Demographic parameters at evolutionary equilibrium[1]

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We reason that natural selection acting under conditions imposed by physical factors (e.g., geometric constraints on growth rate) and community organization (e.g., persistent finite population sizes, equal total biomass of organisms in proportionately equal size ranges) should lead to certain life history features. The initial size of resource-capturing young should be the smallest that permits growth rate to exceed mortality rate so that the age cohort will start to increase in biomass. Production of such young must be an inefficient use of biomass because of metabolism, predation of embryos, the cost of males, and other losses. Mortality rate during juvenile growth should be a power function like growth rate, but always a bit lower so that the age cohort continues to increase and ultimately to compensate for the inefficiency of reproduction. In a constant environment, the individual should stop growing at the size of greatest expected excess of future reproductive resources over size, and thereafter devote all expendable resources to reproduction. Any given size range of animals, such as 1−2 mg or 1−2 kg, should consist of both mature and immature individuals in any community and should be devoting about a third of its investable resources to reproduction and the rest to growth. We use our equations to generate sample life histories. The simple form of our equations organizes these life tables into families of similar schedules with variable generation time.

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Voici la théorie que nous proposons: la sélection naturelle, dans des conditions imposées par certains facteurs physiques (p.ex., les contraintes géométriques qui affectent le taux de croissance) et par l'organisation de la communauté (p.ex., populations d'effectifs finis et persistants, biomasse totale d'organismes égale dans des classes de taille de proportions égales), devrait éventuellement entraîner l'existence de certaines caractéristiques dans la dynamique des populations. La taille initiale des jeunes capables d'utiliser les ressources doit être la plus petite taille qui permette au taux de croissance d'excéder le taux de mortalité, de façon à ce que la biomasse de la cohorte puisse augmenter. La production de ces jeunes doit nécessairement entraîner une utilisation inefficace de la biomasse à cause des pertes par métabolisme, par prédation des embryons, par dépense énergétique des mâles etc . . . Le taux de mortalité durant la croissance des jeunes devrait être une fonction exponentielle à l'image du taux de croissance mais légèrement inférieure, de façon à permettre à la cohorte de continuer sa croissance et, éventuellement, compenser l'inefficacité de la reproduction. Dans un environnement constant, on devrait s'attendre à ce que l'individu cesse de croître au moment où il atteint la taille qui détermine le plus grand écart entre les ressources reproductives futures et la taille, et à ce qu'il consacre alors toutes ses ressources utilisables à la reproduction. Une classe donnée d'animaux, par exemple 1−2 mg ou 1−2 kg, devrait contenir à la fois des individus immatures et des individus adultes et allouer le tiers de ses ressources disponibles à la reproduction, le reste à la croissance. Nos équations permettent de générer des modèles de dynamique de populations. La forme simple de nos équations permet d'organiser ces tables de survie en catégories de stratégies semblables, mais où la durée d'une génération peut varier.

[Traduit par le journal]

Introduction

Some quantitative generalizations about groups of organisms in nature seem to have wide acceptance, but their formulations may be vague and their logical connections with each other have not been seriously considered. The following generalizations are some examples. (1) Populations always remain finite despite a universal capacity for indefinite expansion ($r_{max} > 0$), but often persist for an enormous number of generations ($\bar{r} = 0$). (2) Biological rates are power functions of organism size. They are often assumed to depend on surface area or the two-thirds root of the mass. (3) Exothermic organisms have higher rates of metabolism and other processes at higher temperatures, but different processes remain functionally coordinated within a sometimes broad temperature range. (4) The biomass of age cohorts increases on average at least until maturity (Cushing 1975; Ware 1975; Alverson and Carney 1975). (5) Specific mortality and growth rates are directly related (Williams 1966; Cherepanov 1967; Ware 1975). (6) Natural selection optimizes resource allocation and the timing of events in the life cycle.

Generalizations Nos. 2 and 5 jointly imply that as an animal grows larger, its absolute growth rate increases but its rates of specific growth and mortality decrease. A continuous increase in cohort biomass (generalization No. 5) implies that specific growth continuously exceeds mortality.

This change in mortality with a large increase in size between zygote and maturity must be enormously greater than any change in the opposite direction from senescence. Larval plaice may have instantaneous annual mortality rates about 180 times as great as those of adults (Gulland 1977), while an increase in mortality from senescence is difficult to detect (Cushing 1975).

The power-function dependence of biological rates has been recognized as ". . . one of the few manifestations of a universal law in biology" (Platt and Silvert 1981). Unfortunately there is no consensus on any universal value for the exponential constant. Platt and Silvert (1981) argue from dimensional considerations that rates should depend on size to the power 2/3 for aquatic mammals and to the power 3/4 for terrestrials. Sometimes the 2/3 exponent of surface-area dependence is supported by experimental data, e.g., Jobling (1982) on plaice metabolism, Economos (1979) on cetacean metabolism, and Hutchings and Budd (1981) on nutrient capture by plants. More often

a higher value is suggested, e.g., about 0.75 by Banse (1976) for phytoplankton growth, by Economos (1979) for land mammal metabolism, and by Sebens (1982) for biomass capture by sea anemones. Values well above 0.8 are often observed for fish metabolism (Brett and Groves 1979; Kudrinskaya 1979; Tarby 1981).

In this paper we make use of simplified versions of the generalizations above and two others. We assume that the size ratio of adults to zygotes in a community is large and independent of absolute size (discussed in the interaction of size ranges). We also accept a suggestion of Sheldon et al. (1972) that proportionately equal size ranges of particles in the ocean have about the same total mass. If the only particle between 100 and 200 t in a cubic kilometre of seawater is one 150-t whale, that same cubic kilometre would be expected to contain about 150 t of objects between 1 and 2 kg, 150 t of objects between 1 and 2 mg, and so on. We assume that almost all particles in pelagic waters are either organisms themselves or must be closely correlated with organism abundance (exoskeletal fragments, fecal pellets, etc.). Platt and Silvert (1981) discuss related generalizations about sizes of organisms.

This paper is a preliminary attempt to rationalize these generalizations and to derive more explicit formulations for some of them than have been suggested before. The extremely simplified assumptions that we use are unlikely to be accurate, but may be sufficient for an exploratory venture. Consequences of the relaxation of some of our assumptions are examined briefly after the initial analysis, especially the substitution of seasonally rhythmic change for constant conditions. Our approach differs from other recent modelling of life history evolution (e.g., Leon 1976; and Schaffer 1983), in that we make size rather than age the basic independent variable. In this respect we follow Western (1979), Roff (1981), and Hughes (1984). This approach has a number of advantages. Size is more easily measured than age and may be more closely correlated with survival, maturity, and fecundity. Also, the use of size leads in places to simplifications in the modelling and allows stronger conclusions.

Size—range specialization in the life cycle

In what might be conceived as a stable and homogeneous environment, such as a large mass of seawater, organisms vary in size over many orders of magnitude. A given kind is reliably viable over only a part of the total range. A bluefin tuna, for instance, starts life at a substantial fraction of a milligram and most likely ends it weighing less than 1 t. This is a mere billionfold increase in biomass, a limited part of the total range (bacteria to whales). We interpret this to mean that each species' adaptations permit growth to exceed mortality within a special size range (Fig. 1), and that this is the size range on which the life cycle depends for its completion. Similar reasoning was used by Roff (1981) and applied to vital processes in *Drosophila*. Mathematically we define the range of specialization as that in which a female organism of size s can gather resources for growth at rate $sg(s)$ and can thereby grow according to the differential equation $ds/dt = sg(s)$ if she uses all investable resources for growth. If she is reproducing, she can produce resource-capturing offspring at rate $sg(s)E$, where E is efficiency, independent of s. Size-dependent mortality, $\mu(s)$, within the range of specialization is less than $g(s)$, but the reverse is true outside this range.

Taylor and Williams (1983) showed with a geometric argument that an optimal life history under the above assumptions
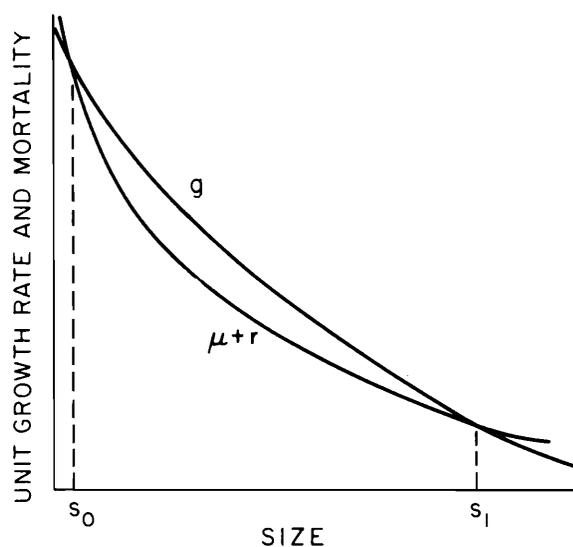

FIG. 1. Plots of unit growth rate (g) and mortality (μ) against size (s) of an organism. The life cycle of the organism is expected to remain in the range (s_0, s_1) in which $g > \mu + r$.

(and with a constant population size) has the following simple form: an organism should grow without reproducing to a certain size y and then, remaining at that size, convert all resources for growth to offspring of some size x. The optimum values of x and y are found by maximizing $w(x,y)$, the total expected number of offspring of a zygote.

Here we indicate how the analysis is modified for increasing or decreasing population size ($r \neq 0$). Let $l(x,s)$ be the survivorship from size x to size s assuming the organism puts all investable resources into growth between x and s. Then a zygote survives to maturity with probability $l(x,y)$ and, when mature, has a constant mortality, $\mu(y)$, and so is still alive time t after maturity with a probability of $e^{-\mu(y)t}$. While mature, it gathers resources for propagules at rate $yg(y)$. The present value (at age of maturity) of all such resources gathered is

$$[1] \quad R(y) = yg(y) \int_0^\infty e^{-\mu(y)t} e^{-rt} \, dt = \frac{yg(y)}{\mu(y) + r}$$

and these are converted, with efficiency E, into offspring of size x. The reproductive value of a zygote is then

$$[2] \quad v(x,y) = l(x,y)e^{-rT(x,y)}ER(y)/x$$

where $T(x,y)$ is the time from zygote to maturity. We can regard $v(x,y)$ as the present value of the expected number of offspring of a zygote (of size x) or as the present value of the expected total mass of offspring produced by a yet undifferentiated unit mass of ovarian material. With this last interpretation we can imagine the unit mass as choosing first the size x of the immediate zygotes (of which it then gets $1/x$) and then, later, choosing the size y of maturity. With this interpretation it is clear that natural selection will choose x and y to maximize v.

We show in the Appendix that v is maximized when (i) $g(x) = \mu(x) + r$ and (ii) $R(s) - s$ is maximized at y. Condition (i) gives the optimal zygote size x and condition (ii) gives the optimal mature size y.

The differential condition corresponding to condition (ii) is $dR/ds = 1$ at $s = y$. The interpretation of this is that growth should cease when an extra unit, δs, of resources into growth no longer produces as large a gain in present value as the gain,
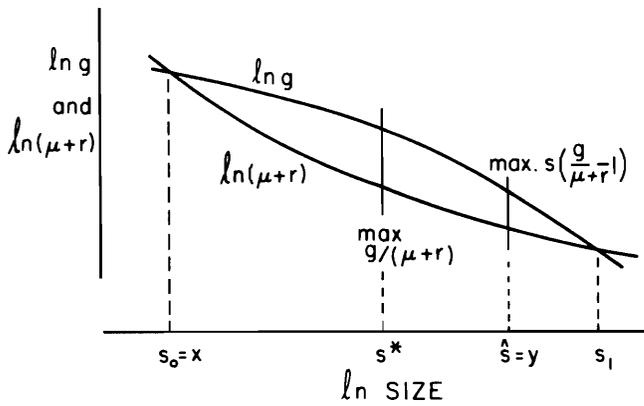
FIG. 2. The same plot as Fig. 1 except on log−log scale. The optimum zygote size x and the optimum mature size y occur at sizes s_0 and $\hat{s}$, respectively.

δR, of putting it into reproduction. In other words, growth should cease when the benefit/cost ratio falls below one. Optimal values of x and y are indicated in Fig. 2. We remark that y always falls between the point s^*, where $g/(\mu + r)$ is maximized, and the point s_1 where $g = \mu + r$. Seasonality and other factors may favour growth beyond y as discussed below.

The interaction of different size ranges

The previous section limited discussion to the life history of a single species. Now we fasten attention on a wide range (20 orders of magnitude) of individual organisms in a continuous medium such as the sea, here assumed homogeneous. Each size category has contributions from species at different life history stages. There will be a steady flow of mass from one size category into others because of growth, predation, and reproduction. Our objective is to quantify this flow in ways consistent with our initial list of generalizations. The results we obtain should be regarded as crude estimates of general averages. We adopt temporarily the assumption of constant population size ($r = 0$), to simplify the equations. The main effect of nonzero r on life history parameters is expected to occur through its effect on optimal values of zygote size x and mature size y given by conditions (i) and (ii). We discuss later the possible magnitude of this effect.

Living organisms will be of two kinds, mature and immature, defined, as above, by the use of investable resources for either growth or reproduction. We will use q to denote the ratio $\mu(s)/g(s)$ of specific mortality and growth rate. Now q will vary between species and over the size range of any given species. In our model, q will appear in two versions:

[3] $\quad \hat{q} = \mu(y)/g(y)$

the value at maturity, and

[4] $\quad \bar{q} = \dfrac{\displaystyle\int_x^y \dfrac{\mu(s)}{g(s)}\dfrac{ds}{s}}{\displaystyle\int_x^y \dfrac{ds}{s}} = \dfrac{1}{\ln(y/x)}\int_x^y \dfrac{\mu(s)}{g(s)}\dfrac{ds}{s}$

a convenient average value of q over the immature portion of the life cycle. We expect $\hat{q}$ and $\bar{q}$ to be reasonably close, but it is not clear which should be larger; since y exceeds that value of s which maximizes $g(s)/\mu(s)$ (a consequence of condition (ii)), $\bar{q}$ will be an average of q values some of which exceed $\hat{q}$ and some of which do not. We will assume that $\hat{q}$ and $\bar{q}$ are independent of species size and somewhat less than 1.

Let $N(s)$ denote community density at size s, so that by definition, there are $N(s)ds$ individuals in the interval $(s, s + ds)$ for small ds. We estimate $N(s)$ from the generalization, discussed above, that the total biomass between s and αs is independent of s, that is, biomass density with respect to log size is constant. Taking $\alpha = 1 + \epsilon$ for small ϵ, the biomass is $sN(s)$ (ϵs). If this is independent of s

[5] $\quad N(s) = n/s^2$

for some constant n. Thus, the community density (on the size axis) varies inversely with size squared.

Our assumption that the ratio $k = y/x$ of adult to offspring size is independent of size is no doubt inaccurate for at least part of the size spectrum (examples discussed later), but may be justified as a first approximation. From the fact that reproductive value of a zygote must be unity, we can estimate reproductive efficiency. Setting $v(x,kx) = 1$ in Eq. 2, with $r = 0$, we get

[6] $\quad l(x,kx)E\,k/\hat{q} = 1$

We can estimate l from the formula, obtained by integrating, Eq. 2A,

[7] $\quad \ln l(s',s'') = -\int_{s'}^{s''} \dfrac{\mu(z)dz}{zg(z)} = \bar{q}\ln(s'/s'')$

where we replace μ/g by its average $\bar{q}$ defined in Eq. 4. Thus, survivorship from zygote to maturity is

[8] $\quad l(x,kx) = 1/k^{\bar{q}}$

and, from Eq. 6, reproductive efficiency is

[9] $\quad E = \hat{q}/k^{1-\bar{q}}$

When $\mu \equiv g$, $q = 1$ and $E = 1$ as expected. Unless reproduction is perfectly efficient, g must exceed μ for juveniles.

For calculating cohort biomass increase during juvenile growth, we let $C(s) = l(x,s)s/x$ be biomass of a cohort of unit mass starting at size x. Since $l(x,s) = (x/s)^{\bar{q}}$ from Eq. 7,

[10] $\quad C(s) = (s/x)^{1-\bar{q}}$

(this is the same as Ware's (1975) equation 2), the cohort biomass increase over the juvenile phase is

[11] $\quad \dfrac{C(kx)}{C(x)} = k^{1-\bar{q}} = \hat{q}/E$

from Eq. 9.

We also want to know the proportion of mature individuals of any size s. Let $I(s)$ and $M(s)$ be the density (along the s axis) of immature and mature individuals, respectively, of size s. We produce an equation for I in terms of M using the fact that every immature individual of size s came from a mature individual of some size z for $s \le z \le ks$. A mature individual of size z produces $Ezg(z)/(z/k) = \hat{q}k^{\bar{q}}g(z)$ offspring per unit time (from Eq. 9), and these survive to size s with probability $l(z/k,s) = (z/ks)^{\bar{q}}$ (from Eq. 7), and remain in $(s,s + ds)$ for the period $ds/sg(s)$. Thus, the number of immature individuals in $(s,s + ds)$ is

$$I(s)ds = \int_s^{ks} (ds/sg(s))\,(z/ks)^{\bar{q}}\hat{q}k^{\bar{q}}g(z)M(z)dz$$

Hence,

[12] $\quad I(s) = \dfrac{\hat{q}}{g(s)s^{1+\bar{q}}}\int_s^{ks} z^{\bar{q}}g(z)M(z)dz$

To solve this for M, we invoke the power function generalization (No. 2) on the form of g, so that

$$[13] \quad g(s) = as^{-\alpha}$$

for some constants a and α. If growth rate is proportional to surface area, then $ds/dt \sim s^{2/3}$ and $g(s)$ is of this form with $\alpha = 1/3$. As noted above, growth and other vital rates are often found to increase with size more quickly than surface area. Thus, we can expect α to be somewhat less than $1/3$ but well above 0. With this assumption on $g(s)$ it can be verified immediately that $M(s) = m/s^2$ solves Eq. 12 (using the fact that $I(s) = N(s) - M(s)$ where N is given by Eq. 5) with the constant m given by

$$[14] \quad \frac{m}{n} = \frac{1 + \alpha - \bar{q}}{1 + \alpha - \bar{q} + \hat{q}(1 - k^{-1-\alpha+\bar{q}})}$$

$$\simeq \frac{1 + \alpha - \bar{q}}{1 + \alpha - \bar{q} + \hat{q}}$$

the approximation valid if k is large. This is an expression for the proportion of mature individuals of any size. It is seen to be independent of s. If we assume that the rate at which an individual captures resources is not greatly affected by the use to which these resources wil be put, we can interpret m/n as the proportion of resources beyond maintenance spent by the community for reproduction. The fraction $1 - m/n$ would be invested in growth. These fractional rates of resource investment would be valid even if some mature individuals are continuing to grow.

We can now get an expression for the birth rate in terms of mature size where birth rate is the number of young born per unit time per individual in the population. Mature individuals produce young at rate $Eyg(y)/x = Eaky^{-\alpha}$ from Eqs. 1 and 13 where $k = y/x$ is assumed independent of size. Since mature individuals comprise a fraction m/n of the population, also size independent by Eq. 14, then

$$\text{birth rate} = Eak(m/n)y^{-\alpha}$$

and depends on size to the power $-\alpha$.

Finally, we derive a formula for the time taken for a zygote to reach maturity, under the assumption of Eq. 13 on the form of the growth function. Letting $T(x,s)$ be the time taken to reach size s, we integrate Eq. 4A to get

$$[15] \quad T(x,s) = \int_x^s \frac{dz}{zg(z)} = \frac{1}{\alpha a}(s^\alpha - x^\alpha)$$

and time to maturity is

$$[16] \quad T(x,kx) = \frac{1}{\alpha a}(k^\alpha - 1)x^\alpha$$

and is proportional to size to the power α. With growth rate proportional to surface area, $\alpha = 1/3$ and time to maturity is proportional to the length difference between parent and offspring. If $\alpha < 1/3$, growth in length would accelerate with increasing size, as long as no reproductive investments are being made.

Note that since mature life-span is given by

$$1/\mu(y) = \frac{1}{\hat{q}g(y)} = y^\alpha/\hat{q}a$$

using Eqs. 3 and 13, then total life-span, being the sum of time to maturity and mature life-span, should also depend on size to the power α.

Various demographic parameters must depend on the value of reproductive efficiency E. We have limited all previous discussion to females. If males are produced in equal numbers and compete equally with females for resources, E must include the factor $1/2$ (cost of males), typical for many animals. Note also that reproduction in our modelling means the production of resource-capturing young. Usually there will be an interval following the zygote stage when the young are not yet feeding, but are metabolizing and suffering predation. Vetter et al. (1983) found a 30% loss of lipids and other biomass reductions in developing drum eggs, and the mortality of fish eggs can sometimes exceed 90% (Harding 1974; Williams et al. 1973). To account for all this the reproductive efficiency E can hardly exceed $1/4$ and may often be $1/10$ or less. Suppose we take $k = 10^6$, $E = 1/10$, and $\alpha = 1/3$ (surface area growth). Equation 9 then allows us to find any number of pairs of values for $\hat{q}$ and $\bar{q}$. Three such pairs $(\hat{q}, \bar{q})$ are 0.80, 0.85; 0.845, 0.845; and 0.93, 0.84. They all give values of m/n (the proportion of mature individuals, from Eq. 14) of roughly 0.35. Thus, approximately one-third of expendable resources are invested by the community in reproduction, two-thirds are invested in growth. Finally, from Eq. 11 cohort biomass should increase from initial resource capture to maturity by a factor of $10\hat{q}$, somewhere between 8 and 10.

A pair of sample life histories (for $r = 0$) are calculated in Table 1, for organisms which take 341 and 786 days to mature and during this time increase in size by a factor k of approximately 1.5×10^5 and 1.5×10^6, respectively. The growth and mortality functions $g(s)$ and $\mu(s)$ both have approximately the form $as^{-1/3}$ for some constant a, and, following Fig. 1, $g = \mu$ at x and s_1, and $g > \mu$ in between. Indeed, we assumed

$$[17] \quad \begin{aligned} \ln g(s) &= f(s) + h(s) \\ \ln \mu(s) &= f(s) - h(s) \end{aligned}$$

where

$$[18] \quad \begin{aligned} f(s) &= \ln(\mu_0) - \frac{1}{3}(\ln(s) - \ln(x)) \\ h(s) &= B(\ln(s) - \ln(x))(\ln(s_1) - \ln(s)) \end{aligned}$$

The constants x, μ_0, B, and s_1 are to be specified. Note that $\mu_0 = \mu(x) = g(x)$ is mortality immediately after birth and B is a positive constant which measures the separation between g and μ. Values of s at different times were calculated by inverting the integral formula, Eq. 15, and survivorship was calculated as $l(x,s)$ from Eq. 7. Biomass increase $C(s)$ was calculated from Eq. 10. For both life histories we used $x = 0.25$ mg and $\mu_0 = 0.4$. The size y at maturity was calculated by maximizing $R(s) - s$ (see condition (ii)). Our values $(\hat{q}, \bar{q})$ for μ/g were 0.89, 0.75 and 0.93, 0.82 for the 1- and 2-year tables (Tables 1A and 1B, respectively) and reproductive efficiency values were 0.045 and 0.07, respectively. We did other simulations varying B and s_1 and always found $\hat{q} > \bar{q}$.

Notice that all equations in our model except the above equation for the time $T(s)$ to size s, depend not on μ and g separately but only on their ratio, which in turn is independent of μ_0. A consequence of this is that any life history generated by our equations gives rise to a whole family of similar life histories with μ_0 multiplied by any constant λ and all ages multiplied by $1/\lambda$. Thus, in Table 1, by multiplying all entries in the first column by two, we get a pair of life histories with times 682 and 1572 days to maturity and mortality at birth

TABLE 1. Sample life histories calculated with the growth and mortality functions of Eqs. 17 and 18. In both cases (A and B) $x = 0.25$ mg and $\mu_0 = 0.4$

Age (days)	Size, s (mg)	Mortality, $\mu(s)$ (per day)	Survivorship, $l(s)$	Relative cohort biomass, $c(s)$
(A) $s_1=10^5$, $B = 0.005$, age at maturity $= 341$ days, mature size $(y) = 38$ g				
0	0.250	0.400	1	1
1	0.366	0.344	0.69	1.009
2	0.516	0.301	0.50	1.032
4	0.943	0.238	0.29	1.11
8	2.47	0.165	0.13	1.32
16	9.69	0.100	0.05	1.86
32	53.0	0.055	0.015	3.17
100	1 239	0.019	0.0018	9.07
365	45 396	0.0067	0.00011	20.3
(B) $s_1=10^6$, $B = 0.0025$, age at maturity $= 786$ days, mature size $(y) = 387$ g				
0	0.250	0.400	1	1
1	0.365	0.348	0.689	1.005
2	0.513	0.307	0.497	1.019
4	0.925	0.247	0.287	1.061
8	2.36	0.176	0.125	1.18
16	8.82	0.110	0.041	1.46
32	45.9	0.062	1.13×10^{-2}	2.07
100	1 049	0.021	1.1×10^{-3}	4.45
365	43 772	0.0065	5.0×10^{-5}	10.1
730	314 350	0.0036	1.0×10^{-5}	13.0

$\mu_0 = 0.2$ per day.

The first life history (Table 1A), with an age of maturity of 341 days, was used to estimate the effect of small $r \neq 0$ on x and y which for $r = 0$ are 0.25 and 38 000, respectively. Using a first-order analysis at $r = 0$ and conditions (i) and (ii), we calculated that for a population that increases by a fraction δ each generation, so that $r = \ln(1 + \delta)/341 \simeq \delta/341$, we have fractional changes

$$\frac{\mathrm{d}x}{x} = 0.07\delta \quad \text{and} \quad \frac{\mathrm{d}y}{y} = -4.1\delta$$

in the zygote and mature sizes. Thus, a population changing in size by 10% every generation ($\delta = \pm 0.1$) would experience a selective pressure to change zygote size by $\pm 0.7\%$ and mature size by $\mp 41\%$. The effect on mature size seems substantial. We remark that our first-order analysis assumed $r \ll \mu$ (for example, we replaced $\ln(1 + r/\mu)$ by r/μ). The above value of δ gives an r of 0.0003, whereas the value of μ at maturity is 0.007. The approximation seems reasonable.

Seasons and other complications

High and middle latitudes are subject to an annual rhythm of temperature change that would affect all of the rates under consideration. For our conclusions to be valid, such ratios as that between mortality and growth would have to remain the same, not only for different communities, but at different seasons in the same community. They should be equally applicable, for instance, to sand lance larvae developing in Long Island Sound at about 0°C in January, and anchovy larvae developing there in the summer at >20°C.

Even in tropical habitats there are seasonal changes in community composition, for example, in the kinds and numbers of any organism's predators, competitors, and food items. We would expect this cycle of associated organisms to produce changes in growth and mortality curves (Figs. 1 and 2), and therefore in the values of s_0 (where $g = \mu + r$ for the first time)

and $\hat{s}$ (the point which maximizes $R(s) - s$). We have shown that if g and μ are time invariant, the optimal size y at maturity is $\hat{s}$ and the optimal zygote size x is s_0. What should y and x be when $\hat{s}$ and s_0 change seasonally? This optimization problem is mathematically quite complicated. We expect organims to adjust their seasonal phase to take advantage of some optimal time of reproduction. For example, they might arrange to attain reproductive maturity at a time when $\hat{s}$ is at or near a seasonal minimum. In this matter of timing there may well be a conflict between the needs of the zygote and the parent to minimize mortality and maximize growth. We hope to tackle these problems in a subsequent publication.

Our modelling relates explicitly to life cycles like those of many fishes and invertebrates, in which parental investment consists only of materials packaged in the egg and ends at zygote production. If parents feed their developing young it would increase juvenile growth rates, and active protection from predators would decrease juvenile mortality rates in comparison with organisms of the same size without parental care. Population stability requires these benefits to the young to be balanced by costs to parents measured as decreased growth or fecundity or as increased mortality. We hope to model this trade-off in a future publication.

Possible application to field data

We observed in Eq. 16 that juveniles of constant shape under constant conditions should grow at a constant linear rate if $\alpha = 1/3$ or at a slightly accelerating rate with a lower value of α. Aquaculturists find that well-fed juvenile fish at tropical temperatures in a size range of 10–100 mm can grow at rates of 0.4–0.7 mm/day (Brown and Gratzek 1980; Payne 1971; Strawn 1961; Uchida and King 1962). Wild mullet juveniles in the 100–300 mm range grow a bit more slowly at similar temperatures, about 0.3 mm/day (Oren 1981). Two-metre juveniles of a tropical shark likewise grew at about 0.3 mm/day (Thorson and Lacy 1982). The data are certainly

consistent with the supposition that linear growth rate is independent of size, as expected with $\alpha = 1/3$. They do not rule out a somewhat higher value, especially since it is unlikely that either the mullet or the sharks were as well fed as the species under culture. A few marine invertebrates that have been investigated show a slightly accelerating linear growth of early juveniles (Theisen 1973; Yamaguchi 1975) implying $\alpha < 1/3$.

Ecologically normal variation in temperature can produce manifold differences in biological rates. It is commonly observed, for instance, that rates of embryogenesis in fishes show an increase of three-fold or more with a 10°C increase in temperature (Coombs and Mitchell 1982; Williams 1975). An egg developing at 5°C would take about 10 times as long from fertilization to hatching as one developing at 25°C. A survey of data on fertilization to hatching survival for marine fishes with planktonic eggs showed no obvious effect of latitude or season (Williams et al. 1973). This must mean that lower temperatures mean less mortality per unit time in addition to slower development. The same 1-day mortality that would allow 50% survival over the 2-day embryonic development of a tropical species would permit a survival of only one in a thousand of a boreal species. Our assumption that rate ratios are independent of temperature is apparently not seriously incorrect. We suggest that the factor a in rate formulations (Eqs. 13, 15, and 16) can be considered a temperature coefficient applicable to both mortality and growth.

Our inferred schedule of mortality with time (Eq. 7) depends on a postulated dependence on size and is independent of age. A feeding juvenile fish of 1 g is thus predicted to have a certain mortality rate regardless of whether it was hatched from a large egg last week or a small egg last year. A given community may well include both kinds of 1-g fish. This picture will certainly prove inaccurate. A 1-week-old fish might not have as advanced sensory and motor capabilities as an older fish of the same size. This would make it more vulnerable to predators and less efficient at foraging, so that its mortality rate would be greater and its growth rate less. We also think that such inaccuracies may be minor compared with the enormous variation in both mortality and growth across the size spectrum. Similar-size juveniles of two species may often be more similar to each other in these respects than those of the same species with manifold size differences.

Many field studies of planktonic egg survival, larval survival, and larval growth have been made. They support widely different interpretations with, no doubt, widely different reliability. Some are biased with respect to season and locality, and much of the sampling may be biased for size classes and age-classes. Delicate younger larvae may be mechanically fragmented by collecting gear and forced through netting; larval ability to avoid capture increases with size. These factors could introduce serious errors into both mortality and growth estimates.

Some studies support our inferences on the general shape of growth and survival functions and the expectation of a steady increase in cohort biomass. Examples are those reviewed by Ware (1975) for mackerel and haddock, and by Gulland (1977) for plaice. Farris' (1961) 3-year study of jack mackerel showed a steady biomass decrease. The actively feeding 3-mm larvae were sampled abundantly all 3 years. In less than 2 months they grew to about 16 mm, perhaps a 130-fold increase in biomass. Survivorship during this period for the 3 years was about 0.00058, 0.00275, and 0.00017. None of the three cohorts even approached the expected increase in biomass. At best (in 1953) the biomass dropped to about a third of its original value. If the observations are representative and if the biomass trend continues for these cohorts, it means that in reproduction, the adults are investing biomass at negative interest and the population must be headed for extinction.

It may be that sampling biases like those listed above contribute to the contradiction between our expectations and Farris' (1961) data, but we suspect that another factor may be more important. Great variation in year class size from similar spawning stocks is commonly observed, and the persistence of populations is made possible by that small proportion of year classes that have many times the median survival. That a 3-year study based on thousands of samples may be judged inadequate indicates the great technical difficulty of studying the demography of natural popuations. The most that can now be said for the mortality rate formulations derived in this paper, in relation to available field data, is that they give the right general shape for survivorship curves (e.g., Cushing 1975; Fig. 2).

Commercially exploitable age groups are more reliably known than larval and early juvenile stages. Cushing (1975) has shown that cohort biomass of young adults (e.g., 4 year olds) in a plaice stock may nearly double in a year. Mortality rate is nearly constant thereafter but growth rate declines to equal mortality at about age 16 years. In most species the age of maximum cohort biomass probably occurs earlier (Alverson and Carney 1975). Older cohorts show an ever steeper decline in biomass. We would expect, contrary to Farris' (1961) data, that larval and juvenile stages also have a net biomass increase as a mean (but not median) condition (Eq. 11).

Our assumption that the adult/offspring biomass ratio k is independent of size is another inaccuracy. Adults of really large organisms (tuna, kelp, trees) are often a million to a billion times the size of offspring. We are not aware that this is often true of organisms in the bacteria to insect range of sizes. So our inferrence from Eq. 14 that the proportion of adulthood ($M/M + I$) is about one-third regardless of size range must be inaccurate, but the discrepancy is noticeable only when k values are commonly less than 10, for example, in communities in which the dominant mode of reproduction is binary fission.

Indeed, let us postulate a dependence of y/x on mature size y of the form $y/x = K(y) = ky^\beta$, where $0 \leq \beta < 1$. Estimates of β for various classes of organisms have ranged from 0.05 to 0.75. Then in all our equations, up to Eq. 11, k can simply be replaced by ky^β. Some care is needed with the integral Eq. 12 for density $I(s)$ of immature individuals. The range of integration is all values of z for which $z/K(z) < s < z$. This translates to a lower limit of integration of s, as before, and an upper limit of $(ks)^{1/1-\beta}$. It is now true that $M(s) = m/s^2$ is approximately a solution of Eq. 12 provided $k^{q-\alpha-1} \ll 1$. This will certainly hold for $k \geq 10$, and Eq. 14 will remain valid.

For example, a sample of marine zooplankton in the $1-2$ mg range might be dominated by crustaceans, and we would expect about a third of them to be adults, the rest larval instars of species with adult sizes greater than 2 mg. A sample from the $1-2$ t range of the same community would be dominated by vertebrates (cetaceans, sharks, sea turtles) and we would expect about a third of them to be adults. A seemingly adult shark or turtle would be using some resources for growth, and should therefore be divided between the mature and immature categories. Since it is clearly true that both the ton and the milligram (and smaller) ranges contain both adult and juvenile organisms, it must be that size is at most weakly related to the proportion of mature organisms in a community.

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Appendix

We wish to find x and y to maximize

$$v(x,y) = l(x,y) \, e^{-rT(x,y)} ER(y)/x$$

We first derive formulae for the derivatives of l. Regarding s as a function of t, obtained by solving $ds/dt = sg(s)$, we have

[1A] $dl(x,s)/dt = -l(x,s)\mu(s)$

by definition of mortality μ. Thus,

[2A] $\partial \ln l(x,s)/\partial s = \dfrac{(dl(x,s)/dt)\,(dt/ds)}{l(x,s)} = -\dfrac{\mu(s)}{sg(s)}$

Similarly, it can be shown that

[3A] $\partial \ln l(x,s)/\partial x = \dfrac{\mu(x)}{xg(x)}$

We next remark that

[4A] $\dfrac{\partial T}{\partial x} = -\left(\dfrac{dx}{dt}\right)^{-1} = \dfrac{-1}{xg(x)}$ and $\dfrac{\partial T}{\partial y} = \left(\dfrac{dy}{dt}\right)^{-1} = \dfrac{1}{yg(y)}$

Now we find x and y to maximize $\ln v(x,y)$. To find x we set

$$\frac{\partial}{\partial x} (\ln l(x,s) - rT(x,y) - \ln (x)) = 0$$

and obtain $g(x) = \mu(x) + r$. It is easily checked that $x = s_0$ gives the maximum (see Fig. 1; $x = s_1$ gives a minimum). To find y we calculate

$$\partial/\partial s \ln v(x,s) = \frac{E}{x} \frac{\partial}{\partial s} (\ln l(x,s) - rT(x,s) + \ln R(s))$$

$$= \frac{E}{x} \left(\frac{\mu(s)}{xg(s)} - \frac{r}{sg(s)} + \frac{R'(s)}{R(s)} \right)$$

$$= \frac{E}{xR(s)} (R'(s) - 1)$$

Thus, $w(x,s)$ will be maximized at y provided the above expression is 0 at $s = y$, >0 for $s < y$, and <0 for $s > y$. This is just the condition that $R(s) - s$ be maximized at y, providing condition (ii).