



# Relation between mortality of young walleye (*Stizostedion vitreum*) and recruitment with different forms of compensation\*

A. L. Jensen

School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48109–1115, USA

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The relation between mortality of young fish and recruitment is important for assessment of the environmental effects of facilities that kill large numbers of young fish, such as electric power stations and hydropower plants. A simulation model with a bioenergetic growth component was applied to examine the relation between mortality of young and recruitment for walleye (*Stizostedion vitreum*) with different forms of population regulation, including: food limited growth, food limited growth with size-dependent mortality, and food limited growth with age at maturity dependent on size. With food limited growth small increases in mortality of young reduced recruitment considerably, but the population slowly approached a new equilibrium. If mortality of young increased when growth was food limited, the population approached a new equilibrium of natality and mortality because with fewer individuals there was more food per individual, and individuals were larger in size and produced more eggs; this feedback adjusted natality to equal mortality. With either mortality or age at maturity dependent on size, large increases in mortality of young resulted in only small decreases in recruitment.

## INTRODUCTION

The relation between mortality of young fish and recruitment is important for assessment of the environmental effects of facilities that kill large numbers of young fish, such as electric power stations and hydropower plants. This relation is difficult to study in the laboratory because population densities in the laboratory are many times higher than in the field, and laboratory environments do not have the complexity of natural environments. Study in the field is difficult because a large number of interrelated factors operate, spatial and temporal variation are high, a single observation per year is obtainable for recruitment, data for early life stages are highly variable and difficult to obtain, and small changes in larval survival rates, changes that are impossible to detect, are biologically significant. This has led to inconclusive results even in detailed studies of fish populations in small lakes (e.g. Serns, 1982, 1984).

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The processes hypothesized for population regulation can be quantified in mathematical models, and the models can be applied to study some aspects of population regulation. For example, models can be applied to compare the levels of compensation provided by different processes that have been proposed for population regulation, they can be applied to determine changes in life history parameters that are necessary for population regulation to occur, and they can be applied to determine changes that need to be detected in the field to identify population processes.

A life history simulation model was applied to determine the relation between recruitment and mortality of young assuming different compensation processes for fish populations that have been proposed in the literature. Changes in recruitment that occurred with increase in mortality of early life stages were simulated assuming: (1) growth dependent on ration, which depends on density, and age specific mortalities, (2) growth dependent on ration, which depends on density, and mortality dependent on size, and (3) growth dependent on ration, which depends on density, and age at maturity a function of size.

The model was applied using data for the walleye

(*Stizostedion vitreum*) population in the western basin of Lake Erie, but some parameters were estimated with data for other walleye populations. The walleye population of Lake Erie is of interest because it is of significant commercial and sport value, it is impacted directly and indirectly by entrainment and impingement, and well documented changes in abundance and growth have occurred during the past 15 years (Muth & Wolfert, 1986).

## THE MODEL

Simple, well established relations among food abundance, growth, and mortality were applied. Most of the components of the model are the same as those applied by Jensen (1989), but a new component was added for age at maturity, and the components were coupled. The model combines Larkin's (1956) predator-prey model, Ursin's (1967, 1979) bioenergetic growth model, Ivlev's (1961) feeding model, the exponential mortality model, and the relation between mortality and size developed by Peterson and Wroblewski (1984).

Each year in the simulations was separated into four different time periods to describe the changing composition of the population during a year. During the winter the population consisted of juveniles and adults, and each age was simulated separately. Egg production occurred in the spring, starting the second time period. After the eggs hatched the third time period began, and the population consisted of larvae, juveniles and adults. Later, in the fourth time period, after the larvae had become young of year (YOY) the population consisted of YOY, juveniles, and adults. Changes in the population of food concentration were calculated each day. At the end of 365 days, ages were incremented by one year.

Eggs are spawned in the spring; the number of eggs produced is:

$$H \sum_{i=x_m}^{x_r} pN(x)W(x) \quad (1)$$

where  $H$  is the average number of eggs per gram of female,  $N(x)$  is the abundance of age  $x$  individuals in the population at the time of spawning,  $W(x)$  is the weight of age  $x$  individuals (g), and  $p$  is the proportion of females in the population. The number of larvae hatching after the incubation period is  $sE$ , where  $E$  is the number of eggs and  $s$  is egg survival.

The relation between predator abundance and prey abundance has been described with many different equations; for fish populations Larkin (1956) concluded that the classical equations of Lotka and Volterra do not apply because they indicate starvation of a predator when a prey species becomes extinct. At equilibrium the predation equations Larkin (1956) recommended give the following relation between the density

of prey ( $N_1$ ) and the density of walleye ( $N_2$ ).

$$N_1 = K_1 - b_1 K_1 N_2 / r_1 \quad (2)$$

where  $r_1$  is the prey population growth coefficient,  $K_1$  is prey density at the carrying capacity, and  $b_1$  measures the impact of predators on prey abundance.

Growth was modeled using a bioenergetic growth model that combines the works of Winberg (1956), Ursin (1967, 1979) and Ivlev (1961). Based on Winberg's (1956) energy balance equation, Ursin (1967) proposed modeling growth as

$$dW/dx = e_f dR/dx - Q \quad (3)$$

where  $dW/dx$  is the growth rate (cal/g day),  $dR/dx$  is ration (cal/g day),  $Q$  is the total metabolic rate (cal/g day), and  $e_f$  is the efficiency of food utilization. Ursin (1967, 1979) modeled the rate of food consumption as

$$dR/dx = b_0 (1 - Af)fhW^m \quad (4)$$

where  $b_0(1 - Af)$  is the amount of food absorbed, which depends on the feeding level,  $f$  is the feeding level,  $0 \leq f \leq 1$ ,  $h$  is a coefficient of food consumption,  $W$  is weight, and  $m$ ,  $b_0$ , and  $A$  are parameters. The rate of metabolism ( $Q$ ) was separated into two components, feeding catabolism and fasting catabolism, given by the following equation (Ursin 1967, 1979)

$$Q = a dR/dx + kW^n \quad (5)$$

where  $a$ ,  $n$  and  $k$  are parameters.

The feeding level was a function of prey abundance, and based on Ivlev's (1961) equation

$$f = 1 - \exp(-SN_1) \quad (6)$$

where  $N$  was prey density and  $S$  was a coefficient. For simplicity, it was assumed that some constant fraction  $b$  of the food ingested was absorbed, then the growth equation became

$$dW/dx = C[1 - \exp(-SN_1)]W^m - kW^n \quad (7)$$

where  $C = (1 - a)bh$ .

Mortality was modeled with the exponential model

$$N(x) = N(x_0) \exp[-Z(x - x_0)] \quad (8)$$

where  $N(x)$  was abundance at age  $x$ ,  $x_0$  was the initial age, and  $Z$  was the instantaneous mortality coefficient. Mortality coefficients were dependent either on age or size.

In simulations where age at maturity was dependent on size, the distribution of weights at a given age was described using the logistic probability distribution

because its shape is similar to the normal distribution and its distribution function,

$$F(x) = 1 - \{1 + \exp[(W(x) - a)/k]\}^{-1} \quad (9)$$

can be found in closed form. In eqn (9) the mean weight is  $a$ , and the variance of weight is  $k^2\pi^2/3$ . The proportion of each age group larger than the weight at maturity was calculated at the time of spawning.

## PARAMETER ESTIMATION

The model was applied to the walleye population of the western basin of Lake Erie, and most of the parameter estimates are the same as in an earlier study (Jensen, 1989). The food concentration for larvae was set at 200 mg/m<sup>3</sup>, and assuming that food concentration increased with the size of walleye, the values for YOY, juveniles and adults were set at 1000, 1500 and 2000 mg/m<sup>3</sup>, respectively. The decreases in prey per walleye, as a result of feeding, were  $1 \times 10^{-7}$  mg/m<sup>3</sup> for larvae,  $5.0 \times 10^{-5}$  mg/m<sup>3</sup> for YOY,  $7.5 \times 10^{-5}$  mg/m<sup>3</sup> for juveniles and  $1 \times 10^{-4}$  mg/m<sup>3</sup> for adults. These values generated walleye abundances similar to those observed in the western basin of Lake Erie. Age at maturity was 4 years and the number of eggs per gram of female was 74 (Eschmeyer, 1950). The oldest age attainable was set at 8 years.

For the relation between the instantaneous mortality coefficient and weight, the parameter estimates of Peterson and Wroblewski (1984) of 1.92 for the coefficient and  $-0.25$  for the exponent were used for adults, juveniles and YOY, but as in Jensen (1989) a coefficient of 20 was used for larvae. In simulations where age at maturity was a function of size, the size at maturity was 1200 g and the variance was 100 g.

In simulations without the Peterson and Wroblewski (1984) mortality size relation, the mortality rates were input parameters and the instantaneous annual rates were 75 for larvae, 5 for YOY, 0.5 for juveniles, and 0.4 for adults. For the other simulations mortality rates were calculated from size.

## RESULTS AND DISCUSSION

The simulations are based on processes for regulation of fish population size proposed in the literature (Beverton & Holt, 1957; Ricker, 1975; Rothschild, 1986; Saila *et al.*, 1987). Simulations were done with: (1) food limited bioenergetic growth and constant age specific mortalities, (2) food limited bioenergetic growth and a size dependent-mortality relation and (3) food limited bioenergetic growth and age at maturity dependent on size. For each simulation mortality was increased for either larvae, YOY, or juveniles. The results reported

are percent of total recruitment after 100 years as a function of percent increase in mortality of either larvae, YOY, or juveniles.

Change in recruitment with increase in mortality of young depends on the compensation process. An inverse relation between walleye population density and growth rate has been well documented (Colby *et al.*, 1979), and large variation in walleye growth rates may occur between year classes and among individuals of the same year class. One of the most important factors affecting growth of walleye is the amount of forage available (Colby *et al.*, 1979).

Relations between recruitment and mortality increases are different for larvae, YOY and juvenile mortality. The relations for larvae are examined first. Relatively small increases in mortality of larvae decreased recruitment substantially with food limited bioenergetic growth and constant age specific mortality coefficients (Fig. 1A), but there was compensation. This limited compensation occurred with no control of population size through predation, disease, competition among species, or special population behavior. With food limited growth, if mortality of young increases slightly, the population approaches a new equilibrium of natality and mortality because with more food per individual the adults are larger in size and produce more eggs.

Dependence of mortality on size is a reasonable assumption for walleye, especially for early life stages where there is extensive predation. Northern pike feed on walleye larvae, and other species such as sauger, bullheads, burbot, and yellow perch feed on walleye YOY (Colby *et al.*, 1979). With food limited bioenergetic growth and a relation between mortality and size the simulations indicate a substantial compensation, and relatively large increases in larval mortality result in only small decreases in recruitment (Fig. 1B).

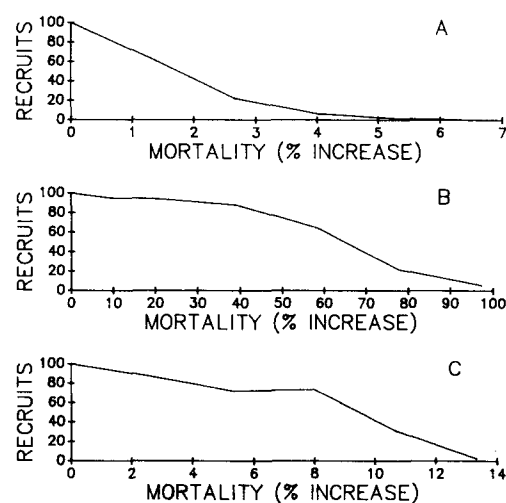


Fig. 1. Percent change in recruits with percent increase in larval mortality with (A) growth dependent on food density; (B) growth dependent on food density and mortality dependent on size and (C) age at maturity a function of size and growth dependent on food density.

Age at maturity varies considerably among walleye stocks, and age at maturity is inversely related to growth rate, which in turn is affected by the amount of food available (Colby *et al.*, 1979). Northern stocks mature later and over a larger number of years than southern stocks and heavily exploited stocks (Colby *et al.*, 1979). A trend towards earlier maturity among more rapidly growing walleye has been reported in Oneida Lake, New York, and a similar trend was observed for heavily exploited stocks in Saginaw Bay (Lake Huron), the western basin of Lake Erie and Dexter Lake, Ontario (Colby *et al.*, 1979). In Lake Erie, the percent of walleye maturing at age 3 increased from 40 to 80 during a period when the stock size declined markedly (Shuter and Koonce, 1977). Age and size at maturity within a given population may vary with both water temperature and food availability (Colby *et al.*, 1979).

In the simulations it was assumed that age at maturity and age at recruitment were the same. With food limited bioenergetic growth and age at maturity dependent on size the decrease in recruitment with increase in larval mortality is much less than when food limited growth is the only compensation process (Fig. 1A and Fig. 1C)), and recruitment actually increased with increase in larval mortality. This increase in recruitment resulted from a decrease in age at recruitment with increase in larval mortality (Fig. 2A); when larval mortality increases fish of a given age are larger and age at recruitment decreases. The number of individuals at younger ages is larger than the number at older ages. Although recruitment can increase when age at recruitment is a function of size, the number of four-year-olds decreases monotonically with increase in larval mortality (Fig. 2B). A flexible age at maturity, as observed in

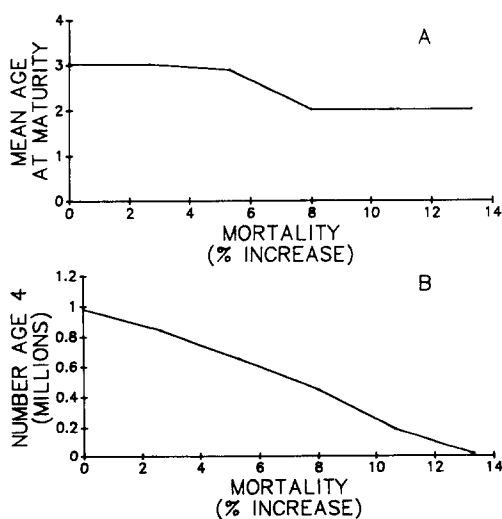


Fig. 2. (A) Relation between percent increase in YOY mortality and mean age at recruitment with age at recruitment dependent on size. (B) Relation between number of 4-year-olds and percent increase in YOY mortality with age at recruitment dependent on size.

walleye and many other species of fish, enables a population to survive a large increase in larval mortality (Fig. 1C).

The relations between mortality and recruitment found for larvae also were found for YOY and juveniles. If compensation is provided only by food limited bioenergetic growth, recruitment decreases rapidly when YOY mortality increases, but there is some potential to compensate for YOY mortality (Fig. 3A). The decrease in recruitment with increase in YOY mortality is much less when there is both food limited growth and size dependent mortality (Fig. 3B). For YOY mortality, food limited growth with an age at maturity that depends on size provides considerable compensation potential (Fig. 3C).

With increase in juvenile mortality there again is little compensation with just food limited bioenergetic growth (Fig. 4A), but more than occurs with increases in YOY or larval mortality. If there is a size mortality relation (Fig. 4B), or if age at maturity is dependent on size (Fig. 4C) there is considerable compensation potential.

A relation between mortality and size is the most effective compensation process for larval mortality. The coefficient in the relation between size and mortality is large for larvae, and abundance of larvae is high, so an increase in larval size that results in a decrease in mortality has a substantial effect on recruitment. For YOY and juvenile mortality, both a size dependent age at maturity and a relation between mortality and size are effective compensatory processes. Mortality during all three life stages appears about equally important; i.e., there does not appear to be a critical life stage.

The compensatory effects of food limited growth alone and in combination with an age at maturity

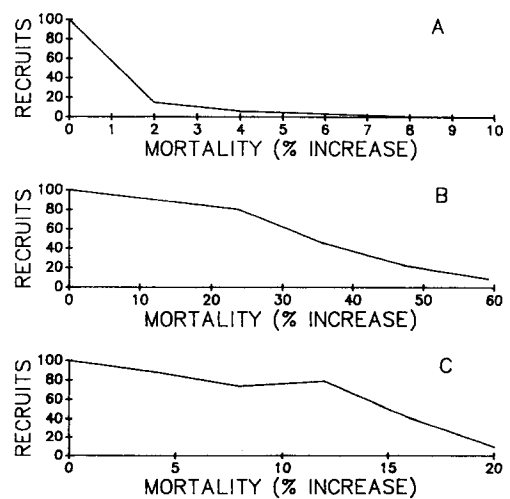


Fig. 3. Percent change in recruits with percent increase in YOY mortality with (A) growth dependent on food density; (B) growth dependent on food density and mortality dependent on size and (C) age at maturity a function of size and growth dependent on food density.

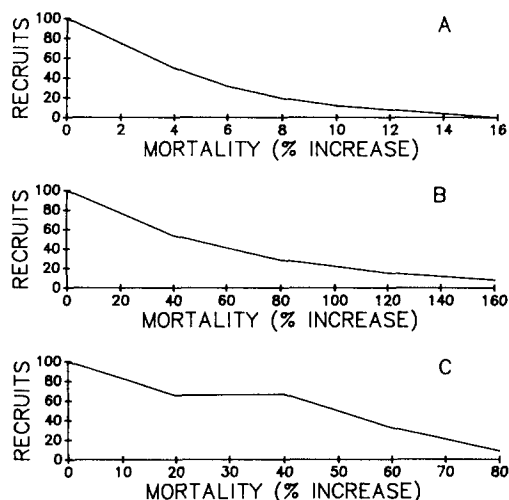


Fig. 4. Percent change in recruits with percent increase in juvenile mortality with (A) growth dependent on food density; (B) growth dependent on food density and mortality dependent on size and (C) age at maturity a function of size and growth dependent on food density.

dependent on size and a relation between size and mortality have been examined. There are many additional processes that can affect population regulation, including a relation between egg and larval survival and nutrition of the spawning adults, a relation between abundance and proportion of a population that is female, cannibalism, and behavioral, physiological, and biochemical relations. All of these processes could be tuned to the environment through natural selection. In addition, predation, interspecific competition, and disease could contribute to regulation of population size.

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