On the Quantitative Genetics of Correlated Characters under Directional Selection in Age-Structured Populations

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On the quantitative genetics of correlated characters under directional selection in age-structured populations

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SUMMARY

The evolution of correlated characters in natural populations depends on the demographic structure of these populations. This is often considerably more complicated than the structure of populations typically addressed by quantitative genetics, involving overlapping generations, age-dependent vital rates, and large fluctuations in recruitment from year to year. It is important to know more about such evolution because human exploitation of natural populations such as fishes is selective and has the potential to cause major changes in their properties. Here the theory of quantitative genetics of correlated characters under directional selection is extended to incorporate some demographic properties of non-equilibrium age-structured populations.

Short-term evolution is described in terms of changes in a matrix of mean breeding values of the traits at each age, and depends on the selection differentials in operation, together with the variances and covariances of breeding and phenotypic values. Because the selection differentials depend on the current mean phenotypic values which are themselves changing as each cohort grows older, the dynamics of mean phenotypic values within cohorts are also followed. Together, the changes in mean breeding and phenotypic values are sufficient to predict the short-term transient evolutionary dynamics of correlated characters in non-equilibrium age-structured populations. The predictions are compared with the dynamics observed in some randomly generated populations, and the application of the theory to evolution in commercially exploited populations of fish is discussed.

1. INTRODUCTION

This paper is motivated by the need to understand how natural fish stocks evolve through their exploitation by man. There are often elements of size specificity in our patterns of exploitation, to the extent that control of net mesh size has become an important tool in the regulation of fisheries (Garrod 1987). Since fishes of a given age clearly vary in size (see, for example, Bannister (1977); Daan (1986)), it is likely that fishing will generate a substantial selection differential on size-related traits in heavily exploited fisheries. Moreover, there is known to be an additive genetic component to size variation in certain cases (Gjedrem 1983; Gjerde 1986), so it is likely that a genetic response to selection will occur in the form of a gradual change in the mean value of these traits during subsequent generations.

At present, we have little idea about the evolutionary dynamics of size and size-correlated traits expected under the contemporary patterns of exploitation. Consequently, it is not clear whether we will have a serious problem on our hands in the forseeable future.

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Our ignorance is partly because the theory needed for predicting such evolution has not been developed. Quantitative genetics, which provides a basis for describing evolution of continuous characters, has grown up primarily in the context of animal and plant breeding, where particular individuals with desirable traits are selected as the parents of the next generation (Falconer 1989). Change in quantitative characters brought about by directional selection in natural populations of fish (and many other organisms) is a good deal more complicated than that in the populations typically considered by animal and plant breeders for several reasons.

The first reason is that natural populations usually have overlapping generations, and contain individuals which reproduce at different rates at different ages. These populations are often far from a demographic steady state, with large fluctuations in numbers from one cohort (yearclass) to the next. Second, fishing may generate selection differentials on several traits, some of which are expressed at the same age (for instance, length and weight), and some in series (for instance, length-at-age 1, length-at-age 2, etc.). Third, the selection differentials themselves change, most obviously with changes in the prevailing patterns of fishing. Less obviously, they also change as the traits evolve, because net meshes are set externally by dialogue between fishermen and regulatory authorities, rather than with reference to the current frequency distributions of the traits.

There is, then, a need for a theory of quantitative genetics for suites of correlated characters expressed at arbitrary ages and undergoing directional selection in non-equilibrium age-structured populations. In this paper some elements of the theory are developed. The building blocks for doing this are first the basic theory of quantitative genetics (Bulmer 1980; Falconer 1989), second the theory of selection on single traits in age-structured populations (Hill 1974; Charlesworth 1980), and third the theory of evolution of correlated characters simultaneously expressed (Lande & Arnold 1983). Some other approaches to the study of selection on size in structured populations are given by Kirkpatrick (1988) and Lynch (1988), and Lande (1982) describes a theory for the evolution of quantitative characters in age-structured populations, given the assumption of demographic equilibrium. The theory described here specifically addresses the short-term dynamics of correlated characters in non-equilibrium populations, and allows the first-order statistics (means) but not the second-order statistics (variances and covariances) to evolve. Although the theory is developed with the problem of fisheries in mind, it should be more widely applicable to the evolutionary dynamics of correlated traits in other kinds of natural populations under directional selection.

1. THEORY

(*a*) *Background*

The theory addresses a population living in a seasonal environment with reproduction occurring in pulses once a year. The sequence of events in each year is: census, the time at which characteristics of individuals are measured, mortality, both selective and non-selective, and reproduction at the end of the year. Individuals live to a maximum age n, so that at any time there is a maximum of $n+1$ cohorts present $(0, 1, \ldots, j, \ldots, n)$.

We consider the evolution of m phenotypic traits in the population. For the time being, it is assumed that the traits are expressed both in females and in males; this assumption is relaxed in a later section. Each trait is expressed at no more than one age; this assumption can be made without loss of generality, since characters expressed at two or more ages can be treated separately and assumed to have a perfect correlation. The traits are numbered $1, 2, \ldots, i, \ldots, m$, in order of the age at which they are expressed, the sequence of traits expressed at the same age being arbitrary.

Each individual at birth has a phenotypic value for every trait. The individual may not survive for long enough to express this phenotype, but the value does in principle exist and could be measured if selective and non-selective sources of mortality were eliminated. Assuming, for simplicity, that there is no interaction between genotype and environment, that dominance deviations are absent, and that there are no non-additive interactions between loci, then the phenotypic values can be partitioned into a breeding value (the mean value which the progeny of this individual will have) and an independent environmental deviation. The individual is therefore characterized both by its breeding value and its phenotypic value for every trait.

Evolution is measured in terms of changes through time in the mean breeding value of each trait. At the time of census the mean breeding values of individuals at age j are given by the column vector $(\bar{a}_{1j}, \ldots, \bar{a}_{mj})^T$. So the population is fully characterized by $n+1$ such vectors, one for each age. These vectors are collected together in order of increasing age, to give a matrix $\boldsymbol{A}_t$ of order m by $n+1$, for the mean breeding values at the start of year t:

$$\boldsymbol{A}_t = \begin{bmatrix} \bar{a}_{10} & \cdots & \bar{a}_{1n} \\ \vdots & & \vdots \\ \bar{a}_{m0} & \cdots & \bar{a}_{mn} \end{bmatrix}_t .$$

It is necessary to keep track of the mean breeding value of a trait even when it is not being expressed because such a trait may still be changing due to selection operating on traits which *are* currently expressed by virtue of non-zero covariances in its breeding value with these traits. Such changes depend on the covariance matrix of breeding values $\boldsymbol{G}$, of order m by m:

$$\boldsymbol{G} = \begin{bmatrix} \operatorname{var}(a_1) & \cdots & \operatorname{cov}(a_1, a_m) \\ \vdots & & \vdots \\ \operatorname{cov}(a_1, a_m) & \cdots & \operatorname{var}(a_m) \end{bmatrix}.$$

Matching the matrix of mean breeding values, is a matrix of mean phenotypic values, $\boldsymbol{X}_t = [\bar{x}_{ij}]_t$, at the start of year t also of order m by $n+1$. At birth (the first column), these mean values are assumed to be the same as the mean breeding values at birth. As the cohort grows older, the mean phenotypic value of trait i changes, first due to selection operating directly on trait i itself at the age when it is expressed, and secondly at this and other ages by virtue of the phenotypic covariances between trait i and other traits when selection operates on the latter. These phenotypic covariances are given by the matrix $\boldsymbol{P}$ of the same form as $\boldsymbol{G}$ above.

The reason for keeping track of both the mean breeding values and mean phenotypic values is that, as a cohort grows older in the presence of directional selection, the identity between mean breeding values and mean phenotypic values disappears. Yet both play a part in evolution because the selection differential depends in part on the mean phenotypic value before selection, and the response to selection depends on the mean breeding value. One therefore needs both the mean breeding values and the mean phenotypic values to predict future states of the population.

(*b*) *Selection differentials*

Suppose that directional selection is applied to the population shortly after the start of year t. The observed selection differential on trait i expressed at age j is given by the difference between the mean phenotypic value before and after selection at the age at which the trait is expressed, $s_{ijt} = \bar{x}^{*}_{ijt} - \bar{x}_{ijt}$, where * denotes 'after selection'. The selection differentials are taken together as elements of a matrix of selection differentials, $\boldsymbol{S}_t$, of order m by $n+1$. Since a selection differential clearly cannot be applied to a trait when it is not being expressed, $\boldsymbol{S}_t$ can only contain non-zero elements at positions matching the age of expression of the traits. But this in no way precludes changes at age j in traits which are expressed at ages other than j. Indeed such changes are to be expected as long as there are non-zero covariances in their values and those of traits under selection at age j, as shown in the next section.

The observed change in the mean phenotypic value of trait i when expressed at age j is the outcome of selection acting directly on trait i and that acting indirectly via other correlated traits also being expressed at age j. Following Lande & Arnold (1983), the selection differentials on all traits expressed at age j in year t are partitioned into directional selection gradients, $\boldsymbol{\beta}_{jt}$:

$$\boldsymbol{\beta}_{jt} = \boldsymbol{P}_j^{-1}\boldsymbol{s}_{jt},$$

where $\boldsymbol{P}_j$ is the block from the phenotypic covariance matrix which refers to traits expressed at age j and $\boldsymbol{s}_{jt}$ is the column vector obtained by extracting from $\boldsymbol{S}_t$ the selection differentials on the traits expressed at age j. Notice that there can be no selection differential or selection gradient for traits not expressed at age j. To obtain the selection gradients operating in all $n+1$ cohorts in year t, we use a modified form of the phenotypic covariance matrix, $\dot{\boldsymbol{P}}$, of order m by m, which contains non-zero elements only for those traits expressed at the same age, comprising blocks on the diagonal of $\boldsymbol{P}$

$$\dot{\boldsymbol{P}} = \mathrm{diag}\,(\boldsymbol{P}_0, \ldots, \boldsymbol{P}_j, \ldots).$$

As long as $\dot{\boldsymbol{P}}$ is non-singular, the matrix of directional selection gradients operating at all ages in year t is then given by $\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t$.

(*c*) *Mean values after selection*

In general there are two kinds of trait within each cohort in year t: those currently being expressed and those not expressed. Both kinds of trait can change due to selection in year t, the former as a direct result of their own selection gradients and covariances with other traits also being expressed (Lande & Arnold 1983), and the latter as a result of their covariances with the former. The changes in mean breeding values depend on the regression of breeding values on phenotypic values; these changes are given by the product $\boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t$ once all $n+1$ cohorts have been collected together. Thus the mean breeding values after selection are given by

$$\boldsymbol{A}^{*}_t = \boldsymbol{A}_t + \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t.$$

Similarly, the mean phenotypic values of unexpressed traits can change. The changes in both expressed and unexpressed traits are given by the product $\boldsymbol{P}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t$ when all $n+1$ cohorts are combined, leading to

$$\boldsymbol{X}^{*}_t = \boldsymbol{X}_t + \boldsymbol{P}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t.$$

These equations assume that the breeding values and phenotypic values have a multivariate normal distribution.

Clearly, many of the changes described by the equations above are cryptic, unobserved because the cohort is at an age when the trait is not expressed. Yet we need to keep track of them all irrespective of when they are expressed for several reasons. First the changes are cumulative; as the cohort grows older, mean values can depart more and more from their values at birth whether or not the traits are expressed. Second, parents reproducing at a given age j contribute their current breeding values to their offspring; in this regard it is immaterial whether or not traits are expressed at age j. Third, the selection differentials on traits expressed at age j depend in part on the mean phenotypic values of these traits at age j; these values could be quite different from the values at birth due to cryptic changes before the cohort reaches age j.

It is worth noting the form of these equations in certain special cases.

(*a*) One trait expressed in a single cohort population. Here the relation for the mean breeding value takes the form

$$a^{*}_t = a_t + \frac{\mathrm{var}\ (a)}{\mathrm{var}\ (x)}s_t,$$

or

$$\Delta a_t = \frac{\mathrm{var}\ (a)}{\mathrm{var}\ (x)}s_t,$$

where Δa_t is the selection response. This is the well-known result from quantitative genetics (usually given as $R = h^2S$), the ratio of the two variances being the heritability (h^2) of the trait (Falconer 1989).

(*b*) When all the traits are expressed at the same age, the mean values are given by

$$\boldsymbol{A}_t^* = \boldsymbol{A}_t + \boldsymbol{G}\boldsymbol{P}^{-1}\boldsymbol{S}_t$$
$$\boldsymbol{X}_t^* = \boldsymbol{X}_t + \boldsymbol{S}_t.$$

This is essentially the result given by Lande & Arnold (1983), although it is given in a slightly modified form to allow $n+1$ cohorts to be present.

(*c*) When one trait only is expressed at each age and $m = n+1$, the matrix of selection gradients is diagonal with element i being $s_{ijt}/var(x_i)$ where $i = j+1$. Thus the change in mean breeding value of a trait k not expressed at age j $(k \neq j+1)$ is $s_{ijt} \cdot \mathrm{cov}\,(a_i, a_k)/\mathrm{var}(x_i)$. It can be seen that this change depends only on the directional selection gradient on trait i and the covariance of the breeding values of trait i and trait k.

(*d*) *Population dynamics*

The final step in the sequence of events in year t is to generate a newborn cohort and to increase the age of each cohort already present by one year. To take the population through this step, we define a transition matrix $\boldsymbol{T}_t$, of order $n+1$ by $n+1$:

$$\boldsymbol{T}_t = \begin{bmatrix} p_0 & 1 & & 0 \\ \vdots & & \ddots & \\ p_{n-1} & 0 & & 1 \\ p_n & 0 & & 0 \end{bmatrix}_t .$$

Here the element p_{jt} is the probability with which a newborn individual inherits a given gene from a parent of age j so that $\Sigma p_{jt} = 1$, and the line of elements of value unity above the leading diagonal advances the age of all cohorts already present by one year, except the cohort at age n which disappears (Hill 1974; Charlesworth 1980). Notice that Charlesworth's (1980) notation is adopted so that the sum of each column is unity; $\boldsymbol{T}_t$ is then the transpose of a stochastic matrix (Lancaster 1969). The matrix is a simplified form of that used by Hill (1974) and Charlesworth (1980) because it does not treat separately the contributions of females and males; some relaxation of this assumption is possible and is considered separately below.

The element p_{jt} of $\boldsymbol{T}_t$ must allow for the rate of reproduction at age j (b_j, assumed for simplicity to be independent of year t here), the number of individuals in the cohort at birth and the risk of mortality from birth up to the time of reproduction at age j, including all selective as well as non-selective mortality. Thus

$$p_{jt} = \frac{N_{jt}\,\overline{W}_{jt}\,b_j}{\sum\limits_j N_{jt}\,\overline{W}_{jt}\,b_j}, \tag{1}$$

where N_{jt} is the number of individuals surviving at the start of year t and is defined recursively by

$$N_{jt} = N_{j-1,t-1}\,\overline{W}_{j-1,t-1}. \tag{2}$$

The term $\overline{W}_{jt}$ is the proportion of individuals aged j which survive from the start of year t to the time of reproduction, referred to as the mean fitness below. Evidently we can expect p_{jt} (and hence $\boldsymbol{T}_t$) to vary from year to year, depending on factors such as fluctuations in yearclass strength, changes in fishing patterns, and the previous history of selection.

In keeping with the focus on short-term dynamics, it is assumed that the distributions of breeding and phenotypic values of newborn individuals have the same covariance matrices $\boldsymbol{G}$ and $\boldsymbol{P}$ as previous cohorts. Additionally, we have to assume that the distribution of breeding values is multivariate normal in newborns; this can be no better than an approximation because the distribution is obtained as a mixture of the breeding values of parents of different ages and these in general would have different means. Given these assumptions, the weightings in the first column of $\boldsymbol{T}_t$ generate the mean breeding values of newborn individuals when premultiplied by the matrix of mean breeding values after selection ($\boldsymbol{A}_t^*$) (Hill 1974; Charlesworth 1980). At the time of reproduction there are no changes in mean breeding values within cohorts older than age 0, so elements above the leading diagonal of $\boldsymbol{T}_t$ have the value unity. Thus the complete recurrence relation for the dynamics of the mean breeding values from census t to $t+1$ is given by

$$\boldsymbol{A}_{t+1} = (\boldsymbol{A}_t + \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t)\,\boldsymbol{T}_t. \tag{3}$$

This equation shows in a simple explicit way how the evolution of correlated characters depends on the directional selection in operation ($\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t$), the genetic structure ($\boldsymbol{A}_t$ and $\boldsymbol{G}$) and the demographic properties ($\boldsymbol{T}_t$) of the population.

The matrix for the mean phenotypic values at time $t+1$ is obtained in two parts. The first part makes use of the matrix product $\boldsymbol{T}_t\,\boldsymbol{C}$ to increase the age of cohorts $0, \ldots, n-1$ by one year; $\boldsymbol{C}$ is a diagonal matrix of order $n+1$ by $n+1$ with elements of value unity except for the first which has value zero. The second part inserts the column of mean phenotypic values of newborn individuals; this is by definition equal to the first column of $\boldsymbol{A}_{t+1}$, because the mean phenotypic values and mean breeding values must be the same before any selection takes place. It is given by the matrix product $\boldsymbol{A}_{t+1}\,\boldsymbol{C}'$, where $\boldsymbol{C}'$ of order $n+1$ by $n+1$ has the first element with value unity and zeros elsewhere. Thus the full equation is given by

$$\boldsymbol{X}_{t+1} = (\boldsymbol{X}_t + \boldsymbol{P}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t)\,\boldsymbol{T}_t\,\boldsymbol{C} + \boldsymbol{A}_{t+1}\,\boldsymbol{C}' \tag{4}$$

The first part of the right hand side in effect keeps track of the within-generation dynamics of the mean phenotypic values, and the second part provides initial values for each new cohort.

Equations 3 and 4 can be used iteratively to predict the evolution of correlated traits in the short term under directional selection in non-equilibrium age-structured populations. Equation 3 alone is sufficient to predict the response to a single round of selection. However, if we wish to project the evolutionary dynamics further into the future under continuing selection, the mean phenotypic values need to be modelled as well (equation 4). The reason for this is that the selection matrix $\boldsymbol{S}_t$ requires information on the mean phenotypic values of traits before selection *at the age when they are expressed*. These mean values may be quite different from those at birth by virtue of non-zero phenotypic covariances with other traits expressed and selected earlier in life.

(*e*) *Asymptotic properties*

Suppose that a single bout of selection occurs in year 0 and none thereafter. What will be the asymptotic response to this selective event? Assume that there is a steady state matrix $\boldsymbol{T}$ describing the dynamics of the population in the absence of selection. Although selection acts in year 0 only, there is still a sequence of n iterations at the beginning during which the transition matrix is observed to change as the selected cohorts work their way through the population (cf. Hill 1974). Denoting these matrices $\boldsymbol{T}_0$, $\boldsymbol{T}_1, \ldots, \boldsymbol{T}_{n-1}$, we have for $t > n$

$$\boldsymbol{A}_t = (\boldsymbol{A}_0 + \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_0)\,\boldsymbol{T}_0 \ldots \boldsymbol{T}_{n-1}\,\boldsymbol{T}^{t-n}. \tag{5}$$

It is known from the theory of stochastic matrices that $\boldsymbol{T}^{\infty} = \boldsymbol{uv}\alpha^{-1}$, where $\boldsymbol{v}$ is the left dominant eigenvector of $\boldsymbol{T}$, scaled so that all elements are unity, $\boldsymbol{u}$ is the right dominant eigenvector scaled with the first element at unity (Lancaster 1969), and the term α is the mean generation time (Hill 1974; Charlesworth 1980). The asymptotic mean breeding values ($\boldsymbol{A}_{\infty}$) are thus given by

$$\boldsymbol{A}_{\infty} = (\boldsymbol{A}_0 + \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_0)\,\boldsymbol{T}_0 \ldots \boldsymbol{T}_{n-1}\,\boldsymbol{uv}\alpha^{-1}. \tag{6}$$

It is unnecessary to keep track of the dynamics of mean phenotypic values here, since the selection differentials are taken to be zero after year 0.

An asymptotic result for the change in mean breeding values from one year to the next ($\Delta\boldsymbol{R}_{\infty}$) can also be determined under the assumption of constant selection differentials $\boldsymbol{S}_t = \boldsymbol{S}$ for all t. As before there is a sequence of n iterations during which the transition matrices are changing as cohorts present at the start work their way through the population, denoted by $\boldsymbol{T}_0, \ldots, \boldsymbol{T}_{n-1}$. Subsequently every cohort experiences the same selective mortality so the transition matrix is constant (denoted $\boldsymbol{T}_s$), i.e. $\boldsymbol{T}_t = \boldsymbol{T}_s$ for $t > n$. (It is assumed that all cohorts start life with the same number of individuals.) As $t \to \infty$ the change in mean breeding values becomes

$$\Delta\boldsymbol{R}_{\infty} = \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}\left\{\left(\sum_{j=0}^{n-1}\boldsymbol{T}_j \ldots \boldsymbol{T}_{n-1}\right)(\boldsymbol{T}_s - \boldsymbol{I}) + \boldsymbol{T}_s\right\} \times \boldsymbol{u}_s\boldsymbol{v}_s\alpha_s^{-1}, \tag{7}$$

where $\boldsymbol{I}$ is the identity matrix of order $n+1$ by $n+1$, $\boldsymbol{v}_s$ is the left dominant eigenvector of $\boldsymbol{T}_s$, $\boldsymbol{u}_s$ is the right dominant eigenvector, and α_s is the mean generation time.

How useful the asymptotic response is under continuing selection is debatable. It ignores the change in mean phenotypic values within cohorts (equation 4). It makes no allowance for changes in the selection differentials which one would expect as the mean breeding values evolve. Neither does it allow for the changes in population dynamics which come about as the selection differentials change. On the other hand, Hill (1974) pointed out that in the context of a single quantitative character $\Delta\boldsymbol{R}_t$ can converge rapidly to $\Delta\boldsymbol{R}_{\infty}$, so the asymptotic result could provide a good approximation to $\Delta\boldsymbol{R}_t$ much of the time.

(*f*) *Sex-dependent dynamics*

The assumption that females and males have the same evolutionary dynamics can be relaxed in various ways. To deal with sex-specific processes, Equations 3 and 4 need to be recast so that the mean breeding values and mean phenotypic values are defined separately for each sex. The values are aggregated into block matrices of order m by $n_{\female}+n_{\male}+2$

$$\tilde{\boldsymbol{A}}_t = [\boldsymbol{A}_{\female}\boldsymbol{A}_{\male}]_t \quad \text{and} \quad \tilde{\boldsymbol{X}}_t = [\boldsymbol{X}_{\female}\boldsymbol{X}_{\male}]_t.$$

These treat females and males as separate cohorts, and for the sake of generality we may allow their maximum lifespans to differ so that there are different numbers of cohorts of females and males, $n_{\female}+1$ and $n_{\male}+1$, respectively. All traits are assumed to occur in both sexes, although it will be seen below that some traits may be expressed in one sex alone.

The transition matrix needs to take into account the contribution of genes that females and males separately make to their female and male offspring. It is given by the block matrix

$$\tilde{\boldsymbol{T}}_t = \begin{bmatrix} \boldsymbol{T}_{\female\female} & \boldsymbol{T}_{\female\male} \\ \boldsymbol{T}_{\male\female} & \boldsymbol{T}_{\male\male} \end{bmatrix}_t,$$

of order $n_{\female}+n_{\male}+2$ by $n_{\female}+n_{\male}+2$ (Hill 1974; Charlesworth 1980), the blocks being of the form given by Charlesworth (1980). The block $\boldsymbol{T}_{\female\male t}$, of order $n_{\female}+1$ by $n_{\male}+1$, represents the transitions from females at time t to males at time $t+1$, and the other blocks are defined similarly.

With separate sexes formulated as above, the dynamics of mean breeding values are given by

$$\tilde{\boldsymbol{A}}_{t+1} = (\tilde{\boldsymbol{A}}_t + \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\tilde{\boldsymbol{S}}_t)\,\tilde{\boldsymbol{T}}_t. \tag{8}$$

where the selection differentials are given separately for each sex as $\tilde{\boldsymbol{S}}_t = [\boldsymbol{S}_{\female}\boldsymbol{S}_{\male}]_t$ in a matrix of order m by $n_{\female}+n_{\male}+2$. The dynamics of mean phenotypic values are given in two parts, as in equation 4:

$$\tilde{\boldsymbol{X}}_{t+1} = (\tilde{\boldsymbol{X}}_t + \boldsymbol{P}\dot{\boldsymbol{P}}^{-1}\tilde{\boldsymbol{S}}_t)\,\tilde{\boldsymbol{T}}_t\tilde{\boldsymbol{C}} + \tilde{\boldsymbol{A}}_{t+1}\tilde{\boldsymbol{C}}', \tag{9}$$

where $\tilde{\boldsymbol{C}}$ (respectively $\tilde{\boldsymbol{C}}'$) of order $n_{\female}+n_{\male}+2$ by $n_{\female}+n_{\male}+2$ is a diagonal matrix with elements of value unity (respectively zero) except that in column 0 and $n_{\female}+1$ they have value zero (respectively unity). Note that $\tilde{\boldsymbol{T}}_t$ like $\boldsymbol{T}_t$ is the transpose of a stochastic matrix so the asymptotic results obtained earlier still apply with minor modifications.

By using equations 8 and 9, several extensions of the earlier sex-independent dynamics become possible.

(*i*) *Vital rates dependent on sex*

It is often the case that females and males of a given age have different vital rates; for instance, in the cod (*Gadus morhua*) males frequently mature at an earlier age than females (see, for example, Jørgensen (1988)). Even if the sexes experience the same selection differentials ($\boldsymbol{S}_{\female t} = \boldsymbol{S}_{\male t}$), the evolutionary dynamics are influenced by their different vital rates because their relative contributions to breeding values of newborns are weighted differently over age. The matrix $\tilde{\boldsymbol{T}}_t$ keeps track of these different weightings. Notice however that sex-dependent vital rates would not on their own lead to differences between female and male cohorts in mean breeding and phenotypic values if the sex ratio of offspring is independent of parental age.

(*ii*) *Selection differentials dependent on sex*

Differences between female and male cohorts in mean breeding values and phenotypic values come about if the sexes experience different selection differentials ($\boldsymbol{S}_{♀t} \neq \boldsymbol{S}_{♂t}$). Behavioural differences between the sexes could be responsible for this. Alternatively, different selection pressures on the sexes could accompany their different vital rates. For instance, selection pressures associated with spawning are only experienced by mature individuals; if, as in the case of the Northeast Arctic stock of cod, females and males start their annual migrations to the spawning grounds at different ages (Bergstad *et al.* 1988; Jørgensen 1988), there are likely to be differences between the sexes in the selection differentials. A detailed treatment of the evolutionary dynamics of such cases would entail separate estimation of the female and male elements of $\tilde{\boldsymbol{S}}_t$ and the use of equations 8 and 9.

(*iii*) *Sex-dependent expression of traits*

Certain traits are expressed in one sex only. Clearly, there can be no selection differential on such a trait in the sex in which it is not expressed, and in general this leads to the property: $\boldsymbol{S}_{♀t} \neq \boldsymbol{S}_{♂t}$. To the extent that the genes controlling the trait are autosomal, both sexes contribute to the value of the trait in offspring, even though expression is absent in one sex. Equations 8 and 9, which keep track of both sexes provide an appropriate method of describing the evolutionary dynamics, on the understanding that the selection differential must always be zero in the sex in which the trait is not expressed. (Mean phenotypic values for the trait do not exist in the sex in which it is not expressed; these are left in equation 9 for notational convenience only and have no effect on the evolutionary dynamics.)

3. EXAMPLES

To show the path of evolution predicted by the model, two numerical examples are given below. In both cases the path predicted is compared with that observed in populations in which the life of every individual is followed explicitly. The breeding and phenotypic values of these individuals are generated by using pseudo-random numbers, to provide an independent check on certain aspects of the model. Although it would be preferable to use data from exploited fish stocks in these examples, the information needed is not all available (see concluding comments). Numerical values have therefore been chosen simply to reflect a declining rate of growth with increasing age, and the probable low heritability of body size.

Table 1. *Numerical values for parameters used in modelling the evolutionary dynamics of four quantitative traits. See example 1*

$$\boldsymbol{A}_0 = \begin{bmatrix} 2 & 2 & 2 & 2 \\ 10 & 10 & 10 & 10 \\ 14 & 14 & 14 & 14 \\ 16 & 16 & 16 & 16 \end{bmatrix} = \boldsymbol{X}_0$$

$$\boldsymbol{P} = \begin{bmatrix} 0.1 & 0.1 & 0.1 & 0.1 \\ 0.1 & 4.0 & 4.0 & 4.0 \\ 0.1 & 4.0 & 6.0 & 6.0 \\ 0.1 & 4.0 & 6.0 & 8.0 \end{bmatrix} \quad \dot{\boldsymbol{P}} = \begin{bmatrix} 0.1 & 0 & 0 & 0 \\ 0 & 4.0 & 0 & 0 \\ 0 & 0 & 6.0 & 0 \\ 0 & 0 & 0 & 8.0 \end{bmatrix}$$

$$\boldsymbol{G} = \begin{bmatrix} 0.02 & 0.02 & 0.02 & 0.02 \\ 0.02 & 0.80 & 0.80 & 0.80 \\ 0.02 & 0.80 & 1.20 & 1.20 \\ 0.02 & 0.80 & 1.20 & 1.60 \end{bmatrix} \quad \boldsymbol{T} = \begin{bmatrix} 0 & 1 & 0 & 0 \\ \frac{1}{6} & 0 & 1 & 0 \\ \frac{1}{3} & 0 & 0 & 1 \\ \frac{1}{2} & 0 & 0 & 0 \end{bmatrix}$$

(*a*) *Example 1: response to a single round of selection*

(*i*) *Model*

Suppose that there exists a population of fish in which individuals live to a maximum age of three years ($n = 3$) and are subjected to length-specific harvesting. Since exploitation depends only on length and not on age, there are four traits which could in principle be under selection: length-at-age 0, …, length-at-age 3 ($m = 4$). Table 1 gives assumed values at the start of year 0 for the mean breeding values and mean phenotypic values ($\boldsymbol{A}_0$ and $\boldsymbol{X}_0$, respectively), the additive genetic covariances and phenotypic covariances ($\boldsymbol{G}$ and $\boldsymbol{P}$, respectively), and the transition matrix $\boldsymbol{T}$. We make the assumption that there has been no selection recently, so that $\boldsymbol{A}_0 = \boldsymbol{X}_0$. With the additive genetic and phenotypic variances given, the heritability of length at each age is 0.2. Notice that the transition matrix is given under the assumption that, apart from changes due to selection, it remains constant from year to year; the changes required to account for selection are described below.

We suppose that selection occurs in year 0 due to exploitation. What mean breeding values are expected at the start of year 1, 2, …, arising from this single round of selection?

The first step is to define the selection differential on each trait. In general, the mean phenotypic value for trait i in individuals of age j after selection in year t is

$$\bar{x}^*_{ijt} = \bar{W}_{jt}^{-1} \int \cdots \int x_{ijt}\, W(\boldsymbol{x}_{jt}) f(\boldsymbol{x}_{jt})\, \mathrm{d}\boldsymbol{x}_{jt}, \tag{10}$$

where

$$\bar{W}_{jt} = \int \cdots \int W(\boldsymbol{x}_{jt}) f(\boldsymbol{x}_{jt})\, \mathrm{d}\boldsymbol{x}_{jt}. \tag{11}$$

Here $f(\boldsymbol{x}_{jt})$ is the joint probability distribution for all traits expressed at age j, and $W(\boldsymbol{x}_{jt})$ is the corresponding probability of survival; $\bar{W}_{jt}$ is the mean fitness for an individual of age j in year t, and the integration is over all phenotypes expressed at age j.

In the example here, selection occurs only in year 0, so the subscript t is dropped from equations 10 and 11, as is the subscript i since $i = j+1$. Suppose that the threshold length at which individuals become liable to harvesting is k cm, and that the probability of surviving the period of harvesting is θ for vulnerable individuals.

Assuming that the distributions of phenotypes are normal with means $\bar{x}_j$ and variances σ_j^2, and rescaling so that $y_j = (x_j - \bar{x}_j)/\sigma_j$ and $k_j = (k - \bar{x}_j)/\sigma_j$, we have

$$\bar{y}_j^* = \overline{W}_j^{-1}\left\{-\frac{(1-\theta)}{\sqrt{2\pi}}\exp\left(-\frac{k_j^2}{2}\right)\right\},$$

where

$$\overline{W}_j = \int_{-\infty}^{k_j}\frac{1}{\sqrt{2\pi}}\exp\left(-\frac{y_j^2}{2}\right)\mathrm{d}y_j + \theta\int_{k_j}^{+\infty}\frac{1}{\sqrt{2\pi}}\exp\left(-\frac{y_j^2}{2}\right)\mathrm{d}y_j.$$

This gives the selection differential expected on the trait expressed at age j as $\bar{y}_j^*\sigma_j$. It is assumed that harvesting is the only cause of mortality; the generalization to incorporate non-selective mortality is straightforward.

Suppose, for the sake of argument, that the threshold length is $k = 14$ cm, and that a proportion $\theta = 0.4$ of the vulnerable individuals survive harvesting. Then the matrix of selection differentials in year 0 is $\boldsymbol{S}_0 = \mathrm{diag}(0 \; -0.066 \; -0.838 \; -0.970)$. Because there is only one trait expressed at each age, the matrix $\dot{\boldsymbol{P}}$ is obtained by replacing with zeros all apart from the diagonal elements of $\boldsymbol{P}$ (table 1). The inverse $\dot{\boldsymbol{P}}^{-1}$ is then

$$\dot{\boldsymbol{P}}^{-1} = \mathrm{diag}\;(10 \quad 0.25 \quad 0.167 \quad 0.125),$$

and the matrix of selection gradients operating on each trait at each age in year 0 is

$$\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_0 = \mathrm{diag}\,(0 \quad -0.016 \quad -0.140 \quad -0.121).$$

The next step is to make allowance for the effects of the selected cohorts on the elements in the first column of the transition matrix (equations 1 and 2). It is assumed that recruitment is a constant N so that $N_{0t} = N$ for all $t > 0$ and at $t = 0$ $N_{j0} = N$ for $j = 0, \ldots, 3$. Since selection occurs in year 0 only, the mean fitness $\overline{W}_{jt} = 1$ for $t > 0$. At $t = 0$, the mean fitnesses are 1, 0.986, 0.7 and 0.544 for ages 0, 1, 2, and 3, respectively. As there is no non-selective mortality, the b_js are proportional to the elements in the first column of $\boldsymbol{T}$ (table 1). From equations 1 and 2, the first columns of the transition matrices $\boldsymbol{T}_0$, $\boldsymbol{T}_1$, $\boldsymbol{T}_2$, $\boldsymbol{T}_3, \ldots$, are then

$$\begin{array}{llllll} \text{year 0:} & (0 & 0.245 & 0.348 & 0.406)^T, \\ \text{year 1:} & (0 & 0.197 & 0.389 & 0.414)^T, \\ \text{year 2:} & (0 & 0.167 & 0.336 & 0.497)^T, \\ \text{year 3:} & (0 & 0.167 & 0.333 & 0.5)^T. \\ \quad\vdots & & \vdots & & \end{array}$$

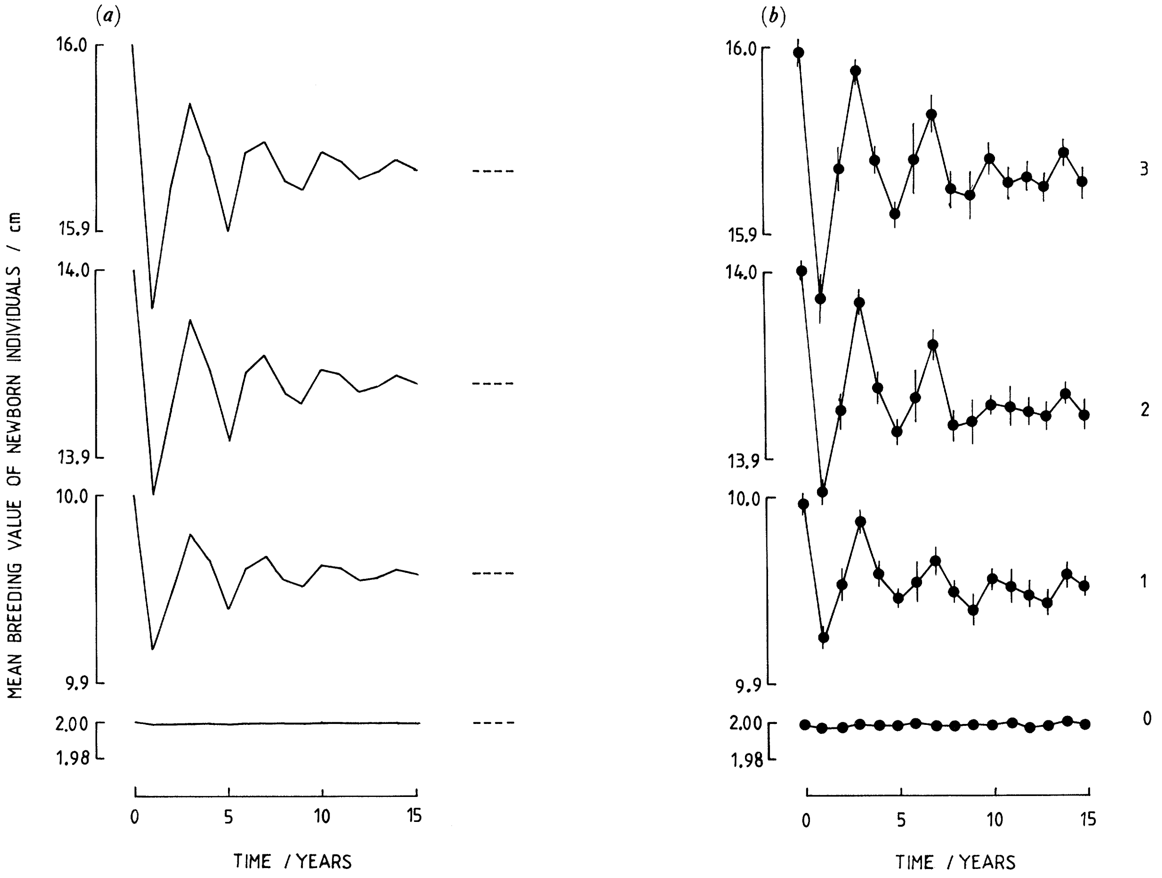

Figure 1. Response to a single round of directional selection on body length of fish in year 0. The population comprises four age classes and selection can take place at each age. The graphs give the mean breeding values for length-at-age 0, 1, 2, 3 in individuals at birth. (*a*) Timecourse for population predicted by equation 5; discontinuous lines are asymptotic values predicted by equation 6. (*b*) Timecourse observed in simulated populations in which the lives of individuals were followed explicitly as described in the text; each point gives the mean (±1 standard error) of 5 simulations.

The evolutionary dynamics of the population given by equation 5 are shown in figure 1 *a*. There is very little change in length-at-age 0 because there is no selection operating on this trait directly and the additive genetic covariances with the other traits on which selection does act are very small. On the other hand, there are substantial changes in the other traits. The oscillations in these come about because all parents from the 1, 2 and 3-year-old cohorts contribute to the mean breeding value of offspring, yet their mean breeding values have been altered to different extents by selection in year 0, depending on which trait was expressed in year 0. For instance, the mean breeding values of the 0-year-old cohort were unchanged by selection in year 0; as this cohort grows older and contributes increasingly to the production of newborn individuals, the mean breeding values of newborns increase (years 2 and 3). None the less, the oscillations are strongly damped, and the population is already close to its asymptotic values (1.999, 9.96, 13.94, 15.93, obtained from equation 6) by year 15.

(*ii*) *Populations simulating the lives of individuals*

The dynamics expected from theory are compared with those observed in simulated populations in which the lives of individual fishes were followed explicitly. Each individual fish was assigned at birth a breeding value for length-at-age $0,\ldots,3$ $(a_0,\ldots,a_3)$, defined recursively by

$$a_j = a_{j-1}+g_{j-1} \quad \text{for} \quad j>0.$$

Here g_{j-1} is the increment in length from age $j-1$ to age j, taken to be a random variable with a normal distribution, and a_0 is the length of a newborn individual, also a normal random variable. Each individual was also assigned at birth a phenotypic value for length-at-age $0,\ldots,3$ $(x_0,\ldots,x_3)$:

$$x_0 = a_0+e,$$

$$x_j = a_j+e_{j-1} \quad \text{for} \quad j>0,$$

where e is a random deviation arising from effects of the environment on newborn individuals, and e_{j-1} is the random environmental deviation which comes about between age $j-1$ and age j. These environmental deviations are assumed to have normal distributions with zero means. The random variables a_0, g_0, g_1, g_2, e, e_0, e_1 and e_2 are independent but in view of the way they are combined to give length-at-age $0,\ldots,3$, the breeding and phenotypic values $a_0,\ldots,a_3$, $x_0,\ldots,x_3$, have positive covariances.

All simulations were started with 5000 individuals in each cohort (20000 individuals all told). Parameters for the normal distributions were set initially as in table 2, giving matrices of expected values $\boldsymbol{A}_0$, $\boldsymbol{X}_0$, $\boldsymbol{G}$ and $\boldsymbol{P}$ the same as those in table 1. In year 0, a proportion 0.6 of the individuals with a currently expressed phenotypic value $\geqslant 14$ cm were chosen at random for harvesting. To put it another way, the probability of removing an individual aged j with a phenotypic value $\geqslant 14$ cm at age j $(j = 0,\ldots,3)$ was 0.6. The harvest pattern is therefore equivalent to that used in the model above ($\theta = 0.4$, $k = 14$ cm). After year 0, there was no further harvesting.

Table 2. *Mean* (μ) *and variance* (σ^2) *of normal distributions for generating values of the independent random variables in populations simulating the lives of individuals*

(The random variables are: a_0, length-at-age 0; g_{j-1}, growth increment from age $j-1$ to age j; e, environmental deviation of newborn individuals; e_{j-1}, environmental deviation from age $j-1$ to age j. The values were obtained using the pseudo-random number generator in the statistical package Minitab (Ryan *et al.* 1985).)

	μ	σ^2		μ	σ^2
a_0	2	0.02	e	0	0.08
g_0	8	0.78	e_0	0	3.12
g_1	4	0.4	e_1	0	1.6
g_2	2	0.4	e_2	0	1.6

At the end of each year, reproduction took place, giving rise to a newborn cohort of 5000 individuals. The breeding and phenotypic values of these new individuals were generated in four steps. First, the breeding value of length at each age of each surviving parent was weighted by the current contribution of the parent to reproduction. To match the elements of $\boldsymbol{T}$ in table 1, one can suppose for instance that 0, 1, 2, 3 year-old parents contribute to 0, 10, 20, 30 offspring, respectively. (The generalization to randomly distributed numbers of offspring at each age does not introduce new behaviour to the dynamics of mean breeding and mean phenotypic values.) Second, the mean and variance of each weighted distribution of breeding values was determined; there are four of these distributions, one for each length-at-age. The means and variances were then used to obtain parameters for the normal random variables a_0, g_0, g_1, g_2 in the newborn cohort. Third, given these parameters, 5000 values of a_0, g_0, g_1, g_2 were generated, and summed as described above to give breeding values a_0, a_1, a_2, a_3 for each individual in the new cohort. The intermediate step involving the growth increments retained the general additive genetic covariance properties of the population, but allowed both the means and the variances of the breeding values to change from one generation to the next. Fourth, each newborn individual was assigned a phenotypic value for length-at-age $0,\ldots,3$ by incorporating environmental deviations e, e_0, e_1, e_2, taken from independent normal distributions as described above; the parameters for these distributions remained unchanged (table 2).

Figure 1 *b* gives the average behaviour (± 1 standard error) of five simulated populations. The mean breeding values for length-at-age 1, 2 and 3 undergo damped oscillations as expected from theory (figure 1 *a*) and overall there is close agreement between the theoretically predicted behaviour and that observed in practice.

(*b*) *Example 2: response to repeated selection*

(*i*) *Model*

In this model it is assumed that selection, rather than being confined to year 0, occurs in every iteration. Apart from this, the population has the same properties as those in the previous example, with $\boldsymbol{A}_0$, $\boldsymbol{X}_0$, $\boldsymbol{G}$, $\boldsymbol{P}$ and

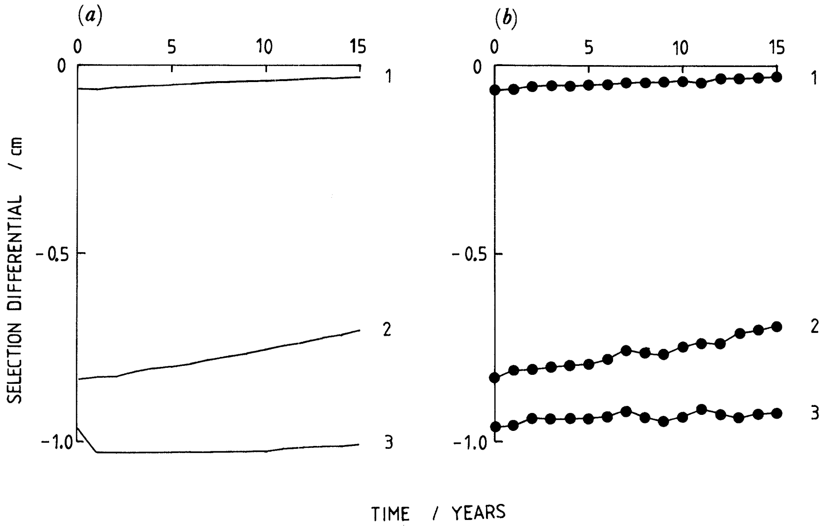

Figure 2. Selection differentials on body length of fish under continuing directional selection. The population consists of four age classes and selection differentials are generated at age 1, 2 and 3, fish at age 0 being too small to be caught. (*a*) Timecourse predicted by model. (*b*) Timecourse observed in simulated populations in which the lives of individual fish were followed explicitly as described in the text; each point gives the mean of 5 simulations, all standard errors being less than 0.02 cm.

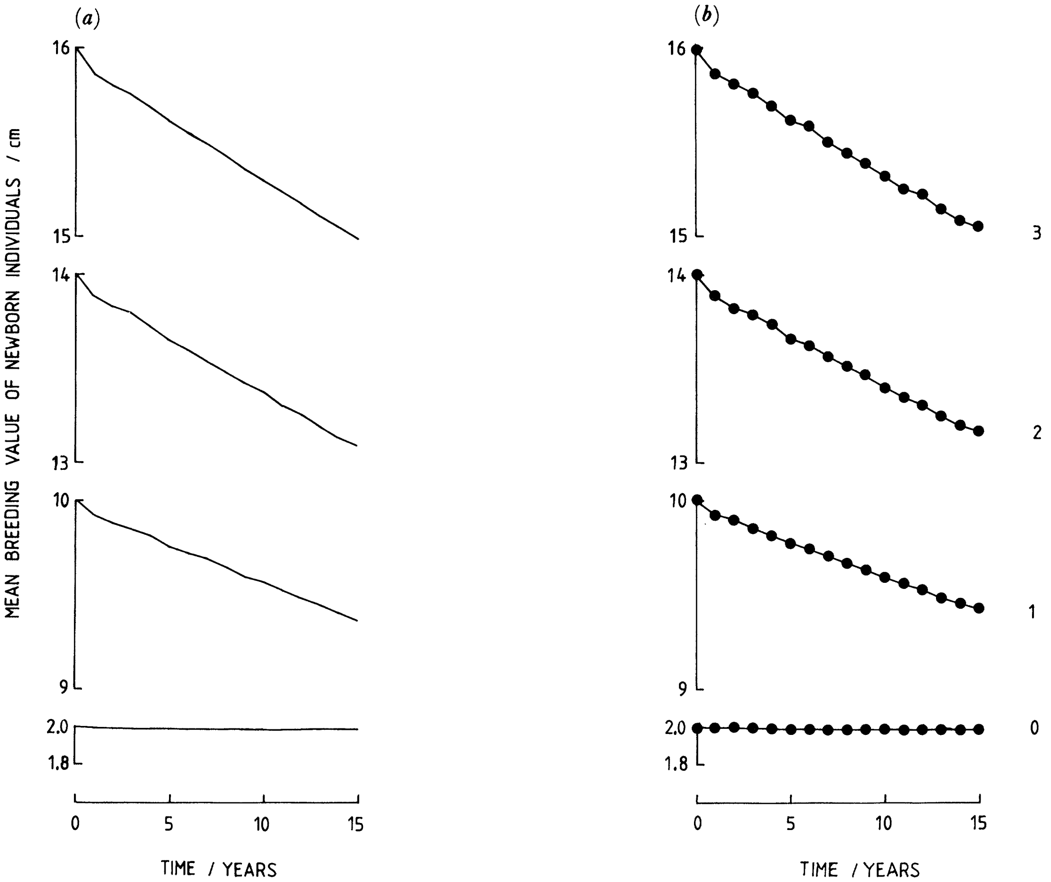

Figure 3. Response to continuing selection on body length of fish. The population comprises four age classes and selection can take place at each age. The graphs give the mean breeding values for length-at-age 0, 1, 2, 3 in individuals at birth. (*a*) Timecourse for populations predicted by equations 3 and 4. (*b*) Timecourse observed in simulated populations in which the lives of individuals were followed explicitly as described in the text; each point gives the mean of 5 simulations, all the standard errors being less than 0.02 cm.

$\boldsymbol{T}$ as in table 1. As before, selection takes the form of removing individuals of length $\geqslant 14$ cm ($k = 14$ cm) with probability $1-\theta = 0.6$, but this now happens every year.

The dynamics of mean breeding values are given by equations 3 and 4. In using these equations, we need to bear in mind that the matrix of selection differentials $\boldsymbol{S}_t$ changes from year to year as the mean phenotypic values change. As noted earlier, change in the mean phenotypic value of a trait j (and hence $\boldsymbol{S}_t$) comes about within a cohort as it ages due to selection operating on other correlated traits expressed before trait j, and also between cohorts as the mean phenotypic value of trait j in newborn individuals changes in concert with their mean breeding value. The time course of the selection differentials, shown in figure 2*a*, shows small changes at age 1 and 3 and a somewhat larger reduction at age 2; there is no selection at age 0. The transition matrix $\boldsymbol{T}_t$ also changes from year to year, depending on the proportions of each cohort which have survived selective mortality up to the present time. Equations 1 and 2 keep track of these changes. In general, $\boldsymbol{T}_t$ continues to change as long as the population is evolving, because the mean fitnesses $\overline{W}_{jt}$ on which the p_{jt}s depend are themselves changing.

The dynamics of the mean breeding values at birth, determined iteratively from equations 3 and 4, show a continuing decline in mean length-at-age 1, 2 and 3 (figure 3*a*), corresponding to the continuing selection against large individuals. There is very little change in length-at-age 0, as one would expect from the lack of any selection differential on the trait and the very low covariance of its breeding value with those of other traits.

There is a close match between the response to selection obtained by using equations 3 and 4 and the response predicted by the asymptotic approximation (equation 7), despite the additional assumptions of the latter. Consider for instance the iteration $t = 10$ to $t = 11$. The change in mean breeding values obtained from equations 3 and 4 is

$$\boldsymbol{A}_{11} - \boldsymbol{A}_{10} = \begin{bmatrix} -0.001 & -0.001 & -0.001 & -0.001 \\ -0.039 & -0.037 & -0.040 & -0.041 \\ -0.057 & -0.054 & -0.059 & -0.060 \\ -0.064 & -0.059 & -0.065 & -0.066 \end{bmatrix}.$$

Assuming that $\boldsymbol{S} = \boldsymbol{S}_{10}$, $\boldsymbol{T}_s = \boldsymbol{T}_{10}$ and that by $t = 10$ the system is at steady state with respect to population dynamics, the asymptotic response is

$$\Delta \boldsymbol{R}_\infty = \boldsymbol{G}\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}\boldsymbol{u}_s\boldsymbol{v}_s\alpha_s^{-1},$$

so

$$\Delta \boldsymbol{R}_\infty = \begin{bmatrix} -0.001 & -0.001 & -0.001 & -0.001 \\ -0.039 & -0.039 & -0.039 & -0.039 \\ -0.057 & -0.057 & -0.057 & -0.057 \\ -0.063 & -0.063 & -0.063 & -0.063 \end{bmatrix},$$

which corresponds closely to the matrix above.

(*ii*) *Populations simulating the lives of individuals*

The dynamics predicted from the model are compared with those observed in populations containing individuals with randomly generated breeding and phenotypic values. These populations were constructed in precisely the same way as those in the previous example, except that harvesting took place every year, removing as before 0.6 of the individuals with a currently expressed phenotypic value $\geqslant 14$ cm.

The behaviour predicted by the model can be no more than an approximation to the average dynamics of these simulated populations because the latter allow changes in the covariance matrices to come about. Such changes arise for two main reasons. First, as a single cohort ages, selection alters the distributions of phenotypic values, and hence the distributions of breeding values. By the time the cohort is old, its observed covariance matrices can therefore differ appreciably from $\boldsymbol{P}$ and $\boldsymbol{G}$. Second, the variances of breeding values in newborn cohorts are free to change under selection, whereas they are assumed to be constant in the model.

One of the effects of the changing distributions of phenotypic values within cohorts is that the phenotypic variance of length-at-age 3 had already been reduced by the age at which the trait was expressed in the selected populations. This reduction came about through the positive phenotypic covariance of the trait with those expressed earlier in life, in conjunction with the selection operating at these earlier ages. A consequence was that the observed selection differential at age 3 was about 10% less in absolute value than that predicted (figure 2*b*). Apart from this, there is a close match between the observed and predicted selection differentials over the course of time. For short-term prediction of evolutionary dynamics the discrepancy in the selection differential makes little difference (figure 3*b*), but the match between the observed and predicted dynamics would become less close in the longer term.

4. CONCLUDING COMMENTS

Equations 3 and 4 provide a model for predicting the evolution of a set of correlated quantitative traits in a non-equilibrium age-structured population. There are, however, some caveats about the model which need to be borne in mind. First, there is an assumption that the phenotypic value of an individual can be partitioned into a breeding value and an independent environmental deviation. Interactions between genotype and environment, dominance deviations and non-additive interactions between loci are not considered, and it should be borne in mind that long-term directional selection could mould the genetic architecture generating non-additive interactions within and between loci (Lawrence 1984). Second, it is assumed that there is a scale on which breeding values, environmental deviations and phenotypic values have a multivariate normal distribution. For the breeding values of newborns this cannot be better than an approximation because these distributions are obtained by mixing the distributions from parents of different ages which in general would have different means.

Another important assumption is that the phenotypic value of an individual has no effect on fitness in the absence of the directional selection pressure applied. Since some traits such as length-at-age are often correlated with vital rates, extension of the theory to relax this assumption would be well worthwhile (see Lande 1982).

The theory is aimed at predicting short-term transient evolutionary dynamics, because it is such changes which are of most interest in the management of exploited stocks of fish. The focus is therefore on first-order statistics, while holding the second-order statistics constant. Second-order statistics can however change in the short term. First, when directional selection is introduced, it immediately generates gamete phase disequilibrium, causing a reduction in the variances and covariances of breeding values (Falconer 1989). The effect of this is small as long as heritabilities are low and the selection differential is not too large. Second, when the same character is expressed at a series of ages and experiences directional selection at each age, its phenotypic variance is diminished at each stage and may be substantially reduced by the time the cohort is old. Over longer periods of time, second-order statistics would be expected to change as gene frequencies change, and such changes would need to be considered in modelling the longer-term evolutionary dynamics.

Equations 3 and 4 identify the information needed from fisheries to predict the ways in which exploited stocks evolve. Some pieces of information are more readily obtained than others. For instance, by combining knowledge of the life history of a stock with estimates of the numbers at age routinely collected in the management of some fisheries, an estimate of $\boldsymbol{T}_t$ could be made. In addition the matrix of selection differentials $\boldsymbol{S}_t$ could be estimated by direct monitoring of the mean phenotypic values of traits before and after a period of selection. Since $\dot{\boldsymbol{P}}$ contains only the variances and covariances of traits at the age when they are expressed, this matrix can also be estimated from the phenotypic values prior to selection as can the matrix of directional selection gradients $\dot{\boldsymbol{P}}^{-1}\boldsymbol{S}_t$. On the other hand, there is much more uncertainty over the matrices which deal with breeding values, $\boldsymbol{A}_t$ and $\boldsymbol{G}$; these require data from breeding experiments at present unavailable in commercially exploited fish stocks. Still more problematic is the full phenotypic covariance matrix $\boldsymbol{P}$; to estimate this we need the phenotypic values of individuals from a control, unharvested population. Until more is known about $\boldsymbol{A}_t$, $\boldsymbol{G}$ and $\boldsymbol{P}$, there is bound to be much doubt about the evolutionary dynamics of exploited fishes.

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