FOREWORD AND RETROSPECTIVE: LIFE HISTORIES, EVOLUTION AND SALMONIDS[1]

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[1] In memory of Paul F. Elson and Robert H. MacArthur who helped me on my way.

I. Origins of this *Foreword*.

This book is about salmonid fishes and the ways in which studying salmonids can inform general problems in evolution. My own involvement with salmon dates to the fall of 1969 when, at the urging of Professor J. T. Bonner, I attempted to apply my then nascent ideas on life history evolution to the genus *Salmo*. The occasion was the weekly ecology brown bag at which I had been scheduled to speak, and the ensuing discussion focused on the adaptive merits of semelparous *vs.* iteroparous reproduction. Dr. Bonner, it transpired, spent his summers in Nova Scotia where he enjoyed angling for salmon. He was impressed by the tremendous obstacles elsewhere[2] encountered by these fish when they returned from the ocean to spawn. Even though *S. salar* is technically iteroparous, it was apparent that individuals often had but a single crack at reproduction (Belding 1934). I should go to the Maritimes, he proposed; solicit the assistance of P. F. Elson, a fisheries biologist at the research station in St. Andrews; learn about salmon. Perhaps, there were data that would inform the theory I was developing. Perhaps I would gain insight as to why *Oncorhynchus* is obligatorily semelparous and *Salmo* not.[3] And so, when the spring semester ended, I drove north, knowing little enough about the organisms I had chosen to study, but convinced, as only a graduate student can be, that they would doubtless conform to my expectations. In due course, I met Dr. Elson who took me under a fatherly wing. With his assistance and encouragement, data were gathered, the theory refined and results published (Schaffer and Elson 1975; Schaffer 1979a). Thereafter, I moved on to other taxa (Schaffer and Schaffer 1977, 1979) and other questions (Schaffer 1985). Thirty years later, an invitation arrived to write this *Foreword*. Let me begin by thanking the editors for affording me an opportunity to revisit a formative stage in my scientific career.

II. Theory of Life History Evolution.

Nature of the Problem. According Merriam-Webster [http://www.refdesk.com/], demography is the statistical study of human populations especially with reference to size

[2] Nova Scotia's rivers themselves are short, gentle affairs.

[3] At the time, only semelparous species (Pacific salmon) were assigned to *Oncorhynchus* (Neave 1958).

and density, distribution, and vital statistics." Such studies need not be restricted to humans. One can just as well construct life tables for animals (Deevy 1947) and plants (Harper 1977) although in the latter case, especially, the situation may be complicated by ambiguity as to just what constitutes an individual. Such technicalities aside, one of the more interesting aspects of non-human demography is the fact that age-specific schedules of reproduction and mortality can vary dramatically among closely related species and even among populations of the same species. Some of this variation is nothing more than the proximate reflection of differences in environmental quality. But this is not the whole story. Animal and plant life histories are also the products of evolution, having been moulded to a greater or lesser degree by natural selection. Regarding this second source of demographic variation, it is important to bear in mind that characters such as egg size and number, gestation period, generation time, *etc.*, are often correlated with traits such as body size (Bonner 1965; Calder 1984; Schmidt-Nielsen 1984) upon which selection also can act. As a result, inferring the phenotypic targets of past selection can be problematic. It follows that the biologist seeking adaptive explanations of particular life history phenomena is wise to focus on closely allied forms that differ principally with regard to the characters in question. Put another way, the sensible adaptationist, as opposed to ideologically inspired caricatures (Gould and Lewontin 1979) thereof, is guided by the expectation that "*related* species will differ in the direction of their respective optima."[4]

Early Investigations. The late 1960s and early 70s were years of heady optimism for evolutionary ecologists who believed that simple mathematical models could offer a useful accounting of the broad-brush stroke patterns observable in nature (Kingsland 1985). Forever associated with this conviction will be the name of Robert Helmer MacArthur whose Mozartsian career spanned a scant 15 years.[5] Best known for his interest in biogeography (MacArthur and Wilson 1967; MacArthur 1972) and competitive exclusion (May and MacArthur 1972; MacArthur 1958, 1969, 1970; MacArthur and Levins 1967),

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4 This is an amended version of Levins' (1966) "Principle of Optimality," the emendation being addition of the word, "related."

5 Struck down in his prime, MacArthur left the intellectual playing field, like the runner of Housman's poem, never having experienced defeat.

MacArthur also contributed (1962; MacArthur and Wilson 1967) to the *corpus theoretica* now known as the theory of life history evolution (Roff 1992; Stearns 1976, 1977, 1992). This line of inquiry traces to the work of Lamont Cole (1954) who was among the first to advocate a comparative approach to the study of animal demographics. Especially, Cole sought to understand the adaptive significance of divergent schedules of reproduction and mortality, in which regard, he presumed that fitness, the elusive "stuff" of evolution, is usefully approximated by the rate at which an asexual individual and its identical descendants multiply under the assumption of unchanging probabilities of reproduction and survival. As discussed by Leslie (1945, 1948), Keyfitz (1968) and others, this rate is determined by the so-called "stable age equation,"

$$1 = \sum_{i=0}^{n} \lambda^{-(i+1)} \ell_i B_i \qquad (1)$$

where, ℓ_i is the probability of living to age *i*, and B_i is the *effective* fecundity of an *i* year-old.[6,7]

Equation (1) is a polynomial equation of degree *n*+1 from which it follows by the Fundamental Theorem of Algebra that there are *n*+1 (possibly complex and not necessarily distinct) values of λ for which the equality holds. These values are called "roots," and we may arrange them in order of decreasing magnitude, *i.e.*, $|\lambda_1| \geq |\lambda_2| \geq ... \geq |\lambda_{n+1}|$.[8] If one neglects post-reproductive age classes, the Peron-Frobenius theorem (Gantmacher 1959) guarantees that λ_1 is real, positive. Moreover, we can usually replace the inequalities, $\lambda_1 \geq |\lambda_2| \geq ... \geq |\lambda_{n+1}|$, with *strict* inequalities, $\lambda_1 > |\lambda_2| > ... > |\lambda_{n+1}|$, in which case, λ_1

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6 For purposes of exposition, I suppose a time step of a year and further that the population is censused annually. The numbers of individuals in the various age classes are thus the numbers alive at census time. By this accounting, the probability that an individual survives from birth to first census is absorbed by the *B*'s, which become "effective fecundities." Moreover, ℓ_0 necessarily equals 1.

7 In some texts, the rate at which the population multiplies, λ, is replaced by e^r, thereby emphasizing the relation of Eq (1) to its continuous analog, $1 = \int e^{-rx} l_x m_x dx$ (Fisher 1930), in which case, the *m*'s are (no longer effective) fecundities.

8 Recall that the magnitude of a complex number is the square root of the squares of its real and imaginary parts added together, *i.e.*, if $z = x \pm iy$, $|z| = (x^2 + y^2)^{1/2}$.

Cole's Paradox:

Cole asserted that "for an annual species, the absolute gain in intrinsic population growth … achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter." His argument was as follows:

Consider an annual plant, which produces B_a seeds and then dies, and a corresponding perennial which produces B_p seeds and itself survives with probability one to reproduce the following year and again with probability one, the year after that, *ad infinitum*. The annual and its descendants multiply yearly at rate $\lambda_a = B_a$; the perennial and its descendants, at rate $\lambda_p = B_p+1$. Energetically, seeds are "cheap" compared to adaptations that permit plants to overwinter. Why then, asked Cole, aren't perennials replaced by annual mutants which "trade in" the energy required for long life for a small increment in seed production?

The answer (Charnov and Schaffer 1973) is that the *B*'s are "effective fecundities," *i.e.*, the numbers of seeds that germinate and themselves survive to set seed. That is, $B_a = cb_a$, and $B_p = cb_p$, where *b*'s are the numbers of seeds produced, and *c* is the aforementioned germination-survival probability. For the annual population to grow more rapidly than the perennial, it is therefore necessary that $b_a > b_p + 1/c$, or, in the case that adults survive with probability $p < 1$, that $b_a > b_p + p/c$. Often, $c << p$, in which case, $(p/c) >>1$. Then, superiority of the annual requires $b_a >> b_p$, which is to say, an increase in fecundity substantially in excess of a single seed.

is the rate at which the population ultimately multiplies.[9] It is this final fact which justifies identification of λ_1 with fitness.

Equating fitness with λ_1 enabled Cole to inquire as to the circumstances favoring alternative schedules of birth and death. In particular, he argued that delaying the onset of reproduction would generally be disadvantageous, in which regard, he posed his famous

[9] Eq (1) is the characteristic equation of the *linear* growth process, $\mathbf{N}(t+1) = \mathbf{A}\,\mathbf{N}(t)$, where the **N**'s are vectors, the elements of which are the numbers of individuals in the different age classes at times *t* and *t+1*, and **A** is the so-called "population projection" or "Leslie" matrix. Provided that λ_1 exceeds the other λ's in magnitude, it follows that as $t \to \infty$, $\mathbf{N}(t) \to c_1\lambda_1^t\mathbf{N}_1$ where, c_1 is a constant reflective of the population's initial age structure. . According to this, $\mathbf{N}_1$, which is an eigenvector defined by the relation, $\mathbf{A}\,\mathbf{N}_1 = \lambda_1\mathbf{N}_1$, specifies the "stable age distribution."

paradox (text box) concerning the ubiquity of the perennial habit. Implicit in Cole's analysis was the notion of *trade-offs*: over the course of evolution, he imagined, current fecundity can be exchanged for subsequent survival and reproduction, an idea that George Williams (1966a) later made explicit via the concept of "reproductive effort." Of course, many mutations result in fitness diminutions all round, *i.e.*, reductions in *both* reproduction and survivorship. *Modulo* the effects of small population size, such variations are eliminated by selection - which is what Levins (1968) meant when he observed that it is only those genotypes corresponding to points on the margins of a fitness set which matter.

What about potentially beneficial variations? To first approximation (Crow and Kimura 1970; Charlesworth and Williamson 1975), the likelihood of a favorable mutation's being fixed depends on its selective advantage, which, in the present case, reflects the values of the partial derivatives,

$$(\partial\lambda_1 / \partial B_i) = (\ell_i / \lambda_1^i) / V_T \qquad (2a)$$

and

$$(\partial\lambda_1 / \partial p_i) = ((\ell_i / \lambda_1^i) / V_T)(v_{i+1} / v_0) \qquad (2b)$$

(Hamilton 1966; Emlen 1970; Caswell 1979).[10] Here,

$$(v_i / v_0) = (\lambda_1 / \ell_i) \sum_{j=1}^{\infty} \lambda_1^{-(j+1)} \ell_j B_j \qquad (3)$$

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[10] For the reader uncomfortable with derivatives generally, and with partial derivatives in particular, we offer the following. If the value of y depends on a second quantity, x, the derivative, dy/dx, evaluated at $x = x_0$, is the rate at which y changes in response to a small variation in x when $x = x_0$. If y depends on a number of quantities, say, w, x and z, then the *partial* derivative, $\partial y/\partial x$, is the same rate of change, but with the values of the other variables fixed.

is the *reproductive value* (Fisher 1930) of an *i* year-old, which is simply the expectation of current and future offspring discounted by appropriate powers of λ_1.[11] Correspondingly,

$$V_T = \sum_{i=0}^{\infty} (i+1)\lambda_1^{-(i+1)} \ell_i B_i \tag{4}$$

is the *total reproductive value* of a population that has achieved stable age distribution.

Equations (2a) and (2b) suggest two principal conclusions:

1. Increased reproduction at earlier ages confers greater benefits to fitness than comparable increases at later ages. This reflects the fact that, so long as $\lambda_1 \geq 1$, the term, (ℓ_i/λ_1^i), necessarily declines with age.
2. The benefits of increased survival are often greatest at intermediate ages. This is because $(\partial\lambda_1/\partial p_i)$ depends on reproductive value, which generally peaks at, or shortly after, the age of first reproduction (Fisher 1930).

Fixation of Advantageous Mutants in the Presence of Density Dependence. Thus far, we have assumed constant rates of reproduction and survival. This is appropriate for populations growing exponentially. Of course, real world populations do not multiply indefinitely. Rather, their growth rates are arrested by a variety of limiting factors, the effect of which is to reduce reproduction and increase mortality. It is important therefore to inquire as to what happens when life history parameters manifest *density dependence*, *i.e.*, when λ_1 depends on both population numbers and phenotype. To this end, we study the fate of an advantageous mutant arising in a population at equilibrium with respect to both age structure and density. In what follows, we denote the wild type phenotype φ_0; the mutant phenotype, φ' and the corresponding equilibrium densities (carrying capacities), K_0 and K'. Please refer to Figure 1.

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[11] Eq (3) is the definition one finds in the textbooks and, as such, has perplexed generations of students. A more useful rendering of this expression can be had as follows: Let p_i be the probability of surviving from age *i* to *i+1*, *i.e.*, $p_i = \ell_{i+1}/\ell_i$. Now multiply the chicken scratches under the sum, *i.e.*, the terms following the "∑," by the quantity in brackets outside it. Then $v_i/v_0 = B_i/\lambda_1 + p_iB_{i+1}/\lambda_1^2 + p_ip_{i+1}B_{i+2}/\lambda_1^3 + \ldots$, whence follows the verbal definition given above.

When the mutant first appears, the wild type is in approximate equilibrium, and $\lambda_1(\varphi_0, K_0) \approx 1$.. At the same time, the mutant's rate of increase, by virtue of its being advantageous, exceeds 1. That is, $\lambda_1(\varphi', K_0) > 1$. More precisely, the mutant manifests a selective advantage,

$$s = [r(\varphi', K_0) - r(\varphi_0, K_0)] \approx \Delta\varphi(dr/d\varphi)\big|_{N=K_0} > 0 \qquad (5)$$

where $r \equiv \ln \lambda_1$. Since $s > 0$, the number of mutants increases and, with it, the population's overall size. At the same time, increasing density forces reductions in the rates of increase of *both* phenotypes. Now $\lambda_1(\varphi_0, K') < 1$, and the number of wild type individuals begins to decline. Still, $N < K'$, and the number of mutants continues to increase, albeit more slowly. Eventually, the wild type dies out, and population size stabilizes at the new carrying capacity, $N = K'$, which is larger than the old. At this point, the mutant's frequency, $p = 1$, and its rate of multiplication, $\lambda_1(\varphi', K') = 1$.

Regarding this scenario, there are two principal caveats. In the first place, we assume the substitution process to be *slow*, where by "slow," we mean *quasi-static*, *i.e.*, slow enough that both density and age structure track their respective equilibria. We also require that the fitness of the mutant exceed that of the wild type on the entire range of population densities, $[K_0, K']$. According to this, substitution of a favorable mutant is formally equivalent to interspecific competition when the zero-growth isoclines do not cross. Absent this assumption, we are into the world of *r*- *vs.* *K*- selection as these concepts are traditionally formulated (MacArthur and Wilson 1967; Pianka 1970).

When "phenotype," *i.e.*, φ, refers to the *B*'s or *p*'s above, we may use Equations (2a) and (2b) to evaluate $dr/d\varphi = (1/\lambda_1)(\partial\lambda_1/\partial\varphi)$. This ignores the possibility of trade-offs, for example, between current fecundity and subsequent reproduction and survival. If there are trade-offs, these must be taken into account as discussed in (Schaffer 1979b). To summarize, the machinery developed for the density-independent case can be applied to density-dependent situations given satisfaction of certain assumptions.

Life History Evolution as an Optimization Problem. The notion of reproductive effort was first linked to Cole's mathematics by Gadgil and Bossert (1970) who framed life history evolution in terms of costs and benefits. Specifically, they considered the set of age-specific reproductive expenditures, $\boldsymbol{E} = [E_0, \ldots, E_n]$, and assumed explicit dependencies of the fecundities, B_i, and survival probabilities, $p_i = (\ell_{i+1}/\ell_i)$, on **E**. The computer was then used to determine the expenditures, $\boldsymbol{E}^* = [E_0^*, \ldots, E_n^*]$, maximizing λ_1. As discussed by subsequent authors (Taylor *et al.* 1974; Leon 1976; Schaffer 1983), this is an *optimization problem* (Bellman 1957; Leitmann 1966; Intrilligator 1971) whereby a set of "controls," the E_i, are adjusted to maximize an "objective function," λ_1.

Because the dependence of λ_1 on the controls, $\boldsymbol{E} = [E_0, \ldots, E_n]$, is via their effect on the B's and p's, viewing life history evolution as an optimization problem focuses our attention on the functional dependencies, $B_i(E_i)$, $p_i(E_i)$, *etc*. Concerning these, we note the following:

1,. Effective fecundity will generally be an *increasing* function of reproductive effort at the current age and possibly a decreasing function of expenditure at prior ages. That is, $\partial B_i/\partial E_i > 0$ and $\partial B_i/\partial E_j \leq 0$, for $j < i$.
2. In the special case that $B_{i+1} = g_i(E_i)B_i$, the rate, g_i, at which fecundity multiplies from one year to the next will be a *decreasing* function of reproductive effort at the current age, *i.e.*, $\partial g_i/\partial E_i < 0$.
3. Post-reproductive survival will also be a *decreasing* function of reproductive effort at the current age and possibly a decreasing function of expenditure at prior ages. That is, $\partial p_i/\partial E_i < 0$, and $\partial p_i/\partial E_j \leq 0$ for $j < i$.

This brings us to one of the more interesting subjects in life history theory, namely the adaptive significance of "big bang reproduction" (semelparity) whereby a single, often spectacular, bout of breeding is followed by the organism's obligate demise. Concerning this matter, Gadgil and Bossert suggested that such a strategy should be favored by concave, *i.e.*, *accelerating,* dependencies (positive second derivatives) of effective fecundity and post-breeding survival on reproductive effort. Conversely, they proposed that convex, *i.e.*, *decelerating*, dependencies (negative second derivatives), should favor more modest levels of reproduction and, hence, post-reproductive survival and iteroparity. The distinction is illustrated in Figure 2 for the special case in which the functions, $B_i(E_i)$ and $p_i(E_i)$, are the same for all age classes, and there is a common reproductive effort, $E = E_0 = E_1 = \ldots = E_n$.

Under these assumptions, and in the limit that the number of age classes, $n \to \infty$, the multi-dimensional optimization problem collapses (Schaffer 1974a) to the simpler chore of maximizing

$$\lambda(E) = B(E) + p(E). \tag{6a}$$

If effective fecundity, $B(E)$, multiplies at rate, $g(E)$, each year, this expression generalizes to

$$\lambda(E) = B(E) + p(E)g(E) \tag{6b}$$

(Schaffer 1974; Schaffer and Gadgil 1975). In either case, there is a trade-off between current and future components of fitness: current fecundity and subsequent survival [Equation (6a)] or current fecundity and subsequent survival multiplied by the yearly rate at which fecundity multiplies [Equation (6b)].

Returning to Figure 2, we note that when $B(E)$ and $p(E)$ are concave (Figure 2a), the optimal expenditure, E^*, is either 0 or 1. Often, both of these so-called "boundary" solutions correspond to local maxima in $\lambda(E)$. Conversely, when $B(E)$ and $p(E)$ are convex (Figure 2b), E^* will often be intermediate between 0 and 1. That is, one has the "interior" solution, $0 < E^* < 1$.

The dependencies in Figures 2a and 2b are very simple. Figures 2c and 2d illustrate more complicated possibilities. Here, as in Figure 2a, there can be two expenditures corresponding to local maxima in fitness. Of these, one is always a boundary solution, *i.e.*, $E^* = 0$ (Figure 2c) or 1 (Figure 2d), while the other is often an interior solution, *i.e.*, $0 < E^* < 1$.

Of the four fecundity curves in Figure 2, the sigmoid function (Figure 2c) is arguably the one most often occurring in nature. Sigmoidal dependence combines the idea of "start-up costs" to reproduction with the notion of diminishing returns when expenditure is high. With regard to start-up costs, we note that in most organisms the commitment to breed entails an initial investment that, of itself, yields nothing in the way of viable offspring. In anadromous fishes, for example, this investment, involving physiological changes that facilitate returning to freshwater, an often costly upstream migration, *etc.*, can be substantial. Intraspecific competition - among males for females and among females for nesting sites - will also serve to increase the range of effort values for which fecundity evidences an accelerating dependence on expenditure. In extreme cases, such factors may have the effect of making the entire function concave as in Figure 2a.

Other factors can be expected to have the opposite effect, *i.e,* to promote diminishing fecundity returns at high effort values (the decelerating portion of the curve). Examples include competition among sibs for resources (including parental attention) and the tendency of numerous, tasty offspring to attract natural enemies.

With regard to post-reproductive survival, the functional dependencies most frequently occurring in nature are arguably convex functions of the sort shown in Figure 2b. Biologically, such curves correspond to the idea that the consequences to post-breeding survival of increasing reproductive expenditure only become significant when investment exceeds some threshold. But here again, changing biological and environmental circumstances can mould the dependency. For example, organisms in poor condition to begin with may manifest abrupt declines in post-breeding survival at intermediate levels of expenditure – in which case the dependency will be convex-concave as shown in Figure 5 of (Schaffer and Rosenzweig 1977). Conversely, the onset of reproduction may involve the initiation of morphological changes or behaviors that place the animal at immediate risk – think breeding coloration in birds - even though the energetic investment itself is modest. Then, survivorship may evidence an initial drop, in which case the curve will be concave-convex as shown in Figure 4 of (Schaffer and Rosenzweig 1977). If sufficiently pronounced, such effects can make the curve entirely concave (Figure 2a).

Regarding such considerations, we make two observations: The first is that they are difficult to quantify in the field (Schaffer and Schaffer 1977). Second, they can be confusing to think about, essentially because one is attempting to squeeze too much biology into a single variable. These are issues to which we will return in Sections III and IV. For the present, we reiterate that even the simplest model life histories can manifest alternative solutions to the same circumstances. With more than one age class (see below), the possibilities for multiple optima proliferate.

Characterizing an Optimal Life History. My own contribution to life history evolution with age structure was technical. As a student, I absorbed MacArthur's dictum that undue reliance on the computer is an invitation to counter-example. "What would you do," he once asked a visiting systems ecologist describing the results of an elaborate computer simulation, "if someone pulled the plug?" And so, I fretted about what was going on inside Gadgil's computer. Eventually, I convinced myself (Schaffer 1974a, 1979b) that selection acts to maximize reproductive value at all ages, a result which I later discovered had previously been conjectured by Williams (1966a).[12] More precisely, it turns out that the reproductive value, (v_i/v_0), of each age class is maximized with respect to the expenditure, E_i, at *that* age.[13] In symbols,

$$\operatorname*{Max}_{\mathbf{E}}(\lambda_1) \Longleftrightarrow \operatorname*{Max}_{E_i}(v_i/v_0), \text{ all } E_i. \qquad (7)$$

which is read, "maximizing λ_1 by adjusting *all* of the expenditures is equivalent to maximizing each reproductive value, v_i/v_0, with respect to E_i. At about the same time, Taylor *et al.* (1974) and Pianka and Parker (1975) independently came to the same conclusion.

Intuitively, Equation (7) makes sense - reproductive value being the age-specific expectation of current and future reproduction discounted by appropriate powers of λ_1. One can further show (Schaffer 1974a) that these two components of fitness, *i.e.*, current and future reproduction, are exchangeable: That is, maximizing (v_i/v_0) with respect to E_i also maximizes the sum, $B_i + p_i(v_{i+1}/v_0)$, where the second term, $p_i(v_{i+1}/v_0)$, is sometimes

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[12] This result requires that varying reproductive effort at age *i* is without consequence to reproduction and survival at previous ages (Schaffer 1979b). On the face of it, this would seem always to be the case: time, after all, does not run backwards. In fact, there are instances when, so far as natural selection is concerned, the hand on the dial really does turn counter-clockwise. Specifically, when there is extended parental care, resources expended on this year's offspring can adversely affect the growth and survival of their older siblings. This reduces the parents' effective fecundity at previous ages. Similarly, if last year's offspring fail to disperse, as in the case of organisms that propagate "vegetatively" (plants, corals, *etc.*), they may compete with this year's progeny.

[13] Eq (7) was misinterpreted (Schaffer 1981; Yodzis 1981) by Caswell (1980) who imagined the claim to be that the optimal expenditure at each age maximizes the reproductive value of *all* the age classes.

referred to as the "residual reproductive value," *RRV*, of an *i* year-old. The complement to Equation (7) is thus

$$\underset{\mathbf{E}}{\mathrm{Max}}\,(\lambda_1) <=> \underset{E_i}{\mathrm{Max}}\,[B_i + p_i(v_{i+1}/v_0)],\ \text{all } E_i. \qquad (8)$$

Equation (8) is the analog of Equations (6) appropriate to cases in which there are distinguishable age classes. Among other things, it allows for the definition (Schaffer and Gadgil 1975; Schaffer 1979a) of costs and benefits. In particular, with a small increase, ΔE_i, in reproductive expenditure at age *i*, we can associate the

$$\text{Benefit}\,(\Delta E_i) = \Delta B_i \approx \Delta E_i(\partial B_i/\partial E_i) \qquad (9a)$$

and the

$$\text{Cost}\,(\Delta E_i) = \Delta RRV_i \approx -\Delta E_i\{\partial[p_i(v_{i+1}/v_0)]/\partial E_i\} \qquad (9b)$$

Predictions of Simple Models. While Equations (7) and (8) speak to the nature of an optimal life history, they cannot be used to compute one directly. This is because the optimal reproductive expenditure for any *particular* age class depends on the reproductive expenditures at *all* ages.[14] As discussed below, this leads to the study of curves (surfaces) of *conditional optima* whereby one computes the optimal value of E_i for representative reproductive expenditures at the other ages (Schaffer and Rosenzweig 1977). Before turning to such matters, however, let us first review what can be learned from single age class models. In this instance, the following results can be deduced:

1. **Semelparity *vs.* Iteroparity (Schaffer 1974a; Schaffer and Gadgil 1975).** We have already remarked upon the fact that the evolution of "big-bang" reproduction is predicted under circumstances that make for concave, *i.e.*, accelerating dependencies of life table parameters on reproductive expenditure (Figures 2a,

[14] This is because E_i*, for example, depends on (v_{i+1}/v_0) which, in turn, depends on λ_1 and hence on all the *E*'s.

2d). So far as I am aware, the existence of accelerating dependencies in a natural population has yet to be demonstrated convincingly. Still, one can speculate as to the biological circumstances that would have this effect. In the case of semelparous Agavaceae, Schaffer and Schaffer (1977, 1979) proposed (and with some empirical support) that accelerating dependencies of effective fecundity on effort may result from competition among flowering plants for pollinators. Similarly, concavity of the fecundity function in Pacific salmon may result from competitive interactions among reproductives (see below). In such cases, reproductive success depends, not on an individual's reproductive effort *per se*, but on his/her effort relative to that of other individuals in the population. This suggests a connection between behavioral components of reproductive expenditure and dispersal as discussed in (Schaffer 1977).

2. **Allocation in Proportion to Relative Returns (Schaffer 1974a; Schaffer and Gadgil 1975).** This is the theory's most general prediction: Increasing fecundity per unit investment favors greater reproductive effort (Figure 3a); increasing post-reproductive survival or year-to-year growth in fecundity per unit investment favors reduced reproductive expenditure, which is to say, greater allocation to maintenance and growth (Figure 3b).
3. **Effects of Juvenile (Pre-reproductive) *vs.* Adult (Post-reproductive) Mortality (Schaffer 1974a; Schaffer and Gadgil 1975).** This is a special case of the previous result. As such, it merits separate mention because it serves to emphasize the fact that the fecundities in Equation (2) are *effective* fecundities, *i.e.*, the numbers of offspring that survive to be counted as young-of–the year at census time. Accordingly, increasing (decreasing) survival rates among juveniles will select for greater (lesser) rates of reproductive expenditure. This is in contrast to changing survival rates among adults that select in the opposite direction.
4. **Under Density Dependence, Optimal Reproductive Strategies Maximize Carrying Capacity (Schaffer and Tamarin 1973).** This is the life historical realization of MacArthur's (1962) reformulation of Fisher's (1930) Fundamental Theorem of Natural Selection. Two examples are given in Figure 4. Here we plot optimal expenditure as a function, $E^*(N)$, of density and equilibrium density as a

function, *N*(E)*, of reproductive effort. In the first instance (Fig. 4a), density is assumed to reduce juvenile survival and hence effective fecundity; in the second (Fig. 4b), increasing population numbers are assumed to reduce post-reproductive survival. In both cases, the optimal expenditure changes with population size so as to maximize the carrying capacity, which is what MacArthur's more general analysis predicts. At the same time, the means by which this maximization is accomplished differ: in the first case, optimal reproductive effort declines with density; in the second, optimal expenditure increases. At first glance, the second result would seem to be at odds with the theory of *r*- and *K*- selection which holds that *r*-selected species produce more young and are generally shorter lived than their *K*-selected counterparts. The discrepancy vanishes on consideration of the fact that under conditions of crowding, it is the youngest individuals that usually experience the most additional mortality.

5. **Year to Year Variation in Relative Returns is Selectively Equivalent to Reducing the Mean Return in a Constant Environment (Schaffer 1974b).** Suppose the effective fecundity, *B(E)*, and survival, *p(E)*, functions are subject to year-to-year variations that result from environmental fluctuations. Choosing the population's *geometric* mean rate of increase,

$$\overline{\lambda_g} = \lim_{n\to\infty}\left(\prod_{i=0}^{n}\lambda_i\right)^{(1/n)}$$

as our criterion of optimality yields the following results:

a) Variation in effective fecundity per unit investment selects for reduced reproductive expenditure;

b) Variation in post-reproductive survivorship and growth favors increased reproduction.

These results are sometimes cited (Stearns 1976) as an evolutionary example of "bet-hedging." In fact, the arguments from which they follow have nothing to do with risk minimization (Schaffer 1974b). More generally, if variations in reproduction and survivorship per unit expenditure are predictable, selection will favor adaptations that allow organisms to "read" the environment and respond adaptively.

Optimal Allocation with Age Structure. With the addition of age-structure, the problem of deducing general results becomes more difficult. As noted above, this is because the optimal reproductive expenditure for any *particular* age class, depends on next year's reproductive value, and thus on the reproductive expenditures at *all* ages. Taking this complication into account, yields the following results:

1. **Selective Consequences of Altered Returns Per Unit Investment Depend on the Age Classes Affected (Schaffer 1974a; Schaffer and Rosenzweig 1977).** As before, increasing effective fecundity for the *current age class* favors increased reproductive expenditure *at that age,* whereas increasing post-reproductive survival and/or growth per unit effort for the current age class selects for reduced expenditure (again, at that age). In addition, increasing fecundity *or* survivorship per unit investment at *earlier* age classes *increases* the optimal current expenditure. This is because these changes increase λ_1 and thereby reduce subsequent reproductive value, (v_{i+1}/v_0). Conversely, increasing fecundity or survivorship at *later* age classes *reduces* the optimal current expenditure because such changes increase subsequent reproductive value. These results are summarized in Table I.
2. **Reduced Reproductive Effort in Older Individuals Can be Adaptive.** Gadgil and Bossert (1970) proposed that optimal effort invariably increases with age, a conclusion which suggests that declining expenditures in older individuals are a maladaptive consequence of aging. Subsequently, Fagen (1970) produced a counter-example and observed that almost *any* age-specific pattern in optimal effort is possible depending on the way in which the functions, $B_i(E_i)$ and $p_i(E_i)$ vary with age. In retrospect, one imagines that Gadgil and Bossert were misled by the fact that their model life histories assumed a maximum age following which death is obligate. Provided that fecundity increases monotonically with effort, the optimum expenditure for this final age class is necessarily 100% - *i.e.*, in terms of Equation (8), $(v_{i+1}/v_0) = 0$ for all values of E_i, which should thus be chosen to maximize B_i. It

follows that optimal effort increases from the penultimate to the final age class, and, oftentimes, the pattern cascades back to the younger age classes.

From a computational point of view, assuming a fixed life span may be convenient. However, on biological grounds, it is often more realistic to suppose that even the oldest individuals have a non-zero probability of surviving another year. In such cases, there is no maximum age class *per se*, and optimal reproductive investment can decline in the later age classes. In particular, reduced per unit effort fecundity in older individuals, as typically results from aging, can favor reductions in reproductive effort. This suggests a distinction between organisms in which body size and fecundity increase throughout life, and those in which body size and reproductive potential plateau. Some sample computations are presented in Table II wherein we report some results for a five age-class model. Under the assumption of continuing age-dependent increases in potential fecundity, optimal effort increases with age regardless of what one assumes about the final age class.[15] Conversely, when fecundity per unit investment peaks at intermediate ages, the Gadgil-Bossert only obtains if one assumes the obligate demise of individuals in the oldest age class. Absent this assumption, *i.e.*, if one regards the oldest age class as "adults" which survive from one year to the next with constant probability, optimal expenditure can manifest the up-down pattern noted above.[16] These results underscore the selective link between senescence, as the term is usually understood, *i.e.*, the onset of degenerative disorders of the sort targeted by geriatric medicine, and optimal life history evolution.[17]

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15 The set of optimal reproductive efforts, ***E****, were computed using a "down-hill simplex" algorithm (Press et al. 1992) to minimize $(1/\lambda_1)$. Note, however, that nothing having been proved, the proposed generality is purely conjectural.

16 With an infinite number of "adult" age classes, the stable age equation (1) becomes

$$1 = \sum_{i=0}^{a-1} \lambda^{-(i+1)} \ell_i B_i + \left(\lambda^{-a} \ell_a B_a\right) / \left(\lambda - p_a\right)$$

Here a is the age at which individuals achieve "adulthood," while B_a and p_a are respectively adult fecundity and the probability of survival from one year to the next.

17 While the mathematics of senescence (Hamilton 1966) and life history evolution are essentially equivalent, from a biological perspective the two topics are rather different. In the first case, one is concerned with

Optimal Effort for Multiple Age Classes.

Thus far, we have emphasized the evolution of reproductive expenditure at individual age classes, either in single age class models, or in the context of multi-age class models, with expenditures at the other age classes implicitly held constant. To complete our discussion, we consider selection on the entire set of reproductive expenditures, $\boldsymbol{E} = E_0, \ldots , E_n$. That is, we treat the life table as a whole. To do this, we introduce the notion of *curves (or surfaces) of conditional optima* that specify the optimal value reproductive effort at a particular age for some suitably chosen set of expenditures at the other ages (Schaffer 1974a; Schaffer and Rosenzweig 1977). We emphasize that this approach is neither esoteric nor difficult to implement. In practice, one identifies an age class of interest and computes the optimal reproductive effort at *that* age for a large number of expenditures at the *other* ages. For example, in the case of two age class models, one calculates the curve of optimal expenditures, $E_0*(E_1)$, at age 0 for representative values of E_1 and the corresponding curve, $E_1*(E_0)$, for representative values of E_0. The resulting curves are then plotted in the E_0-E_1 plane and inspected. Points at which the curves intersect maximize λ_1 with respect to both expenditures and consequently correspond to optimal life histories. With three age classes, the curves become surfaces in E_0-E_1-E_2 space; and, with $n+1 > 3$ age classes, hypersurfaces in E_0 - … -E_n space. In an entirely analogous fashion, one can compute curves (surfaces) of conditional *minima* in fitness. From the viewpoint of adaptive topographies (Wright 1968), intersections of curves (surfaces) of conditional optima correspond to *peaks* on an adaptive landscape; intersections of curves (surfaces) of conditional minima, to *valleys*; and intersections of conditional maxima with minima, to *saddles*.

Figure 5 shows the result of applying this approach to a two-stage life history in which there is a single juvenile age class followed by an infinite number of adult age classes wherein individuals survive with constant probability from one year to the next.[18]

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adaptations that delay the onset of morbidity and mortality; in the latter, with the allocation of available resources to competing functions.

18 In terms of note #17, we consider the case in which $a = 1$.

Four examples, corresponding to each of the single class models of Figure 2, are given. In each case, reproductive effort pairs, (E_j, E_a), are color-coded according to the visible spectrum with dark red denoting low values of fitness and dark violet, high. The thick white lines, actually closely spaced crosses, are curves of conditional optima, E_j*(E_a) and E_a*(E_j); the thin white lines, curves of conditional minima, $E_j^{\#}(E_a)$ and $E_a^{\#}(E_j)$. In Figure 5a, we consider *accelerating* dependencies of effective fecundity and post-reproductive survival on reproductive effort. In this case, there is a single global minimum in fitness with the consequence that optimal life histories, (E_j, E_a) = (0,0), (0,1), *etc*., are all boundary solutions corresponding to zero reproduction or the maximum possible at the different age classes. In Figure 5b, we consider *decelerating* dependencies of fecundity and survival on reproductive effort. Here, there is a single, *interior maximum* in fitness. Figures 5c and 5d treat cases in which effective fecundity and post-reproductive survival are more complex. Here, the fitness landscapes evidence multiple peaks and valleys.

As further discussed in the following section, studying curves of conditional optima allows one to think more clearly about the evolution of life histories as a whole. In particular, this approach, facillitates the elaboration of falsifiable predictions regarding the selective consequences of changing environmental circumstances affecting reproduction, growth and survival.

Optimal Age of First Reproduction. One consequence of the theory is that it generates predictions regarding the optimal age of first reproduction, a character more readily quantified than small variations in reproductive expenditure. In this regard, recall that when effective fecundity functions are sigmoidal (Figure 2c), there can be two values of reproductive effort corresponding to local maxima in λ_1. Of these, one is always zero, in which case, the organisms don't reproduce, while the second is often intermediate between 0 and 100%. In such cases, factors that *increase* optimal reproductive expenditure within an age class also act to *lower* the optimal age of first reproduction. Conversely, factors that *reduce* optimal expenditure within age classes favor *delays* in the onset of breeding. Computations illustrating these effects for the two-stage life history studied in Figure 5 (but with the possibility of year-to-year increases in effective fecundity among adults) are given in Figures 6 and 7. Figure 6 documents the fecundity effect. With increasing fecundity per unit expenditure in **both** stages of the life cycle, the optimal life history can shift from one in which only adults reproduce to one in which both age classes manifest high expenditures. Figure 7 documents the effect of increasing the rate – again, in **both** life cycle stages - at which fecundity multiplies from one age to the next. Here, the shift is in the opposite direction: increasing this rate selects for delayed reproduction. To complete the story, we note that increasing post-reproductive survival per unit expenditure also selects for delayed reproduction (not shown).

III. Limitations.

As discussed, for example, by Roff (1992) and Stearns (1977, 1992), the theory as here elaborated ignores a great deal of biological detail. Rather than review this material, I here focus on the following, more fundamental deficiencies:

1. Insufficiency of Reproductive Effort as a Descriptor of Allocation. Use of a single set of control variables, $\boldsymbol{E} = \{E_1, \ldots, E_n]$, ignores the fact that there are multiple functions to which resources can be allocated. For example, in modeling plant life histories, it is useful to distinguish allocation to reproduction, growth and storage (Schaffer *et al.* 1982; Chiariello and Roughgarden 1983; Schaffer 1983). In short, the E_i, in Equations (7) and (8) should really be E_{ij}, where the second subscript refers to the physiological function targeted.

2. Insufficiency of Reproductive Effort as a Descriptor of Reproductive Style. This is an extension of #1, the point being that energy allocated to reproduction can itself be partitioned in various ways. We have already alluded to this fact in reviewing the functional dependence of fecundity on effort. Thus, in many species, one wants to distinguish energy expended on different aspects of reproduction, *e.g.* to distinguish mate competition from the actual production of offspring, the cost of birthing, from *post-partem* parental care, *etc*.

3. Total Effort *vs*. Effort per Offspring. This is a further extension of # 1. Most organisms produce multiple young, with the consequence that selection can act on both the effort expended per offspring and the **total** effort.[19] In the absence of age structure, this leads to

[19] In fishes, an important determinant of effort per offspring is egg size. To first order, the total caloric expenditure in females is thus $n \times e$ where n is the number of eggs.

$$\lambda(E,e) = B(E,e) + g(E)p(E) \qquad (6c)$$

where E is total reproductive effort, and e is the caloric expenditure per offspring. With E held constant, maximizing $\lambda(E,e)$ collapses to the “clutch size problem” as it was studied in the 1950s and 60s by David Lack (1966) and his associates. In this case, and with a cap on juvenile survival, $c(e)$, the optimal expenditure per offspring, e^*, is the value of e at which $c(e)$ is tangent to the line,

$$c = e\,k\,, \qquad (10)$$

of greatest k as shown in Figure 5a. This so-called “marginal value-solution” (Charnov 1976) was proposed independently by Smith and Fretwell (1974) and Schaffer and Gadgil (1975). The latter authors also considered the way in which competition among juveniles selects for increased parental expenditure. What happens if we allow both expenditures, *i.e.*, total and *per* offspring, to vary? One answer is shown in Figure 5b wherein we assume that offspring survival depends only on e. Then the optimal effort per offspring, e^*, is independent of the total expenditure. On the other hand, the optimal total expenditure, $E^*(e)$, depends on e. In particular, $E^*(e)$ rises and falls as shown in the figure, and, in fact, is maximal when $e = e^*$. There is no mystery to this: e^* maximizes effective fecundity, $B(E,e)$, and, so long as post-reproductive survival depends only on the total expenditure, the consequence of setting $e = e^*$ is to maximize $E^*(e)$.

As discussed by Parker and Begon (1986) and McGinley (1989), more complex dependencies result when juvenile survival depends not only on effort per offspring but also on the total number of offspring produced. For additional discussion such matters in the context of salmonids, see Einum *et al*. (2003 – *this volume*).

4. Insufficiency of Age as a Descriptor of Potential Reproduction, Growth and Survival. Especially in organisms with indeterminate growth, size is often of equal, if not greater importance, than age in determining components of fitness. If size is the principal determinant, one can replace Equation (1) with the corresponding equation that describes the growth of a population in which individuals are categorized by size or "stage.” If both factors are important, an "age by stage" description is required.

5. Dose-Response Relations. In many species, patterns of reproductive expenditure depend on environmental circumstance. In such cases, what is selected among is not a set of age specific reproductive efforts, but rather a set of "dose-response" relations, the "dose" being the environmental state, often as reflected by the organism's size or condition, and the "response," the age-specific expenditure. Such relationships - also called "norms of reaction" (Hutchings 2003 – *this volume*) - vary between and within species. For example, some desert birds (these notes are being written in Tucson, Arizona) are notoriously flexible with regard to the onset of breeding, in which regard they are influenced by variations in rainfall. Other species respond primarily to photoperiod and are locked into fixed breeding seasons. Likewise, a positive correlation between pre-reproductive growth rates and the age of first reproduction is widely observed in both plants (Harper 1977) and animals (Alm 1959).

6. Insensitivity of Fitness to Variations in Allocation. As usually articulated, life history theory makes no reference to the expected degree of dispersion about a putative optimum. In fact, one expects that the selective pressures that mould life histories in nature are often minuscule, *i.e.*, adaptive topographies of the sort shown in Figures 5-7 will be quite flat. In this case, finite population effects *guarantee* that real world populations will be sub-optimal. The question then becomes not whether natural populations exhibit optimal behavior – they won't - but rather the degree to which deviations from optimality preclude validation of the theory.

7. Life History Evolution and Nonlinear Population Dynamics. The theory reviewed here antedates the realization (May 1976; Schaffer 1985) that ecological populations can manifest complex dynamics independent of environmental fluctuations. With regard to life history evolution, nonlinearity introduces the twist of deterministic fluctuations in population density and, hence, selective pressures which, over the short term, are predictable. There is also the contrapuntal issue as to the consequences to population dynamics of variations in life history.

IV. The Theory Applied to Atlantic Salmon.

Age of First Spawning. As discussed by Stearns and Hendry (2003 – *this volume*), salmonid life histories make interesting grist for the theorist's mill. As a graduate student, I deduced predictions regarding the effects of environmental factors expected to influence the optimal (sea) age of first reproduction in anadromous North American Atlantic salmon. The predictions were tested by comparison with data from over 100 stocks obtained from, or with the assistance of, what was then the Fisheries Research Board of Canada. In particular, I considered the selective consequences of the following environmental factors:

- **a)** The energetic demands of the up-stream migration as indexed by river length;
- **b)** The rate at which fish from different rivers gain weight in the ocean after their first summer at sea;
- **c)** The intensity of coastal and estuarine fishing as indexed by the numbers of commercial nets.

Because angling statistics were the principal source of data for most rivers, I relied largely on the mean weight of angled fish as a *proxy variable* for the age of first return. So long as the frequency of repeat spawners is low (generally true), this procedure is wholly defensible [see Table I of Schaffer and Elson (1975)], the increase in weight resulting from each additional summer at sea being large compared to variations in weight among fish of the same (sea) age.

With regard to these factors, it was predicted that the optimal age of first spawning should

- **a)** Increase with river length - because increased energetic demands of migration depress effective fecundity per unit reproductive effort;[20]
- **b)** Increase with ocean growth rate - because this increases residual reproductive value per unit expenditure;
- **c)** Decrease with the intensity of commercial fishing - because larger (= older) fish are more likely to be trapped than smaller (= younger) individuals.[21, 22]

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20 River length is, of course, but the crudest of measures of the cost of migration. Subsequently, N. Jonsson *et al*. (1991) suggested that mean annual discharge is a better indicator. For further discussion of migratory cost, see Chapter 2 (*this volume*) and references therein.

21 Obviously, if older fish are preferentially removed from the spawning run, the mean age of returning fish will drop, a prediction for which optimality theory is manifestly unnecessary. In fact, what is being predicted is that the numbers of fish returning to spawn at an early age, as indicated by census *before they hit the nets*, will increase. As discussed in (Schaffer and Elson 1975) this prediction is supported by increasing numbers of grilse taken in a research trap on the N. W. Miramichi from 1961 to 1969, even as the numbers of 2 sea-year first spawners.

To confirm that these predictions do, in fact, derive from the theory, we refer back to the two-stage life history model of the preceding section. In the context of Atlantic salmon, think of these equations as modeling the adult (post-smolt) phase of the life cycle with everything that goes on in the river and during the first summer at sea being collapsed into the effective fecundity function of the first age class. In this spirit, we view the "juvenile" age class as "grilse," fish that spend a single summer in the ocean before returning to the river, and the "adult" age classes as "salmon," fish that spend two or more summers at sea before spawning.

Figure 6 addresses the river length effect on assumption that the more demanding the swim upstream, the greater the fraction of reproductive effort (*sensu lato*) that must be allocated to migration as opposed to reproduction *per se*. With migratory costs high (long rivers), fecundity per unit effort is reduced and fitness maximized by one sea-year fish not returning to spawn (Figures 6a and 6b). Conversely, with migratory costs low, fecundity per unit effort is high and selection favors reproduction by both age classes (Figures 6c and 6d).

Figure 7 addresses the ocean growth rate effect. Here the rate at which fecundity can increase from year to the next, *i.e.*, the growth function, $g_i(E_i)$, is varied. For low rates of post-reproductive growth potential, reproduction by both age classes is favored (Figures 7a, 7b). For higher values of this function, an optimal life history is one in which only "salmon" reproduce (Figures 7c, 7d).

Finally, in Figure 9, we study the selective consequences of commercial fishing. Since commercial gear preferentially removes larger individuals, we model the effect of coastal and estuarine fishing by reducing *both* the effective fecundity and post-reproductive survival functions of older individuals. The not unexpected result is a shift from life histories in which one sea-year fish do not reproduce (Figures 9a, 9b) to those in which they do (Figures 9c, 9d).

To varying degrees, all three predictions were supported by the data. The results of subsequent studies (Thorpe and Mitchell 1981; Scarnecchia 1983; Fleming and Gross 1989; Myers and Hutchings 1987b; N. Jonsson *et al.* 1991a; L'Abée-Lund 1991; Hutchings

[22] For an engaging (and insightful!) discussion of the many other consequences of human exploitation, see Young (2003 – *this volume*).

and Jones 1998) of *S. salar* and other salmonids, however, were mixed. The follow-up investigations focused principally on the first prediction [but see Myers and Jones (1987) and Hutchings and Jones (1998)], *i.e.*, on the effect of increasing costs of migration imposed as indexed by length of the river or mean annual discharge. This is something of a pity, inasmuch as the original analysis suggested that river length effects are subject to masking or accentuation by the other variables.[23] In particular, river length, while strongly correlated with delayed reproduction in some regions (*Baie de Chaleur*, North Shore of the Gulf of St. Lawrence), evidenced no such relationship in others (New Brunswick and Newfoundland). In discussion, Elson and I suggested that this variation might reflect regional differences in commercial fishing pressure,[24] and growth rates in the ocean. With regard to the latter point, populations from regions manifesting a significant effect of river length also evidenced the highest post-grilse growth rates at sea, a finding subsequently confirmed by Hutchings and Jones (1998) in a study notable for its inclusion of data from both European and North American stocks. Such synergy is, in fact, to be expected, *i.e.*, if fish grow less rapidly at sea, the benefits of postponing reproduction are diminished.

Variation in Inter-Spawning Intervals. One of the patterns reported by Schaffer and Elson (1975) was the observation (their Figure 7) that inter-spawning intervals, *i.e.*, the number of summers spent at sea between migrations into freshwater, was positively correlated with the mean age of first return. This finding was subsequently confirmed for Norwegian Atlantic salmon by N. Jonsson *et al.* (1991) who ascribed it to the fact that

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23. There was also some confusion. For example, regarding our use of angling statistics (fish weight) as a proxy variable for the age of first spawning, Fleming and Gross (1989) and, to a lesser extent, N. Jonsson *et al*. (1991), imagined that what was being predicted was variation in fish size *per se*. Thus, the former authors reported as contradicting our results the observation that the size of returning female Coho salmon (*Oncorhynchus kisutch*) varies *inversely* with river length. In fact, all of the fish in their study spent the same number of summers at sea with the consequence that the reported variations in body size are irrelevant to the life historical predictions we were trying to test.

24 As noted above, commercial nets and weirs preferentially remove larger (= older) fish from the spawning run and therefore select for an early age of first spawning. In fact, there is evidence that this has happened. For example, in the case of the Northwest Miramichi, the principal salmon river in New Brunswick, there is good reason (Hunstman 1939; Elson 1957) to believe that the decades prior to those for which I was able to obtain data witnessed dramatic declines in the abundance of 2- and 3-sea year virgin fish. By way of contrast, long-term angling records kept by the Moise Salmon Club (North Shore) indicate little change in the composition of the spawning run from 1930 to 1970 (Schiefer 1971).

larger (= older) fish require a longer period of ocean feeding to mend.[25] The twist that life history theory brings to the discussion is that factors (reduced fecundity per unit effort, increased post-reproductive growth rate) that select for delayed reproduction should also select for increasing intervals between reproductive episodes.

Life in the River. Contemporary science being the collective endeavor that it is, graduate students embarking upon what they believe to be a novel course of investigation often discover as their work progresses (and to their not inconsiderable chagrin!) that they are *not alone*. In my own case, a thesis (Schiefer 1971) relating heightened freshwater growth rates among parr to increased rates of pre-migratory sexual maturation and early return from the sea was submitted to the University of Waterloo even as I worked to complete my own dissertation. These observations were in accord with the widely held belief (Huntsman 1939) that growth rates in freshwater are an important determinant of the period salmon spend at sea before returning to the river. They are also consistent with the theory elaborated above: greater pre-reproductive growth rates increase fecundity per unit investment for all age classes and thereby favor increased reproductive expenditure and an earlier age of first spawning. This point was first made in the paper with Elson. Later (Schaffer 1979a), I extended the argument by considering a model in which river and ocean stages of salmonid life histories were explicitly distinguished. The latter analysis further predicts that the age at which young salmon go to sea should vary inversely with growth rates in the river, which prediction is consistent with the observation that the age of ocean-bound smolts increases with latitude (Power 1969; Schaffer and Elson 1975).

Males *vs.* Females. One of the more interesting discussions in the salmonid life history literature [see Gross (1996), Fleming and Reynolds (2003 – *this volume*)] revolves about the adaptive significance of precocious maturation by male parr. This phenomenon appears to reflect the fact that parr can slip past territorial adult males and fertilize some fraction of the female's eggs (Jones 1959; Fleming and Gross 1994). That comparable forces may also be at work among adult fish is suggested by the fact that, even though the mean age of

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[25] My own take on this was to emphasize the fact that increased inter-spawning intervals were associated with increased losses in growth due to spawning which, in turn, correlated with increased migratory costs as evidenced by river length. Supporting this interpretation is the observation by N. Jonsson *et al.* (1991) that post-spawning survival declines with the age of first return.

returning adults varies from river to river, the average sea age of returning males is almost invariably less than that of returning females (Schaffer 1979a).

V. Pacific Salmon *vs.* Atlantic Salmon and Trout.

While post-spawning mortality approaches 100% in some populations of *S. salar*, there are other populations in which multiple returns to the river are the norm, and it is not unheard of for individuals to reproduce five times or more (Ducharme 1969). This is in contrast to Pacific salmon (*Oncorhynchus*) in which anadromous individuals are obligately semelparous.[26, 27] During the upstream migration, apparently irreversible changes occur (Neave 1958; Foerster 1968; Groot and Margolis 1991): individuals stop feeding; the digestive tract is resorbed; and the jaws, especially in males, elongate to form a fearsome kype. In some species, males also develop a pronounced hump and there is the acquisition, to varying degrees depending on species, of characteristically gaudy spawning colors in both sexes. In thinking about the adaptive significance of these changes, I was first drawn to images of indomitable sockeye (*O. nerka*) fighting their way a thousand miles inland as they traverse rivers such as the Snake and Columbia in western North America. Under such circumstances, one can well imagine effective fecundity functions of the sort shown in Figure 2a, with anything less than a maximum effort resulting in the individual's death *before* it reaches the spawning grounds. Further reflection, however, suggests that such considerations do not explain the origin of semelparity in this group.

In the first place, anadromous rainbow or "steelhead" trout (*O. mykiss*), cohabit the same river systems and, in some cases, make the same grueling upstream migrations. Yet this species, like *S. salar*, with which it was previously grouped as *S. gairdneri*, is iteroparous. It follows that, if the adaptive significance of semelparity in *Oncorhynchus* relates to the rigors of migration, one must confront the fact that these factors, while

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26 In what follows, I use the term "semelparity" to refer to the obligate demise of post-spawning *adults*, *i.e*., fish which have gone to sea and then returned to brackish or freshwater. This usage reflects the observation that, as in *S. salar*, male juvenile Pacific salmon can reproduce more than once as parr (Unwin *et al*. 1999) and further that some Pacific salmon returning to spawn have previously reproduced as parr (Tsiger *et al.* 1994).

27.There *may* be occasional exceptions. For instance, Ricker (1972) cites published reports of purportedly "mending," *i.e.*, post-spawning chinook (*O. tshawytscha*) adults taken in salt water.

operative on the ancestors of contemporary Pacific salmon, had no such effect on the line leading to steelhead trout. In addition, many Pacific salmon, for example, silver (coho) salmon (*O. kisutch*) in California, spawn in short, coastal streams (Shapovalov and Taft 1954). For these populations, getting back out to sea would seem to be no more of a problem than it is for multiple spawning *S. salar* in the rivers of southeastern Canada. Similarly, landlocked populations of *Oncorhynchus* generally undertake little in the way of spawning migrations. Yet, like their anadromous cousins, these populations are semelparous. In short, the distribution of reproductive and migratory habit suggests that the evolution of semelparity in *Oncorhynchus* is unrelated to migratory stress. This forces us to look to other possible explanations. Among them, are the following:

1. **Semelparity in contemporary *Oncorhynchus* is mal-adaptive, having been retained only because the ability to re-evolve repeated reproduction has been lost (Crespi and Teo 2002).** This is the "hen's tooth"explanation. It holds that big bang reproduction in extant populations is reflective of selective regimes past. In this case, migratory stress may, indeed, have been the critical factor in the evolution of semelparity, but the ability to re-evolve the iteroparous habit was subsequently lost. This hypothesis raises the fascinating question as to whether or not heretofore unreported vestiges of *Oncorhynchus'* iteroparous heritage persist in extant populations of the Japanese species, *O. masou* and *O. rhodurus*, which are generally held (Neave 1958; Stearley and Smith 1993; McKay *et al.* 1996; Oakley and Phillips 1999; Osinov and Lebedev 2000) to be primitive for the group.
2. **Semelparity and iteroparity in salmonids represent multiple optima in allocation schedules (Schaffer 1979a).** According to this, both strategies are adaptive, *i.e.*, that they correspond to alternative adaptive peaks in the here and now. The advantage of this explanation is that, with effective fecundity functions as in Figure 2d, alternative optima corresponding to iteroparous and semelparous reproduction are predicted. The problem is that with so many populations isolated to varying degrees by the tendency of individuals to return to the waters of their birth (Hendry *et al.* 2003a – *this volume*), one expects at least occasional jumps from one adaptive peak to the other. In short, the hypothesis of alternative

evolutionary optima in contemporary populations is inconsistent with the phylogenetic distribution of parity modes.

3. **Semelparity in *Oncorhynchus* is adaptive by virtue of the acquisition of traits that increase effective fecundity per unit effort, thereby selecting for increased effort (Crespi and Teo, 1002).** Recently this idea was advanced by Crespi and Teo (2002), who conjectured that increased egg size in *Oncorhynchus*, to the extent that it serves to increase effective fecundity, may have selected for greater reproductive expenditure. The question left unanswered is whether or not the effect would be sufficient to drive optimal levels of expenditure to the maximum. More precisely, increasing juvenile survival does not make for concavity in the effective fecundity function.
4. **Semelparity in *Oncorhynchus* is adaptive by virtue of the acquisition of traits that make post-reproductive survival unlikely regardless of reproductive expenditure (Crespi and Teo, 2002).** Such traits would make for concave dependencies of residual reproductive value on current reproductive expenditure (Figure 2), thereby increasing the likelihood of selection for maximum reproductive expenditure. In this regard, Crespi and Teo (2002) suggest that Pacific salmon are characterized by more extensive ocean foraging than Atlantic salmon and trout and that this would likely act to reduce post-reproductive survival. An alternative hypothesis, for which there is currently no evidence, is that physiological innovations in Pacific salmon may preclude post-spawning resumption of a salt water existence (see Hendry et al. 2003b – *this volume*). On the face of it, this hypothesis would seem to stumble on the fact that immature Pacific salmon make the transition to marine environments as a matter of course. Still, experience teaches that the loss of plasticity with age is a common feature of biological systems.
5. **Semelparity in *Oncorhynchus* is adaptive by virtue of the acquisition of traits that make for accelerating dependencies of effective fecundity on reproductive expenditure independent of the costs of migration into fresh water (Willson, 1997; Crespi and Teo, 2002).** This possibility is discussed by Willson (1997) and Crespi and Teo (2002) who emphasize the importance of competition for mates

among males and nesting sites among females who further defend their eggs after fertilization. Among salmonids, these traits appear to be most highly developed in Pacific salmon, suggesting that semelparity in these species is essentially a consequence of sexual selection (Fleming and Reynolds 2003 – *this volume*).

Of these five possibilities, which are not, of course, mutually exclusive, it is the last that is arguably the most intriguing. In the first place, intraspecific competition provides a mechanism that can keep driving populations toward higher and higher levels of reproductive investment, in effect manufacturing accelerating fecundity curves (Figure 2a) along the way. This is becausereproductive success in such circumstances is a function of an individual's relative (as opposed to absolute) expenditure. Second, this hypothesis is consistent with the exaggerated secondary sexual characters (kype, hump and gaudy spawning colors) which distinguish semelparous *Oncorhynchus* as a group. It further suggests a tie in with the observation that semelparous salmonids generally breed under higher densities than their iteroparous allies. Specifically, high densities of spawners favor increased competition for mates and nesting sites, territorial defense of fertilized eggs and increased *per offspring* allocation by females in the form of larger eggs - which is to say, the innovations of which we have been speaking. So perhaps the problem's solution is already in our grasp. And perhaps not. For, as A. Hendry has emphasized in correspondence, the situation is really quite complex, both with regard to the selective agents that may have triggered the process and the sequence in which traits were acquired. And of course, there is the not so minor consideration that, viewed across the animal kingdom, sexual selection doesn't always "run away." In short, the matter remains murky, for which reason, this essay concludes, not with an answer, but with an open question. It is an appropriate way to end a prolegomenon, though clearly not so satisfying as being able to trumpet "Problem solved!" Maybe next time.

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Table I. Consequences to Current Optimal Reproductive Effort, E_i^*, of Increased Effective Fecundity and Survival per Unit Investment.

Life History Parameter Affected:					
Current Age		**Later Ages**		**Earlier Ages**	
$B_i(E_i)$	$p_i(E_i)$	$B_j(E_j)$	$p_i(E_j)$	$B_j(E_j)$	$p_j(E_j)$
Consequence to E_i^*					
↑	↓	↓	↓	↑	↑

Table II. Age-Specific Optimal Effort, E_i^*.

	Age Class:				
	0	**1**	**2**	**3**	**"Adults"**
Potential Fecundity Increases With Age					
Maximum Return on Investment					
β_i =	0.50	1.00	2.00	3.00	4.00
Optimal Effort					
Adults Die After One Year					
E_i^* =	0.34	0.36	0.45	0.57	1.00
Adults Survive with Probability p_A					
E_i^* =	0.34	0.35	0.43	0.53	0.66
Potential Fecundity Declines in Old Age					
Maximum Return on Investment					
β_i =	0.50	1.00	2.00	1.00	0.50
Optimal Effort					
Adults Die After One Year					
E_i^* =	0.37	0.44	0.73	0.76	1.00
Adults Survive with Probability p_A					
E_i^* =	0.37	0.44	0.72	0.72	0.63

1. $B_i(E_i) = \beta_i(2E_i - E_i^2)$; $p_i(E_i) = \pi_i(1-E_i^2)$; π_i = [0.50, 0.60, 0.70, 0.65, 0.50].

Captions to the Figures.

Figure 1. Fitness, $r(\varphi,N)=(1/N)(dN/dt)$, plotted against density for wild type and mutant phenotypes, φ_0 and φ'. In the course of evolving from φ_0 to φ', the population's equilibrium density increases from K_0 to K'.

Figure 2. Optimal reproductive expenditure under different assumptions regarding the trade-off between current effective fecundity, B(E), and subsequent survival, p(E), for populations growing according to Eq(6a). Optimal expenditures are values of *E* at which $\lambda(E) = B(E) + p(E)$ is maximal. **a.** B(E) and p(E) are *accelerating* functions (*positive* second derivatives) of *E*. In this case, $\lambda(E)$ passes through a minimum, $E^{\#}$, and the optimal expenditure is 0 *or* 1. **b.** The dependencies, B(E) and p(E) are *decelerating* functions (*negative* second derivatives) of *E* with the consequence that the optimum expenditure, E^*, is often *between* 0 and 1. **c.** and **d.** More complex dependencies. In **c**, $E^* = 0$ or $0 < E^* < 1$; in **d**, $0 < E^* < 1$ or $E^* =1$. Functions and parameter values used to compute these figures as follows: **a.** $B(E) = \beta E^2$; $\beta= 1.0$; $p(E) = \pi (1-E)^2$, $\pi = 0.7$. **b.** $B(E) = \beta (2E-E^2)$, $\beta = 1.0$; $p(E) = \pi (1-E^2)$, $\pi = 0.7$. **c.** $B(E) = \beta (3E^2 - 2E^3)$, $\beta = 1.0$; $p(E) = \pi (1-E)$, $\pi = 0.7$. **d.** $B(E) = \beta E$; $\beta = 1.0$; $p(E) = (1-2E^2+2E^3)$, $\pi = 0.9$.

Figure 3. Consequences to optimal reproductive expenditure, E*, of per unit effort reductions in effective fecundity, B(E), and post-reproductive survival, p(E), in a model without age structure. **a.** Reducing B(E) reduces E*. **b.** Reducing p(E) increases E*.

Figure 4. Optimal reproductive effort, E*(N), and equilibrium density, N*(E), under alternative assumptions regarding the effects of increasing population size. **a.** Increased density reduces pre-reproductive survival. Optimal effort declines with density. $\lambda(E,N) = B(E,N) + p(E) = \beta e^{-cN} (2E-E^2) + \pi(1-E^2)$; $c = 0.5$; $\beta = 5.0$; $\pi = 0.8$. **b.** Increased density diminishes post-reproductive survival. Optimal effort increases with density. $\lambda(E,N) = B(E) + p(E,N) = \beta (2E-E^2) + \pi e^{-cN} (1-E^2)$; $c = 0.5$; $\beta = 0.95$; $\pi = 0.8$.

Figure 5. Adaptive topographies and optimal reproductive expenditures in a two stage (juvenile-adult) life history. The coordinate axes, E_j and E_a, are juvenile and adult reproductive effort. Reproductive effort pairs, (E_j, E_a), are color coded by $\exp(\lambda_1)$ according to the visible spectrum with dark red denoting low fitness values and dark violet, high. The thick white lines are curves of *conditional optima*, $E_j^*(E_a)$ and $E_a^*(E_j)$ whereon λ_1 is maximized. The thin white lines are curves of *conditional minima* whereon λ_1 is minimized. **a.** The effective fecundity and post-reproductive survival functions are *accelerating* functions of reproductive effort as in Figure 2a. In this case, there is a single global *minimum* in fitness and multiple optimal life histories. The latter correspond to zero or 100% reproduction at each age. **b.** The effective fecundity and post-reproductive survival functions are *decelerating* functions of reproductive effort as in Figure 2b. Here, there is a single global maximum in fitness. **c.** Effective fecundity is a sigmoid function of effort; post-reproductive survival declines linearly as in Figure 2c. In this case, there are two prominent adaptive peaks, the tallest of which corresponds to no reproduction by juveniles and high effort by adults. **d.** Effective fecundity is a linear function of effort; post-reproductive survival, a reverse sigmoid as in Figure 2d. Effective fecundity and post-reproductive survival functions as in Figure 2.

Figure 6. Effective Fecundity Effect. Changing adaptive topographies and optimal reproductive expenditures in response to increasing fecundity potential (effective fecundity per

unit effort) in a two-stage life history. Curves of conditional optima and minima and reproductive effort pairs, (E_j, E_a), color-coded as in Figure 5. Life history functions, $B_i(E_i)$ and $p_i(E_i)$ as in Figure 2c (fecundity a sigmoidal function of effort; post-reproductive survival, a linear function with $\pi_j = 0.8$; $\pi_a = 0.9$). Post-reproductive growth function, $g_i(E_i) = 1 + \gamma_i(1\text{-}E_i)$, with $\gamma_j = \gamma_a = 2.0$. **a.** $\beta_j = \beta_a = 0.5$. **b.** $\beta_j = \beta_a = 2.0$; **c.** $\beta_j = \beta_a = 3.0$; **d.** $\beta_j = \beta_a = 5.0$. With fecundity per unit effort low, juveniles should not reproduce. As potential fecundity increases, the optimal life history shifts to one in which reproductive effort is high at both stages in the life cycle.

Figure 7. Post-Reproductive Growth Rate Effect. Changing adaptive topographies and optimal reproductive expenditures in response to increasing post-reproductive growth potential in a two-stage life history. Curves of conditional optima and minima and reproductive effort pairs, (E_j, E_a), color-coded as in Figure 5. Life history functions, $B_i(E_i)$ and $p_i(E_i)$ as in Figure 2c with $\beta_j = \beta_a = 1.5$ and $\pi_j = 0.8$; $\pi_a = 0.9$. Post-reproductive growth function, $g_i(E_i)$, as in Figure 7. **a.** $\gamma_j = \gamma_a = 0.0$. **b.** $\gamma_j = \gamma_a = 0.5$; **c.** $\gamma_j = \gamma_a = 1.0$; **d.** $\gamma_j = \gamma_a = 2.0$. For low growth potential, the optimal life history corresponds to large reproductive expenditures by juveniles and adults. With increasing growth potential, the optimal life history shifts to one in which the onset of reproduction is delayed, *i.e.*, juveniles no longer reproduce.

Figure 8. Evolution of effort per offspring, *e*, and the joint evolution of total effort, *E*, and *e*. **a.** Optimal value, *e**, of *e* is that for which juvenile survival, c(e), is tangent to the straight line, c = e k, of greatest *k*. **b.** Covariation of effort per offspring and total reproductive expenditure. Because e* maximizes effective fecundity, the optimal total expenditure, E*(e), is maximal at e = e*. For these calculations, which are purely illustrative, it is assumed that $c(e) = \sigma e^2 - \tau e^3$; $e < \sigma/\tau$; $c(e) = \sigma^3/\tau^2$, $e \geq \sigma/\tau$; with $\sigma = 0.2$, and $\tau = 1.5$.

Figure 9. Commercial Fishery Effect. Changing adaptive topographies and optimal reproductive expenditures in response to increasing commercial fishing pressure as modeled by reductions in fecundity and post-reproductive survival per unit effort among adults in the two-stage life history model of Figures 5-7. Curves of conditional optima and minima and reproductive effort pairs, (E_j, E_a), color-coded as in Figure 5. Life history functions, $B_i(E_i)$ and $p_i(E_i)$ as in Figure 2c with $\beta_j = 1.0$ and $\pi_j = 0.8$. Post-reproductive growth function, $g_i(E_i)$, as in Figure 7 with $\gamma_j = \gamma_a = 2.0$. **a.** $\beta_a = 1.6$; $\pi_a = 0.9$. **b.** $\beta_a = 0.8$; $\pi_a = 0.45$. **c.** $\beta_a = 0.4$; $\pi_a = 0.225$. **d**. $\beta_a = 0.2$; $\pi_a = 0.1125$. Diminishing adult components of fitness lowers the optimal age of first reproduction.

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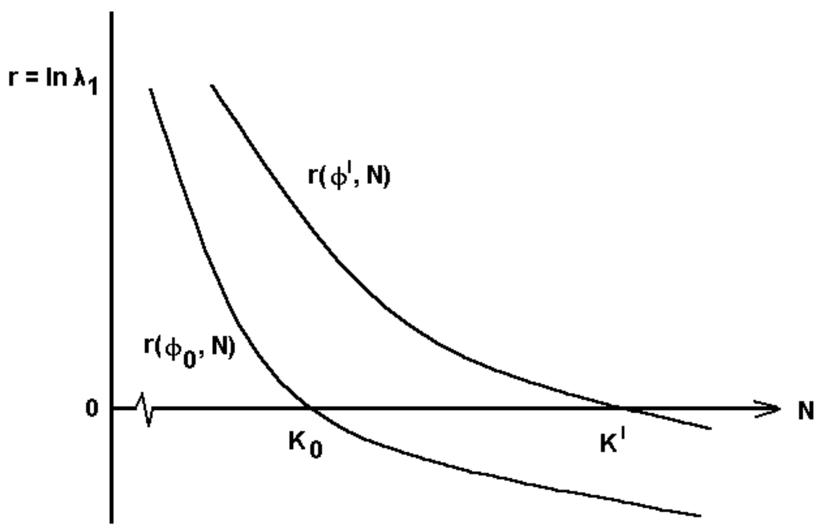


Figure 1. Fitness, r(φ,N)=(1/N)(dN/dt), plotted against density for wild type and mutant phenotypes, φ_0 and φ′. In the course of evolving from φ_0 to φ′, the population's equilibrium density increases from K_0 to *K*′.

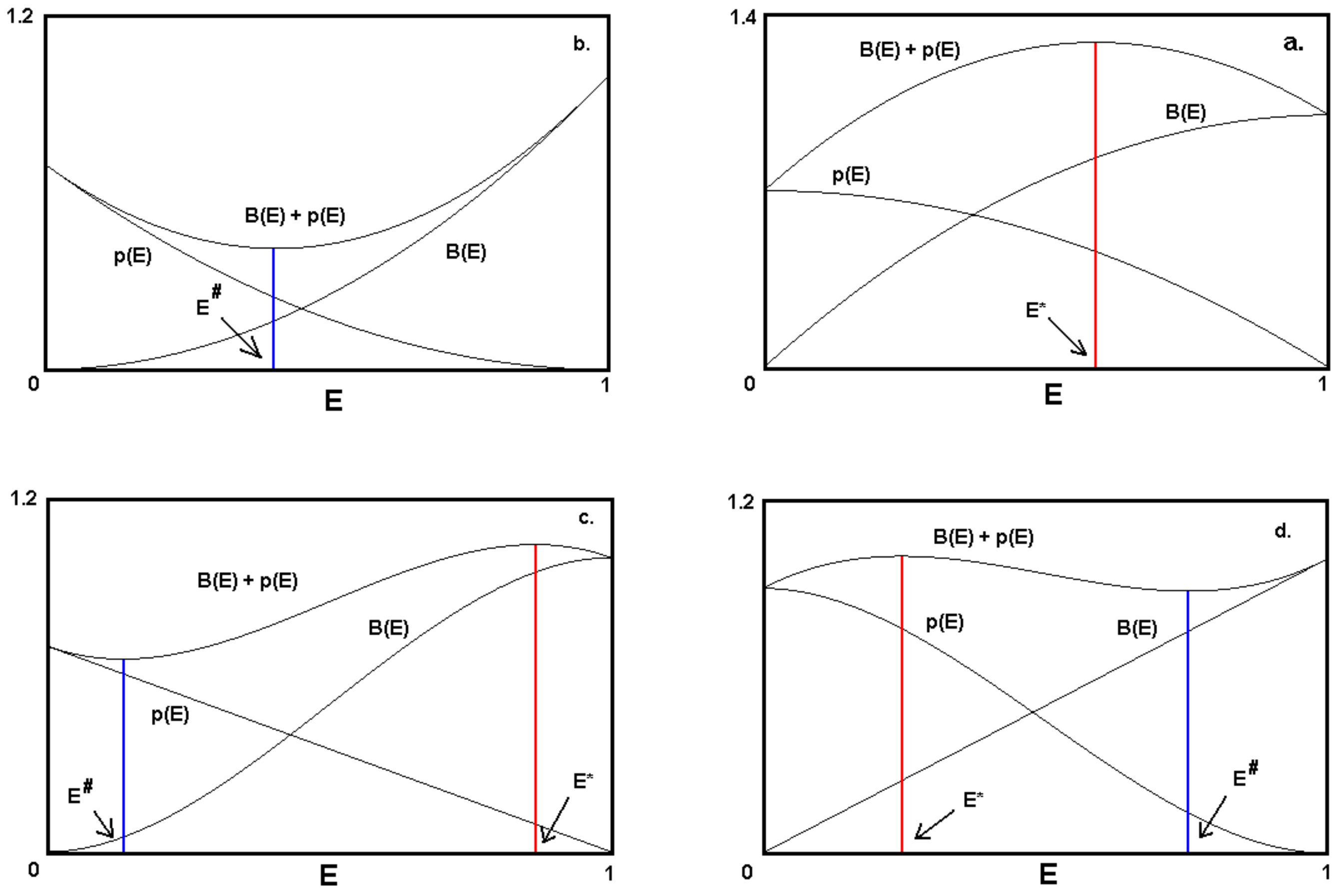


Figure 2. Optimal reproductive expenditure under different assumptions regarding the trade-off between current effective fecundity, B(E), and subsequent survival, p(E), for populations growing according to Eq(6a). Optimal expenditures are values of *E* at which $\lambda(E) = B(E) + p(E)$ is maximal. **a.** B(E) and p(E) are *accelerating* functions (*positive* second derivatives) of *E*. In this case, $\lambda(E)$ passes through a minimum, $E^{\#}$, and the optimal expenditure is 0 *or* 1. **b.** The dependencies, B(E) and p(E) are *decelerating* functions (*negative* second derivatives) of *E* with the consequence that the optimum expenditure, E^{*}, is often *between* 0 and 1. **c.** and **d.** More complex dependencies. In **c**, $E^{*} = 0$ or $0 < E^{*} < 1$; in **d**, $0 < E^{*} < 1$ or $E^{*} = 1$. Functions and parameter values used to compute these figures as follows: **a.** $B(E) = \beta E^2$; $\beta = 1.0$; $p(E) = \pi (1-E)^2$, $\pi = 0.7$. **b.** $B(E) = \beta (2E-E^2)$, $\beta = 1.0$; $p(E) = \pi (1-E^2)$, $\pi = 0.7$. **c.** $B(E) = \beta (3E^2 - 2E^3)$, $\beta = 1.0$; $p(E) = \pi (1-E)$, $\pi = 0.7$. **d.** $B(E) = \beta E$; $\beta = 1.0$; $p(E) = (1-2E^2+2E^3)$, $\pi = 0.9$

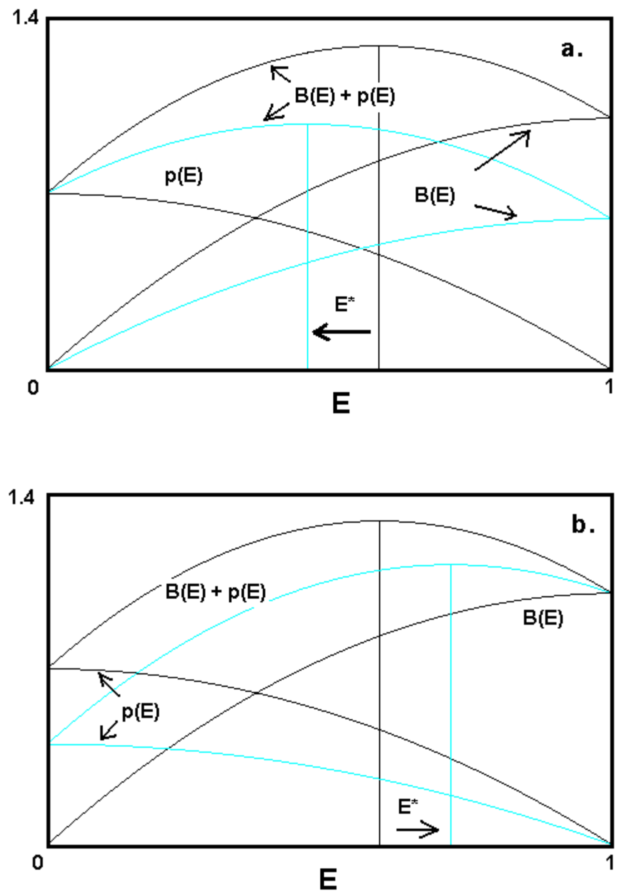


Figure 3. Consequences to optimal reproductive expenditure, E*, of per unit effort reductions in effective fecundity, B(E), and post-reproductive survival, p(E), in a model without age structure. **a.** Reducing B(E) reduces E*. **b.** Reducing p(E) increases E*.

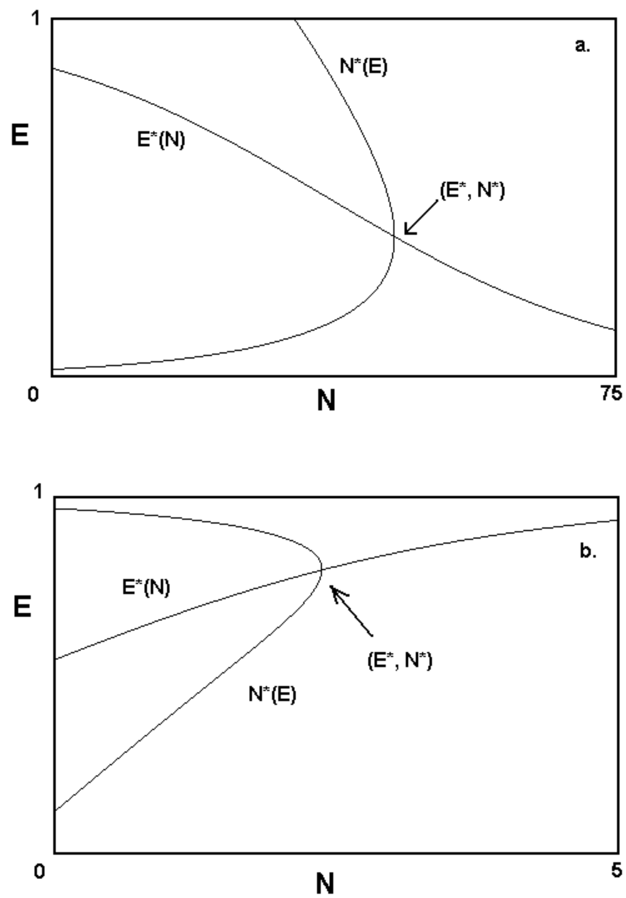


Figure 4. Optimal reproductive effort, E*(N), and equilibrium density, N*(E), under alternative assumptions regarding the effects of increasing population size. **a.** Increased density reduces pre-reproductive survival. Optimal effort declines with density. $\lambda(E,N) = B(E,N) + p(E) = \beta e^{-cN} (2E-E^2) + \pi(1-E^2)$; $c = 0.5$; $\beta = 5.0$; $\pi = 0.8$. **b.** Increased density diminishes post-reproductive survival. Optimal effort increases with density. $\lambda(E,N) = B(E) + p(E,N) = \beta (2E-E^2) + \pi e^{-cN} (1-E^2)$; $c = 0.5$; $\beta = 0.95$; $\pi = 0.8$.

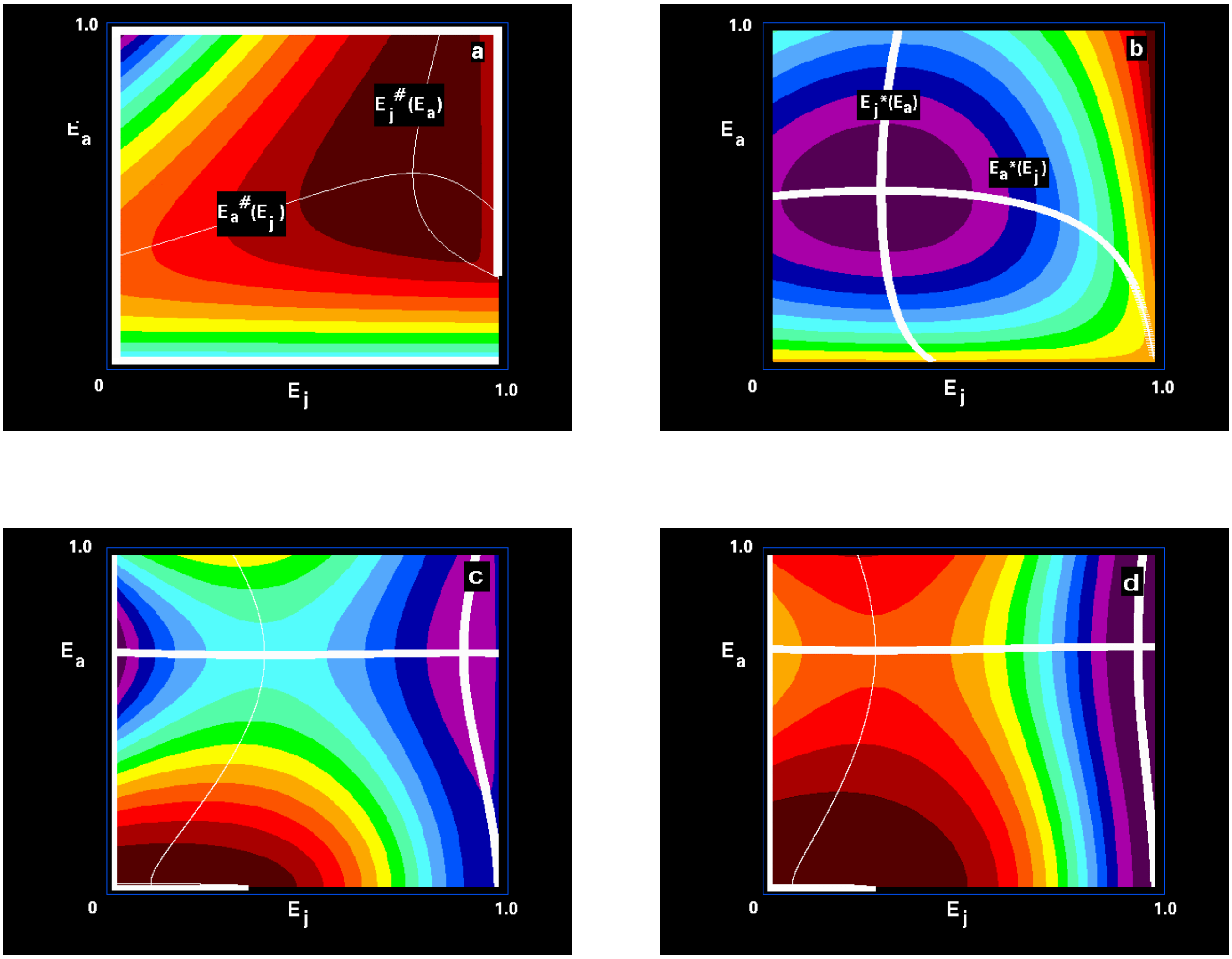
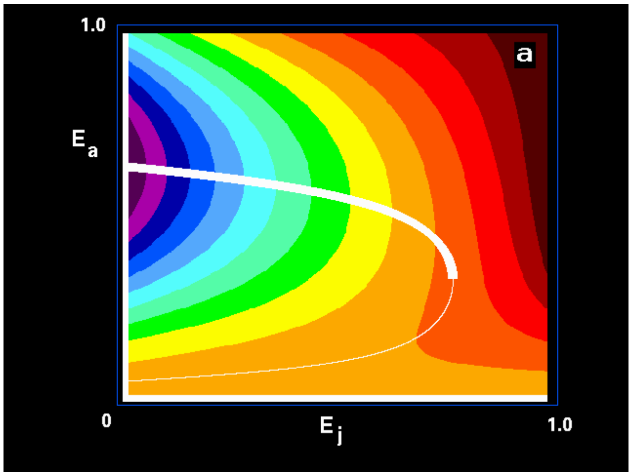


Figure 5. Adaptive topographies and optimal reproductive expenditures in a two stage (juvenile-adult) life history. The coordinate axes, Ej and Ea, are juvenile and adult reproductive effort. Reproductive effort pairs, (E_j, E_a), are color coded by $\exp(\lambda_1)$ according to the visible spectrum with dark red denoting low fitness values and dark violet, high. The thick white lines are curves of *conditional optima*, $E_j{*}(E_a)$ and $E_a{*}(E_j)$ whereon λ_1 is maximized. The thin white lines are curves of *conditional minima* whereon λ_1 is minimized. **a.** The effective fecundity and post-reproductive survival functions are *accelerating* functions of reproductive effort as in Figure 2a. In this case, there is a single global *minimum* in fitness and multiple optimal life histories. The latter correspond to zero or 100% reproduction at each age. **b.** The effective fecundity and post-reproductive survival functions are *decelerating* functions of reproductive effort as in Figure 2b. Here, there is a single global maximum in fitness. **c.** Effective fecundity is a sigmoid function of effort; post-reproductive survival declines linearly as in Figure 2c. In this case, there are two prominent adaptive peaks, the tallest of which corresponds to no reproduction by juveniles and high effort by adults. **d.** Effective fecundity is a linear function of effort; post-reproductive survival, a reverse sigmoid as in Figure 2d. Effective fecundity and post-reproductive survival functions as in Figure 2.



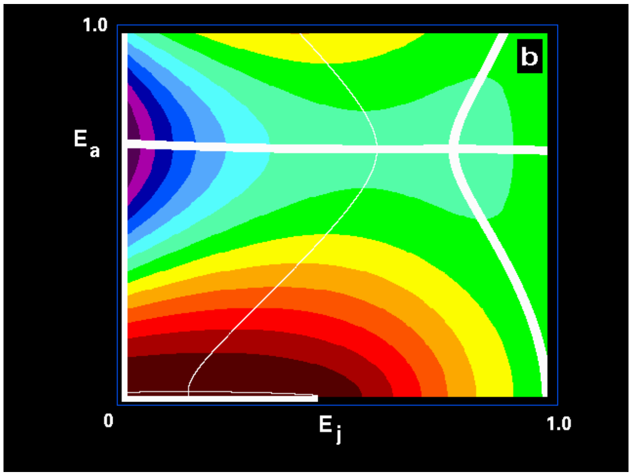


Figure 6. Effective Fecundity Effect. Changing adaptive topographies and optimal reproductive expenditures in response to increasing fecundity potential (effective fecundity per unit effort) in a two-stage life history. Curves of conditional optima and minima and reproductive effort pairs, (E_j, E_a), color-coded as in Figure 5. Life history functions, $B_i(E_i)$ and $p_i(E_i)$ as in Figure 2c (fecundity a sigmoidal function of effort; post-reproductive survival, a linear function with $\pi_j = 0.8$; $\pi_a = 0.9$). Post-reproductive growth function, $g_i(E_i) = 1 + \gamma_i(1-E_i)$, with $\gamma_j = \gamma_a = 2.0$. **a.** $\beta_j = \beta_a = 0.5$. **b.** $\beta_j = \beta_a = 2.0$; **c.** $\beta_j = \beta_a = 3.0$; **d.** $\beta_j = \beta_a = 5.0$. With fecundity per unit effort low, juveniles should not reproduce. As potential fecundity increases, the optimal life history shifts to one in which reproductive effort is high at both stages in the life cycle.

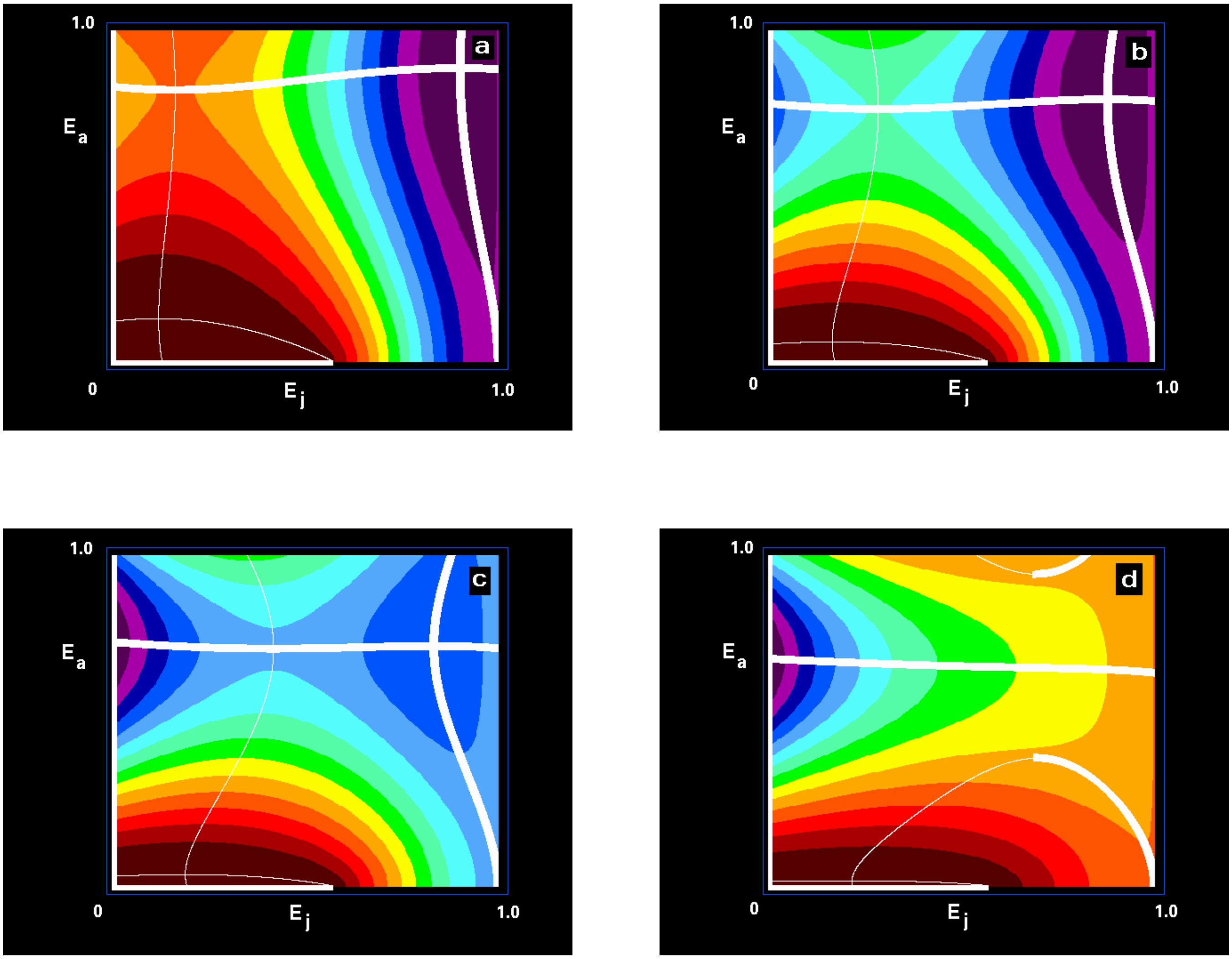


Figure 7. Post-Reproductive Growth Rate Effect. Changing adaptive topographies and optimal reproductive expenditures in response to increasing post-reproductive growth potential in a two-stage life history. Curves of conditional optima and minima and reproductive effort pairs, (E_j, E_a), color-coded as in Figure 5. Life history functions, $B_i(E_i)$ and $p_i(E_i)$ as in Figure 2c with $\beta_j = \beta_a = 1.5$ and $\pi_j = 0.8$; $\pi_a = 0.9$. Post-reproductive growth function, $g_i(E_i)$, as in Figure 7. **a.** $\gamma_j = \gamma_a = 0.0$. **b.** $\gamma_j = \gamma_a = 0.5$; **c.** $\gamma_j = \gamma_a = 1.0$; **d.** $\gamma_j = \gamma_a = 2.0$. For low growth potential, the optimal life history corresponds to large reproductive expenditures by juveniles and adults. With increasing growth potential, the optimal life history shifts to one in which the onset of reproduction is delayed, *i.e.*, juveniles no longer reproduce.

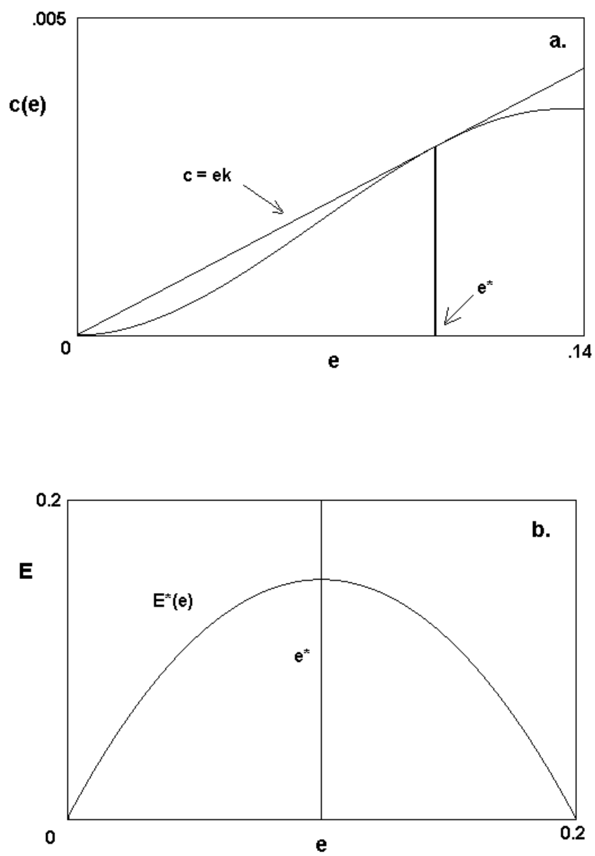


Figure 8. Evolution of effort per offspring, *e*, and the joint evolution of total effort, *E*, and *e*. **a.** Optimal value, *e**, of *e* is that for which juvenile survival, c(e), is tangent to the straight line, c = e k, of greatest *k*. **b.** Covariation of effort per offspring and total reproductive expenditure. Because e* maximizes effective fecundity, the optimal total expenditure, E*(e), is maximal at e = e*. For these calculations, which are purely illustrative, it is assumed that $c(e) = \sigma e^2 - \tau e^3$; $e < \sigma/\tau$; $c(e) = \sigma^3/\tau^2$, $e \geq \sigma/\tau$; with $\sigma = 0.2$, and $\tau = 1.5$.

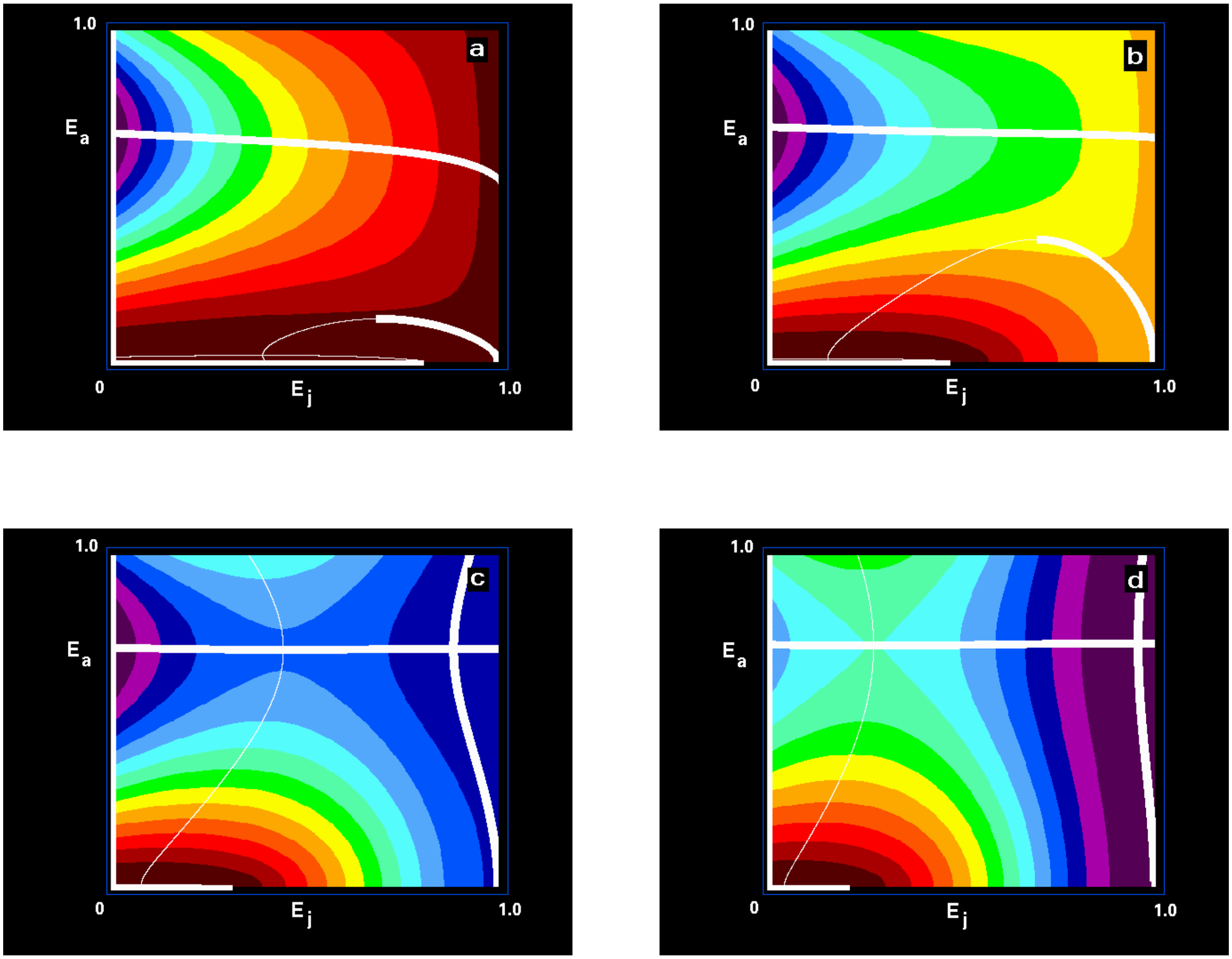


Figure 9. Commercial Fishery Effect. Changing adaptive topographies and optimal reproductive expenditures in response to increasing commercial fishing pressure as modeled by reductions in fecundity and post-reproductive survival per unit effort among adults in the two-stage life history model of Figures 5-7. Curves of conditional optima and minima and reproductive effort pairs, (E_j, E_a), color-coded as in Figure 5. Life history functions, $B_i(E_i)$ and $p_i(E_i)$ as in Figure 2c with $\beta_j = 1.0$ and $\pi_j = 0.8$. Post-reproductive growth function, $g_i(E_i)$, as in Figure 7 with $\gamma_j = \gamma_a = 2.0$. **a.** $\beta_a = 1.6$; $\pi_a = 0.9$. **b.** $\beta_a = 0.8$; $\pi_a = 0.45$. **c.** $\beta_a = 0.4$; $\pi_a = 0.225$. **d**. $\beta_a = 0.2$; $\pi_a = 0.1125$. Diminishing adult components of fitness lowers the optimal age of first reproduction.