

EVALUATING THE CONSEQUENCES OF REPRODUCTION IN COMPLEX SALMONID LIFE CYCLES

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ABSTRACT

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Reproduction by individuals at different stages in the life cycle contributes differentially to population growth. This paper shows how to evaluate these contributions in complex life cycles, in which individuals may be classified by size or developmental stage as well as age. Population growth is measured by the maximum eigenvalue of a projection matrix corresponding to a life cycle graph. The sensitivity of this eigenvalue to changes in reproduction can be expressed as a simple function of the demographic parameters describing the life cycle. The sensitivity of growth rate to reproduction declines with age, at a rate which is inversely proportional to survival and directly proportional to growth rate itself. The importance of alternate developmental pathways is related to the reproductive values of the stages to which those pathways lead. The latter observation is used to examine the possibility that natural selection in response to increased fishing pressure at sea is responsible for the recent increase in precocious maturation by male parr in the Atlantic salmon (*Salmo salar*) of the Matamek River, Quebec.

INTRODUCTION

Reproduction obviously contributes to population growth, and if the life cycle of an organism includes reproduction by different developmental stages, one may expect these stages to contribute differentially to that growth. This paper shows how to evaluate the relative magnitude of these contributions, with application to the complex life cycles of salmonid fishes. These methods are potentially useful to aquaculturists and population managers concerned with maximizing yield by manipulating reproductive output. They also have important evolutionary implications, since the relative contribution of a reproductive pathway to population growth is also its relative contribution to individual fitness. Natural selection is expected to act upon the life cycle in response to the pattern of these contributions. At the end of this paper, we will use this approach to examine the possibility that recent shifts in the life cycle of a population of Atlantic salmon (*Salmo salar*) may be due to such selection.

METHODS

To assess the sensitivity of population growth rate to reproduction, we will utilize a demographic theory which describes the life cycle in graphical form (Fig. 1). For detailed discussion of this theory, see Caswell (1978, 1982a,b, 1985) and Hubbell and Werner (1979). Schaffer (1979) has applied similar methods to salmonid life cycles. Each node in the life cycle graph represents a demographically relevant stage in the life cycle. In traditional life table analysis, these stages are age classes, but many organisms (including salmonids) are more appropriately classified by such other factors as size or developmental stage. The arrows connecting the nodes indicate the transitions open to an individual during one time interval.

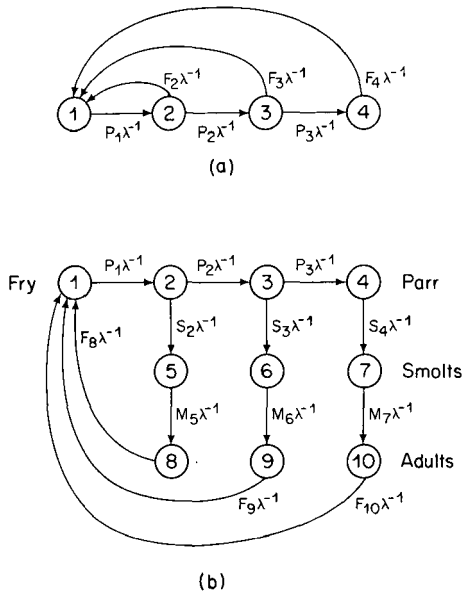


Fig. 1. Two life cycle graphs. (a) A simple age classified population. The numbered nodes represent age classes, P_i is the survival probability and F_i the per-capita reproductive output of an i -year old. (b) A more complex graph representing the life cycle of an anadromous, semelparous salmonid. P_i denotes survival probability, S_i the probability of survival and smoltification, and M_i the probability of successful maturation and survival to spawning.

The coefficients on the arrows contain two components, one relating to population growth, the other describing the transition probability. The asymptotic population growth rate implied by the conditions described by the graph is denoted by λ ; the negative exponent (e.g., $-\alpha$) on λ is the number of time units required for the transition. The coefficient multiplying $\lambda^{-\alpha}$ gives the number of individuals in the recipient stage at time $t+\alpha$ per individual in the donor stage at time t ; it may be a survival probability or a measure of reproductive output, depending on the transition.

This graph is equivalent to a matrix population model of the type developed by Leslie (1945) and later expanded to classification by stage rather than age (Lefkovich, 1965). The population growth rate λ is the maximum eigenvalue of the matrix, and is found by solving the characteristic equation, which may be derived from the matrix or from the graph (Hubbell and Werner, 1979; Caswell, 1982a). The stable stage distribution is given by the corresponding right eigenvector w and the reproductive value distribution by the left eigenvector v . These eigenvectors may be evaluated numerically by readily available computer algorithms, or their general formulae may be written down directly from the graph (Caswell, 1982a).

The value of λ reflects the total structure of the life cycle graph. The contribution of each transition to population growth can be evaluated by determining the sensitivity of λ to a change in the corresponding transition coefficient. This sensitivity can be expressed in terms of the eigenvectors; given w and v we can write down the sensitivity of λ to changes in any coefficient in the matrix (Caswell, 1978, 1985). For a coefficient a_{ij} representing a transition from node j to node i (note order of subscripts), we have

$$\partial\lambda/\partial a_{ij} = v_i w_j / \langle w, v \rangle \quad (1)$$

if the transition requires only a single time step and

$$\partial\lambda/\partial a_{ij} = \lambda^{-\alpha+1} v_i w_j / \langle w, v \rangle \quad (2)$$

if it requires α time steps. In these formulae, $\langle w, v \rangle$ denotes the scalar product of w and v ; since this is constant for a given life cycle it cancels out of comparative calculations.

Space does not permit us to discuss in detail the calculation of w and v from the life cycle graph (see Caswell, 1982a,b, 1985). However, the following simplified formulae are valid for life cycles (including those to be considered here) in which all reproductive pathways pass through a single stage. The entries w_i of w are given by

$$w_1 = 1 \quad w_x = \sum T_{1x}^i \quad (3)$$

and the entries v_i of v are given by

$$v_1 = 1 \quad v_x = \sum T_{x1}^i \quad (4)$$

In these formulae, the following definitions apply: (a) T_{1x}^i is the transmission of the i th path between node 1 and node x , calculated by multiplying coefficients along the path and absorbing "self-loops" at any node by dividing all incoming arrows by $(1 - \text{self-loop coefficient})$; (b) T_{x1}^i is the transmission of the i th path from n_x back to n_1 , calculated as in (a) except that self-loops are absorbed by dividing all outgoing arrows by $(1 - \text{self-loop coefficient})$.

The interpretation of (3) and (4) is biologically reasonable; the abundance of any stage in the stable stage distribution depends on the success of individuals in getting from birth (n_1) to that stage. The reproductive value

of a stage depends on its success in transmitting new individuals to n_1 . In both cases, the contributions of all possible pathways are summed.

We will now apply these analyses to three different life cycle graphs. Our primary concern is to demonstrate the method and derive general conclusions; these models are not intended as detailed descriptions of real populations.

APPLICATIONS

A simple age classified model

The life cycle in Fig. 1(a) describes an age classified population, with no alternative developmental pathways. The reproductive output terms F_i connect stage i and stage 1, so from (1) we know that the sensitivities $\partial\lambda/\partial F_i$ are proportional to the elements in the stable age distribution (i.e., $\partial\lambda/\partial F_i = v_1 w_i / \langle w, v \rangle$). From (3) the stable age distribution is given by

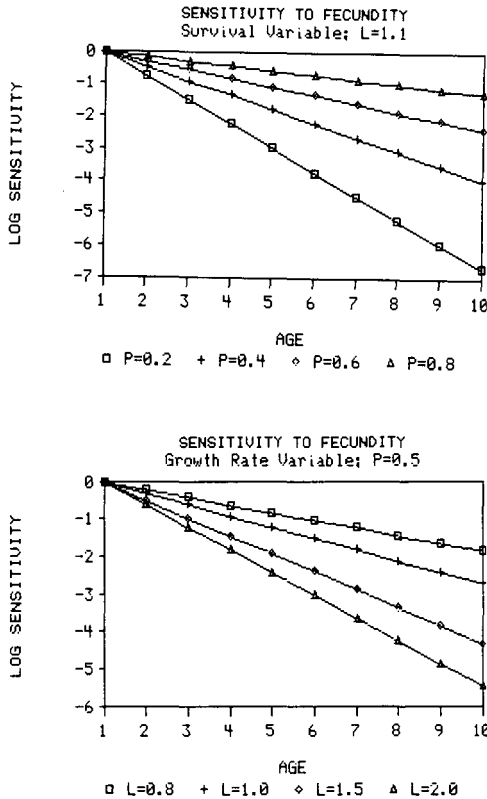


Fig. 2. Relative sensitivity of λ to changes in age specific fecundity for an age classified population as a function of survival rate P and population growth rate λ (denoted by L in the figures). The importance of reproduction to λ falls off exponentially with age, at a rate which is inversely proportional to P and directly proportional to λ .

$w_1 = 1$, $w_x = P_1 P_2 \dots P_{x-1} \lambda^{-x+1}$. As long as $\lambda > 1$, abundance in the stable age distribution is a decreasing function of age. Thus reproduction at later ages always has a smaller impact on λ than that at earlier ages. The difference can be dramatic; a survey of laboratory life table data for a variety of organisms (Caswell, 1978, 1985) shows that the decline in sensitivity with age is roughly exponential, and may span as much as 7 orders of magnitude. Fig. 2 shows a calculation of the effects of changes in λ and P for a simple case in which the survival probability is age-invariant.

This conclusion is independent of the details of the life cycle, as long as it can be graphed in the form in Fig. 1(a). Indeed, the conclusion that $\partial\lambda/\partial F_i$ is proportional to w_i is true in general, regardless of the life cycle.

An anadromous salmonid life cycle

Fig. 1(b) is an idealized model for an anadromous semelparous salmonid. The stages of the life cycle are parr of several ages, which survive as parr with probabilities P_i and survive and smoltify with probabilities S_i . The smolts survive to maturity, with probability M_i , and the resulting adults have reproductive outputs F_i which may depend on the age at which they went to sea.

The relative sensitivity of λ to changes in the F_i is directly proportional to w_8 , w_9 , and w_{10} . From this and from the fact that w is calculated by summing the transmissions of pathways from n_1 to n_x it follows that the relative importance of reproduction by the three reproductive classes depends on the survival probabilities of the parr and smolts. If survival probability is low, w_{10} will be much less than w_9 , which in turn will be much less than w_8 ; the sensitivities of λ to F_{10} , F_9 , and F_8 follows the same trend.

The growth rate of the population also has an important effect, since more rapidly growing populations tend to be more dominated by young individuals. Thus reproductive output itself, by altering λ , can affect the sensitivity to reproduction. As an example of this effect, a set of arbitrary survival probabilities and fecundities were inserted into Fig. 1(b), the sensitivities were calculated numerically, and the results are shown in Fig. 3(a).

Note that this method can evaluate the sensitivity of population growth to reproduction which is, at the time of the evaluation, only potential. In Fig. 1(b), for example, there is no reproduction by parr (n_2-n_4), but we can directly calculate the way in which λ would change if such reproduction were to be added.

Within the adult age classes, λ is most sensitive to F_8 ; the effects of F_9 and F_{10} are about equal and an order of magnitude less. Sensitivity within the parr follows the same pattern. The effect of reproduction by parr is always greater than that of adult reproduction. As fecundity increases, thereby increasing λ , the absolute sensitivity decreases, but the disparity between the different sensitivities increases.

The parameters used in this model gave the adult stages quite different

fecundities (in a ratio of 1:15:20). In such situations, a direct comparison of sensitivities may be misleading, since a unit change in F_8 represents a much greater proportional change than does the same unit change in F_{10} . This can be taken into account by calculating the proportional change in λ caused by a proportional change in F_i , which is given by $\partial \ln \lambda / \partial \ln F_i = (F_i / \lambda) \partial \lambda / \partial F_i$. These proportional sensitivities are known as elasticities in the economics literature. When the elasticities of F_8 – F_{10} are calculated, the results are as shown in Fig. 3(b). They vary much less than the corresponding sensitivities, and their rank order, in contrast to that of the sensitivities, changes as λ increases.

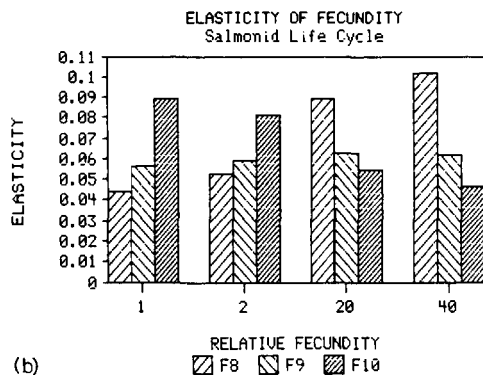
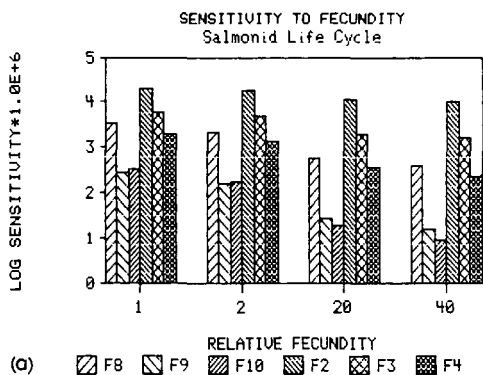


Fig. 3. (a) Sensitivities of λ to changes in F for the salmonid life cycle in Fig. 1(b). Parameter values were set at $P_1=0.1$, $P_2=P_3=0.3$, $S_2=0.3$, $S_3=0.2$, $S_4=0.5$, $M_5=0.5$, $M_6=0.2$, $M_7=0.3$, and fecundities were set in a ratio $F_8:F_9:F_{10}=1:15:20$, with the absolute magnitude varied over a range of values as indicated on the abscissa (1 corresponds to $F_{10}=250$). (b) Elasticities, or proportional sensitivities, of λ to reproductive output.

Precocious maturation by male parr

The previous examples showed the relative importance of reproduction given that the individuals had in fact reached the stage in question. We can

also examine the contribution of alternate developmental pathways by which an individual may arrive at reproduction.

Such alternate pathways are found in male Atlantic salmon, which may mature precociously as parr, sometimes at very high frequencies (Jones, 1959; Dalley et al., 1983), or normally as sea-run adults. Between 1967 and 1982, the Atlantic salmon population of the Matamek River (on the north shore of the Gulf of St. Lawrence in Quebec) exhibited a significant increase in precocious maturation (Montgomery et al., in prep.), from 31% to 75%.

Of the several hypotheses proposed to explain this life history shift (Montgomery et al., in prep.) one is based on natural selection. Intense fishing pressure at sea should, all other things being equal, favor genotypes which avoid that mortality by maturing in the river. All other things are not equal, of course. Presumably the costs of precocity include decreased reproductive output associated with small size and increased mortality due to the investment of energy in gonad development (Leyzerovich, 1973; Mitans, 1973). Selection will respond to the net balance of these costs and benefits. On this hypothesis, for example, the failure of females to mature as parr is due to the fact that eggs are more energetically costly than sperm, and hence that small size is more expensive to a female than a male.

In the absence of information on the genetic structure of the Matamek River population, we cannot directly evaluate the genetic component of the observed phenotypic shift. We can, however, evaluate the plausibility of selection as an explanation, by examining the balance between the costs and benefits of precocious maturation. The operation of selection requires only genetic variation and selective advantage; since genetic variation in precocity is known to exist (Thorpe et al., 1983; Gjedrem, 1984; Iwamoto et al., 1984), we can focus our attention on the selective advantage, measured by the net effect on fitness (λ), of an increase in precocity.

Fig. 4 shows a stylized life cycle graph for a male Atlantic salmon. Fry mature precociously with probability M , or undergo normal development with probability $(1-M)$. It requires α years to develop to the smolt stage and β years to develop to precocious maturity. For simplicity, we have made the conservative assumption that precocious males do not subsequently smoltify and reproduce as adults. We will assume that the annual survival rate for immature parr is given by ϕ , regardless of an individual's eventual maturity, so that $P_1 = \phi^\alpha$ and $P'_1 = \phi^\beta$. There is some evidence that precocious parr experience heavier mortality than immature parr. Leyzerovich (1973) found that the survival of precocious males held in large tanks was 88–95% of that of immature males. Mitans (1973) estimated precocious male survival, based on the age distribution and sex ratios of parr and smolts in the field, at 55–57% that of immature males. Under at least some hatchery conditions, however, the difference becomes negligible (Saunders et al., 1982). Based on these reports, we set $P_4 = c\phi$, where the parameter c ($0 \leq c \leq 1$) measures the extent to which precocity reduces survival.

Our task is to calculate $\partial\lambda/\partial M$. Since M appears in both a_{21} and a_{41} , we have

$$\partial\lambda/\partial M = P'_1\partial\lambda/\partial a_{41} - P_1\partial\lambda/\partial a_{21}$$

which can be evaluated using (2) as

$$\partial\lambda/\partial M = (P'_1\lambda^{-\beta+1}w_1v_4 - P_1\lambda^{-\alpha+1}w_1v_2)/\langle w, v \rangle$$

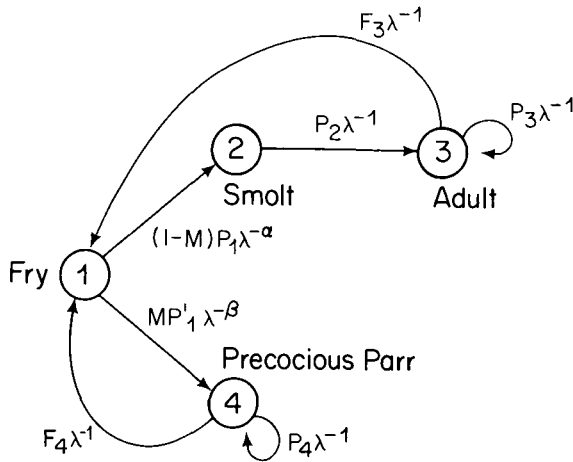


Fig. 4. A life cycle graph for male Atlantic salmon, including precocious maturation of parr. The analysis in this paper assumes $P_3 = 0$.

Selection favors an increase in M if $\partial\lambda/\partial M > 0$. This is determined by the relative magnitude of v_2 and v_4 , which can be obtained directly from the graph ($v_2 = P_2F_3\lambda^{-2}$, $v_4 = F_4/(\lambda - P_4)$), using (4). The resulting equations can be arranged in a number of ways; since it is intuitively clear that the net selective pressure will be influenced by the relative reproductive outputs of the two stages, in relation to the survival at sea and in the river, we choose to express the conditions for $\partial\lambda/\partial M > 0$ as

$$F_4/F_3 > P_2[\phi^{\alpha-\beta}\lambda^{\beta-\alpha-2}(\lambda - c\phi)] \quad (5)$$

Estimates of some of these terms are available. The average age of smolts leaving the Matamek River over the last 15 years is close to 3, so we will take $\alpha=3$ as first approximation. In a sample of 1375 male parr from the Matamek River, pooled over the period 1967–1982, the proportion mature as a function of age were: age 1+: 26% ($n=469$), 2+: 55% ($n=758$), 3+: 84% ($n=125$), 4+: 100% ($n=133$), 5+: 100% ($n=5$). Since close to 50% of the 2+ parr were mature, we will take $\beta=2$ as a first approximation to the median age at maturity of precocious parr.

Using $\alpha=3$ and $\beta=2$, (5) simplifies to

$$F_4/F_3 > P_2[\phi\lambda^{-3}(\lambda - c\phi)] \quad (6)$$

Unless the population is increasing or decreasing very rapidly (and the Matamek River population does not seem to be), we can set $\lambda \approx 1$, and (6) reduces to

$$F_4/F_3 > P_2\phi(1-c\phi) \quad (7)$$

Fig. 5 shows this critical value of F_4/F_3 as a function of P_2 , ϕ , and c . Rough estimates of P_2 are available for some Atlantic salmon stocks. Chadwick et al. (1978) estimate that approximately 3.5% of a year class of Newfoundland smolts survive natural and fishing mortality to spawn. Reddin (1981), in an analysis of Labrador and Newfoundland stocks, estimates an annual exploitation rate of 40–70%, and a natural mortality rate of about 80%, implying an overall survival rate in the neighborhood of 8%. Thus it seems that we can take 0.05–0.1 as a reasonable range for P_2 . Based on the estimates cited above, the cost of precocious maturation (c) appears to fall in the range 0.5–1.0. Estimates of parr survival rates (ϕ) seem harder to obtain. Figures in Dymond (1963) suggest values in the order of 0.1–0.5. From Fig. 5, we see that the ratio F_4/F_3 must be in the range 0.03–0.1 for selection to favor precocity.

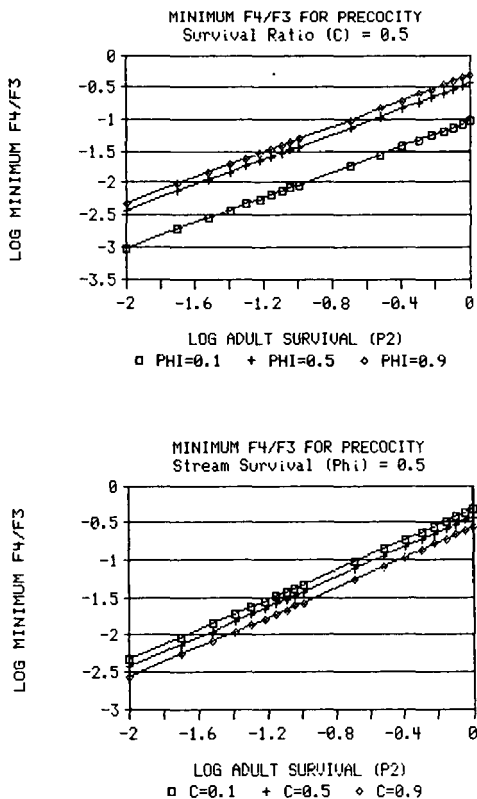


Fig. 5. Critical value of the ratio of precocious parr to adult male fecundity (F_4/F_3) required in order for natural selection to favor an increased incidence of precocity, as a function of adult survival at sea (P_2), parr survival in the river (ϕ), and the survival cost of precocious reproduction (c). These figures assume that $\lambda \approx 1.0$.

Estimating the fecundity of male parr and adults is very difficult. Given that precocious parr are in much closer contact with the eggs during spawning than is an adult male, a simplistic estimate can be based simply on the relative gonad mass of the two stages. The gonad weight of precocious male parr in the Matamek River reaches a peak in September, averaging $4.05 \text{ g} \pm 0.26 \text{ g}$ ($n=87$). We have insufficient data to estimate adult male gonad weight in the Matamek River, but based on a typical gonadosomatic index of 5% (S. McCormick, pers. commun., 1984) and a typical body weight of 2 kg, a figure of 100 g is probably not far off as a rough estimate of gonad weight. Thus we estimate that $F_4/F_3 \approx 0.04$.

On this basis, we conclude that the relative fecundities of parr and adults are such that natural selection under recent conditions of mortality at sea should in fact favor an increased incidence of precocity. We can use these figures to calculate the threshold value of P_2 which will trigger this selection. If $F_4/F_3 = 0.4$, and taking $c = \phi = 0.5$, we find that the critical value for $P_2 \approx 0.11$. Interestingly, Murray (1958) and Carlin (1955) give estimates of the return of tagged smolts (in Newfoundland and Sweden, respectively) in the early nineteen-fifties which imply P_2 values in the range 0.14–0.19. If these are an accurate reflection of conditions prior to recent increases in oceanic exploitation, they suggest that the increase in precocity would have been triggered recently, as the Matamek River data suggest.

Models of this sort make many assumptions; they should properly be regarded not as quantitative descriptions of the population, but rather as means for exploring the qualitative consequences of the structure of the life cycle. Of the three most questionable assumptions, two have little effect on the validity of our conclusions. First, we have ignored the possible effects of density on the life cycle parameters. However, our assumption that $\lambda \approx 1$ is equivalent to examining the selective pressures on precocity at equilibrium, if density dependence is important. Second, our analysis ignores frequency dependent effects arising from the interaction of the sexes. The analysis is based on the life cycle graph of a male salmon; obviously the per-capita fecundity of a male eventually depends on the relative abundance of males and females. Indeed, since females will not spawn with precocious parr in the absence of a mature male, there is the potential for a three-way frequency dependent interaction between adult males, precocious parr, and adult females. By ignoring this frequency dependence, we are tacitly assuming that females are present in sufficient numbers that their abundance is not limiting to adult male fecundity, and that mating male–female pairs are present in sufficient numbers that their abundance is not limiting to precocious parr fecundity. We can legitimately make this assumption by focusing attention on the initial stages of the evolution of increased precocity, at which point precocious males are relatively rare, and asking whether the incidence of precocity in this situation should increase. We need not consider here the eventual equilibrium attained when precocious parr become common relative to adult males.

Our most questionable assumption involves the use of λ as a measure of fitness; it requires that the population be at or near its stable structure. This assumption is manifestly false, since the age distribution of the Matamek River population is nowhere near stable (Montgomery et al., in prep.). Moreover, the evolutionary analysis of populations far removed from their stable structures is very much an open problem. In the only case we know of in which the consequences of violating this assumption were examined empirically [a plant population analyzed by Caswell and Werner (1978)], there was very little effect, but it is not known how widely this one example may be generalized.

CONCLUSIONS

We arrive at several general conclusions. The importance of reproduction by different stages is proportional to the representation of those stages in the stable stage distribution, and thus depends on survival probabilities and population growth rate in a predictable manner. The differences may span many orders of magnitude, especially if survival is low or growth rate high. The elasticities of reproduction may show different patterns from the sensitivities. The sensitivity of λ to choices between different pathways to reproduction depends on the relative reproductive values of the target stages. Applying these methods to the Matamek River Atlantic salmon population suggests that natural selection is a plausible explanation for the recent increase in the incidence of precocious maturation of male parr. We believe that these methods have great potential importance in understanding the dynamics of salmonid populations.

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