

Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchill)

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Mechanisms that might compensate for changes in mortality are well known but documentation of their operation and determination of their relative capacities is difficult. In this study the potential of lake whitefish to compensate for fishing mortality is quantified using a conventional fishery stock assessment model. The mechanisms examined are proportion of females, fecundity, survival of eggs and larvae, decrease in age at maturity and growth. The change in each of these parameters necessary to maintain constant recruitment with increasing fishing pressure is determined. Decrease in age of maturity and increased survival of larvae and eggs have the greatest potential for compensation. The total capacity for compensation appears large even when the mechanisms are considered alone. A review of several lake whitefish population studies indicates a large variation in the vital statistics. There is a close relation between total mortality and growth. There is also a close relation between growth and age at maturity. The analyses indicate that increased fishing results in increased growth which then results in a lower age at maturity. This feedback mechanism enables lake whitefish to respond to changes in environmental conditions and on average to maintain a birth rate in balance with mortality.

I. INTRODUCTION

Study of exploited populations provides an opportunity to examine how fish populations survive large fluctuations in mortality. Mechanisms that could operate to offset the impact of fishing mortality are well known, but documentation of their operation is difficult. In conventional stock assessment studies it is assumed that recruitment remains constant, but fishing has a large impact on the age structure and thus on the reproductive potential of exploited stocks and recruitment can remain constant only through density dependent compensation. The level of fishing that can be supported by a population depends on the extent to which various mechanisms are able to compensate for exploitation. In this study, the magnitude of change in the vital statistics necessary to compensate for fishing mortality is determined for lake whitefish, *Coregonus clupeaformis*. The impacts of fishing on population size, age structure and reproductive potential are reviewed and then the changes in growth rate, sex ratio, fecundity, age at maturity and survival of eggs and larvae necessary to compensate for different levels of exploitation are determined. A review of lake whitefish population studies provides estimates of the variation in vital statistics that might be available for compensation.

II. REVIEW OF THE MODEL AND IMPACT OF FISHING

The analytical model for stock assessment developed by Beverton & Holt

(1957) has been applied widely and its development and application are discussed in detail by Gulland (1969). The model separates yield into three components—growth, reproduction and mortality. The equations for yield, numbers and individual weight are:

$$\begin{aligned}\frac{dY}{dx} &= FNW \\ \frac{dN}{dx} &= -(F + M)N, x \geq x_c \\ dN &= -FN, x_r < x < x_c \\ \frac{dW}{dx} &= 3 W_\infty K e^{-Kx} (1 - e^{-K(x - x_0)})^2,\end{aligned}$$

where Y = yield to the fishery; F = instantaneous fishing mortality coefficient; M = instantaneous natural mortality coefficient; N = number of individuals of age x ; W = weight of an average individual of age x ; W_∞ = average asymptotic weight; K = growth parameter; and x_0 = theoretical age when length equals zero. Biomass of the exploited stock is given by the equation

$$B = \int_{x_r}^{\infty} N(x) W(x) dx = R W_\infty e^{-M(x_c - x_r)} \sum_{n=0}^3 \frac{U_n e^{-nK(x_c - x_0)}}{F + M + nK} \quad (1)$$

where $U_0 = 1$, $U_1 = -3$, $U_2 = 3$ and $U_3 = -1$. In this study, equation (1) is used to relate biomass and fishing mortality.

Jensen (1979) applied the dynamic pool model for assessment of the lake whitefish stock in northern Lake Michigan. The parameter estimates obtained are summarized in Table I, which also lists estimates of several parameters not found in the biomass equation. These parameters are necessary for later simulations and include the number of eggs per unit of biomass, E , which was estimated as 17 384 kg⁻¹ (Cucin & Regier, 1965); the duration of the egg stage Δt_1 , and the duration of the larvae stage, Δt_2 , which were estimated as 0.452 and 0.071 years respectively (Hart, 1930); and the age at maturity, x_m , which was estimated at age 4 in northern Lake Michigan (Patriarche, 1977). The number of recruits, R , was set at 1000.

Exploitation causes substantial change in a population. The age structures of an unexploited population and an exploited population with the instantaneous fishing mortality coefficient at $F = 0.60$ are shown in Fig 1. Heavy exploitation reduces the number of older individuals in the population and these large fish produce large numbers of eggs. Exploitation results in a large decrease in the biomass of the standing stock (Fig. 2) and if egg production is assumed proportional to biomass, egg production follows the same pattern as biomass and decreases greatly with exploitation.

A more complete description of the impact of fishing on reproduction is given by the reproductive value, V_x (Fisher, 1930) which is defined as

$$V_x = \int_x^w \frac{l(t)m(t)}{l(x)} dt$$

TABLE I. Estimates of model parameters

Parameter	Symbol	Value
Asymptotic weight	W_{∞}	3.50
Instantaneous natural mortality coefficient	M	0.40
Growth parameter	K	0.30
Recruitment	R	1000
Recruitment age	x_r	4.0
Age when length equals zero	x_0	0.01
Eggs per unit biomass	E	17 384
Egg mortality coefficient	M_1	17.75
Larvae mortality coefficient	M_2	10.00
Duration of egg stage (years)	Δt_1	0.453
Duration of larvae stage (years)	Δt_2	0.077
Duration of pre-recruit stage	Δt_3	3.471
Age of maturity	x_m	4.0
Pre-recruit mortality	M_3	0.55

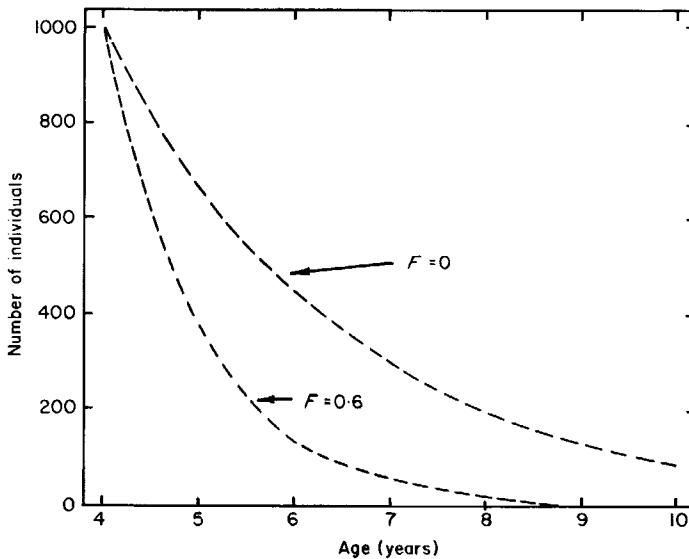


FIG. 1. Age structure of an unexploited and heavily exploited ($F=0.6$) lake whitefish population showing the decrease in the number of older individuals with exploitation.

where $l(t)$ = probability of survival to age t ; $m(t)$ = number of eggs produced per female of age t per year; and w = oldest age attainable.

The reproductive value is the expected number of eggs that an individual of age x will generate during the remainder of its lifetime. V_0 is the net reproductive rate. Under the assumption that egg production is proportional to weight, i.e. $m(t) = E \cdot W(t)$, and the assumption that growth and mortality are given by the Beverton & Holt (1957) dynamic pool model, the reproductive value becomes

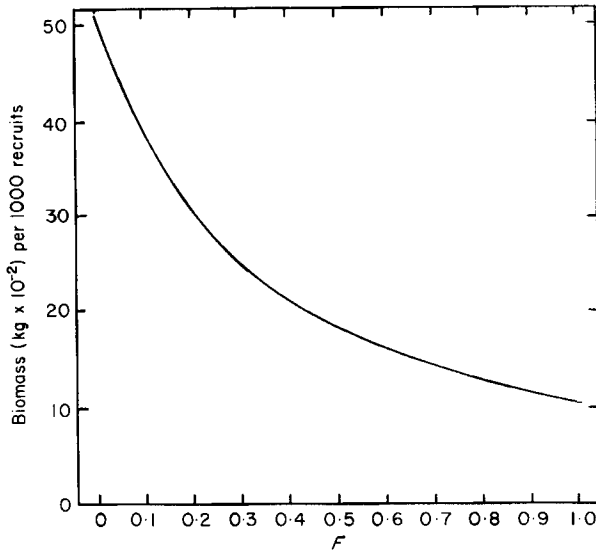


FIG. 2. Decrease in biomass of an exploited population with increase in fishing mortality.

$$V_x = E W_\infty \sum_{n=0}^3 \frac{U_n e^{-nK(x-x_0)}}{F + M + nK} \left[1 - e^{-(F + M + nK)(w - X)} \right]$$

The above equation was applied to calculate V_x over the lifespan under different levels of exploitation; the results are shown in (Fig. 3).

The expected number of eggs produced per individual increases asymptotically with age, but this increase in fecundity with age is balanced against a decrease in

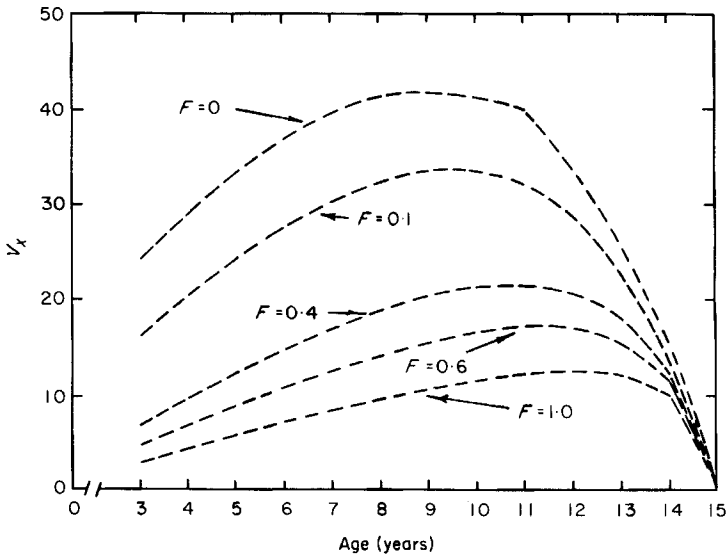


FIG. 3. Reproductive potential as a function of age for several fishing mortality coefficients.

number of years of life remaining as the individuals grow older. With no exploitation the reproductive value increases to a maximum at about age 9 and then begins to decrease. Exploitation has a large impact on the reproductive potential of a fish population. The age at which the maximum reproductive value occurs is higher when fishing mortality is high because individuals do not live as long and the limitation of lifespan has less of an impact. The expected number of eggs that an individual will produce is reduced by fishing, e.g. the expected number of eggs that an individual of age 3 will produce is about 25 without a fishery and decreases to less than 5 with $F=0.60$. These changes in reproductive potential, that occur as a result of fishing, require that density dependent compensatory changes occur in the vital statistics to maintain a constant recruitment.

III. POTENTIAL FOR COMPENSATION RESULTING FROM CHANGES IN VITAL STATISTICS

The potential for possible compensatory mechanisms to maintain constant recruitment as fishing mortality is increased can be examined by determination of the change in the related variables necessary to maintain constant recruitment. The relation between recruitment and stock biomass is given by the equation

$$R = p E B e^{-M_1 \Delta t_1 - M_2 \Delta t_2 - M_3 \Delta t_3} \quad (2)$$

where the only new symbol is the proportion of mature females, p . All terms are described in Table I. Equation (2) is the basis for calculation of the changes in vital statistics that are necessary to maintain a constant recruitment, R . An increase in fishing mortality will decrease the biomass of the mature stock. Biomass is calculated using the biomass equation [equation (1)]. The changes in the number of eggs per unit of biomass, egg mortality, larvae mortality and pre-recruitment mortality necessary to maintain a constant number of recruits with the reduced biomass is determined.

As fishing mortality increases the number of recruits also could be maintained by an increase in the growth parameter and a decrease in the age of maturity which act to replace biomass of the mature stock lost to the fishery. These relations also are examined.

Solution of equation (2) for the proportion of females gives

$$p = \frac{R \exp(M_1 \Delta t_1 + M_2 \Delta t_2 + M_3 \Delta t_3)}{B E}$$

in which p is a function of B . Changes in biomass that result from changes in F are calculated using equation (1). Application of the above equation shows that change in the proportion of females can compensate for only small changes in mortality of the exploited stock (Fig. 4). A population consisting nearly entirely of females could not compensate for the observed fishing mortality in northern Lake Michigan.

From equation (2), the relation between eggs per unit of biomass and biomass is

$$E = \frac{R \exp(M_1 \Delta t_1 + M_2 \Delta t_2 + M_3 \Delta t_3)}{p B}$$

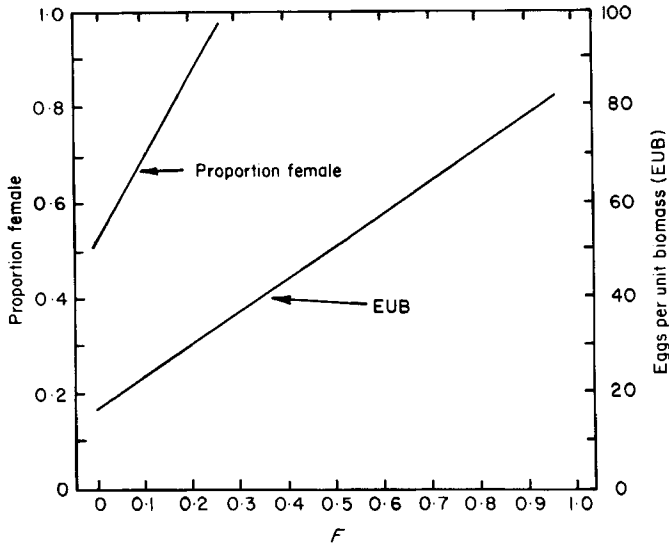


FIG. 4. Change in the proportion of females and number of eggs per unit of biomass necessary to compensate for fishing mortality.

Application of the above relation shows that change in number of eggs per unit of biomass also results in only a small capacity to compensate for exploitation (Fig. 4) given the observed range of eggs per unit of biomass (Table IV).

The combined egg and larvae mortality necessary to maintain a constant recruitment can be calculated but data for separation of this mortality into egg mortality and larvae mortality are not available. The partitioning of mortality between eggs and larvae has a large effect on the potential for compensation afforded by change in larvae mortality, so two cases are considered for both egg and larvae mortality. These two cases are high egg mortality with low larvae mortality and low egg mortality with high larvae mortality. If the instantaneous larvae mortality rate is assigned a value of 10, the instantaneous egg mortality rate necessary to maintain constant recruitment is 17.75. If the egg mortality rate is assigned a value of 10, the larvae mortality rate necessary to maintain constant recruitment is 55.47. This value seems unreasonably high; to maintain constant recruitment with low egg mortality a very high larvae mortality is necessary.

First, the relation between egg survival and fishing mortality is examined. From equation (2),

$$M_1 = \frac{-1}{\Delta t_1} \left[M_2 \Delta t_2 + M_3 \Delta t_3 + \ln \left(\frac{R}{p B E} \right) \right]$$

Application of this equation shows that change in egg mortality is potentially a powerful compensatory mechanism, whether egg mortality is high or low relative to larvae mortality (Fig. 5). The observed fishing mortality in northern Lake Michigan could be offset by a small decrease in egg mortality.

Egg mortality, as formulated in the model, consists of several separate factors that include: the proportion of mature females that spawn, the proportion of

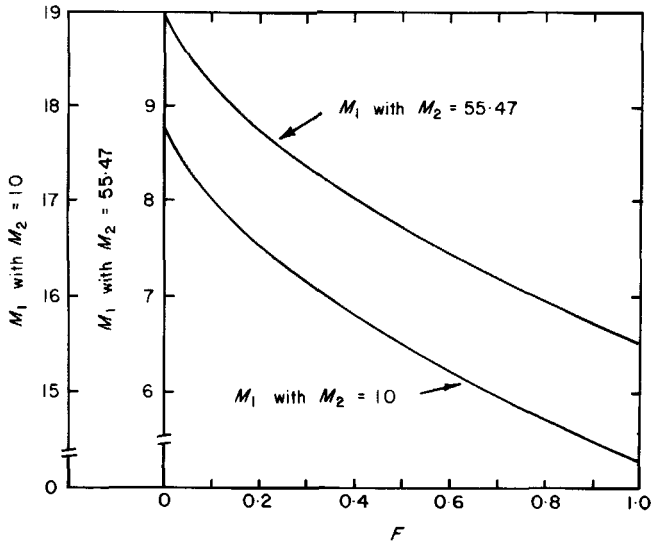


FIG. 5. Decrease in egg mortality necessary to compensate for fishing mortality. Curves are plotted for two different levels of egg mortality under exploited conditions ($M_1 = 17.7$ and $M_1 = 10$).

spawned eggs that are viable, the proportion of viable eggs fertilized and survival of fertilized eggs. For study of regulatory mechanisms, the impact of the first three factors alone is of interest. Survival of eggs can be written as

$$e^{-M_1 \Delta t_1} = p_1 p_2 p_3 e^{-M'_1 \Delta t_1},$$

where p_1 = proportion of mature females that spawn; p_2 = proportion of eggs produced that are viable; p_3 = proportion of viable eggs fertilized and M'_1 = egg mortality coefficient adjusted for the above factors.

The three proportions above were combined into one proportion denoted as p_s . The relation between this proportion and biomass is

$$p_s = \frac{R \exp(M'_1 \Delta t_1 + M_2 \Delta t_2 + M_3 \Delta t_3)}{p B E}$$

The value of p_s without exploitation was set at 0.075, which occurs if in an unexploited population $p_1 = 0.50$, $p_2 = 0.50$ and $p_3 = 0.30$. These are reasonable values for p_1 and p_3 (Van Oosten, 1956; Hart, 1930; Kennedy, 1953; Quadri, 1955). Values for p_2 have not been reported. These three factors acting together have a substantial potential for compensation (Fig. 6).

For larvae mortality, from equation (2), solving for M_2 gives

$$M_2 = \frac{-1}{\Delta t_2} \left[M_1 \Delta t_1 + M_3 \Delta t_3 + \ln \left(\frac{R}{p E B} \right) \right].$$

Application of the above equation indicates that if egg mortality is high compared to larvae mortality, change in larvae mortality affords little compensation for an increase in exploitation (Fig. 7). If egg mortality is

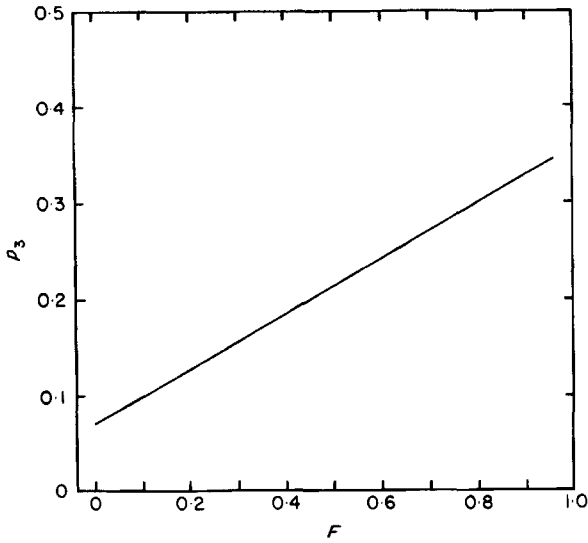


FIG. 6. Increase in the combined proportion p_3 , which is the proportion spawning \times proportion of viable eggs \times proportion of eggs fertilized, necessary to compensate for fishing mortality.

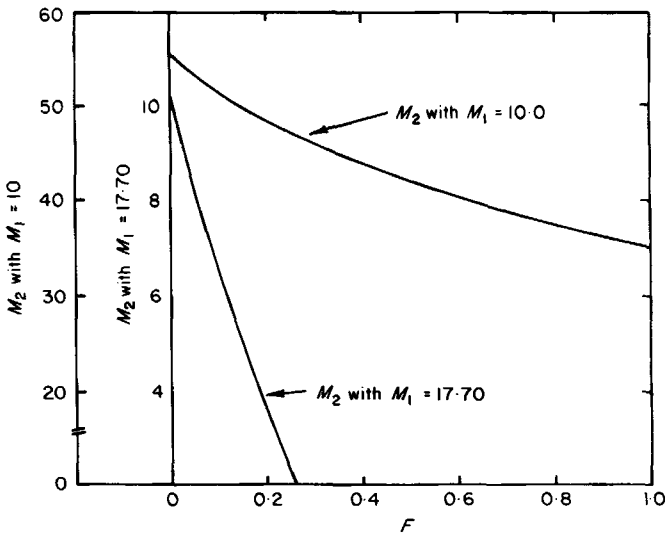


FIG. 7. Decrease in larvae mortality necessary to compensate for fishing mortality. Curves are plotted for two different levels of mortality under unexploited conditions ($M_2 = 10$ and $M_2 = 55.57$).

low compared to larvae mortality, change in larvae mortality becomes a potentially powerful compensatory mechanism (Fig. 7).

Change in age at maturity increases the biomass of the spawning stock to offset the biomass lost to the fishery. If the age at maturity is larger than the age at entry into the fishery, which is true for lake whitefish, the biomass of the mature stock, denoted as $B(F, x_m)$, is given by

$$B(F, x_m) = \int_{x_m}^{\infty} N(x)W(x) dx,$$

which, after substitution for $N(x)$ and $W(x)$ and integration gives

$$B(F, x_m) = W_{\infty}R \exp [-M(x_c - x_r) - (F + M)(x_m - x_c)] \sum_{n=0}^3 \frac{U_n e^{-nK(x_m - x_0)}}{F + M + nK}.$$

The above equation cannot be solved to express the age at maturity, x_m , in terms of F , so for a range of F values Newton's method was applied to find a value of F such that $B(F, x_m) - B(O, x'_m) = 0$, where x'_m is the age of maturity without fishing. Change in age at maturity is potentially a powerful compensatory mechanism (Fig. 8).

Change in the growth rate also increases the biomass of the mature stock. The biomass equation [equation (1)] cannot be solved to express the growth rate, K , as a function of fishing mortality so Newton's method was applied to calculate F for a range of K values such that $B(O, K') - B(F, K) = 0$, where K' is the growth coefficient without a fishery. Assuming $K' = 0.20$, change in the growth rate alone could compensate for a low rate of exploitation (Fig. 8).

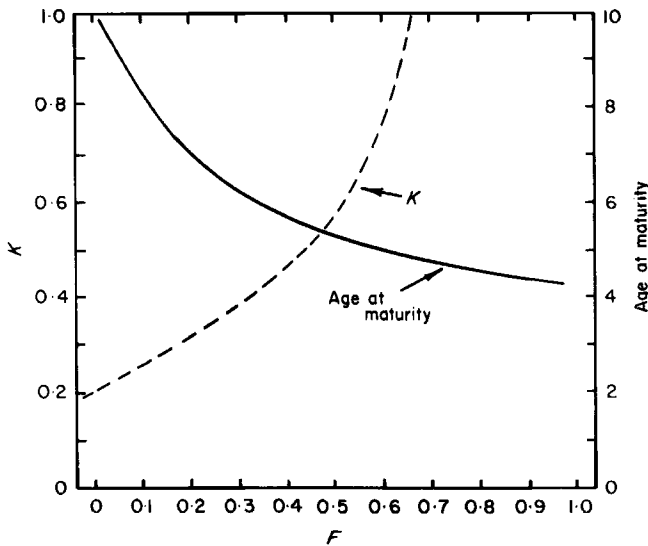


FIG. 8. Increase in the growth rate and decrease in the age of 50% maturity of females necessary to compensate for fishing mortality.

IV. DISCUSSION

Exploitation causes large changes in the age structure and reproductive potential of a population. Density dependent compensatory mechanisms operate to maintain the balance of recruitment and mortality. Annual mortality rates for

lake whitefish range from 0.06 to 82% (Table II). Yet all of these populations sustain themselves—they neither increase without limit nor become extinct. Studies of lake whitefish populations from widely different environments (references cited in Tables II, III, IV & V) indicate three different population types. In heavily exploited populations from large lakes the values of K are intermediate, asymptotic lengths are high and lengths at maturity are high, but ages at maturity are low. In large northern lakes with unexploited populations the values of K are low, asymptotic lengths are low and ages at first maturity are high. Populations in highly exploited small lakes have high K values, early ages at maturity and lower asymptotic lengths than populations in unexploited large lakes. In all environments, exploitation is associated with faster growth and an earlier age at maturity.

Exploitation reduces intraspecific competition and results in faster growth (Healy, 1980). Rapid growth of individuals under the favourable conditions produced by exploitation could trigger mechanisms that might exist to produce more female offspring. Under heavy exploitation a substantial increase in the proportion of females was reported for chubs, *Coregonus hoyi*, in Lake Michigan, a species closely related to lake whitefish (Brown, 1970). The observed proportions of females among many populations of lake whitefish (Table III) indicates a high variation but changes in the proportion of females over the proportions observed could compensate little for exploitation. This is not an important mechanism.

Increase in the growth rate alone could result in only a small degree of compensation (Fig. 8) and the observed variation in growth rate indicates that change in growth alone cannot be an important compensatory mechanism. However, an increase in the growth rate is related to increased fecundity and a lower age at maturity. Fecundity is easy to measure and it has been extensively studied.

Better conditions for growth, produced by a decrease in intraspecific competition resulting from exploitation, do produce a higher age specific fecundity in lake whitefish (Healey, 1980). Several laboratory studies have shown that egg production is related to the ration of the adults for a range of fish species. Bagenal (1969) showed that increased food consumption resulted in increased fecundity of brown trout, *Salmo trutta*, Wootton (1973) demonstrated that a higher ration produced an early age at maturity, a larger proportion of spawners and a higher age specific fecundity in stickleback, *Gasterosteus aculeatus*. Size or weight of eggs did not change. Smith *et al.* (1978) found increased fecundity and larger eggs in fathead minnows, *Pimephales promelas*, fed larger rations. Larger females produced larger eggs. Schoenherr (1977) showed fecundity of gila topminnows, *Poeciliopsis occidentalis*, increased with food supply. In lake whitefish there is a wide range in egg production per unit of biomass (Table IV) but change in fecundity can provide only a small capacity to compensate for exploitation (Fig. 4). Change in fecundity is not an important compensatory factor in lake whitefish.

There is much variation in the age of maturity among various stocks of lake whitefish (Table VI). The age at which 50% of females mature varies from ages 2.5 to 11. The two unexploited populations have ages of 50% female maturity of 11 and 9.2, whereas the heavily exploited stocks in the Great Lakes have an age of 50% maturity of about 3 or 4 (Table VI). Among 14 populations for which data

TABLE II. Total mortality rates, Z, for several exploited and unexploited lake whitefish populations

Locality	Z	Exploited	Reference
Shakespeare Lake	0.20	no	Ricker (1947)
Lake Superior	0.30*	no	Edsall (1960)
Lake Nipigon	0.45	no	Ricker (1947)
Great Bear Lake	0.54	no	Kennedy (1949)
Hottah Lake	0.62	no	Wong & Whillans (1973)
Lake Opeongo	0.65*	no	Ricker (1947)
Alexie Lake	0.65	no	Healey (1975)
Chitty Lake	0.78	no	Healey (1975)
Baptiste Lake	0.82	no	Healey (1975)
Drygeese Lake	0.82	no	Healey (1975)
Nueltin Lake	0.84	no	Kennedy (1963)
MacEwan Lake	1.35	no	Kennedy (1963)
Lake La Ronge	0.69	yes	Quadri (1968)
Lake Ontario	0.73	yes	Christie (1963)
Great Slave Lake	0.84*	yes	Kennedy (1953)
Great Slave Lake	0.87*	yes	Bond & Turnbull (1973)
Buck Lake	0.89	yes	Bidgood (1972)
Red Lakes	0.65	yes	Peterka & Smith (1970)
Lake Winnipeg	0.51	yes	Kennedy (1954)
Lake Winnipeg	1.56	yes	Davidoff <i>et al.</i> (1973)
Lake La Martre	1.05	yes	Bond (1973)
Lake Huron	0.97	yes	Cucin & Regier (1965)
Lake Huron	1.47	yes	Budd (1956)
Pigeon Lake	1.08	yes	Bidgood (1972)
Pigeon Lake	1.39*	yes	Miller (1947)
Lake Erie	1.24	yes	Van Oosten & Hile (1947)
Lake Erie	1.35	yes	Lawler (1965)
Lake Huron	0.82	yes	Budd (1956)
Lake Huron	2.21	yes	Spangler (1970)
Lake Huron	2.66	yes	Budd & Cucin (1962)
Lake Michigan	2.81	yes	Roelofs (1958)
Lake Michigan	1.00*	yes	Jensen (1979)

*Mortality rates applied together with corresponding growth rates of Table V to estimate regression equation parameters (Fig. 10).

TABLE III. Female proportions of spawning stocks of lake whitefish

Location	Proportion	Reference
Shakespeare Lake	0.46	Hart (1931)
Great Slave Lake	0.51	Kennedy (1953)
Lake La Ronge	0.48-0.51	Quadri (1968)
Lesser Slave Lake	0.37-0.69	Bell <i>et al.</i> (1977)
Lake Superior	0.48-0.86	Dryer (1964)
Lake Superior	0.50-0.55	Edsall (1960)
Lake Erie	0.41-0.57	Van Osten & Hile (1947)
Trout Lake, WI	0.62	Hile & Deason (1934)

on growth rates and age at maturity are available, there is a close relation between these variables (Fig. 9). The equation

$$x_m = -1.73 - 3.85 \ln K$$

fits these data well. The regression is significant ($P < 0.0012$) with a coefficient of determination of $R^2 = 0.60$. On the average, an increase in the growth rate results in a lower age at maturity. For six populations for which data are available (Tables II, V) there is also a close relation between the total mortality rate and the growth rate (Fig. 10). The equation

$$\ln K = -3.15 + 1.75 Z$$

fits these data well. The regression is significant ($P < 0.008$) and the coefficient of determination is $R^2 = 0.86$. These results indicate that over a wide range of environments an increase in the total mortality rate results in a higher rate of growth which results in an earlier age at maturity. This same result was reported for brook trout, *Salvelinus fontinalis* (Jensen, 1971).

A decrease in the age of maturity from 10 to 4 or 5 will offset a large increase in fishing mortality (Fig. 8). The entire fishing mortality experienced by whitefish in northern Lake Michigan could be more than offset by a decrease in age at maturity if the age at maturity was 10 in the absence of a fishery. Change in age at maturity is potentially a powerful compensatory mechanism and observed variation in age at maturity (Table VI) indicates that this may in fact be an important mechanism.

In the fisheries literature, a decrease in larvae mortality is assumed to be the major mechanism of compensation for exploitation (Beverton & Holt, 1957). This does not appear to be the case for lake whitefish. Under reasonable conditions of high egg mortality and low larvae mortality, change in larvae mortality can compensate little for fishing (Fig. 7). Change in egg mortality has a

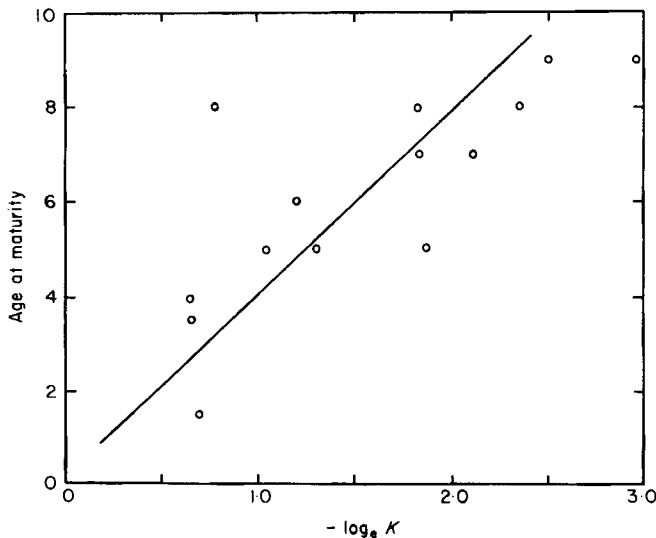


FIG. 9. Relation between growth coefficient and the earliest age at maturity for several populations of lake whitefish.

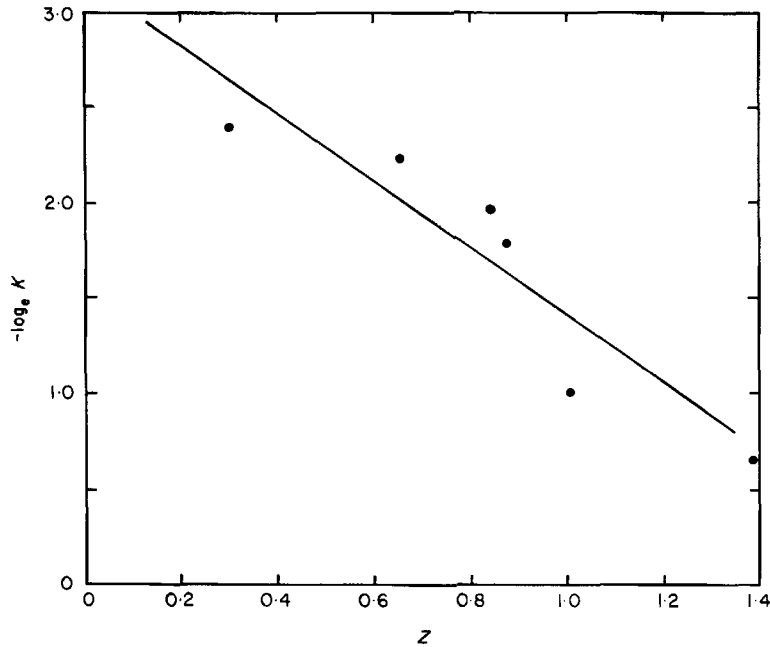


FIG. 10. Relation between instantaneous total mortality rate and growth coefficient (data from Tables II, V).

much larger potential for compensation than change in larvae mortality, even when egg mortality is low.

Egg mortality was separated into several components. One component is the actual survival of the fertilized eggs. The remaining components are the proportion of females spawning, viability of eggs and percentage of eggs fertilized. This second group of components can be influenced by the conditions of growth experienced by adult whitefish. There is considerable variation in these components. In two studies, successful fertilization ranged from 30 to 100% (Van Oosten, 1956) and from 62 to 100% (Hart, 1930). Kennedy (1953) and Quadri (1955) reported that about 50% of mature females spawned annually in unexploited populations. Assuming that under unexploited conditions $p_1 = 0.5$,

TABLE IV. Egg production per unit of female biomass of lake whitefish

Location	Eggs per Unit Biomass ($\text{kg} \times 10^{-3}$)	Reference
Lake Ontario	21.8	Christie (1963)
Lake Erie	34.3	Lawler (1961)
Lake Huron	17.0	Cucin & Regier (1965)
Lake La Ronge	15.8	Quadri (1968)
Hunter Bay	19.9	Quadri (1968)
Small Alberta Lake	18.0	Bidgood (1973)
Small Alberta Lake	27.7	Bidgood (1973)

TABLE V. Parameters for the von Bertalanffy growth equation for several different lake whitefish populations

Locality	W_{∞}	K	x_0	Reference
Lake Superior	2.75	0.09	-2.3	Edsall (1960)
Green Bay	3.37	0.31	0.1	Mraz (1964)
Lake Michigan	4.7-5.32	0.20	0.2-0.3	Mraz (1964)
Lake Superior	1.87	0.32	-0.7	Dryer (1964)
Lake Superior	4.67	0.26	-0.2	Dryer (1964)
Lake Superior	5.14	0.24	-0.9	Dryer (1964)
Lake Superior	3.25	0.28	-0.9	Dryer (1964)
Lake Michigan	2.40	0.42	0.9	Brown (1968)
Lake Michigan	3.43	0.31	0	Brown (1968)
Lake Michigan	3.80	0.30	0	Brown (1968)
Pigeon Lake	-	0.52	0.5	Miller (1949)
Lake Wabamung	-	0.42	0.5	Miller (1949)
Great Slave Lake	-	0.14	-	Kennedy (1953)
Great Slave Lake	-	0.17	-	Bond & Turnbull (1973)
Trout Lake	-	0.10	-	Hile & Deason (1934)
Great Bear Lake	-	0.09	-	Kennedy (1949)
Lake Openongo	-	0.11	-	Kennedy (1943)
Cliff Lake	-	0.18	-	Fenderson (1964)
Lake Openongo	-	0.61	-	Kennedy (1943)
Cliff Lake	-	0.96	-	Fenderson (1964)

TABLE VI. Age at maturity for lake whitefish females

Locality	Earliest age	Age when 50% mature	Reference
Great Bear Lake	6	6.8	Kennedy (1949)
Great Slave Lake	4	6	Healey (1975)
Lake Opeongo	2	4	Kennedy (1943)
Cliff Lake	3	5.2	Fenderson (1964)
Clear Lake	4	4	Fenderson (1964)
Great Slave Lake	5	9.2	Kennedy (1953)
Lesser Slave Lake	4	6.0	Bell <i>et al.</i> (1977)
Lake Superior	5	6.2	Dryer (1964)
Lake Superior	10.0	11	Edsall (1960)
Lake Michigan	-	4.2	Brown (1968)
Lake Michigan	2	2.5	Brown (1968)
Green Bay	3	3	Mraz (1964)
Lake Erie	3	3	Van Oosten & Hile (1947)
Lake Huron	3	6	Van Oosten (1939)
Lake Opeongo	1	1	Kennedy (1943)
Cliff Lake	1	1	Fenderson (1964)

$p_2=0.5$ and $p_3=0.3$, change in these parameters has a large potential for compensation (Fig. 6).

If population size is regulated by conditions of growth in the mature stock, it is necessary for compensation to occur through factors other than survival of eggs and larvae. Unless production of young is so great that crowding or cannibalism are important factors, the conditions experienced by adult fish should not impact on mortality rates of eggs and larvae.

Except for larvae and egg mortality, the mechanisms of compensation examined here are related to the conditions of growth of the mature stock. This creates a feedback mechanism for regulation of population size relative to the availability of resources for growth of individuals in the mature stock. For example, because age at maturity is dependent on size there is feedback between the mortality rate, which acts on growth, and reproduction. Increased mortality reduces intraspecific competition and increases growth which results in a younger age at maturity and perhaps an increased age specific fecundity. A favourable environment for growth of mature females also might result in higher quality eggs, a greater proportion of females spawning and a larger number of fertilized eggs. These factors acting alone or together, without aid of a decrease in larvae or egg mortality, could more than compensate for the observed level of fishing in northern Lake Michigan. These mechanisms would provide whitefish with a mechanism to respond quickly to changes in the environment that either enhance or diminish the conditions for growth.

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