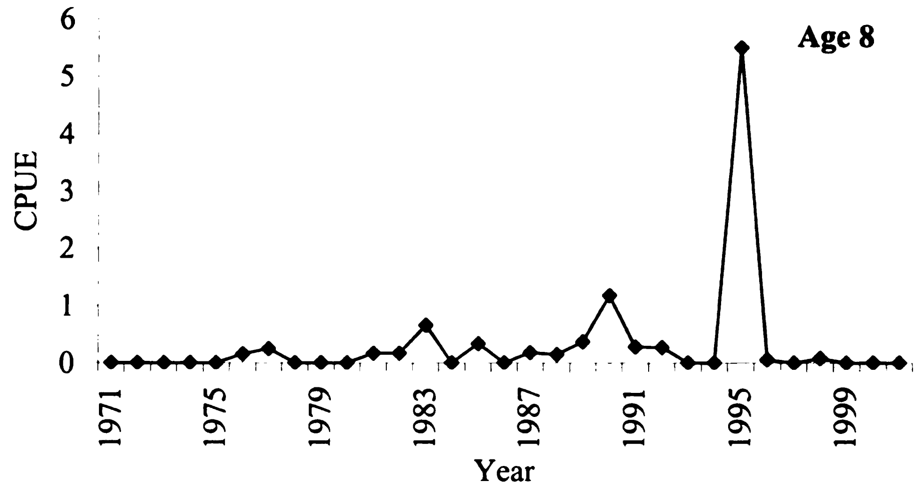


Figure 5. Temporal changes in CPUE of age 7 and age 8 yellow perch in Inner Saginaw Bay, Lake Huron.

Model evaluation

The following models represent the hypotheses listed in Table 1. Some hypotheses involve more than one model. Generally speaking, hypotheses are presented in the same order as listed in the table. Parameter number and estimates are listed in

Appendix A. In this section, models are evaluated based on (1) their "visual" fits to the observed data, and (2) the residual summed squares (RSS) that were minimized during the optimization procedure. Residual summed squares are listed in Table 3. In the following section, the same models are ranked and weighted according to Akaike's Information Criteria (AIC).

The null hypothesis

Model 1. A simple exponential model

This is the simplest model, in which one parameter, age 0 survival rate, was estimated and treated as a constant over time. It was not based on fish density, but was estimated based on a rate that would provide the best overall fit of modeled CPUE to observed CPUE.

Although a constant survival rate of age 0 yellow perch likely does not occur, this model represents the null hypothesis, in which all rates remain constant over time, and are not dependent on fish density. In this model, survival rate was estimated as 0.0003, and abundance increased exponentially because constant survival rates caused the population to increase continuously (Figure 7). Visually, the model did not match the data well because it was incapable of modeling annual fluctuations in density.

Age 0 survival hypotheses

Model 2. Free fitting age 0 survival rate for every year

In this model, age 0 survival rate was estimated for each year, while all other survival and growth rates in the model were held constant. This model was

Model No.	Model Description	P[1]	RSS[2]	Like Comp[3]	Par Comp[4]	AICc[5]	AICc Rank	AIC diffs[6]	Exp(-diff/2)[7]	Akaike weights
1	Constant age 0 surv[8]	1	308277	391.80	393.80	393.94	14	9.97	0.0069	0.002660
2	Variable age 0 surv	30	124881	363.79	423.79	2283.79	29	1899.82	0.0000	0.000000
3	Variable age 0 surv + pert[9]	30	105411	358.53	418.53	2278.53	28	1894.56	0.0000	0.000000
4	Constant age 0 surv + pert	2	207604	379.55	383.55	383.97	1	0.00	1.0000	0.388131
5	Age 0 comp[10] surv (mod[11])	2	271632	387.88	391.88	392.31	10	8.33	0.0155	0.006018
6	Age 0 comp surv (obs[12])	2	312162	392.19	396.19	396.62	18	12.64	0.0018	0.000697
7	Age 0 comp surv (mod) + pert	3	231190	382.88	388.88	389.77	7	5.80	0.0551	0.021397
8	Age 0 comp surv (obs) + pert	3	204770	379.12	385.12	386.01	3	2.03	0.3616	0.140363
9	Age 0 comp growth (mod)	4	305910	391.56	399.56	401.10	21	17.13	0.0002	0.000074
10	Age 0 comp growth (mod) + pert	5	208936	379.74	389.74	392.14	11	8.17	0.0168	0.006531
11	Age 0 surv (obs) + age 0 growth (mod) + pert	8	197127	377.94	393.94	400.49	22	16.51	0.0003	0.000101
12	Depensation at age 0 (obs)	4	391556	399.21	407.21	408.75	25	24.78	0.0000	0.000002
13	Depensation at age 0 (obs) + pert	5	371424	397.58	407.58	409.98	26	26.00	0.0000	0.000001
14	Age 1 comp surv (mod)	3	282352	389.08	395.08	395.97	17	11.99	0.0025	0.000965
15	Age 1 comp surv (obs)	3	276856	388.47	394.47	395.36	16	11.38	0.0034	0.001309
16	Age 1 comp surv (mod), 3 yr delay	3	262197	386.78	392.78	393.67	13	9.70	0.0078	0.003042
17	Age 1 comp surv (obs), 3 yr delay	3	234884	383.37	389.37	390.26	8	6.29	0.0431	0.016736
18	Age 1 comp surv (obs), 5 yr delay	3	226459	382.24	388.24	389.13	6	5.16	0.0760	0.029481
19	Age 1 comp surv (obs), 7 yr delay	3	226446	382.24	388.24	389.13	5	5.15	0.0760	0.029507
20	Age 1 comp surv (obs), 5 yr delay + pert	4	196596	377.86	385.86	387.39	4	3.42	0.1808	0.070166
21	Age 1 comp growth (mod)	5	288256	389.72	399.72	402.12	23	18.15	0.0001	0.000045
22	Age 1 comp growth (mod) + pert	6	200184	378.42	390.42	393.92	15	9.94	0.0069	0.002691
23	Age 1 surv (mod), 5 yr delay + age 1 growth (obs) + pert	8	195688	377.71	393.71	400.26	20	16.28	0.0003	0.000113
24	Depensation at age 1 (obs) + pert	6	481966	405.65	417.65	421.15	27	37.18	0.0000	0.000000
25	Age 2-4 comp surv (mod) + pert	3	196549	377.85	383.85	384.74	2	0.76	0.6825	0.264900
26	Age 2-4 comp surv (mod), 5 yr delay + pert	3	242189	384.32	390.32	391.21	9	7.24	0.0268	0.010411
27	Age 2-4 comp growth (obs) + pert	6	221001	381.48	393.48	396.98	19	13.01	0.0015	0.000581
28	Age 2-4 surv (mod) + age 2-4 growth (obs) + pert	8	210058	379.91	395.91	402.45	24	18.48	0.0001	0.000038
29	Age 1 (mod/5 yr delay) and age 2-4 (mod) comp surv + pert	6	194997	377.60	389.60	393.10	12	9.13	0.0104	0.004042

[1]parameter number, [2]residual sum of squares, [3]likelihood component of AICc, [4]parameter penalization component of AICc, [5]corrected Akaike Information Criteria, [6,7]values used to calculate Akaike weights, [8]survival, [9]perturbation, [10]compensatory, [11]using modeled density, [12]using observed density.

Table 3. Models and their fitness components, for which the smallest RSS, Like Comp, Par Comp, and AICc = the best fitting model.

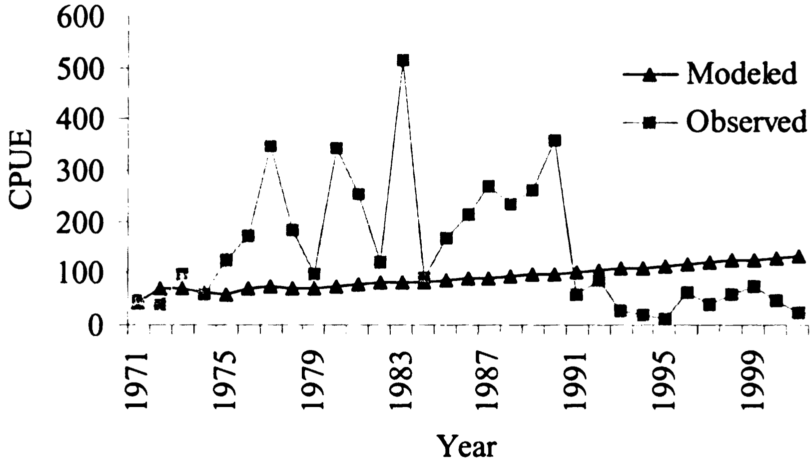
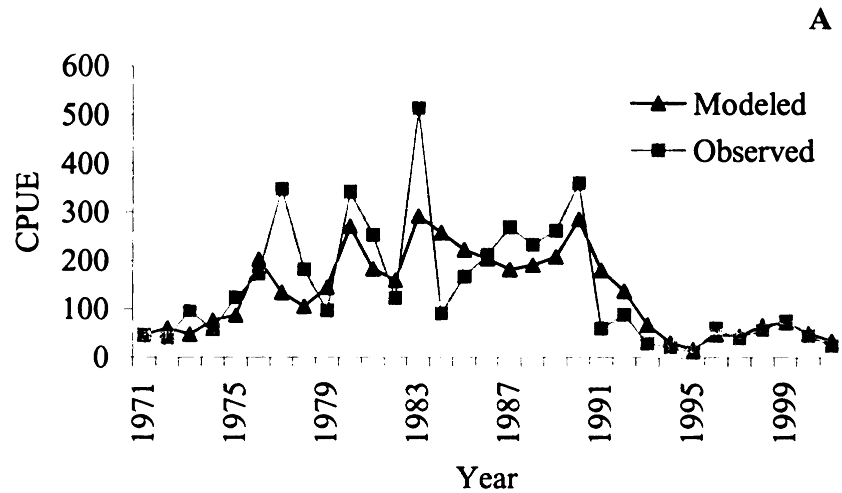


Figure 6. Model 1: Constant age 0 survival.

more flexible than Model 1 because it fit thirty parameters (one age 0 survival rate for each year), and because each survival estimate was not dependent on any value, such as fish density. This does not, however, mean that the survival rates were not related to density; hence the model was considered to be "free fitting", rather than density independent.

In this model, abundance closely matched the observed data (Figure 7A). As indicated by the RSS, the model provided a good fit to the observed data (Table 3). This close fit was possible because (1) age 0 survival rates in fish populations can have a strong impact on the total abundance in subsequent years, and (2) age 0 survival rate is fit independently for each year, allowing for tremendous flexibility of parameter values. Age 0 survival rate estimates varied widely (0.000001 to 0.00011, mean = 0.00018), with the lowest rates occurring between 1992-1994. These low rates were the model's attempt to match the large drop in observed abundance that occurred after 1991. When estimated survival rates were compared to CPUE, there was significant evidence that they may be density dependent (Figure 7B).



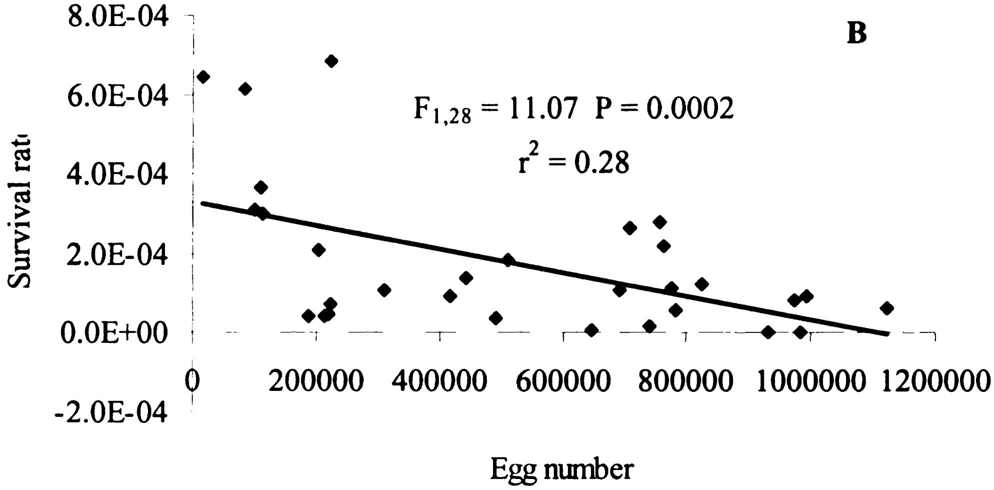


Figure 7. Model 2: Variable age 0 survival (A) and survival rate from age 0 to age 1 versus egg number (B).

Unlike the last model, this model was capable of modeling annual fluctuations in yellow perch abundance. It was capable of matching low abundance in the 1991s, but it could not simulate the "sudden" drop in abundance that occurred in 1991. Despite the influence age 0 survival rate can have on a population and the "free fitting" nature of this model, the model could not simulate this sudden change. One way to model this change is to reduce the survival of yellow perch across all age groups, thereby simulating a perturbation to the entire population.

Model 3. Free fitting age 0 survival rate every year with a perturbation

Model 3 was identical to Model 2, except a perturbation was added in 1991. This perturbation consisted of a reduction in CPUE that was applied to all age groups in 1991. In this model, as well as all subsequent models with a perturbation, CPUE at age was not modeled for 1991, but was fixed at an abundance that was approximately 10 times less than CPUE at age for models without perturbations. The same reduced CPUE values were used in all models with a perturbation, rather than "fitting" the perturbation for each model. This was done to maintain consistency among models with the perturbation, and to reduce additional model complexity. The amount of the reduction was determined in preliminary models by testing several factors and selecting the one that best simulated the sudden change in overall abundance that occurred in 1991. The perturbation was applied to a model prior to optimization and essentially acted as if the model contained an additional starting point (i.e., 1971 CPUE was the first starting point and 1991 CPUE was a second starting point).

Visually, this model (Figure 8A) matched the observed data slightly better than Model 2 (Figure 7), and the RSS also indicated a better fit (Table 3). This closer fit was possible because the perturbation enabled the model to match the drop in abundance in 1991. Age 0 survival rates varied widely across a similar range as Model 2. As with Model 2, when estimated survival rates were compared to CPUE (Figure 8B), there is an indication of density dependence, although the overall relationship was not significant. I also fit a nonlinear regression line to the data and found the linear relationship had a better fit.

Model 4. Model 1 with a perturbation

The above perturbation appeared to be a necessary feature of the free-fitting models; therefore, it was added to Model 1, creating a model with two parameters. The new model (Model 4) provided a better match to the observed data (Figure 9) than Model 1 (Figure 6). Based on RSS, it also had a dramatically better fit than without the perturbation (Table 3).

Model 5 – Model 8. Compensatory survival of age 0 yellow perch

In this suite of models, the age 0 survival rate (survival from egg to age 1) for each year was dependent on the density of age 0 yellow perch (eggs) from the previous year. All of these models estimated at least two parameters (intercept and slope of the linear relationship between age 0 survival rate and egg density).

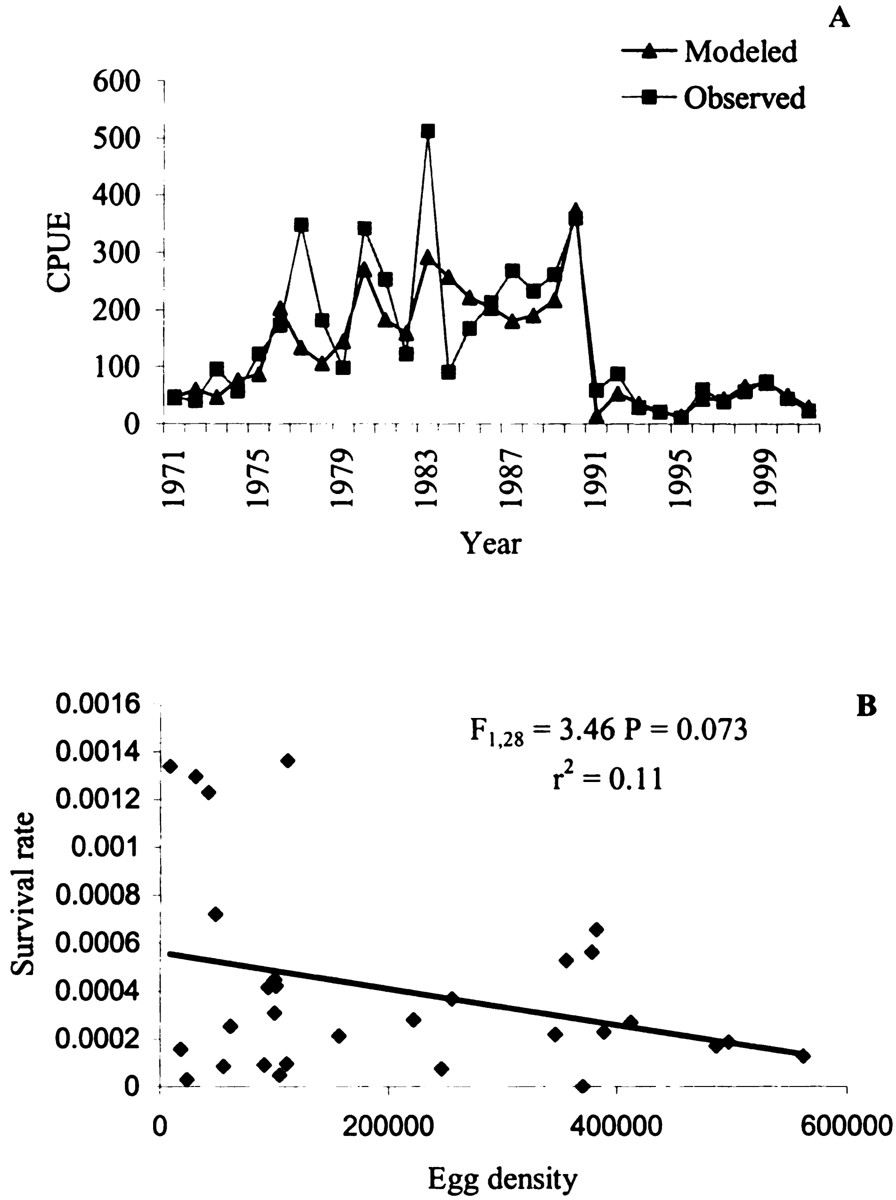


Figure 8. Model 3: Free fitting age 0 survival every year with a perturbation (A) and Model 3 survival rates versus egg density (B).

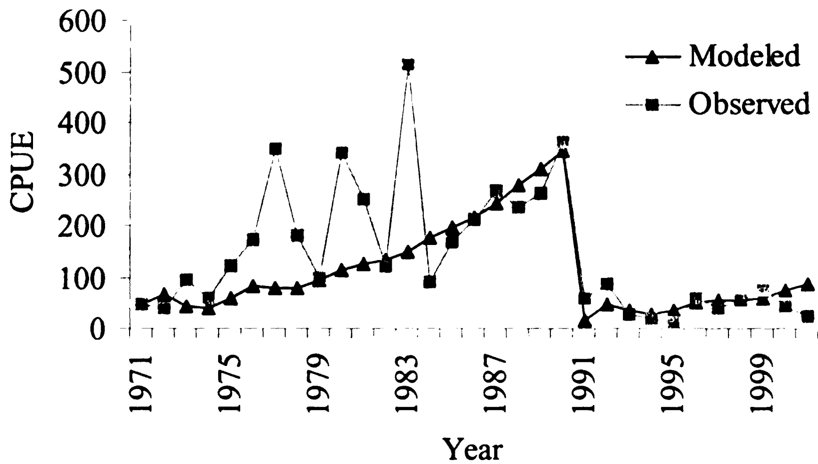


Figure 9. Model 4: Constant age 0 survival with a perturbation in 1991.

In these models, age 0 survival rate was dependent on either egg density predicted within the model (one version of the model), or egg density estimated from the observed data (another version of the model). In all of the age 0 models, observed egg number, as determined from the fecundity and abundance of mature females from the previous year, was variable. This variability produced models with visible cycles in abundance (Figure 10A), which may be indicative of compensatory survival of age 0 yellow perch; however, the models were very unstable. Age 0 survival rates were either zero, or too high; therefore, egg number was log-transformed prior to estimating the parameters of the survival rate equations. This produced a model (e.g., Model 5, Figure 10B) with reasonable age 0 survival rates, but the variability in egg number was greatly reduced.

In Model 5, age 0 survival rate was dependent on egg density predicted within the model. In Model 6, age 0 survival rate was dependent on egg density estimated from the observed data. Both Model 5 and Model 6 (Figure 10A and Figure 10B) were visibly similar to the null model (Model 1; Figure 7). Based on RSS, Model 5 fit the observed data slightly better than Model 1 (Table 3). Model 5 also had a better fit to the observed data than Model 6 (Table 3) because it was able to come closer to some of the data points in the earlier years. For this pair of models, the use of observed egg density to simulate greater annual variability in egg density did not appear to benefit model fit.

Survival rates were distributed differently between the two models. They decreased over time from 0.00046 to 0.00023 in Model 5; but remained virtually constant in Model 6 at 0.00027. A slowly decreasing density of total yellow perch in the model-based formulation (Model 5) caused the survival rate to slowly increase, although it did not fluctuate. In the observed-based formulation (Model 6), a virtually constant value was fit because changes in age 0 density over time likely forced the model to fit a value that kept the model between extremes; therefore, it was very similar to Model 1.

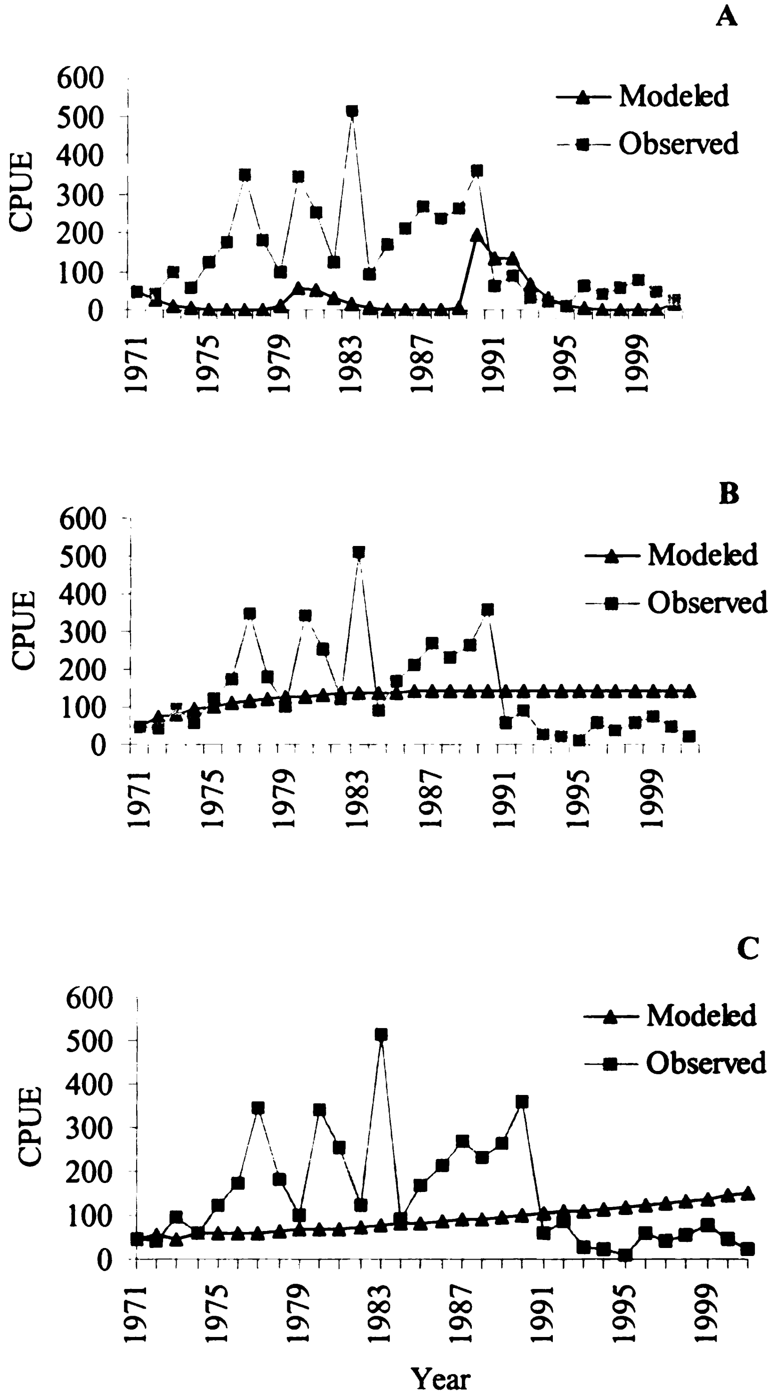
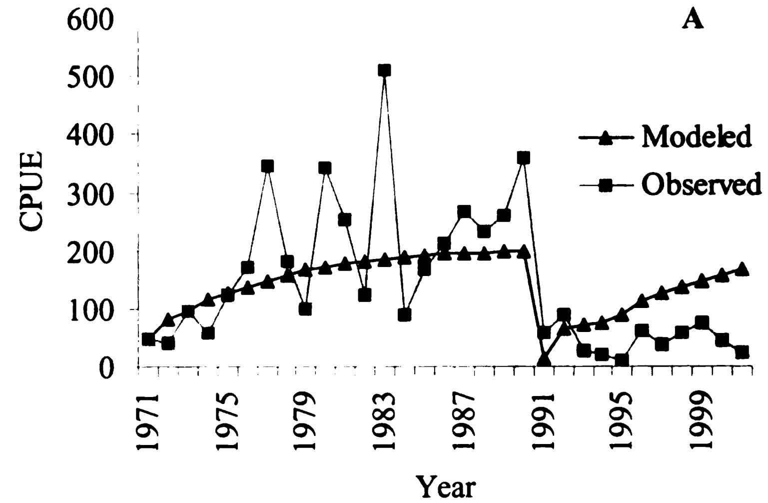


Figure 10. Density dependent survival of age 0 yellow perch without log transformation of egg number (A), Model 5: density dependent survival of age 0 yellow perch, based on modeled, log transformed egg number (B), and Model 6: density dependent survival of age 0 yellow perch, based on observed, log transformed egg number (C).

Model 5 and Model 6 were incapable of fitting the sudden change in abundance that occurred in 1991. When the perturbation (an additional parameter) was added to Model 5 (Model 7) and Model 6 (Model 8), they appeared to fit the observed data better (Figure 11A and Figure 11B), and RSS was lowered (Table 3); however, the model-based



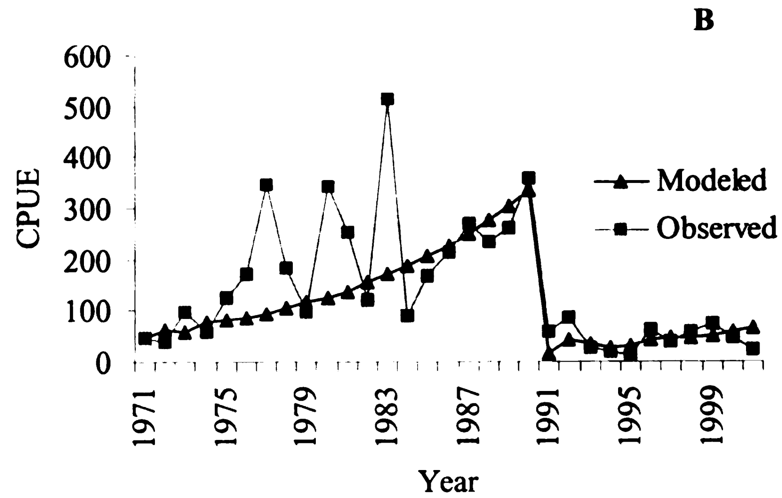


Figure 11. Model 7: density dependent survival of age 0 yellow perch based on modeled egg number, with a transformation (A) and Model 8: density dependent survival of age 0 yellow perch based on observed egg number, with a perturbation (B).

formulation could no longer fit the data as well as observed-based formulation (Table 3). The observed-based formulation probably fit the observed data better because the perturbation enabled the model to use slightly higher age 0 survival rates and provide a slightly better fit to the data points that followed the perturbation.

Model 9 – Model 10: Compensatory growth of age 0 yellow perch, as it impacts future fecundity.

In these models, at least seven parameters were estimated, consisting of intercepts and slopes found within the incremental growth equation. Compensatory growth models based on "modeled" yellow perch abundance provided the best fit to the observed data for these models; therefore, only modeled-based formulations are presented. It was not initially clear that a perturbation was needed.

The model of compensatory growth of age 0 yellow perch (Model 9) did not fit the observed data well (Figure 12A; Table 3). When a perturbation was added (Model 10), the model matched the observed data better (Figure 12B), and, according to RSS, the fit was better (Table 3). As with previous models, the perturbation added an additional parameter to the model, but was needed to accommodate the sudden change in abundance in 1991. Model 10 also had a steeper incline in abundance over the first two decades (Figure 12B).

In all growth models, I examined yellow perch mean length at age (averaged across all years) to determine if it was similar to observed mean length at age. In Model 10, mean length at age was similar to observed mean length at age at young ages;

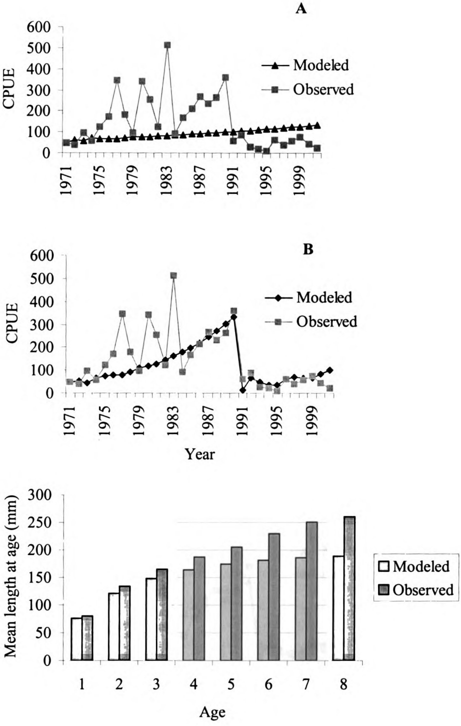


Figure 12. Model 9: Compensatory growth of age 0 yellow perch based on modeled density (A), Model 10: Compensatory growth of age 0 yellow perch based on modeled density with a perturbation (B), and comparison of modeled and observed mean length at age from Model 9.

however, modeled mean lengths remained lower than observed mean lengths at older ages (Figure 12). All remaining growth models showed similar results.

Model 11. Compensatory survival and growth of age 0 yellow perch.

I combined the best-fitting model of compensatory survival of age 0 yellow perch (Model 8) with the best-fitting model of compensatory growth of age 0 yellow perch, as it impacts fecundity, (Model 10). This combined model (Model 11) had a better match to the observed data (Figure 13) and, according to RSS, fit the observed data better than the individual models (Table 3). The number of parameters increased to 8. The combined model was similar to the individual models, except that the predictions had a slightly better fit to the observed abundance points due to the added effects of compensatory growth.

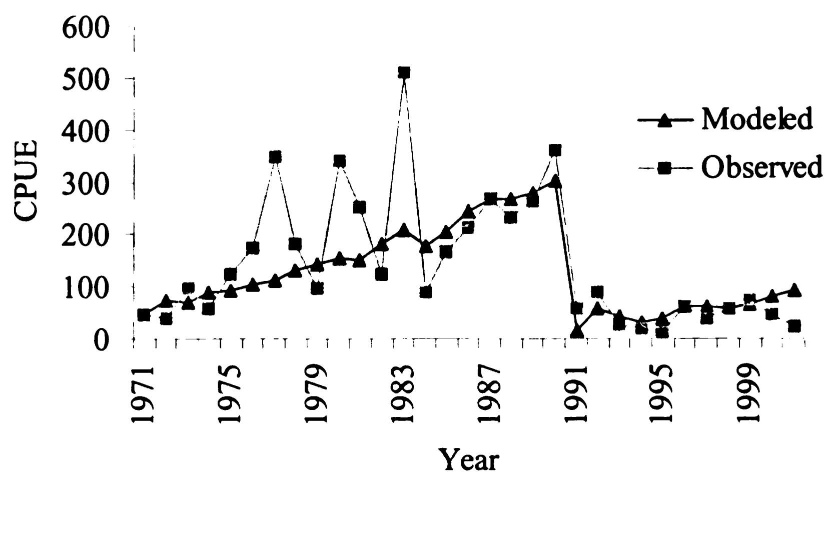


Figure 13. Model 11: Age 0 compensatory survival and growth, with a perturbation.

Depensatory survival of age 0: Model 12-Model 13

When depensation occurred at age 0, (Model 12), the model fluctuated in density similar to observed density, but the fluctuations did not match the observed changes (Figure 14A); therefore, according to RSS, the model did not have a good fit to the observed data (Table 3). Interestingly, this was the first model that was able to produce a significant drop in density in the 1991, yet the drop was immediately followed by a sharp rise in abundance. When a perturbation (additional parameter) was added to the model (Model 13), the sudden drop was modeled more accurately (Figure 14B); however, RSS showed little improvement (Table 3).

Age 1 hypotheses

Model 14 – Model 20. Compensatory survival of age 1 yellow perch

In this suite of models, age 1 survival rate (survival from age 1 to age 2) was based on the density of age 1 yellow perch in the previous year. These models fit at least three parameters. Two of the parameters were the intercept and slope of the linear equation that described the relationship between survival rate and density of age 1 yellow perch. The third parameter was a constant age 0 survival rate. In Model 14 and Model 15, survival rates were dependent on the density of age 1 yellow perch from the model (Model 14) or from the observed data (Model 15).

As with the age 0 models, the model-based formulation (Model 14; Figure 15A), matched the observed data similarly as Model 1 (Figure 7). Age 1 survival rates decreased over time from 0.985 to 0.355 (Mean = 0.451). Although these survival rates were initially high for this age group, the average rate was realistic. In contrast, the

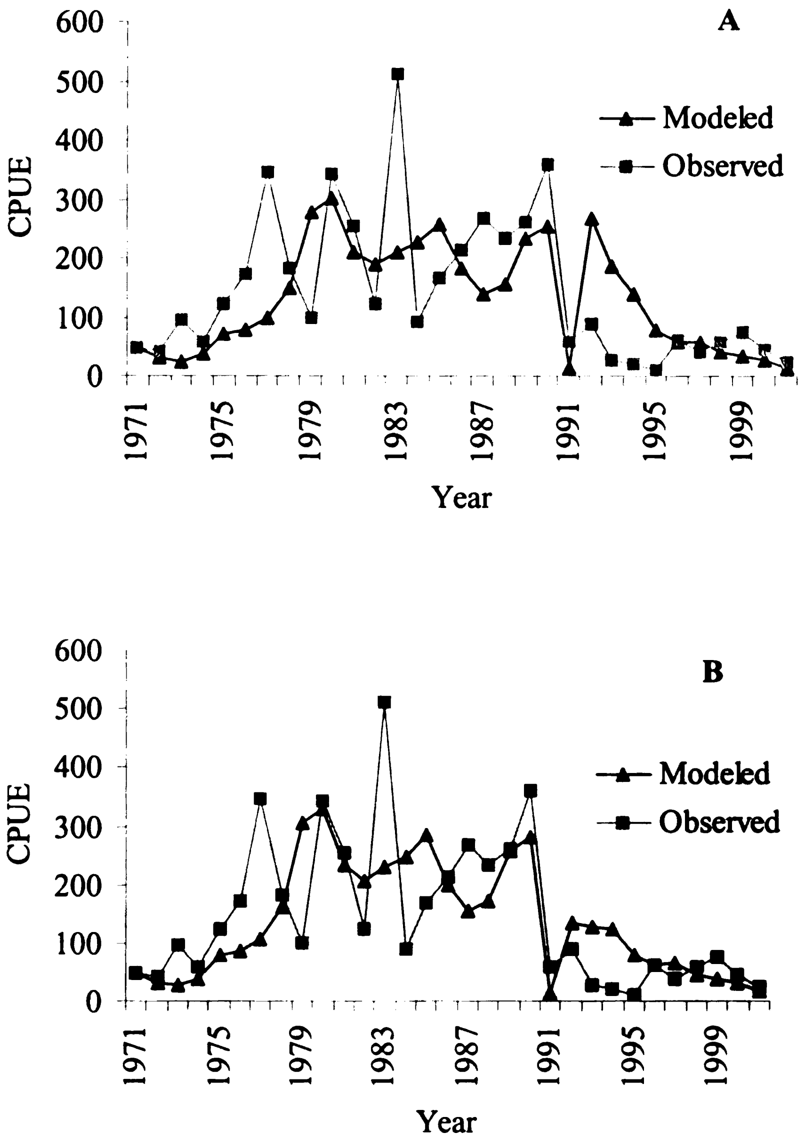
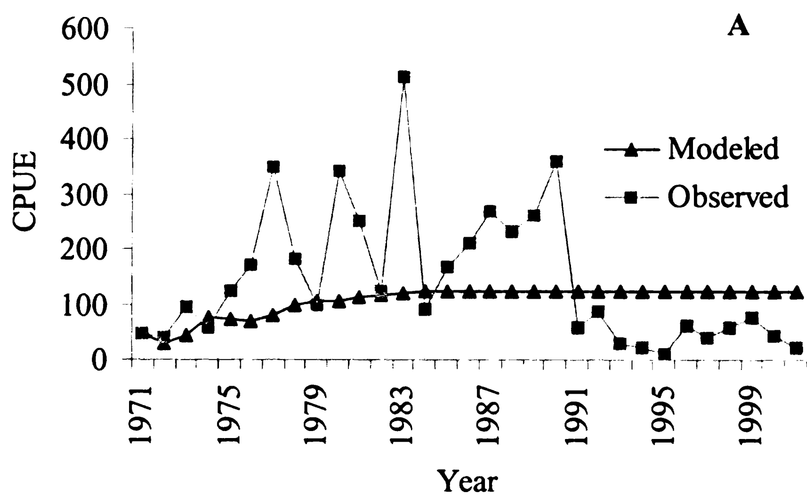


Figure 14. Model 12: Age 0 depensatory survival based on observed density (A), and Model 13: Age 0 depensatory survival based on observed density with a perturbation (B).



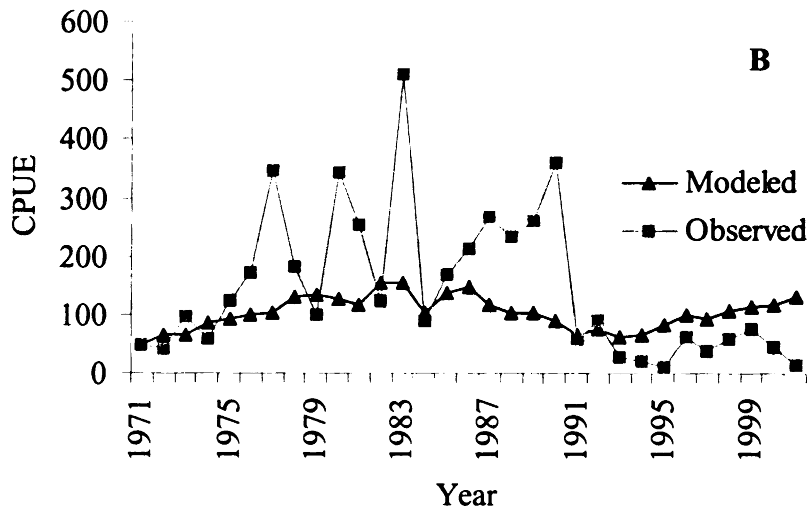


Figure 15. Model 14 and 15: Age 1 compensatory survival based on modeled density (A), and observed density (B).

observed-based formulation (Model 15; Figure 15B) exhibited more reversals in abundance and, according to RSS, was a better fit to the observed data (Table 3). Age 1 survival rates did not steadily decline like they did in Model 14, but increased and decreased densities (range = 0.013 - 0.749; mean = 0.475) based on observed.

When a 3 year time delay was added to Model 14 (Model 16), RSS indicated that it fit the observed data better (Figure 16A; Table 3), so much so, that it had a better match to the observed data and a lower RSS than when a 3 year time delay was added to Model 15 (Model 16B; Figure 16; Table 3). Longer time delays (5 year and 7 year) also performed better on Model 14, rather than Model 15; therefore, longer time delays are only presented for the latter. Five and seven year time delays (Model 18 and 19) impacted Model 14 similarly as the 3-year delay (Figure 17A and 17B). The 7-year time delay provided the best fit, as indicated by RSS (Table 3). The time delays improved the fit of the above models because modeled data points matched the variability in the observed data points much better than previous models; however, these models could not simulate high density in the late 1980s, as well as the sudden drop in 1991.

When the perturbation (additional parameter) was added to the time delay models, the time delay models had a better RSS. A 5-year time delay model with a perturbation (Model 20) had the best match to the observed data (Figure 18) and the lowest RSS (Table 3). This model was now able to fit some of the higher data points in the late 1980s, and incorporate the sudden drop in 1991.

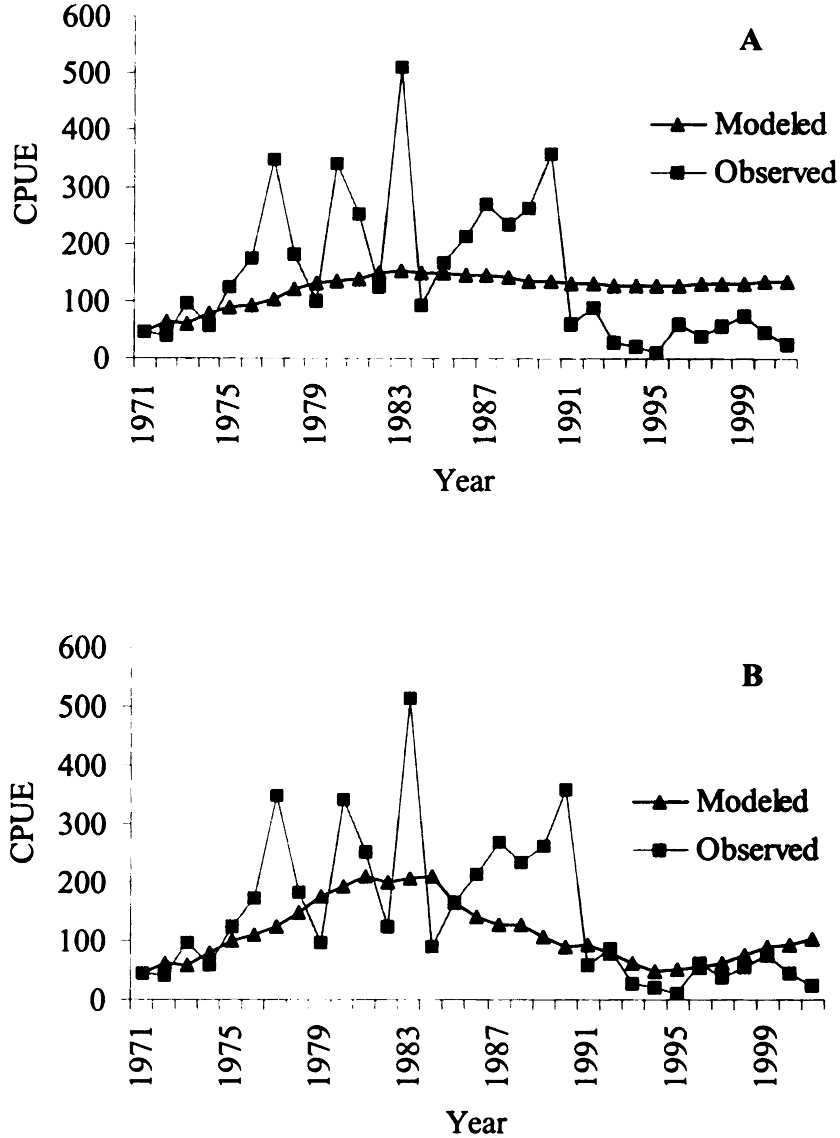
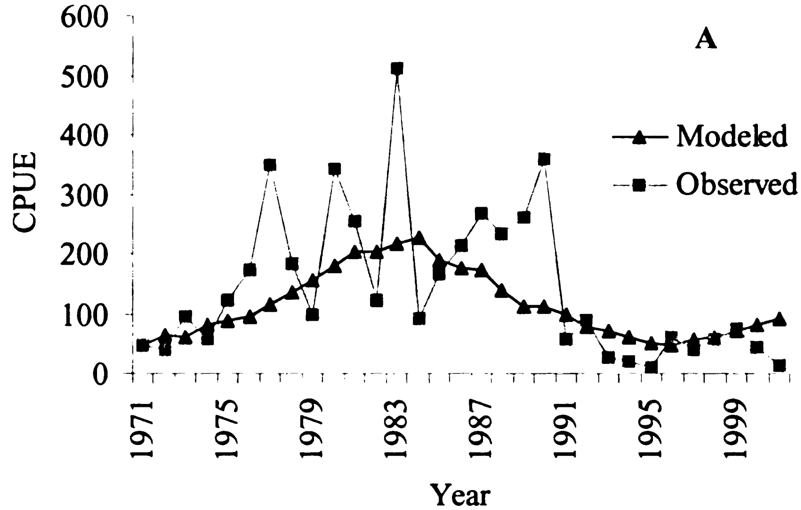


Figure 16. Model 16 and 17: Age 1 compensatory survival with a 3 year time delay based on modeled density (A) and observed density (B).



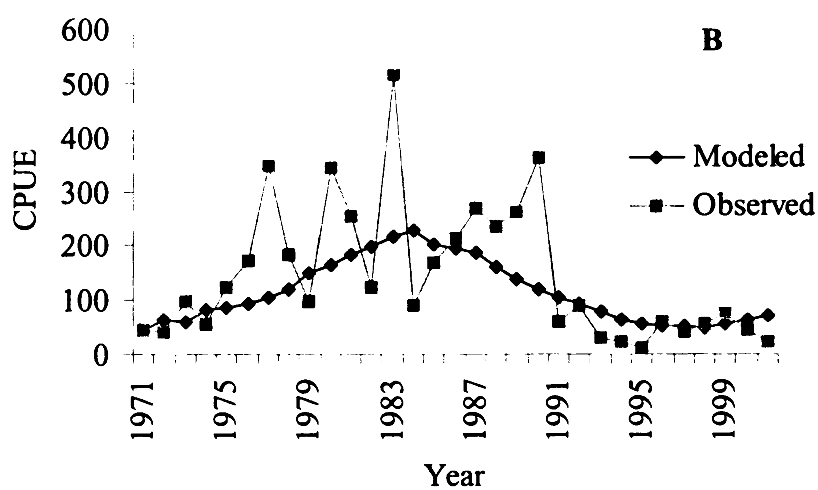


Figure 17. Model 18 and 19: Age 1 compensatory survival based on observed density with a 5 year time delay (A) and a 7 year time delay (B).

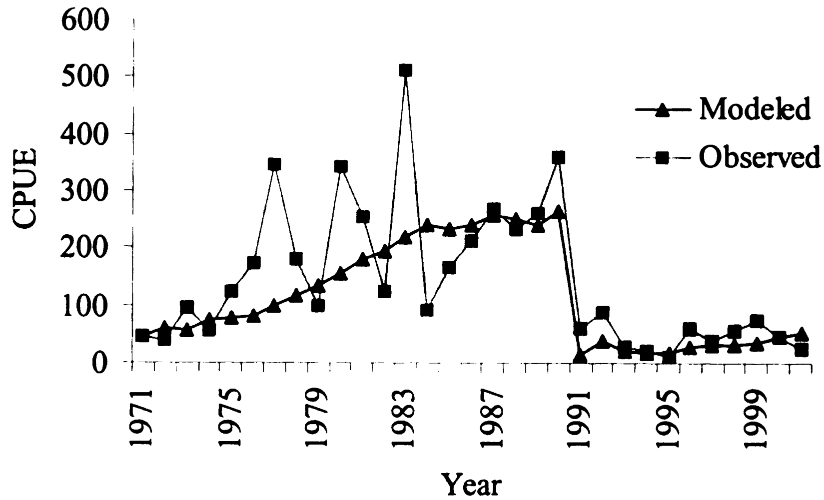


Figure 18. Model 20: Age 1 compensatory survival, based on observed density, with a 5-year time delay and a perturbation.

Model 21 – Model 22: Compensatory growth of age 1 yellow perch, as it impacts future fecundity.

Compensatory growth models based on "modeled" yellow perch abundance provided the best fit (i.e. lowest RSS) to the observed data for these models; therefore, only model-based formulations are presented. The model of compensatory growth of age 1 yellow perch (Model 21) did not match the observed data well (Figure 19A). According to RSS, the fit was not good, either (Table 3). When a perturbation (additional parameter) was added to Model 21, this new model (Model 22) had a better match to the observed data (Figure 19B). The model now had a steeper incline in abundance over the first two decades. According to RSS, the perturbation also greatly improved the fit of the age 1 growth model and this model also fit the observed data better than age 0 growth models (Table 3).

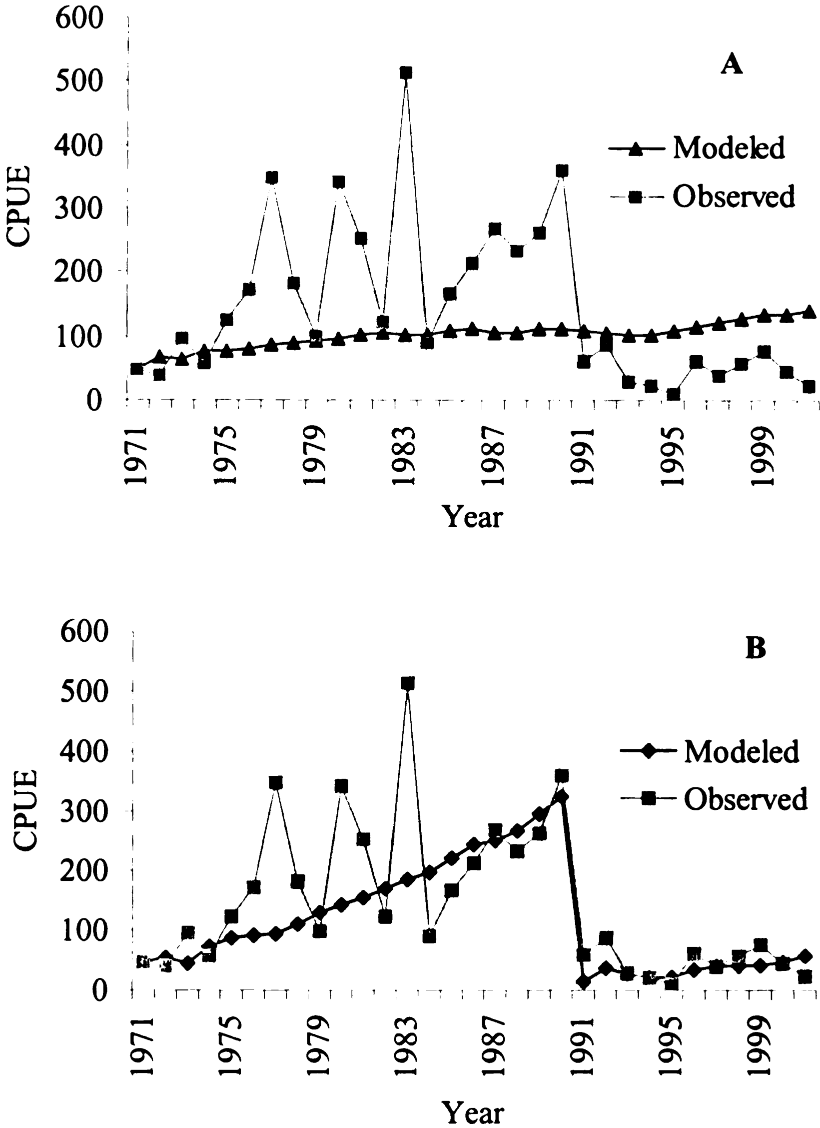


Figure 19. Model 21: Age 1 compensatory growth based on modeled density (A) and Model 22: Age 1 compensatory growth based on modeled density with a perturbation (B).

Model 23: Compensatory survival and growth of age 1 yellow perch.

When I combined the best-fitting model for compensatory survival of age 1 yellow perch (Model 15) with the best-fitting model for compensatory growth of age 1 yellow perch impacting fecundity (Model 22) this combined model (Model 23) matched the observed data slightly better, and had a lower RSS than each individual model (Figure 20; Table 3). The combined model was almost identical to Model 22 (Figure 19B), except that its modeled abundance had a slightly better fit to the observed points due to the added effects of compensatory growth.

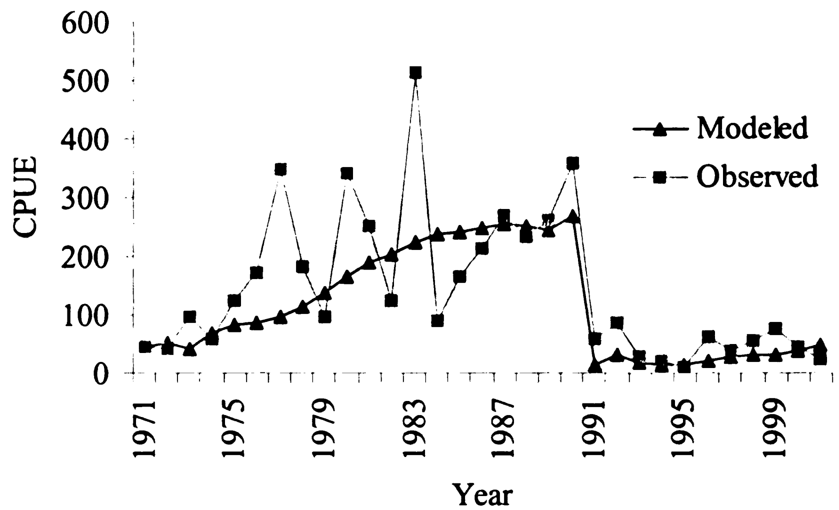


Figure 20. Model 23: Age 1 compensatory survival, with a 5-year time delay, combined with compensatory growth and a perturbation.

Model 24: Depensatory survival of age 1 yellow perch with a perturbation.

When depensation occurred at age 1 (Model 24), the model did not match the observed data well (Figure 21). According to RSS, it also did not provide a good fit (Table 3). As with the age 0 depensatory survival model (Model 12), this model was also not able to simulate the drop in density that occurred in 1991; therefore a perturbation was necessary.

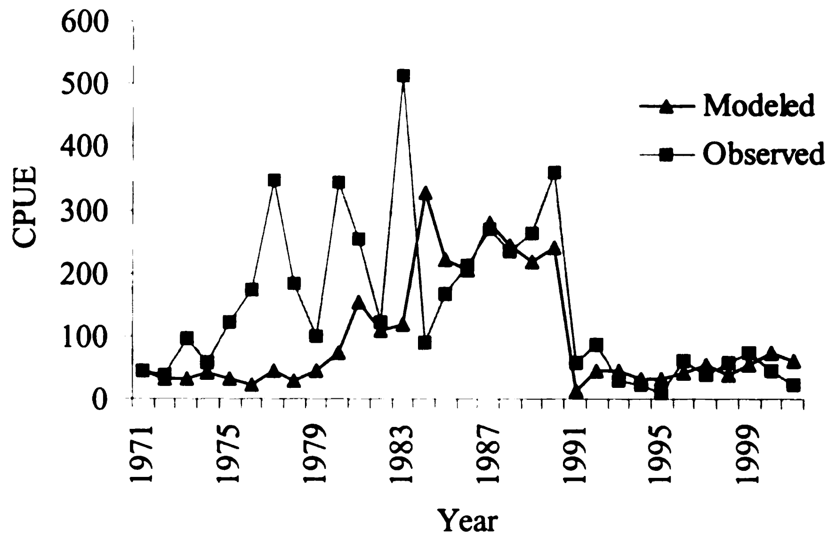


Figure 21. Model 24: Depensatory survival at age 1 with a perturbation.

Age 2-4 hypotheses

Model 25 and 26: Compensatory survival of benthivorous (age 2-4) yellow perch

In these models, age 2-4 survival rates were based on the summed density of age 2-4 yellow perch in the current year. These models had three parameters. Two of the parameters were the intercept and slope of the linear relationship that described the relationship between survival rate and the summed density of age 2-4 yellow perch). The third parameter was the perturbation, which was added to all remaining models because it consistently improved the fit of all previous models. When age 2-4 compensatory survival models were optimized, they produced unrealistic survival rates for older yellow perch. If age 0 survival was fixed at a value of 0.00008, the model provided realistic survival rates of age 2-4 yellow perch; therefore, age 0 survival rate was not freely estimated in these models. Age 2-4 compensatory survival models also fit best (lowest RSS) when compensatory survival rates were based on modeled densities, rather than observed densities; therefore, only modeled densities are presented.

This model (Model 25) provided a relatively good match to the observed data (Figure 22A), and, according to RSS, a fairly good fit (Table 3). Survival rates of age 2-4 yellow perch in this model were quite high (Range = 0.504 – 0.902; mean = 0.705) as compared to estimates made from the observed data (Table 3). In addition, abundance increased in the 1991s much more quickly than what was observed. Nonetheless, the rates varied over time in a way that was consistent with the hypothesis that survival rates were lowest in the 1980s when yellow perch abundance was high. There was no benefit to adding a time delay to this model (Model 26; Figure 22B); however, the model still had a reasonable match and fit to the observed data (Table 3).

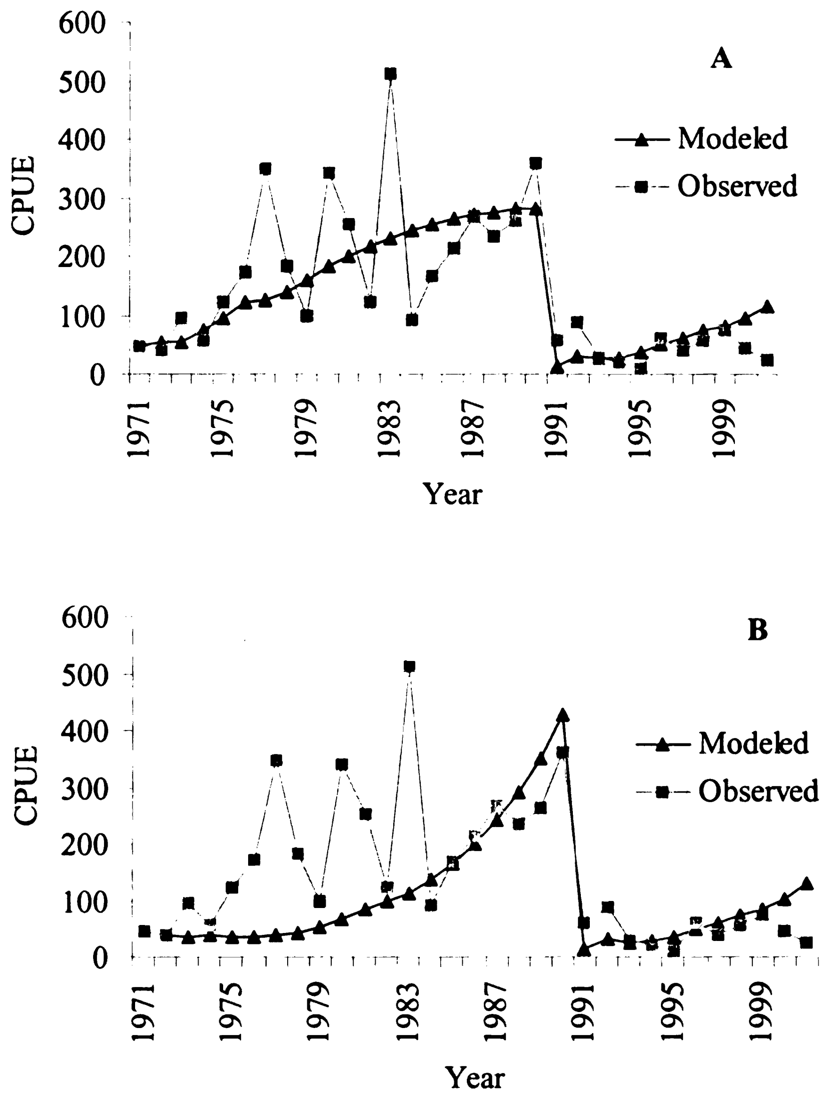


Figure 22. Model 25: Age 2-4 compensatory survival based on modeled density with a perturbation (A) and Model 26: Age 2-4 compensatory survival based on modeled density with a perturbation and 5 year time delay (B).

Model 27: Compensatory growth of age 2-4 yellow perch, as it impacts fecundity

This model was based on observed abundance and included the perturbation. Visually, this model (Figure 23) did not match the data better than previous compensatory growth models that included a perturbation (Model 8 and Model 22), nor did the RSS differ greatly (Table 3). Of all the growth models, compensatory growth of age 1 yellow perch, as it impacts fecundity (Model 22), had the lowest RSS (Table 3). This age 2-4 growth model fit similarly as the age 1 compensatory growth model (Model 22), except that it fit a lower peak in 1991, and tended to increase at the end of the 1990s, like the age 2-4 compensatory survival model.

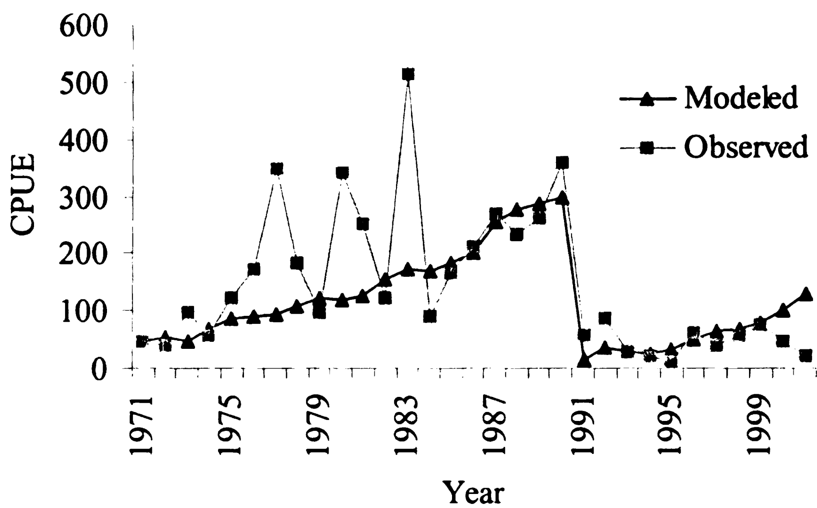


Figure 23. Model 27: Age 2-4 compensatory growth based on observed density, with a perturbation.

Model 28. Age 2-4 compensatory survival and growth

I combined the model of compensatory survival of age 2-4 yellow perch with the lowest RSS (Model 25) with the model of compensatory growth of age 2-4 yellow perch impacting fecundity with the lowest RSS (Model 27), increasing the number of parameters to 9. This combined model (Model 28; Figure 24) did not match the observed data better than the individual models. In contrast to previous survival and growth combination models (Model 11 and Model 23), an age 2-4 combination did not lower the RSS because it could not model the variability in the observed data as well as the other combined models.

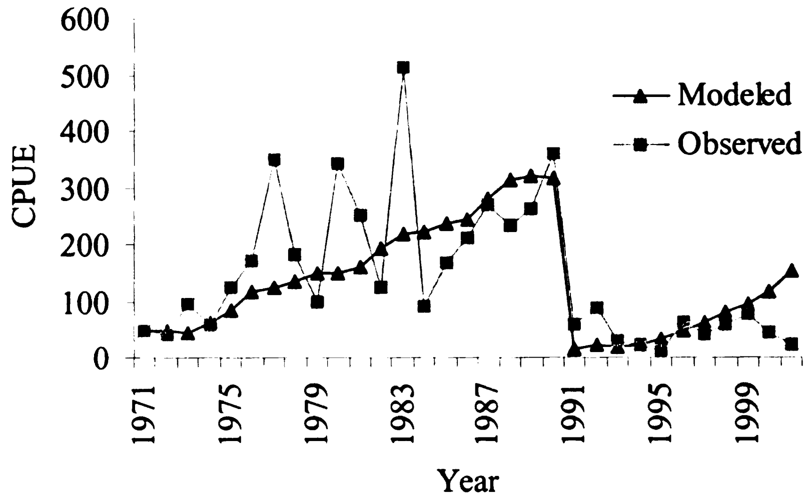


Figure 24. Model 28: Age 2-4 compensatory growth and survival with a perturbation.

A multi-age hypothesis

Model 29: Compensatory survival of two age groups

Of all the compensatory survival models, Model 15 (age 1) and Model 24 (age 2-4) had the lowest RSS. A combination of these two models (Model 28) simulating compensatory survival at more than one age group increased the number of parameters but did not show an improved match with the observed data (Figure 25), and did not lower RSS (Table 3). In fact, Model 24 fit similarly as Model 15, suggesting the constraints on Model 15 overrode any impacts from another model. Multi-age models were not applied to compensatory growth models because the number of constraints became too high, and a solution could not be found.

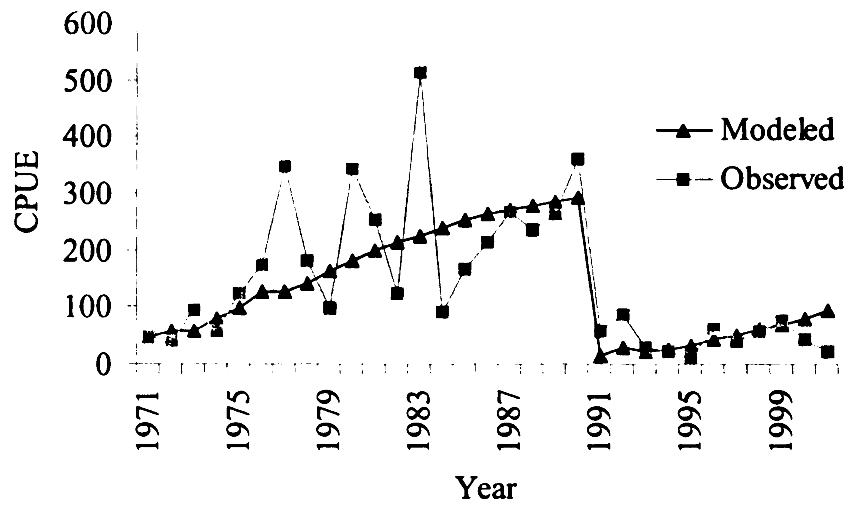


Figure 25. Model 29: Age 1 compensatory survival with a 5-year time delay combined with age 2-4 compensatory survival and a perturbation.

Hypothesis ranking

Table 3 presents several measures used in the process of selecting and ranking models. These measures include (1) a likelihood "component" of the Akaike equation, (2) the likelihood component with the parameter penalization (complete Akaike equation), and (3) a correction for small sample size (corrected Akaike). The likelihood component values tracked the information provided by the residual summed squares, with lower RSS being associated with lower likelihood values, indicating a more likely model. The likelihood values were penalized for parameter number by increasing their value within the Akaike equation, and further penalized because there was a small sample size relative to parameter number, resulting in the corrected Akaike equation. Once the models were ranked, they were compared to the best model and weighted accordingly.

The ten best models, based on Akaike rank are listed in Table 4, alongside the ten best models based on RSS criterion. Some of the models were listed in both tables, thus signifying the strength of their RSS value in combination with a low parameter number.

According to RSS criteria, the best-fitting models were those that best account for the variability in the observed data, and therefore "visually" fit the observed data the best. The best-fitting model was Model 3, where age 0 survival rate is freely fit for each and every year, and a perturbation was included.

According to the Akaike criteria, the best models had a low RSS relative to the amount of parameters. Models that ranked well, according to RSS, often were not included in this list because the RSS was not low enough to compensate for the high parameter number (e.g., Model 3). The models in this list were considered to be the most likely models and were, therefore, explored more thoroughly.

Models that manipulated age 0 and age 1 survival rates dominated the top ten models, with the exception of the second best model, which involved compensatory survival of age 2-4 yellow perch. All involved constant or compensatory survival rates. None of them involved compensatory growth rates (as they impact fecundity), and most involved a perturbation. The best model was not necessarily the dominant model (i.e. its weight value was not 80-99%). In fact, the top models all have relatively high weights, yet they model the observed data differently, as discussed below.

(A)

AICc Rank	Model No.	Model Description	P[1]	RSS	Like Comp[3]	AICc[4]	Akaike weights
1	4*	Constant age 0 surv[5] + pert[6]	1	207604	379.55	383.97	0.388
2	25*	Age 2-4 comp[7] surv (mod[8]) + pert	2	196549	377.85	384.74	0.265
3	8*	Age 0 comp surv (obs[9]) + pert	2	204770	379.12	386.01	0.140
4	20*	Age 1 comp surv (obs), 5 yr delay + pert	2	196596	377.86	387.39	0.070
5	19	Age 1 comp surv (obs), 7 yr delay	3	226446	382.24	389.13	0.030
6	18	Age 1 comp surv (obs), 5 yr delay	3	226459	382.24	389.13	0.029
7	7	Age 0 comp surv (mod) + pert	3	231190	382.88	389.77	0.021
8	17	Age 1 comp surv (obs), 3 yr delay	3	234884	383.37	390.26	0.017
9	26	Age 2-4 comp surv (mod), 5 yr delay + pert	3	242189	384.32	391.21	0.010
10	6	Age 0 comp surv (obs)	3	271632	387.88	392.31	0.006

(B)

RSS rank	Model No.	Model Description	P	RSS	
1	3	Variable age 0 surv + pert	30	105411	Not Applicable
2	2	Variable age 0 surv	30	124881	
3	29	Age 1 (mod/5 yr delay) + age 2-4 (mod) comp surv + pert	6	194997	
4	23	Age 1 surv (mod), 5 yr delay + age 1 growth (obs) + pert	10	195688	
5	25*	Age 2-4 comp surv (mod), + pert	2	196549	
6	20*	Age 1 comp surv (obs), 5 yr delay	3	196596	
7	11	Age 0 surv (obs) + age 0 growth (mod) + pert	10	197127	
8	8*	Age 0 comp surv (obs) + pert	2	204770	
9	4*	Constant age 0 surv + pert	1	207604	
10	28	Age 2-4 surv (mod) + age 2-4 growth (obs) + pert	9	210058	

[1]parameter number, [2]residual sum of squares, [3]likelihood component of AICc, [4]corrected Akaike Information Criteria, [5]survival, [6]perturbation, [7]compensatory, [8]using modeled density, [9]using observed density.
*Model present in both (A) and (B).

Table 4. The ten best models based on AICc criteria (A) and residual sum of squares (B).

The top-ranking model was one of the simplest, containing all constant survival and growth rates, including age 0 survival, but with the added perturbation in 1991. The model that ranked second was a model of compensatory survival rate of age 2-4 yellow perch, based on modeled abundance, and with a perturbation in 1991. The third model included compensatory survival rates of age 0 yellow perch, based on observed abundances, with a perturbation in 1991. This model (and most of the age 0 compensatory survival rate models) did not differ much from the constant model because modeled survival rates varied little over time. The fourth best model included compensatory survival rate of age 1 yellow perch, based on observed abundances, with a five-year time delay, and a perturbation in 1991. All of the best models exhibited an increase in total abundance up until the perturbation, and a very slow increase in abundance following the perturbation, with the exception of the second best model, in which abundance increased more rapidly in the 1991s. The first (Model 4) and the third (Model 8) best models were similar to each other: both exhibited a steady exponential increase in total abundance until the perturbation. Without the perturbation, total abundance increases exponentially without a clear carrying capacity. In contrast, the second (Model 25) and third (Model 20) best models exhibited a logistic increase in abundance, suggesting the population is regulated by a more apparent carrying capacity. These model pairs also showed some similarities to each other when changes in abundance were examined age-specifically (Figure 26 and 27). Qualitatively speaking, it was difficult to determine which model(s) matched age 1 and age 2 the best; however, all of the models matched the overall change in CPUE at age 1, and none of them could match the decreasing abundance of age 2 prior to the perturbation in 1991 (Figure 26).

Model 25 appears to match the overall trend in CPUE at age 3 and at age 4 the better than the other models (Figure 27). Overall, Model 25 matched age-specific changes in abundance the best, although the differences among models were not dramatic.

Auxiliary data

Compensatory survival rate

The ten best models involved either a constant survival rate (Model 4), or compensatory survival rate (remaining top 9 models). Observed data were used to provide additional evidence that survival rates were compensatory. Female instantaneous mortality rates for age 0-4 yellow perch were compared to corresponding CPUE. Gear selectivity influenced the values of the instantaneous mortality rates; therefore they are considered to be "relative", and were some times negative in value (Figure 28 and Figure 29).

There was a significant relationship between instantaneous mortality rate from age 1 to age 2, and age 1 density (Figures 28A); but none for age 2 to age 3 (Figure 28B). Mortality rate from age 3 to age 4 was not significantly related to density (Figure 29A); but there was some indication of a relationship between mortality rate from age 4 to 5 and density (Figure 29B). These results provide additional support for the fourth best model (Model 20) and the second best model (Model 25).

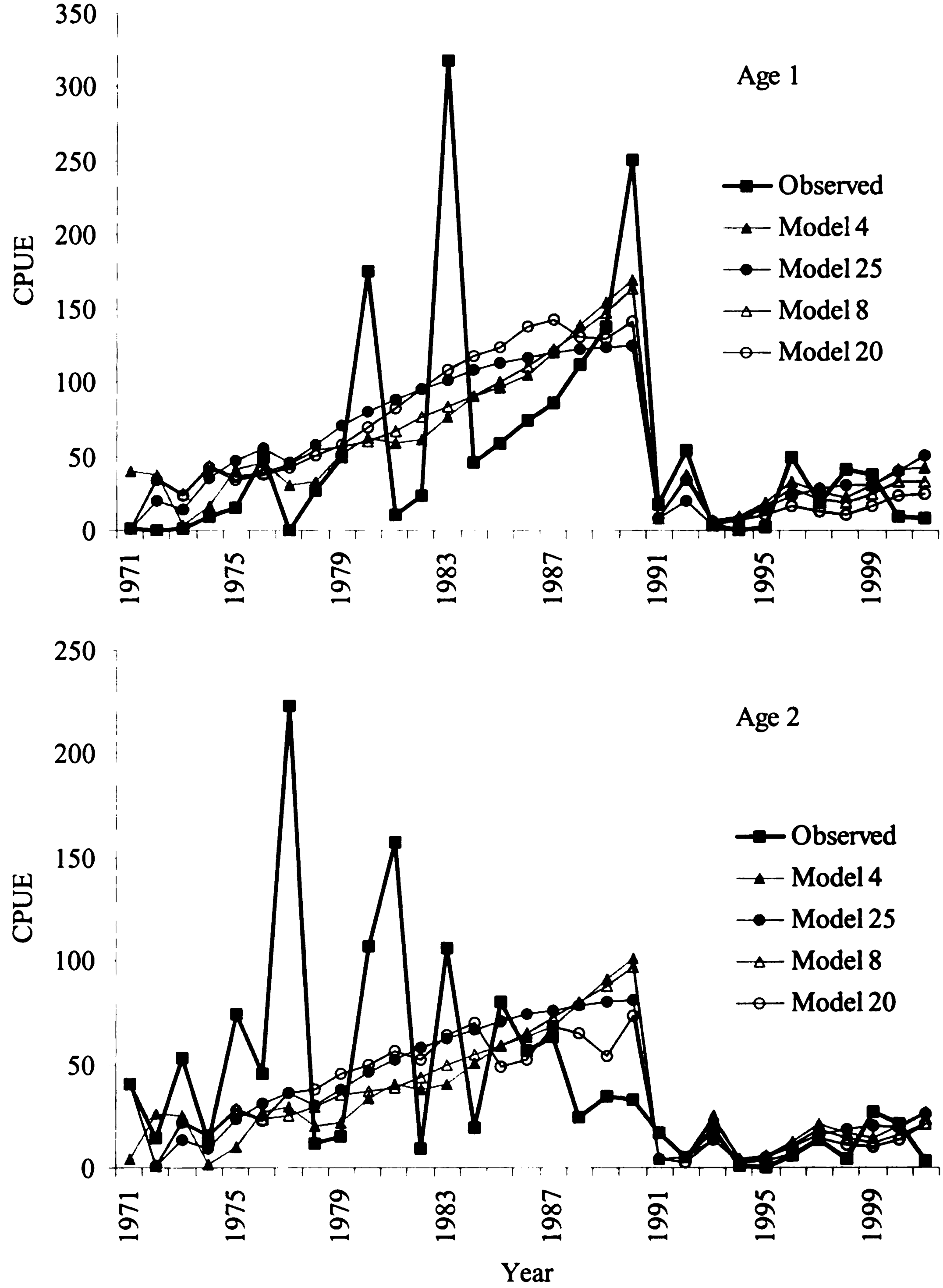


Figure 26. Age 1 and age 2 CPUE from top four models.

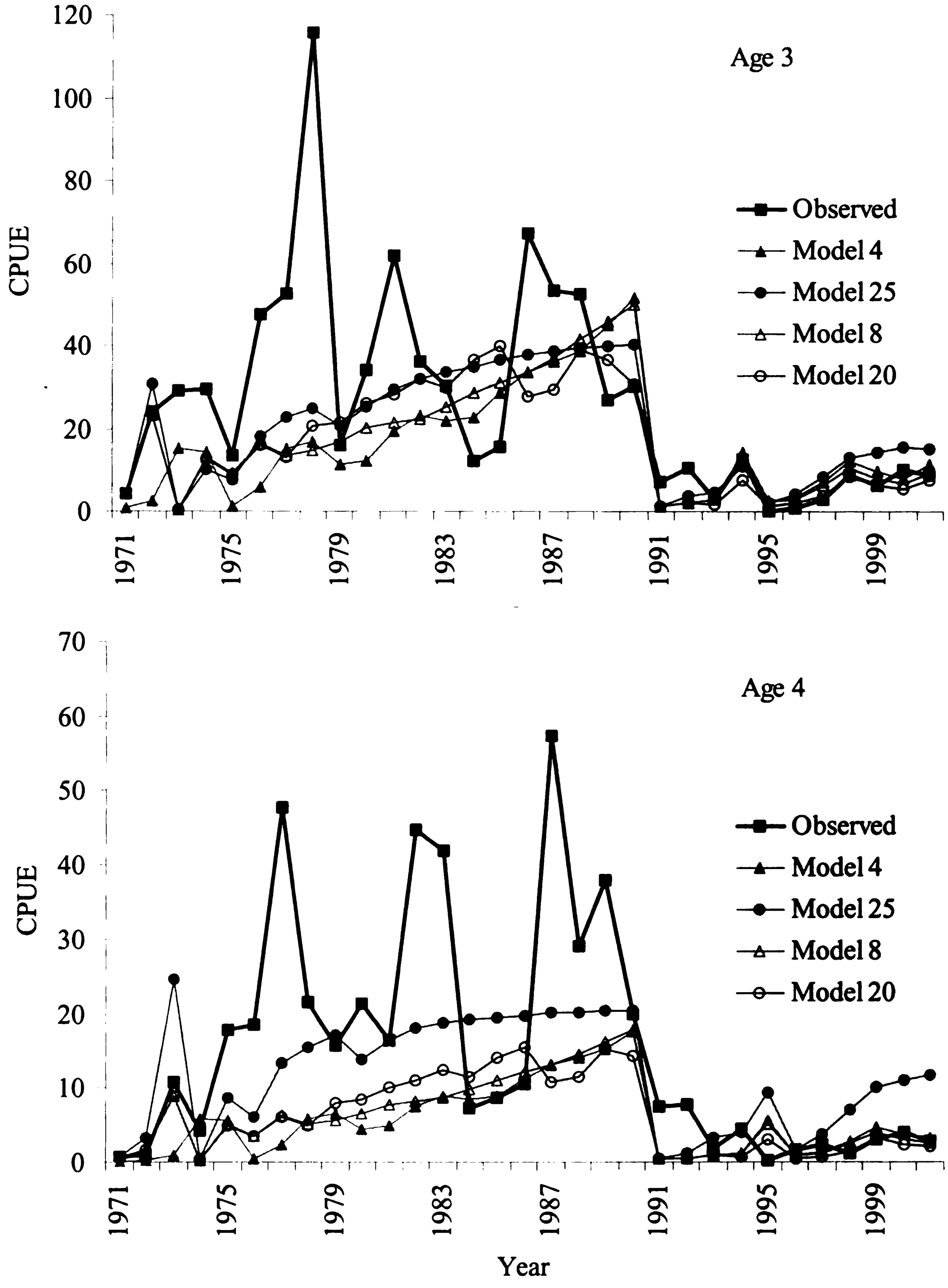


Figure 27. Age 2 and 3 CPUE from top four models.

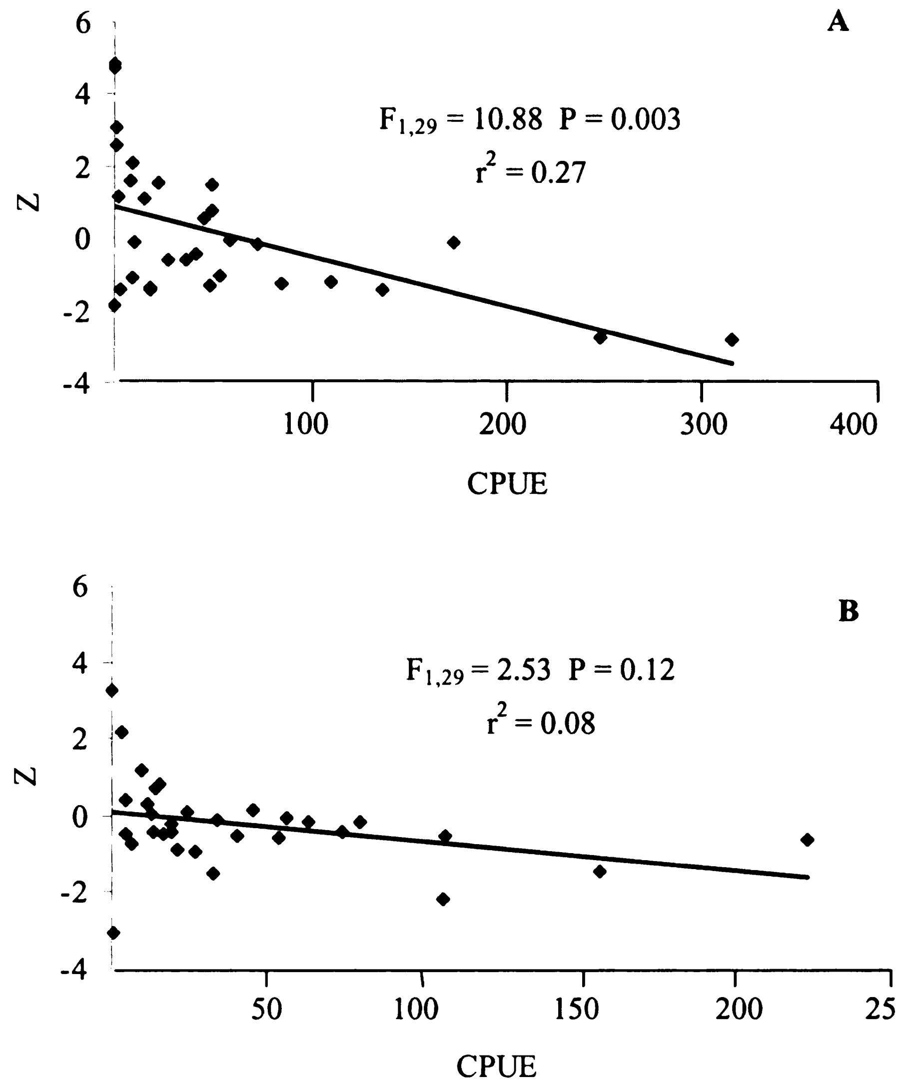


Figure 28. Relative instantaneous mortality rate (Z) versus CPUE of age 1 (A) and age 2 (B) female yellow perch from the observed data. Age 1 CPUE = both sexes * 0.5.

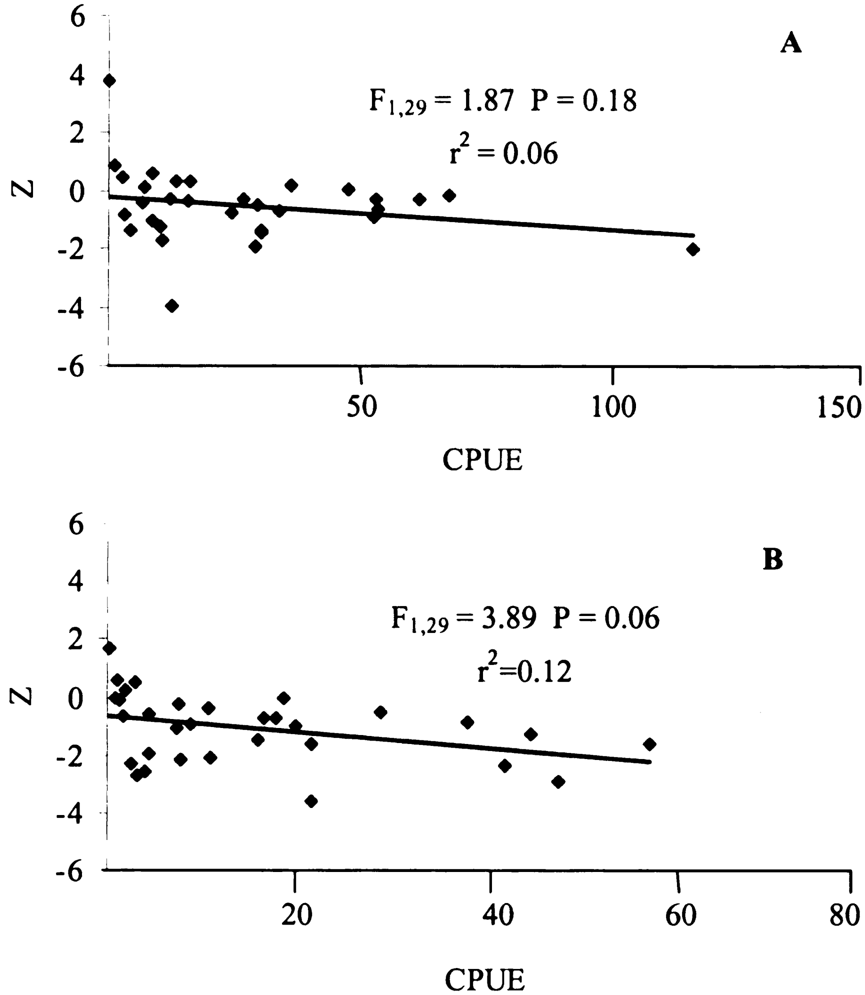


Figure 29. Relative instantaneous mortality rate (Z) versus CPUE of age 3 (A) and age 4 (B) female yellow perch from observed data.

Compensatory growth

Decadal changes in female growth increments over the entire 20th century (Figure 30) suggest compensatory growth may have occurred in age 1-3 yellow perch. Growth increments exhibited a cyclic pattern that may be indicative of compensatory growth if changes were related to fish density. Abundance data were not comparable for these time periods because fish were collected with different gear; however, studies suggest abundance was relatively higher in 1943-51 (El-zarka 1959), 1968-70 (Eschenroder 1977), and the 1980s, as shown in this study. For older yellow perch (age 4-6), growth increments did not exhibit any cyclic pattern, but decreased at a continuous rate.

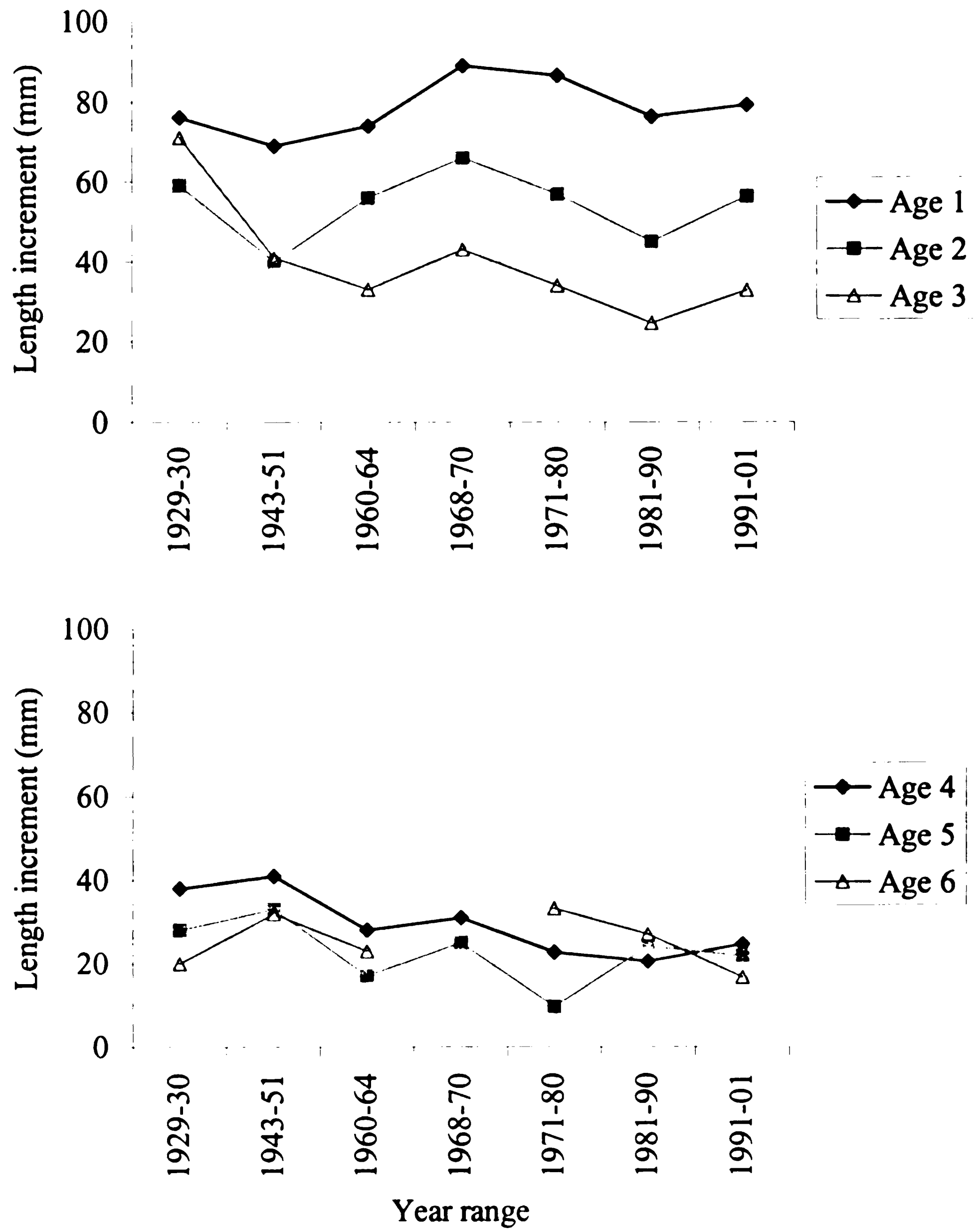
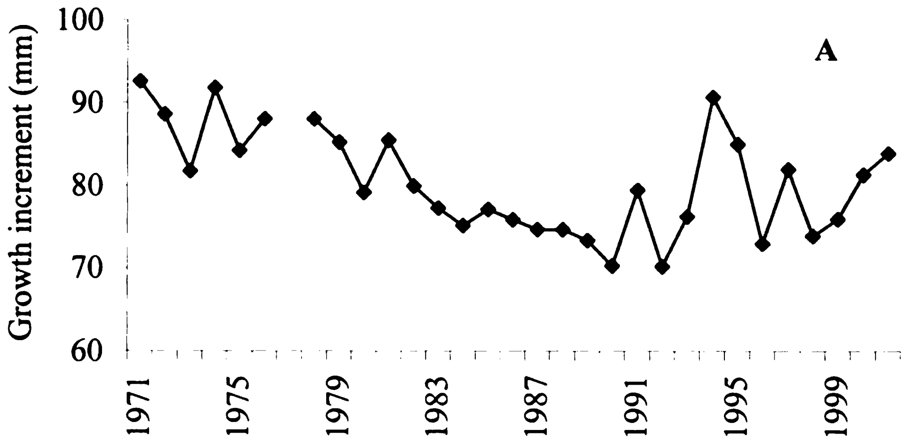


Figure 30. Decadal changes in length increments of age 1-6 yellow perch in Saginaw Bay.

Within the last thirty years, observed annual changes in growth increments of age 0 to age 1, and age 1 to age 2, female yellow perch (Figure 31A and B) suggest growth was lower in the 1980s relative to the surrounding years, which is consistent with changes in CPUE (Figure 2), suggesting a compensatory growth effect on young yellow perch. Older female yellow perch (age 2-3), however, exhibited a pattern of slowly increasing growth over the last thirty years (Figure 32A and B), while growth from age 4-5 decreased recently (Figure 32C). Both of these observations are not consistent with changes in CPUE (Figure 2). Yellow perch growth from age 2-4, on average, appears to have been exceptionally poor within the last thirty years, as evidenced by the very small growth increments in Figure 32A and 32B. In fact, length increments from age 4-5 are actually greater than increments from age 2-4, when it should be less.

When female growth increments from observed data were compared to corresponding CPUE, there was very little indication that density dependent growth occurs (Figures 33 and 34). The lack of significant relationships in the observed data for older yellow perch provides support for the growth models, which were not effective at modeling yellow perch abundance. There is some evidence; however, that young yellow perch (age 0-2) do experience compensatory growth, as seen in the temporal trends in growth increments for recent years, and the temporal trends in mean lengths over the entire 20th century. This may have had a greater impact on survival rate, rather than fecundity, since compensatory growth models in this study did not explain observed CPUE.



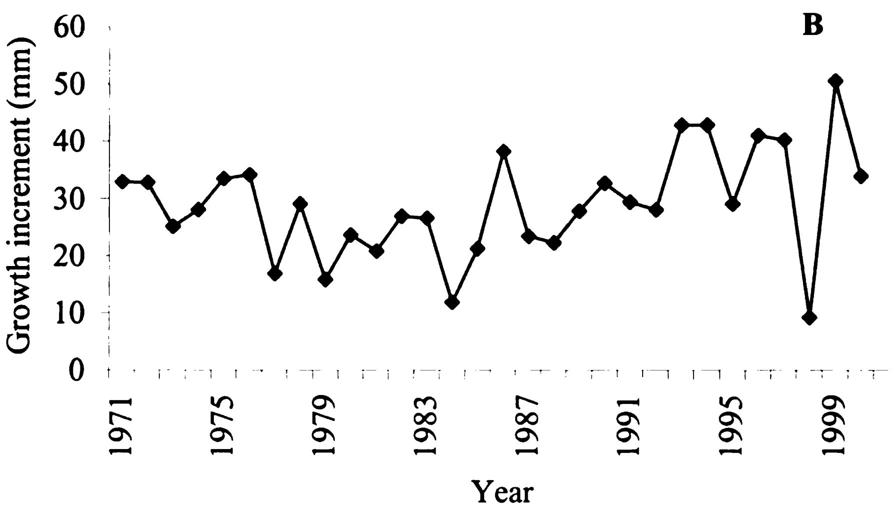


Figure 31. Annual changes in growth increment of female yellow perch, age 0 to age 1 (A) and age 1 to age 2 (B).

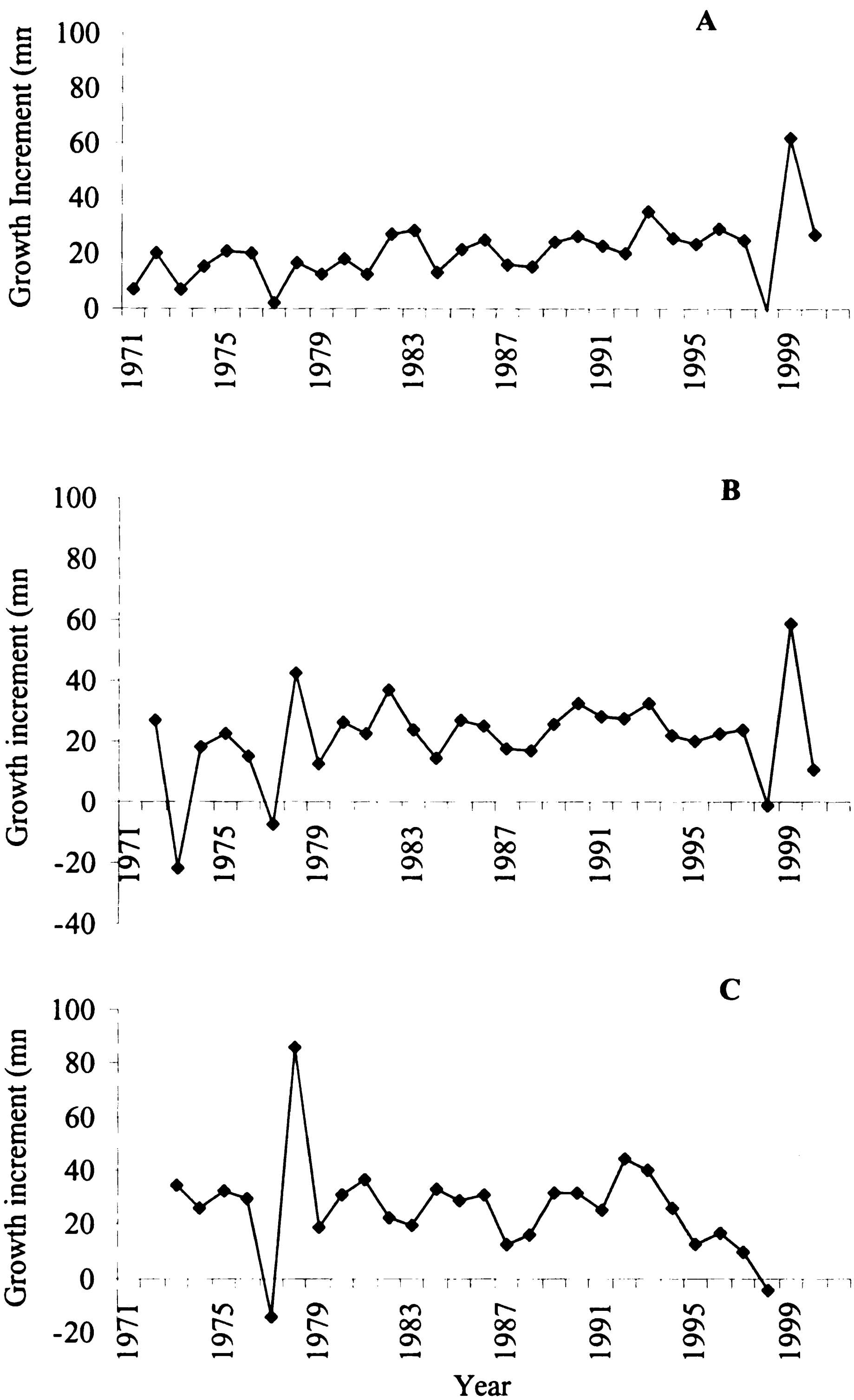
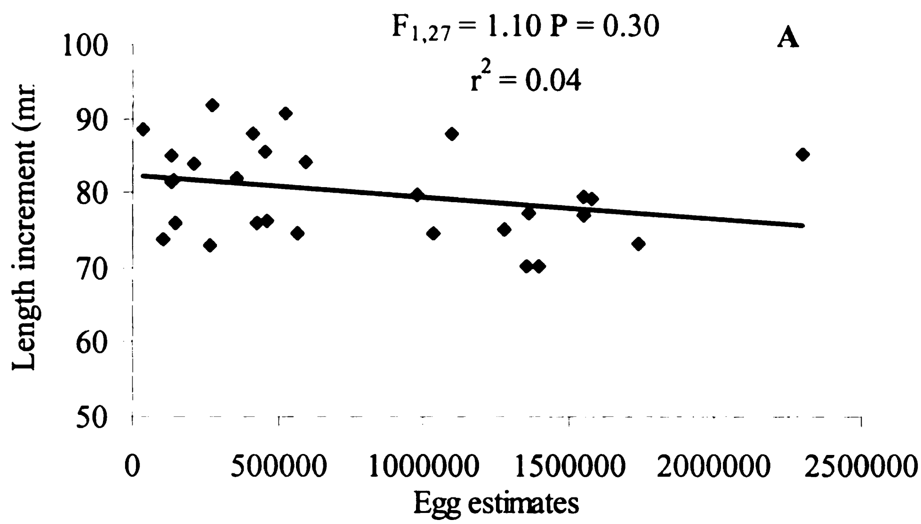


Figure 32. Annual changes in growth increment of female yellow perch, age 2 to age 3 (A), age 3 to age 4 (B), and age 4 to 5 (C).



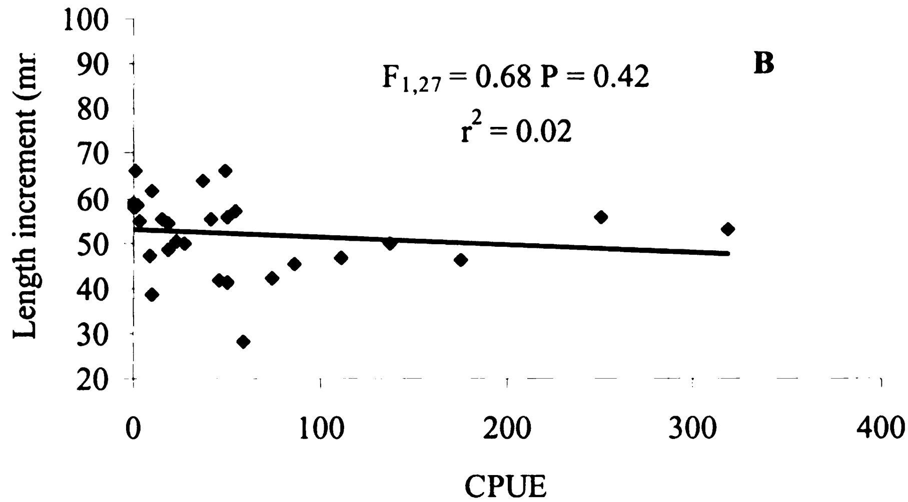


Figure 33. Observed female length increments from age 0 to age 1 (A) and age 1 to age 2 (B) versus egg estimates (A) and observed female CPUE (B).

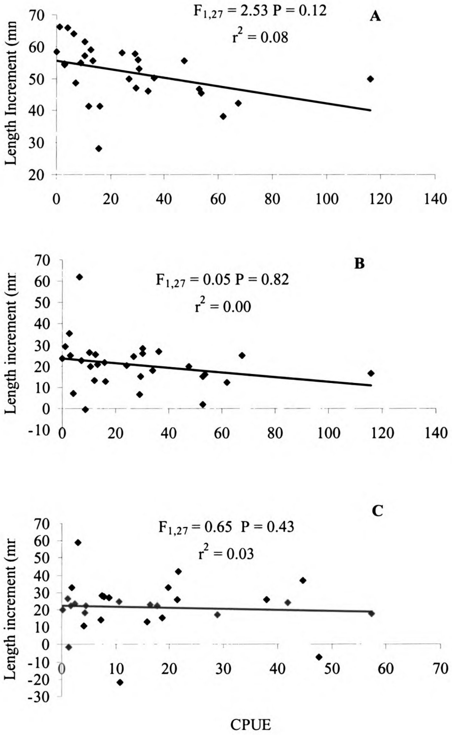


Figure 34. Observed female length increments from age 2 to age 3 (A), age 3 to age 4 (B), and age 4 to age 5 (C) versus observed female CPUE.

DISCUSSION

The goal of this study was to determine how density independent and density dependent processes determine the abundance of yellow perch in Inner Saginaw Bay, Lake Huron, so that fisheries managers can (1) explain observed abundance and (2) predict future abundance. My primary objective was to determine the likelihood and relative weights of various density independent and density dependent models that describe how the abundance of yellow perch changed over time. I compiled a dataset of observed abundance and growth of yellow perch, developed population models that represented competing hypotheses, and determined which models most likely accounted for changes in yellow perch abundance.

The top ranking models matched the general pattern that occurred in the observed abundance; however, they did not fit the observed data in a precise way; therefore, it was somewhat difficult to determine the actual strength of the above processes in influencing yellow perch abundance. Density dependent processes have been shown to occur in some fish populations (Elliot 1985, Bromley 1989, Forrester 1995, Ferrari and Taylor 1996 to name a few); however, it is usually very difficult to detect regulation in animal populations because variability, or "noise", in the data obscures these processes (Murdoch 1994, Turchin 1995). Despite historical arguments over the importance of density dependent processes in determining the abundance of animals (Andrewartha and Birch 1954, Nicholson 1954, Milne 1962), fisheries scientists generally agree that they are important and suggest better methods of detection could help clarify their existence (Rose et al. 2001). For this study, the importance of density independent and density dependent processes was determined by evaluating (1) many models of separate processes at various ages and (2) auxiliary data. The models in this study were evaluated based on (1) their ability to visually match the observed data, (2) the residual summed squared value, (3) the corrected AIC rank, and (4) the weighted ranks. All of these methods identified models that best explain the variation in the observed data, but corrected AIC ranking can be viewed as the best method to account for the trade-off between model fit (likelihood) and the number of fitted parameters (Franklin et al. 2001). The top-ranking models listed in Table 4(A) were selected based on the corrected AIC ranking. If models were selected based on RSS, which does not account for parameter number, one would have assumed the annual free-fitting age 0 survival rate model (Model 2) was the "best" model. This model fit the data well only because it contained multiple free-fitting parameters. If this model had an exceptional fit to the observed data (i.e. very low RSS), its likelihood value would have been strong enough to withstand parameter penalization; however, this was not the case. The modeling process used in this study showed that yellow perch abundance in Inner Saginaw Bay may be weakly regulated with compensatory survival; however, it did not separate the relative importance of density independent and density dependent processes because these twp types of models often fit the data in a similar fashion (i.e., Model 4 and Model 8).

Based on the top-ranking models in this study, some of the dominant processes that determine the abundance of yellow perch in Inner Saginaw Bay include: (1) compensatory survival of age 2-4 yellow perch, (2) compensatory survival of age 0 yellow perch, and (3) compensatory survival of age 1 yellow perch. These are the processes that appear to be important based on how well these models fit the observed data, and the model selection process used in this study. Compensatory growth (as it impacts fecundity) and depensation do not appear to be as important in determining yellow perch abundance in Inner Saginaw Bay.

Despite the above results, the top-ranking model was a model in which all growth and survival rates remained constant (Model 4). It had the highest weight of all of the models; however, its weight (0.388) was not overwhelmingly higher than the other top-ranking models, suggesting other processes are also important. Model 4 simulated changes in yellow perch density with constant rates, including a constant age 0 survival rate. At first, a constant age 0 survival rate does not appear to be biologically realistic because fish populations, in general, often have highly variable age 0 survival rates (Hilborn and Walters 1992). The average of these variable rates over time, however, results in a population that either decreases or increases; therefore, a constant age 0 survival rate may be adequate in describing the overall changes in population abundance.

Model 25 ranked second, with a weight (0.265) that was not much lower than the top-ranking model. This model suggests the population is regulated by compensatory survival of the benthivorous age group, age 2-4. Model 8 and Model 20 (third and fourth best models) suggest compensatory survival at age 0 (Model 8) and age 1 (Model 20) also play a role in population regulation. It appears, however, that age 0 survival is weakly compensatory because Model 8, which explicitly included compensatory survival, simulated abundance almost identically to Model 4, a model with constant rates. The significant linear relationship between survival rates estimated in the free-fitting model (Model 2), and age 0 density, suggests age 0 survival is weakly compensatory.

Of the top four models, Model 25 visually matches the "age-specific" abundance best, thereby reinforcing its rank among the top models. Auxiliary data suggest compensatory survival may be important within this age group; however, these data best support compensatory survival at age 1. In combination with the results of other studies (Diana and Salz 1991; Haas and Schaeffer 1991; Schaeffer et al. 2000), it seems likely that yellow perch in Inner Saginaw Bay have been regulated to some extent by compensatory survival at age 2-4 over the last 30 years. It is not as clear, however, whether compensatory growth causes compensatory survival during that time.

Compensatory survival is commonly controlled by compensatory growth (Goodyear 1980); however, I could not determine if compensatory growth caused compensatory survival in this study because I could not model density dependent impacts on these rates separately within the same model. The auxiliary data in this study, however, suggest the following. If observed yellow perch growth increments over the last thirty years (Figure 30) are compared to yellow perch CPUE over the last thirty years (Figure 2A), the two are not inversely related. In addition, growth of age 3 and 4 yellow perch has steadily declined over the entire century, and has been very low over the last 30 years (Figure 30), suggesting fish density at these ages has not impacted growth as much as other factors, such as the disappearance of *Hexagenia* sp. in the 1960s (Schaeffer et al. 2000). Historical mean length increments of age 1 and age 2 yellow perch suggest fish size has changed in a cyclic pattern over the whole century (Figure 30); however, it is not known whether these changes in growth were dependent on fish density. It may be that the perturbation in 1991 has played the greatest role in determining the abundance of yellow perch in Inner Saginaw Bay.

During the process of modeling yellow perch abundance in Inner Saginaw Bay, I discovered the necessity of the perturbation in 1991. This sudden change in abundance was observed between fall of 1989 and fall of 1990. This perturbation improved the fit of almost every model, and was present in six of the top ten models. It appeared to be a necessary feature to account for the sudden change in abundance that occurred at this time. Without the perturbation, I could not model this change accurately. The need for this process suggests that mortality events affecting the total abundance of yellow perch occur sporadically. Fisheries managers often target recruitment mechanisms to account for changes in fish abundance because small changes in recruitment can have significant impacts on the abundance of fish (Ricker 1975, Cushing 1981). Yet, the need for a perturbation in these models, in which the survival rate of *all* ages of yellow perch was reduced, suggests that poor recruitment alone could not account for the sudden drop in total abundance that occurred in 1991 in the models. Observed age and year specific CPUE shows that the abundance of all age group dropped dramatically between 1990 and 1991.

A perturbation suggests that a poor recruitment rate throughout the 1990s may not explain poor abundance in the 1990s. Instead, abundance was likely low during this time period because the dramatic reduction in stock size in 1991 made it impossible for the population to rebuild itself for some time. A relatively simple model with a perturbation (e.g. Model 25) can adequately explain the changes in abundance that have occurred for this population, rather than a model with variable recruitment. When recruitment was fit for every year (Model 3), age 0 survival rates were not consistently low in the 1990s (Figure 35). The cause of the perturbation is not known. It has been suggested that yellow perch of all ages may have collapsed their food base by 1991 because they became so abundant in the 1980s (R.C. Haas, personal communication). Other possible mechanisms include disease (Mills and Hurley 1990), winterkill (Cooper and Washburn 1946, Tonn and Paszkowski 1986, Hall and Ehlinger 1989), and rapid temperature fluctuations (Busch et al. 1975). Yellow perch in Lake Michigan exhibited a similar drop in abundance around the same time as yellow perch in Inner Saginaw Bay (Makauskas and Clapp 2000), suggesting a regional density independent event could have caused widespread reductions

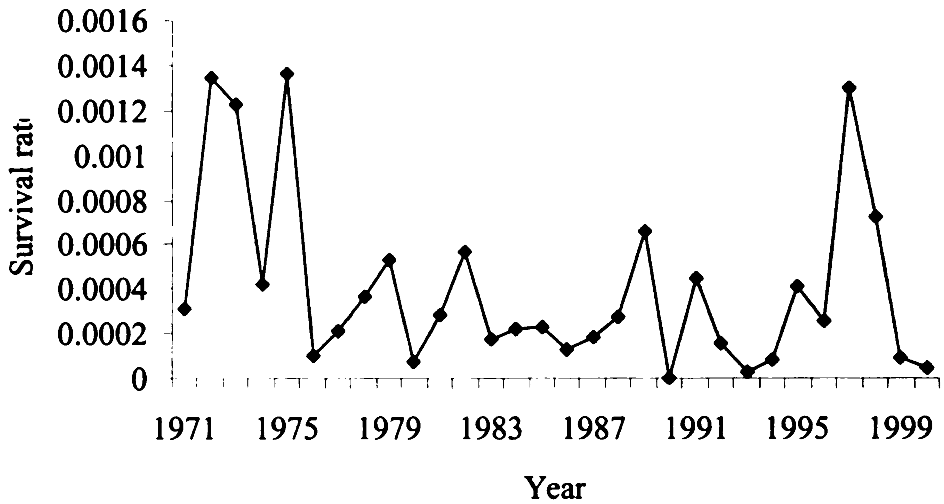


Figure 35. Estimated age 0 survival rates from the free-fitting model with a perturbation (Model 3).

in yellow perch. However, yellow perch populations in Lake St. Clair (Synnestvedt 1996) and in Lake Erie (Tyson and Knight 2001) have flourished in the last decade.

In summary, the results of this study identified the processes that may be important in determining the abundance of yellow perch in Inner Saginaw Bay, Lake

Huron. Compensatory survival at age 2-4 appears to be the dominant regulatory process, although the regulation does not appear to be strong. A reduction in survival across all age groups (perturbation) was needed to match the dramatic drop in abundance that occurred in 1991, suggesting low abundance in the 1990s resulted from a perturbation in 1991, rather than poor recruitment throughout the 1990s. Finally, predictions indicate yellow perch abundance will slowly increase in the future, a recovery that could be hastened if fishing mortality is reduced.

Management Implications

Fisheries managers can target management actions at specific processes and age groups to enhance the population if they know the rates and ages at which regulation occur. The above discussion suggests yellow perch in Inner Saginaw Bay were regulated the most by compensatory survival at age 2-4 in the last thirty years. It is not as clear, however, whether compensatory growth caused compensatory survival during that time, only that growth of this age group has been very poor. Management may be most effective if it were to control the abundance of age 2-4 in a way that produced optimal survival rates. Any management action to improve growth rate, such as habitat improvement, would improve the quality of fish, but may not be a dominant force in determining the abundance of fish.

The models in this study are also beneficial to fisheries scientists as predictive tools. Compensatory impacts can be incorporated into models that predict absolute abundance of yellow perch (e.g. catch-at-age analyses), or they provide relative predictions of future abundance on their own. The best model (constant age survival) and third best model (age 0 compensatory survival) predict future abundance to continuously increase in the near future (Figure 36), yet they do not include an inevitable upper threshold. The second best model (age 2-4 compensatory survival rate) and third best model (age 1 compensatory survival rate) predict a more logistic change in abundance, in which density increases, but eventually levels off at some point (Figure 37).

These predictions are consistent with the different behavior that these model "pairs" exhibit. In Model 2 and Model 8, there is no clear carrying capacity, and the population is reduced by a single event that has a strong impact on survival rate (the perturbation). In contrast, Model 25 and Model 21 exhibit a logistic pattern, suggesting the population was regulated by a more apparent carrying capacity. In these models, the population was self-regulating, was interrupted by a catastrophic event, and continued to self-regulate itself following the perturbation. For yellow perch in Inner Saginaw Bay, both of these behaviors are likely occurring. When managers know the relative contributions that density independent and density dependent processes make to fish abundance, they are able to separate events into those that they can control (density dependent processes), and those that they cannot control (density independent processes). The density dependent models in this study did not show strong relationships between density dependent rates and observed abundance of yellow perch; therefore, managers may not be able to manage for an optimal abundance of yellow perch. Since a perturbation caused a large reduction in abundance of this population, fisheries scientists may wish to collect information that could identify the mechanism(s) that cause a perturbation. Although it is not known whether widespread mortality resulting from a perturbation is more likely to occur when yellow perch abundance is high, increased

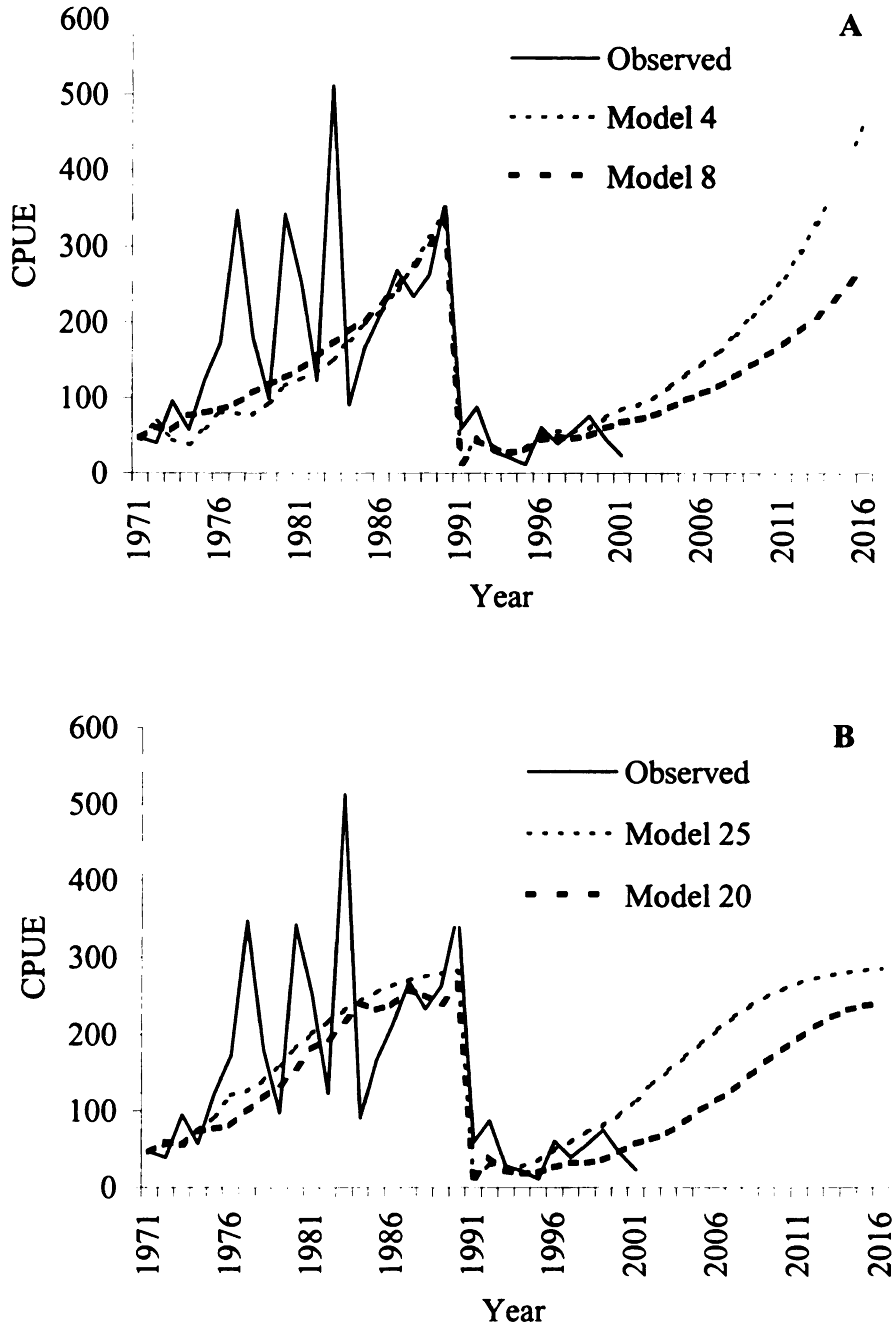


Figure 35. Projected Inner Saginaw Bay yellow perch abundance based on Model 4 (Constant age 0 survival rate with a perturbation) and Model 8 (Age 0 compensatory survival with a perturbation) (A), and Model 25 (Age 2-4 compensatory survival with a perturbation) and Model 20 (Age 1 compensatory survival with a 5 year time delay and a perturbation) (B).

abundance of yellow perch prior to the perturbation in this study suggests this may be a factor. When yellow perch abundance in Inner Saginaw Bay increases to levels similar to the last period of high abundance in the 1980s, fisheries researchers should retain fish for disease evaluation, and collect detailed information on ice cover, temperature changes, and food availability.

An immediate management concern for yellow perch in Inner Saginaw Bay is whether this population has the ability to increase, given that abundance has remained consistently low in the last ten years. The models suggest these fish are capable of better survival at low abundance; however, many of the models show an increased abundance sooner than what was observed in the 1990s. The perturbation in 1991, which affected all age groups, reduced abundance enough that it may take many years for yellow perch to be recruited into the fishery, grow and replenish the stock. If recruitment is consistently poor due to density independent events, this process will be prolonged and it may take some time for the population to rebound. The population may, however, rebound more quickly if birth rates increase and/or survival rates increase. If fishing mortality is reduced, it may be possible for the population to rebound more quickly than if fishing mortality remains at the current level. Managers need to consider a reduction in fishing pressure if they want the population to rebound more quickly.

APPENDICES

Appendix A. List of parameters (and their fitted values) for each model.

Model 1: Constant age 0 surv
1 parameter:
Age 0 survival rate = 0.0003.

Model 2: Variable age 0 surv
30 parameters:

30 age 0 survival rates:

1971	1972	1973	1974	1975	1976	1977	1978
0.0003	0.0006	0.0006	0.0002	0.0007	0.00005	0.0001	0.0002

1979	1980	1981	1982	1983	1984	1985	1986
0.0003	0.00004	0.0001	0.0003	0.0001	0.0001	0.0001	0.0001

1987	1988	1989	1991	1991	1992	1993	1994
0.0001	0.0001	0.0002	0.00002	0.0001	2.8E-06	1.0E-06	7.7E-06

1995	1996	1997	1998	1999	2000
0.0001	0.0001	0.0004	0.0003	0.00004	0.00004

Model 3: Variable age 0 surv + pert
30 parameters:
29 age 0 survival rates:

1971	1972	1973	1974	1975	1976	1977	1978
0.0003	0.0013	0.0012	0.0004	0.0014	0.0001	0.0002	0.0004

1979	1980	1981	1982	1983	1984	1985	1986
0.0005	0.0001	0.0003	0.0006	0.0002	0.0002	0.0002	0.0001

1987	1988	1989	1991	1991	1992	1993	1994
0.0002	0.0003	0.0007	na	0.0004	0.0002	0.00003	0.0001

1995	1996	1997	1998	1999	2000
0.0004	0.0003	0.0013	0.0007	0.0001	0.00005

Perturbation in 1991.

Model 4: Constant age 0 surv + pert
2 parameters:
Age 0 survival = 0.000383.
Perturbation in 1991.

Model 5: Age 0 comp surv (mod)
2 parameters:
Age 0 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.0001 and b = 1.5389

Model 6: Age 0 comp surv (obs)
2 parameters:
Age 0 survival = exp(-Z) = exp(-a-(b*N)) where a = 8.2247 and b = 0.0001

Model 7: Age 0 comp surv (mod) + pert
3 parameters:
Age 0 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.0001 and b = 1.4984
Perturbation in 1991.

Model 8: Age 0 comp surv (obs) + pert
3 parameters:
Age 0 survival = exp(-Z) = exp(-a-(b*N)) where a = 7.954 and b = 0.0001.
Perturbation in 1991.

Model 9: Age 0 comp growth (mod)
4 parameters:
Age 0 length increment = a1 - b1*length = a2/(b2+density) - (b1*length) where a2 = 15000 and b2 = 200 (constraint: a2>=15000 and 40<=b2<=200) and b1 = 0.4 (constraint: 0.4<=b1<=0.1)
Age 1-8 length increment = 75 - b3*length where b3 = 0.4 (constraint: 0.4<=b3<=0.1)
Age 0 survival rate = 0.0003

Model 10: Age 0 comp growth (mod) + pert
5 parameters:
Age 0 length increment = a1 - b1*length = a2/(b2+density) - (b1*length) where a2 = 15000 and b2 = 200 (constraint: a2>=15000 and 40<=b2<=200) and b1 = 0.4 (constraint: 0.4<=b1<=0.1)
Age 1-8 length increment = 75 - b3*length where b3 = 0.2322 (constraint: 0.4<=b3<=0.1)
Perturbation in 1991.

Model 11: Age 0 surv (obs) + age 0 growth (mod) + pert
8 parameters:
Age 0 survival = exp(-Z) = exp(-a-(b*N)) where a = 7.602 and b = 0.002.
Age 0 growth increment = a1 + b1*length = a2/(b2+density) + (b1*length)
where a2 = 15,0000, b2 = 161, and b1 = -0.4
Age 1-8 growth increment = a3 + b3*length where a3 = 75 and b3 = -0.4.
Perturbation in 1991.

Model 12: Depensation at age 0 (obs)
4 parameters:
N(1) = pSexp((S/g*mS/h2+S2) where p = 0.00017, g = 1.54E+12, m = 0, and
h = 141,969.

Model 13: Depensation at age 0 (obs) + pert
5 parameters:
N(1) = pSexp((S/g*mS/h2+S2) where p = 0.00018, g = 1.54E+12, m = 0, and
h = 141,969.

Model 14: Age 1 comp surv (mod)
3 parameters:
Age 0 survival rate = 0.00004
Age 1 survival rate = exp(-a-(b*N)) where a = 0.0001 and b =0.0138

Model 15: Age 1 comp surv (obs)
3 parameters:
Age 0 survival = 0.0004
Age 1 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.2876 and b = 0.0129

Model 16: Age 1 comp surv (mod), 3-yr delay
3 parameters:
Age 0 survival rate = 0.0004
Age 1 survival rate = exp(-a-(b*N)) where a = 0.0001 and b =0.0040

Model 17: Age 1 comp surv (obs), 3-yr delay
3 parameters:
Age 0 survival = 0.0004
Age 1 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.0001 and b = 0.0051

Model 18: Age 1 comp surv (obs), 5-yr delay
3 parameters:
Age 0 survival = 0.0004
Age 1 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.0001 and b = 0.0031

Model 19: Age 1 comp surv (obs), 7-yr delay
3 parameters:
Age 0 survival rate = 0.00004
Age 1 survival rate = exp(-a-(b*N)) where a = 0.0001 and b =0.0022

Model 20: Age 1 comp surv (obs), 5-yr delay + pert
4 parameters:
Age 0 survival = 0.0003
Age 1 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.0001 and b = 0.0015
Perturbation in 1991.

Model 21: Age 1 comp growth (mod)
5 parameters:
Age 1 length increment = a1 - b1*length = a2/(b2+density) - (b1*length) where a2 = 15000 and b2 = 200 (constraint: a2>=15000 and 40<=b2<=200) and b1 = 0.4 (constraint: 0.4<=b1<=0.1)
Age 2-8 length increment = 75 - b3*length where b3 = 0.4 (constraint: 0.4<=b3<=0.1)
Age 0 survival rate = 0.0004

Model 22: Age 1 comp growth (mod) + pert
6 parameters
Age 1 length increment = a1 - b1*length = a2/(b2+density) - (b1*length) where a2 = 15000 and b2 = 200 (constraint: a2>=15000 and 40<=b2<=200) and b1 = 0.4 (constraint: 0.4<=b1<=0.1)
Age 2-8 length increment = 75 - b3*length where b3 = 0.1765 (constraint: 0.4<=b3<=0.1)
Age 0 survival rate = 0.0003
Perturbation in 1991.

Model 23: Age 1 surv (mod), 5-yr delay + age 1 growth (obs) + pert
8 parameters:
Age 1 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.00001 and b = 0.0014
Age 1 length increment = a1 - b1*length = a2/(b2+density) - (b1*length) where a2 = 15000 and b2 = 200 (constraint: a2>=15000 and 40<=b2<=200) and b1 = 0.4 (constraint: 0.4<=b1<=0.1)
Age 2-8 length increment = 75 - b3*length where b3 = 0.1607 (constraint: 0.4<=b3<=0.1)
Age 0 survival rate = 0.0003
Perturbation in 1991.

Model 24: Depensation at age 1 (obs) + pert
6 parameters:
Age 0 survival = 0.0003
N(1) = pSexp((S/g*mS/h2+S2) where p = 0.6093, g = 1.29E+12, m = 0, and h = 137,418
Perturbation in 1991.

Model 25: Age 2-4 comp surv (mod) + pert
Age 0 survival fixed at 0.00008
3 parameters:
Age 2-4 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.0785 and b = 0.0043
Perturbation in 1991.

Model 26: Age 2-4 comp surv (mod), 5 yr delay + pert
Age 0 survival fixed at 0.00008
3 parameters:
Age 2-4 survival = exp(-Z) = exp(-a-(b*N)) where a = 0.1231 and b = 0.0001
Perturbation in 1991.

Model 27: Age 2-4 comp growth (obs) + pert
6 parameters:
Age 2-4 length increment = a1 - b1*length = a2/(b2+density) - (b1*length) where a2 = 15000 and b2 = 200 (constraint: a2>=15000 and 40<=b2<=200) and b1 = 0.1 (constraint: 0.4<=b1<=0.1)
Age 5-8 length increment = 75 - b3*length where b3 = 0.2528 (constraint: 0.4<=b3<=0.1)
Age 0 survival rate = 0.0003
Perturbation in 1991.

Model 28: Age 2-4 surv (mod) + age 2-4 growth (obs) + pert
8 parameters:
Age 2-4 survival = $\exp(-Z) = \exp(-a-(b*N))$ where a = 0.1182 and b = 0.0025
Age 2-4 length increment = $a1 - b1*\text{length} = a2/(b2+\text{density}) - (b1*\text{length})$ where $a2 = 15000$ and $b2 = 200$ (constraint: $a2>=15000$ and $40<=b2<=200$) and $b1 = 0.1$ (constraint: $0.4<=b1<=0.1$)
Age 5 to 8 length increment = $75 - b3*\text{length}$ where $b3 = 0.1$ (constraint: $0.4<=b3<=0.1$)
Age 0 survival = 0.0001
Perturbation in 1991

Model 29: Age 1 (mod/5-yr delay) and age 2-4 (mod) comp surv + pert
6 parameters:
Age 0 survival rate = 0.0002.
Age 1 survival rate = $\exp(-Z) = \exp(-a-(b*N))$ where a = 7.954 and b = 0.0001.
Age 2-4 survival rate = $\exp(-Z) = \exp(-a-(b*N))$ where a = 0.0783 and b = 0.0036.
Perturbation in 1991.

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