

SIMULATION OF THE POTENTIAL FOR LIFE HISTORY COMPONENTS TO REGULATE WALLEYE POPULATION SIZE

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ABSTRACT

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A bioenergetic life history simulation model was applied to identify components of the walleye (*Stezostedion vitreum*) life history that had a potential for population regulation. The model combined a predator–prey model, a bioenergetic growth model, a relation between mortality and size, and the exponential mortality model to produce a feedback relation among abundance, food concentration, growth, and mortality. Larval mortality, juvenile mortality, and age at maturity were identified as factors with a potential for compensation. As the number of larvae increased, the number of young-of-year (YOY) increased to a maximum and then decreased with further increase in the number of larvae. This occurred because as the number of larvae increased, food concentration decreased, growth rate decreased, and mortality, which was size dependent, increased. As the number of juveniles increased, the number of recruits increased to a maximum, and then with further increase in the number of juveniles the number of recruits decreased. Age at maturity increased exponentially with increase in the number of juveniles because growth decreased. Change in mortality of both adults and YOY had little potential for compensation.

INTRODUCTION

Changes in life history parameters that enable fish populations to adapt to a changing environment are often called population compensation or population regulation. To compensate for mortality caused by exploitation or environmental disturbances some other life history parameter such as the growth coefficient, mortality of other life stages, mortality from other sources, age at maturity, or fecundity, must change. Many studies have documented that these compensatory changes occur. Healey (1980) found

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compensatory changes in the life history parameters of an experimentally exploited lake whitefish (*Coregonus clupeaformis*) population. Jensen and Marshall (1982) found that increases in birth offset increases in mortality in laboratory populations of *Daphnia*. Jensen (1981) examined relations among life history parameters of lake whitefish and found that increased growth was associated with a higher mortality and an older age at maturity. Jensen (1981) concluded that an increase in mortality was associated with an increase in growth and that this resulted in a younger age at maturity. Jensen (1985) examined the potential for different life history parameters to change the net reproductive rate which measures the capacity for compensation. The life history parameters with the largest potential for compensation were age at maturity and larval mortality. The approach used by Jensen (1981, 1985), which relies on available field data, identifies relations among parameters that could result in significant compensation but it does not describe the underlying processes.

In this study a model is applied to determine if relations among abundance, growth, mortality, and size can result in the feedback necessary for population regulation, and to evaluate the relative potential of different processes. The simulation model combines Larkin's (1966) predator-prey model, a bioenergetic growth model similar to Ursin's (1967), Ivlev's (1961) feeding model, the exponential mortality model, and the relation between size and mortality proposed by Peterson and Wroblewski (1984). Application of the model requires estimation of a large number of parameters, but the range of values for many of the parameters are well known. The model was fitted to the walleye population of the western basin of Lake Erie where well documented changes in abundance have produced changes in growth rates, condition factor, and age at maturity (Knight et al., 1984, Muth and Wolfert, 1986).

MATHEMATICAL MODEL

The basis for the simulation model are the assumptions:

- a decrease in abundance results in an increase in food concentration,
- an increase in food concentration results in an increase in growth and size, and
- an increase in growth and size results in a decrease in mortality because mortality is a function of size.

The relation between predator abundance and prey abundance is given by the equations (Larkin, 1966):

$$dN_1/dt = r_1N_1 - r_1N_1^2/K_1 - b_1N_1N_2 \quad (1)$$

$$dN_2/dt = r_2N_2 - r_2N_2^2/K_2 - b_2N_1N_2 \quad (2)$$

where N_1 is prey density, N_2 is predator density, r_1 is the prey population growth coefficient, r_2 is the predator population growth coefficient, K_1 is prey density at the carrying capacity, K_2 is predator density at the carrying capacity, b_1 measures the impact of predators on prey abundance, and b_2 measures the impact of prey on predator abundance. Under equilibrium conditions, where $dN_1/dt = dN_2/dt = 0$, equation (2) gives prey abundance as:

$$N_1 = K_1 - (K_1 b_1 / r_1) N_2 = K_1 - b N_2 \quad (3)$$

where b is the impact of walleye on their food concentration.

The size of a cohort at time t is given by the exponential model:

$$N(x) = N(x_0) \exp[-Z(x - x_0)] \quad (4)$$

where $N(x)$ is abundance at age x , x_0 is the initial age, and Z is the instantaneous mortality coefficient. The instantaneous mortality coefficient is a function of the weight of an individual and is given by the equation of Peterson and Wroblewski (1984) as:

$$Z = 1.92 (0.25W)^{-0.25} \quad (5)$$

where W is wet weight.

Growth was determined using a bioenergetic growth model that combined the works of Winberg (1956), Ursin (1967), and Ivlev (1961). Winberg's (1956) energy balance equation gives the growth equation:

$$dW/dx = e_f R - Q \quad (6)$$

where R is ration (g/year), Q is the total metabolic rate (cal/year), dW/dx is the growth rate (g/year), and e_f is the efficiency of food utilization. Ursin (1967) proposed modelling ration as:

$$R = hfW^m \quad (7)$$

where f is the feeding level, $0 < f < 1$, m is an exponent, and h is a coefficient of food consumption. Depending on the objective in modelling growth, different terms can be developed in more detail. For the purpose of this study it will be assumed that feeding level is a function of food abundance, and based on Ivlev's (1961) equation:

$$f = 1 - \exp(-SN_1) \quad (8)$$

where N_1 is food density, and S is a coefficient. The term for total metabolism is usually separated into two terms: low routine metabolism.

cal = calorie (International Table) = 4.1868 J (def).

and metabolism of specific action. Applying conventional equations for the metabolic terms (Ursin, 1967) gives the growth equation:

$$dW/dx = C[1 - \exp(-SN_1)]W^m - kW^n \quad (9)$$

where C is a parameter that combines several parameters given by Ursin (1967), and n is an exponent.

Abundance of food was calculated for larvae, young of year YOY, and each age group at the beginning of each simulation, and then the growth and mortality equations were applied to calculate daily changes.

ESTIMATION OF PARAMETERS

The model was applied to simulate components of compensation for the walleye population of the western basin of Lake Erie. Walleye run to shallows or tributaries and spawn soon after the ice breaks up (Eschmeyer, 1950). The eggs are 1.5–2 mm in diameter and sink; eggs hatch in 10–12 days, producing larvae 6–9 mm in length, and 10–15 days later the yolk sac is absorbed and free swimming larvae appear in the upper water layers (Eschmeyer, 1950).

Parameters for the Ivlev (1961) curve relating walleye ration to prey abundance were estimated using data for Lake Superior and Shagawa Lake

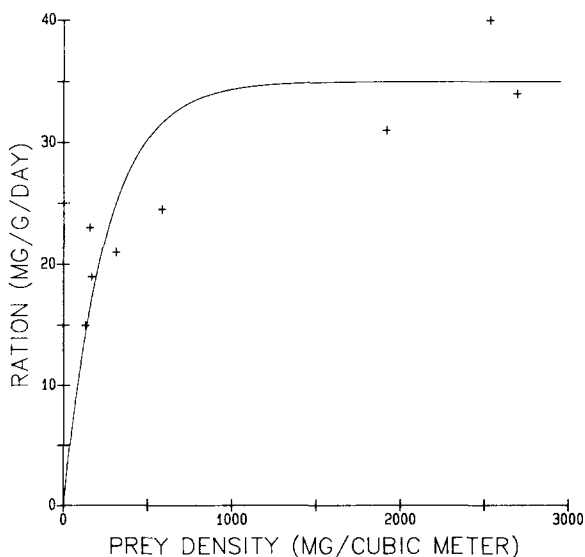


Fig. 1. Observed (Swenson, 1977) and estimated (curve) relation between ration and abundance of food for walleye.

reported by Swenson (1977). In Lake Superior, walleye fed mainly on rainbow smelt (*Osmerus mordax*); prey density was low and daily food consumption was less than 2.5% of body weight. In Shagawa Lake walleye fed mainly on yellow perch (*Perca flavescens*); prey density was high, and the daily food consumption of walleye was 4% of body weight. Fitting the Ivlev (1961) equation:

$$F = F_{\text{inf}} [1 - \exp(-SN_1)] \quad (10)$$

where F is ration on a daily basis, and F_{inf} is the maximum daily ration; using non-linear least squares gave $F_{\text{INF}} = 35 \text{ mg g}^{-1} \text{ day}^{-1}$ and $S = 0.004$. The coefficient of determination was 0.81. The observed and predicted rations are shown in Fig. 1. For Lake Superior, which is cold and non-productive, the prey densities are on the ascending limb of the curve. For Shagawa Lake, a relatively eutrophic lake, the densities are along the asymptote and a decrease in prey abundance in Shagawa Lake would have little effect on production of walleye. In Lake Superior the walleye population may be food limited, but in Shagawa Lake other factors limit growth. The estimate of k of 0.021429/day for a temperature of 15°C was given by Norstrom et al. (1976), and the estimates of m and n of 0.56 and 0.80 were given by Ursin (1967). Norstrom et al. (1976) gave the efficiency of food utilization e_f as 0.80.

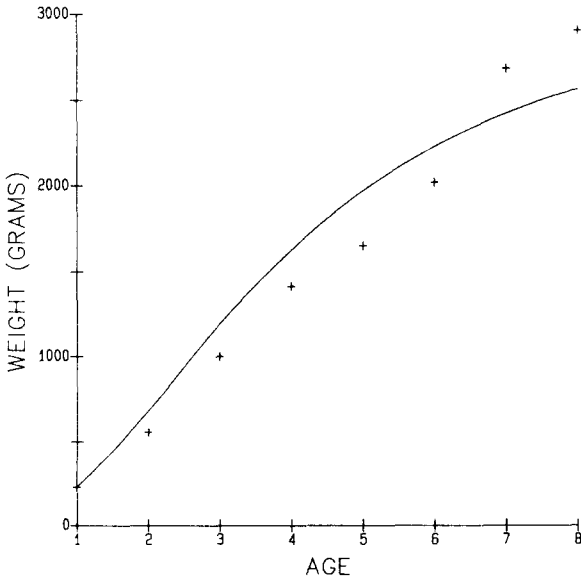


Fig. 2. Observed and fitted growth curve for walleye in the western basin of Lake Erie.

The parameter C was estimated using growth data (Ohio Dep. Nat. Resour., 1985) and non-linear least squares. The growth of walleye has changed (Muth and Wolfert, 1986), and an adjustment in the estimates of C and k was made to give a somewhat better overall fit of the calculated weights to the observed weights. Instead of using $k = 7.82/\text{year}$ and $C = 55/\text{year}$, the parameter estimates used were $k = 6.62/\text{year}$ and $C = 47.25/\text{year}$. The estimates give over estimates of weight for younger fish and under estimates of weight for older fish (Fig. 2).

The following growth parameters were estimated using the Von Bertalanffy (Ricker, 1975) growth equation and the length weight relation for walleye in the western basin of Lake Erie: exponent in length-weight relation = 3.25, initial weight of larvae = 0.005 g, initial size of YOY = 1.32 g, and initial size of juveniles = 16 g. Prey density in the absence of walleye was estimated as $K_1 = 2000 \text{ mg/m}^3$, based on the Ivlev (1961) feeding relation (Fig. 1). The parameter relating walleye abundance and food density was estimated as $b = 0.0001$ by adjusting the calculated growth curve to fit the observed growth data. Age at maturity x_m was estimated as 4 years, and the number of eggs per gram of female, H , was estimated as 74 (Eschmeyer 1950).

RESULTS AND DISCUSSION

All components of compensation examined here depend on the relation between growth and food abundance. The relation between growth and food abundance for walleye has been examined by many authors, including Forney (1976, 1977), Muth and Wolfert (1986), Knight et al. (1984) and Chevalier (1977). In Lake Erie, walleye consume largely YOY gizzard shad (*Dorosoma cepedianum*) and shiners (*Notropis atherinoides* and *N. hudsonius*) (Knight et al., 1984). Gizzard shad are available only during a short period of the year and only during a short period of their lifetime (Bodola, 1966). In the western basin of Lake Erie the abundance of walleye has increased greatly in recent years; their growth has decreased and their age at maturity has increased (Muth and Wolfert, 1986).

In the simulations there is little or no change in growth with decrease in food density when food density is along the asymptote of the ration vs. food abundance Ivlev (1961) curve (Fig. 3), but, as food concentration decreases, ration begins to decrease below the asymptote and growth begins to decrease (Figs. 1 and 3).

To compare simulated growth with growth observed for natural populations, the Von Bertalanffy growth equation (Ricker, 1975):

$$W = W_{\text{inf}}(1 - e^{-Kx})^3 \quad (11)$$

was fitted to the growth data simulated with different food abundances,

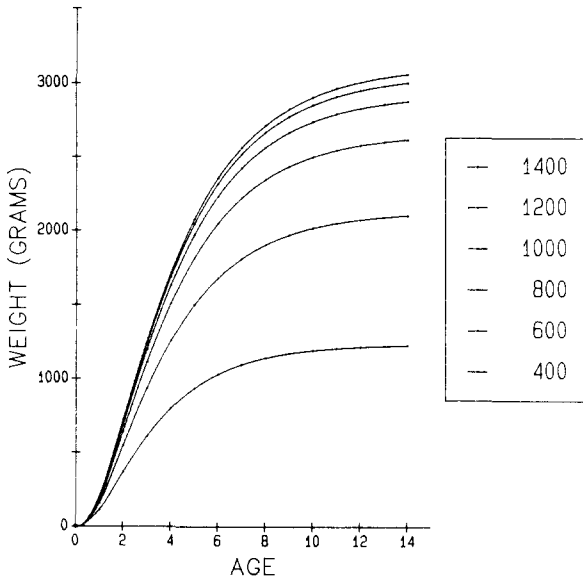


Fig. 3. Simulated growth of walleye for different concentrations of food.

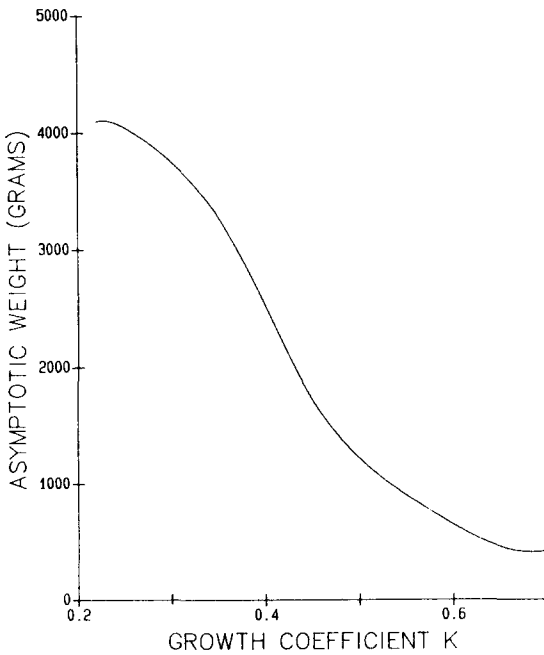


Fig. 4. Relation between asymptotic weight and growth coefficient in simulations of growth for walleye.

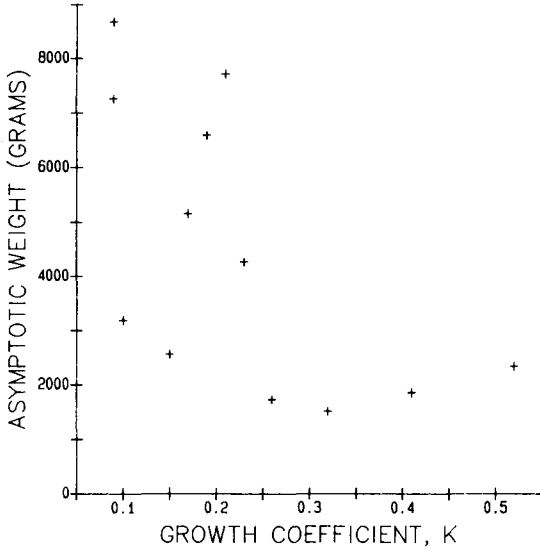


Fig. 5. Observed relation between asymptotic weight and growth coefficient for walleye from different environments.

where K is the growth coefficient, and W_{inf} is the asymptotic weight. In the simulations, for small values of K the asymptotic weight is large, but the maximum asymptotic weight is limited by the asymptote in the Ivlev (1961) feeding equation and the asymptotic weight does not increase without limit as K decreases (Fig. 4). In the simulations, for large values of the growth coefficient K , as K increases the asymptotic weight decreases asymptotically toward zero.

The relation between K and W_{inf} observed for natural populations of walleye is considerably different from that generated by variation of the food concentration (Figs. 4 and 5 and Table 1). The observed relation between K and W_{inf} does not indicate a maximum asymptotic weight at small values of the growth coefficient, and the observed range of both W_{inf} and K among natural populations of walleye are higher than the range in the simulations. The form of the expression for abundance of food in the growth equation limits the impact that food concentration can have on growth. If the large variation in asymptotic weight observed in the field results from environmental variation, rather than genetic variation, then it is probable that the large variation in the field results from variation in temperature rather than from variation in food density. In the bioenergetic growth equation asymptotic weight is given by the relation (Ursin, 1967):

$$W_{\text{inf}} = [C(1 - e^{-SA})/k]^{1/(n-m)} \quad (12)$$

TABLE 1

Growth coefficients (per year), lengths (mm), asymptotic weights (g) for different walleye populations

K	L_{inf}	W_{inf}	Location
0.12	866	7714	Lake Erie
0.10	660	3190	Lake Abitibie
0.09	850	7260	Lake Nipigon
0.26	547	1733	Prairie Provinces
0.41	559	1859	New York Lakes
0.23	722	4271	Wisconsin Lakes
0.09	898	8679	Lake of the Woods
0.17	765	5155	Iowa Lakes
0.19	825	6589	Clear Lakes
0.52	600	2340	Norris Reservoir
0.15	617	2563	Lake Manitoba
0.32	525	1516	Lake Gogebic

Calculated from data in Eschmeyer (1950).

and the coefficient k is temperature dependent in the form:

$$k = k_0 e^{pT} \quad (13)$$

where T is temperature in degrees centigrade, and p and k_0 are parameters (Ursin, 1967). Unlike changes in food density, which have a small effect on asymptotic weight, changes in temperature have a potential for large effects on asymptotic weight because temperature enters the growth equation exponentially.

The parameter estimate 1.92 for the coefficient in the relation between the instantaneous mortality coefficient and weight, given by Peterson and Wroblewski (1984), was used for all life stages except larvae; for larvae this estimate gives mortality coefficients that are too low (Peterson and Wroblewski, 1984). For larvae a parameter estimate of 20 rather than 1.92 gave reasonable estimates of larval mortality. The model of Peterson and Wroblewski (1984) assumes that predation is the only source of larval mortality. Incorporating starvation into the compensation model so that 10% of the larvae died when daily growth was less than 1% of their weight resulted in appropriate levels of larval mortality with a coefficient of 1.92. This indicates that factors other than predation are important for larval survival.

Six potential components of compensation were examined: the relation between recruitment and adult mortality, the relation between recruitment and egg production, the relation between the number of age-1 fish and age at maturity, the relation between the number of larvae and the number of YOY produced, the relation between the number of YOY and the number of

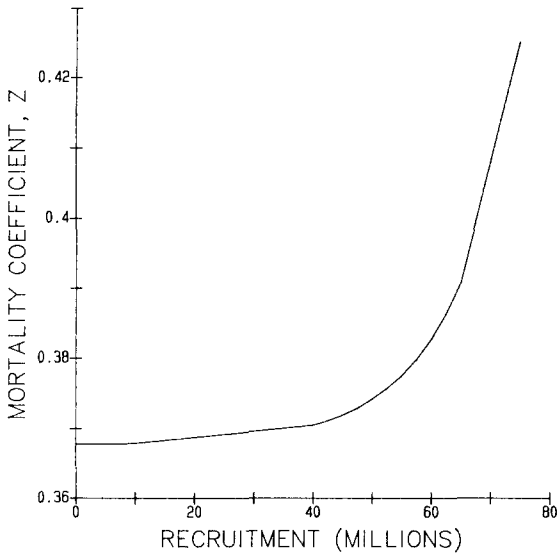


Fig. 6. Simulated relation between recruitment and mortality of adults for walleye.

juveniles produced, and the relation between the number of juveniles and the number of recruits produced.

Mortality of adults increases exponentially with increase in the number of recruits (Fig. 6); the model assumes that as the number of recruits increases the food available for growth of adults decreases, growth of adults decreases, size of adults decreases, and adult mortality which is size dependent increases. Adult fish are large, however, and although the increase in mortality with decrease in size is exponential, the actual increase in mortality is low. On the right in Fig. 6, where mortality begins to increase rapidly with recruitment, there is essentially no growth, and further increase in recruitment does not continue to increase mortality. Change in adult mortality cannot be an important component of compensation.

To examine the relation between population egg production and number of recruits it was assumed that the number of eggs produced per unit of female biomass remained constant as food density decreased. As the number of recruits increased the number of eggs produced increased to a maximum and then decreased slightly (Fig. 7). The decrease in egg production that occurred with large numbers of recruits resulted from the decrease in growth and increase in mortality of adults that occurred at high recruitment levels. At these high recruitment levels there was essentially no growth, and it was reasonable to conclude that, for recruitment levels likely to occur in nature, change in egg production with change in recruitment would be linear and would not be an important component of compensation.

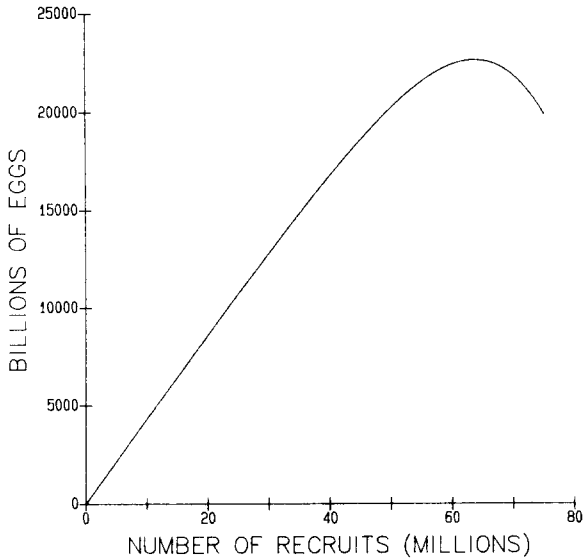


Fig. 7. Simulated relation between recruitment and egg production for walleye. billion (US) = 10^9 .

To examine the effect of density on the age at maturity it was assumed that maturity occurred at 1416 g, which was the mean size of females at the mean age at maturity reported for the western basin of Lake Erie (Eschmeyer, 1950; Ohio Dep. Nat. Resour., 1985). Maturity is related to many factors other than size, but size is an important factor. As the number of juveniles increased age at maturity increased exponentially (Fig. 8). Change in age at maturity could be an important component of compensation because large changes in age at maturity occur with change in the number of juveniles, and change in age at maturity can have a large effect on the net reproductive rate (Jensen, 1985). Muth and Wolfert (1986) reported that in the western basin of Lake Erie age at maturity of walleye increased with an increase in density and a decrease in growth.

As the number of larvae produced increases the number of YOY increases to a maximum and then decreases rapidly (Fig. 9). As the number of larvae increases larval food density and growth decrease; larvae are small and change in larval size has a large effect on larval mortality. Larval mortality can be an important component of compensation, and the change in larval mortality with change in food concentration does not require an assumption of a bottleneck or critical event during the larval life stage. Relations among food abundance, growth, size, and mortality are sufficient to produce a compensatory effect.

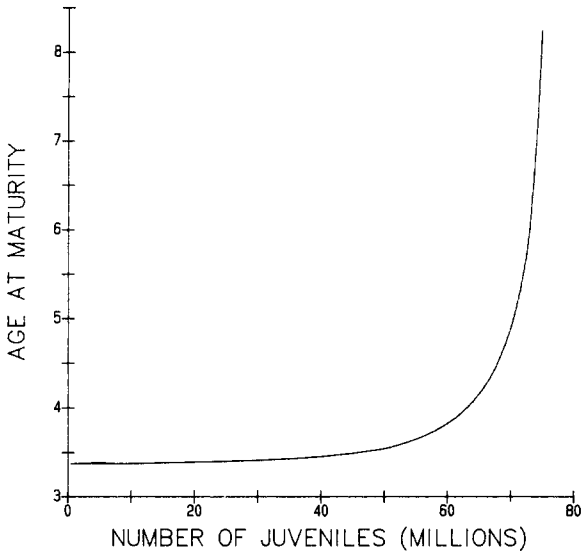


Fig. 8. Simulated relation between the number of juveniles and age at maturity for walleye.

Increase in the number of YOY produces nearly a linear increase in the number of juveniles (Fig. 10); there was a maximum but it occurred where growth was negligible and a maximum would not occur in natural popula-

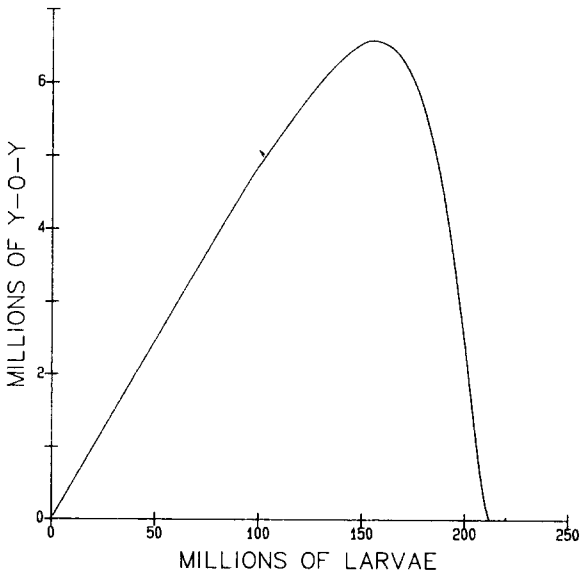


Fig. 9. Simulated relation between millions of larvae and millions of YOY produced for walleye.

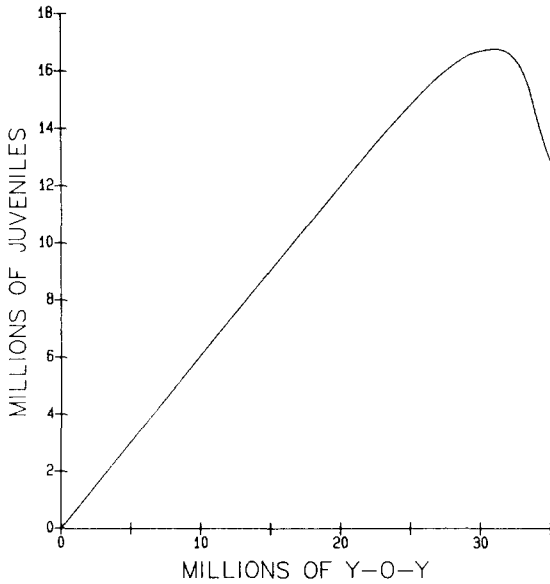


Fig. 10. Simulated relation between YOY and juveniles produced for walleye.

tions. Mortality during the YOY life stage was high, but much lower than that during the larval life stage. The YOY life stage is of short duration, lasting for about 0.5 years. Mortality during the YOY life stage cannot be an important process in compensation.

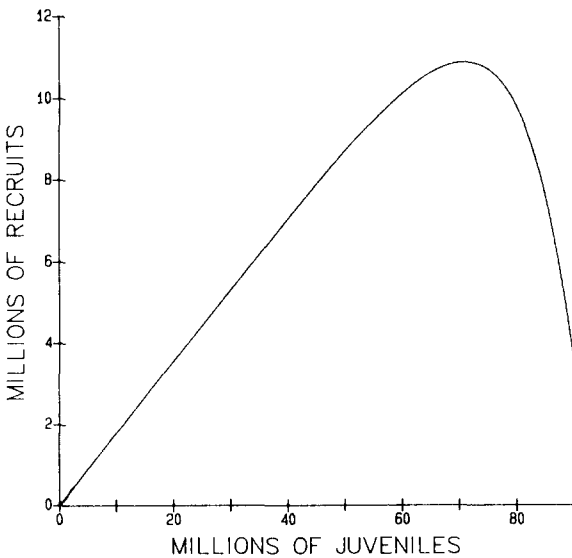


Fig. 11. Number of juveniles and production of recruits for walleye.

The number of recruits increased to a maximum with increase in the number of juveniles; then further increase in the number of juveniles results in a decrease in the number of recruits (Fig. 11). Mortality during the juvenile life stage was lower than mortality during the YOY life stage, but duration of the juvenile life stage was much longer than duration of the YOY life stage. Mortality during the juvenile life stage could have an important regulatory effect.

Relations among abundance, food concentration, growth, and mortality can result in compensation, and the processes likely to be important to compensation are change in the age at maturity, mortality of larvae, and mortality during the juvenile life stage. No critical events or bottlenecks are required to produce regulation.

The above analysis examines only the potential for population regulation resulting from relations among abundance, food density, growth and predation. Population regulation or compensation may result from other density dependent processes such as territorial behavior, secretion of chemicals, and disease.

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