

A General Fishery Model for a Size-Structured Fish Population

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This paper describes a fishery model based on size, rather than age, as the fundamental population variable. The model's key ingredient is a density function related to number of fish within any given size range. A key assumption is that selectivity in the fishery is determined by size, not age, and that fish can reach recruitment size at various ages. The theory easily yields moment equations comparable with those obtained recently by Fournier and Doonan; for example, the general moment equation here is derived in a four-line proof. The paper gives detailed recommendations for tailoring the new model to a specific fishery, where model complexity is determined by the available data. The new theory places earlier models of Deriso and Schnute in the context of generalized cohort analysis, where size-dependent mortality is allowed. In particular, the paper identifies a potential problem with these earlier models and proposes a solution. All results are interpreted biologically to provide both conceptual and analytical tools for stock assessment.

L'auteur présente un modèle des pêches basé sur la taille plutôt que sur l'âge comme principale variable de la population. La composante clé du modèle est une fonction de densité liée au nombre de poissons au sein d'une gamme de tailles donnée. L'une des principales hypothèses est que la sélectivité de la pêche est déterminée par la taille, non par l'âge, et que les poissons peuvent atteindre la taille de recrutement à divers âges. Cette théorie permet facilement d'obtenir des équations de moments comparables à celles récemment obtenues par Fournier et Doonan. Ainsi, une preuve de quatre lignes suffit à obtenir l'équation générale du moment. L'auteur présente des recommandations détaillées pour l'ajustement du nouveau modèle à une pêche précise, la complexité du modèle étant déterminée par les données disponibles. Cette nouvelle théorie situe les modèles antérieurs de Deriso et Schnute dans le contexte de l'analyse généralisée des cohortes qui autorise une mortalité dépendante de la taille. Plus particulièrement, l'auteur souligne le problème que peuvent poser ces modèles antérieurs et propose une solution. Tous les résultats sont interprétés de façon biologique afin d'obtenir des outils tant conceptuels qu'analytiques pour l'évaluation des stocks.

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Recent research has established a mathematical relationship between difference equations directly associated with fishery data and more detailed underlying biological models (Deriso 1980; Schnute 1985; Fournier and Doonan 1987). The object of all this work is to make the link between biology and theory as precise as possible. Unfortunately, from a practical point of view, the theory becomes increasingly complex as more complex biological processes are included in the underlying model. Furthermore, there is even some debate as to the degree of complexity that is useful (Ludwig and Walters 1985).

The simplest model, described by Deriso (1980) and Schnute (1985), is based on the assumption that the fishery has "knife-edged" selectivity. This means that, for some fixed age k , fish of age k or older experience uniform fishing mortality, while fish younger than k are invulnerable to the fishery. There are two unfortunate consequences of this assumption. First, it clearly is too simplistic. For example, if the fishery is managed with a size limit, fish may reach the critical size at various ages. Second, on the analytic side, the assumption forces the modeler to make a fixed choice for k . This fixes the time lag between spawning and recruitment and gives the difference equation a specific structure. In particular, that structure does not include a general autoregressive process in which the current state is allowed to depend on an arbitrary number of earlier states.

Two recent papers have helped resolve the limitations of the simple model described above. First, Fournier and Doonan (1987) placed the model in a much broader context of models containing groups of fish with varying susceptibility to the fishery. Their approach generalizes an earlier "incomplete recruitment" model proposed by Deriso (1980). They obtained a very general set of difference equations for such models and showed that their methods apply to wide range of data when available, such as mean weights and mean square weights from fish samples. In essence, Fournier and Doonan derived difference equations for arbitrarily high-order moments of the population's size distribution. Just as the mean, standard deviation, skewness, and kurtosis are useful characteristics of a statistical distribution, so too they may be informative measures of size distribution within a fish population.

The second recent development in basic theory appears almost incidentally in a manuscript by Walters¹ documenting application software for the models of Deriso (1980) and Schnute (1985). Walters modified the assumption of knife-edged selectivity by assuming that *size*, rather than age, determines the cut-off for selection by the fishery. Although size

¹C. J. Walters. 1986. Microcomputer stock assessment using Schnute's generalization of the Deriso delay-difference mode. User's manual for the computer program "SCHNUTE". Unpubl. ms. 43 p.

selection is an old concept in fisheries literature (e.g. Beverton and Holt 1957, p. 341ff.), Walters appears to be the first to have proposed its application to contemporary models based on difference equations. In his model, fish reach a critical size at various ages; consequently, the present state of the population depends on several past states. Mathematically, this feature allows the model to include a general autoregressive component and brings it closer the modern theory of times series analysis (Box and Jenkins 1970).

Walters presented his difference equation without proof, although his result is intuitively clear from earlier work by Deriso (1980) and Schnute (1985). Changing a major assumption, however, produces a new theory. In this paper, I show that if such a theory is developed systematically, it leads to a remarkably simple and comprehensive model similar to that proposed by Fournier and Doonan (1987). In particular, difference equations for arbitrarily high-order moments of the size distribution can be derived easily. Furthermore, the theory suggests a generalization of cohort analysis that includes size-dependent mortality. Taken together, the results derived here provide a global perspective of single-species fishery models.

Here is a brief outline of the paper. In Section 1, I formulate the main assumptions, which I apply in Section 2 to derive the principal difference equations. In Section 3, I describe how to tailor the model to a specific fishery, where model complexity relates to the data available. Finally, in Section 4, I derive a generalization of cohort analysis from the model hypotheses and show precisely how the difference equations of Deriso (1980) and Schnute (1985) fit into this context. The assumption that mortality is not size selective turns out to be a necessary requirement only for the last two groups of a multigroup model. Throughout the paper, I stress the biological significance of the results, so that the theory can be applied both conceptually and analytically.

The essential feature of the model here is that it is based on size, rather than age. To make this distinction clear, many of the results here are compared with earlier ones for age-structured models. Since the difference equations turn out to be particularly simple, one can assess intuitively their potential for parameter estimation. For example, high-order moments turn out to be informative only for parameters associated with fish growth. Also, the distribution of fish weights can be a useful indicator of natural mortality. Some surprising conclusions emerge from these analyses. For example, I show that the simple model of Deriso (1980) and Schnute (1985) can be deceptively wrong under certain circumstances and that an even simpler one should be used instead.

1. Model Assumptions

In this section, I develop a size-structured model by starting from assumptions familiar in age-structured models and replacing the age a with a suitable measure of fish size. For simplicity, I assume that size refers to weight, although other measures of size (such as length) can be used. The approach taken here might be shortened somewhat by dropping the analogy with age-structured models, but important comparisons between the two types of models would then have to be omitted. Of necessity, the development here involves considerable mathematical notation. The reader may wish to refer frequently to Appendix A, which lists definitions for all notation in the paper.

1A. Growth

The usual growth assumption in an age-structured model (e.g. Schnute 1985) is that the weight w_a at age a follows a von Bertalanffy growth curve:

$$(1.1) \quad w_a = W_\infty [1 - e^{-K(a-a_0)}]$$

where W_∞ , K , and a_0 are three parameters that specify the curve. A short calculation (Ricker 1975, p. 222) from (1.1) shows that

$$(1.2) \quad w_{a+1} = W_\infty(1 - e^{-K}) + e^{-K}w_a.$$

This is a two-parameter relationship between a weight w_a and the succeeding weight w_{a+1} one year later. To obtain the growth model for a weight-structured population from (1.2), replace w_a by w and w_{a+1} by w' . Then (1.2) can be written

$$(1.3) \quad w' = W + \rho w$$

where

$$(1.4a) \quad W = W_\infty(1 - e^{-K})$$

$$(1.4b) \quad \rho = e^{-K}.$$

Although they are both based on von Bertalanffy growth, equations (1.1) and (1.3) have rather different interpretations. In (1.1) the weight w_a at age a is a three-parameter function of the age a . Equation (1.3) does not assume that there is a definite relationship between age and weight. It asserts only that a fish starting at weight w will grow to weight w' within one year. The relationship is linear, having two parameters W and ρ . If there is an underlying age-weight relationship (1.1), then (1.4) can be used to estimate W and ρ from the von Bertalanffy parameters W_∞ and K .

A complete description of the growth model requires one constraint. Deriso (1980) and Schnute (1985) restrict (1.1) to ages above the recruitment age k :

$$(1.5) \quad a \geq k.$$

In this paper, I assume that (1.3) applies to weights above a specified recruitment weight V :

$$(1.6) \quad w \geq V.$$

Thus, (1.3) and (1.6) define a complete growth model in the sense that, for any weight w above the recruitment weight V , (1.3) specifies the succeeding weight w' one year later. The concept is that a fish may reach the weight V at several possible ages; however, once the weight V is reached, the growth curve (1.3) applies. This model contrasts with (1.1) and (1.5) in which the weight at each age conforms to (1.1) after age k .

The essential distinction between the two types of growth models can be summarized symbolically as follows:

Age-structured model: $a \rightarrow w$

Weight-structured model: $w \rightarrow w'$.

In the first case, the weight w is assumed to be a function of the age a . In the second, the weight w' after one year is a function of the starting weight w . Throughout this paper, the prime is used to denote such a function; that is, if u is a weight, then u' is the weight one year later. Furthermore, the tilde symbol is used to denote the inverse of this function; that is, \tilde{u} denotes the starting weight which will result in weight u one year later:

$$(1.7) \quad (\tilde{u})' = u.$$

For example, the growth law (1.3) has the inverse

$$(1.8) \quad \bar{w} = (w - W)/\rho.$$

This particular law is linear, and the linearity makes possible some of the results obtained here. However, other results are valid for any growth law ($w \rightarrow w'$). The main requirement for a growth law is that weights should increase, that is:

$$(1.9) \quad w' > w$$

for any weight $w \geq V$. In (1.3) this is equivalent to the requirement that $\rho > 0$.

A fish starting at weight V will (if it survives) reach weight V' in one year, weight $(V')'$ in two years, and so on. This suggests defining a sequence of weights V_i recursively as follows:

$$(1.10a) \quad V_0 = V$$

$$(1.10b) \quad V_i = (V_{i-1})'.$$

By (1.9), this sequence is increasing and so has a limit V_∞ , which may be either finite or infinite. For example, for the growth law (1.3) it turns out that

$$(1.11) \quad V_i = \frac{1 - \rho^i}{1 - \rho} W + \rho^i V$$

where $(1 - \rho^i)/(1 - \rho)$ reduces to i when $\rho = 1$. Thus, if $\rho \geq 1$, then $V_\infty = \infty$; otherwise, $V_\infty = W/(1 - \rho)$.

The weights V_i in (1.10) can be used to define a series of half-open intervals as follows:

$$[V_0, V_1), [V_1, V_2), \dots, [V_{i-1}, V_i), \dots$$

where the notation $[V_0, V_1)$, for example, denotes the interval that includes V_0 and excludes V_1 . We can think of the recruited population divided into groups, where the i th group consists of fish having weights in the i th interval. Surviving fish in group i move into group $i + 1$ one year later. In the year of recruitment, fish belong to the first group; that is, they have weights in the interval $[V, V')$. (Notice that a newly recruited fish must have weight less than V' ; otherwise, its weight last year would have been at least the recruitment weight V .) The entire recruited population consists of fish with weights in the interval $[V, V_\infty)$.

The theory here is flexible in terms of the number of groups contemplated within the population. Most of this paper is devoted to a two-group model based on new recruits with weights in the interval $[V, V')$ and previously exploited fish with weights in $[V', V_\infty)$. It turns out that the models proposed by Deriso (1980) and Schnute (1985) involve only these two groups. In the paper's final section, I show that generalized cohort models, comparable with those of Fournier and Archibald (1982) and Deriso et al. (1985), can be obtained by extending the number of groups beyond these two.

1B. Population Variables

An age-structured model (e.g. Schnute 1985) involves the fundamental quantity N_a , the number of fish having age a at the start of year t . A basic difference between age and weight is that age is a discrete variable with integer values, while weight is continuous with real values. Consequently, to obtain a weight-structured model, one must replace the fundamental quantity N_a by a density $N(w, t)$. For this density, the integral

$$\int_{w_1}^{w_2} N(w, t) dw$$

represents the number of fish at the start of year t that have

weight somewhere between w_1 and w_2 . Thus, if w is measured in kg, then $N(w, t)$ has units kg^{-1} . Similarly,

$$\int_{w_1}^{w_2} wN(w, t) dw$$

represents the weight (biomass) of fish at the start of year t that have weight between w_1 and w_2 .

Following Schnute (1985), let N_t and N_t^* represent the number and biomass, respectively, of recruited fish in the fishery at the start of year t . Then, by definition, it follows that

$$(1.12) \quad N_t = \int_V^{V_\infty} N(w, t) dw$$

$$(1.13) \quad N_t^* = \int_V^{V_\infty} wN(w, t) dw.$$

As described earlier, the recruited population N_t has two components: newly recruited fish with weights in $[V, V')$ and previously exploited fish with weights in $[V', V_\infty)$. Let R_t and P_t denote the number of fish in each component, respectively, at the start of year t , and let R_t^* and P_t^* represent the corresponding biomasses. Then, by definition,

$$(1.14) \quad R_t = \int_V^{V'} N(w, t) dw$$

$$(1.15) \quad R_t^* = \int_V^{V'} wN(w, t) dw$$

$$(1.16) \quad P_t = \int_{V'}^{V_\infty} N(w, t) dw$$

$$(1.17) \quad P_t^* = \int_{V'}^{V_\infty} wN(w, t) dw.$$

Mathematically, definitions (1.12)–(1.17) correspond to moments of the density $N(w, t)$. This feature plays an important role in the derivation and interpretation of difference equations given later.

A sensitive reader might have concerns about definitions (1.14)–(1.15) for the newly recruited population, since a fish smaller than weight V at the start of year t could grow into the interval $[V, V')$ during the year. Because t is restricted to integer values corresponding to individual years, the model here implicitly assumes that growth occurs instantly at the end of each year. During the year, the population's size structure remains stable, since mortality (fishing and natural) is assumed not be size selective for weights above V . In practice, the recruitment weight V should be chosen with this approximation in mind.

1C. Population Dynamics

An age-structured model always contains one fundamental dynamic equation that describes the process of aging one year. For example, the first assumption in Schnute's (1985) model is

$$(1.18) \quad N_{a+1, t+1} = \tau_t N_a$$

where τ_t is the total survival from fishing and natural mortality during year t . The key feature of this assumption is that survival is independent of age a for $a \geq k$. Biologically, this feature corresponds to knife-edged selectivity; analytically, it makes possible the derivation of a difference equation in the total population N_t .

The counterpart of (1.18) for a weight-structured population

is based on two principles. First, in analogy with age-independent survival, the total survival τ_t is presumed independent of weight w for $w \geq V$. Second, just as a fish of age a must move to age $a + 1$ in one year, so also a fish of weight w must grow in one year to weight w' . These principles imply that

$$(1.19) \quad \int_{w_1'}^{w_2'} N(w, t+1) dw = \tau_t \int_{w_1}^{w_2} N(w, t) dw$$

for every weight interval $[w_1, w_2]$ with $V \leq w_1 < w_2$. This is the fundamental dynamic equation for a weight-structured model. It states that fish in an arbitrary weight interval $[w_1, w_2]$ must, after survival during one year, reach the weight interval $[w_1', w_2']$.

Mathematically, (1.19) is written in integral form. To obtain an equivalent differential form, notice that if w_2 is close to w_1 , then (1.19) implies the approximate equation

$$N(w_1', t+1)(w_2' - w_1') \approx \tau_t N(w_1, t)(w_2 - w_1).$$

Taking the limit as w_2 moves to w_1 gives the exact result

$$(1.20) \quad N(w', t+1) \frac{dw'}{dw} = \tau_t N(w, t)$$

for every $w \geq V$, where the subscript on w_1 has been dropped. Incidentally, the derivative dw'/dw in (1.20) is the Jacobian of the transformation from w to w' .

Equations (1.19) and (1.20) are equivalent forms of the same dynamic assumption for a weight-structured populations. They are valid for any growth law, $w \rightarrow w'$. Furthermore, they can easily be extended to cover the case where mortality is size-selective by assuming that τ_t is a function of size, $\tau_t(w)$. This would require placing τ_t inside the integral on the right side of (1.19), but (1.20) remains valid even when τ_t is replaced by $\tau_t(w)$. I return to this point in Section 4, where I derive generalized cohort analysis; however, in the meantime, I restrict my attention to knife-edged selectivity, for which τ_t is independent of w .

1D. Average Weights

Average weights play an important role in size-structured models. For example, let X_t be the average weight of the entire recruited population at the start of year t ; that is,

$$(1.21) \quad X_t = N_t^*/N_t.$$

Because mortality is presumed not to be size selective for weights above V , this average will not change during the year; thus, X_t also represents the average weight *throughout* year t . Another consequence of knife-edge selectivity is that the weight distribution of the catch follows that of the population; thus, X_t can be estimated directly from a sample of the catch. Incidentally, this discussion shows that it is important to make a judicious choice of the recruitment weight V . In some cases, it may be wise to pick a rather large V and to exclude from the catch fish smaller than V , treating them as part of the natural mortality that precedes recruitment.

In analogy with (1.21), let Y_t and Z_t denote average weights within the newly recruited and previously exploited components of the population, respectively; that is,

$$(1.22) \quad Y_t = R_t^*/R_t$$

$$(1.23) \quad Z_t = P_t^*/P_t.$$

Like X_t , these remain fixed during year t , and they can be

estimated from a sample of the catch. For example, Z_t is the average weight in year t of fish with weight greater than V' .

In age-structured models such as those of Deriso (1980) and Schnute (1985), newly recruited fish all have the same weight V , so that

$$(1.24a) \quad Y_t = V.$$

A more reasonable value of Y_t in a size-structured population might be

$$(1.24b) \quad Y_t = (V + V')/2$$

based on the assumption that new recruits have weights distributed evenly across the interval $[V, V']$. In general, Y_t can be any value between V and V' , depending on the underlying weight distribution. This illustrates one of the differences between age- and size-structured models.

A significant feature of (1.24a)–(1.24b) is that Y_t is *independent of t* . In general, this is true if the new recruits are distributed similarly each year, that is, if there is a function $f(w)$ independent of t such that

$$(1.25) \quad N(w, t) = f(w)N(V, t); \quad V \leq w < V'$$

for every year t . If (1.25) holds for the entire range $V \leq w < V_\infty$, then the averages X_t and Z_t are also independent of t . Stable fish populations typically experience only minor fluctuations in average weights X_t , Y_t , and Z_t . The proofs below suggest that such populations may need to be modeled differently from those in which X_t experiences large variation.

1E. Recruitment

The most fundamental difference between age- and weight-structured models pertains to recruitment. As described in the introduction, the age-structured models of Deriso (1980) and Schnute (1985) involve a specific time lag k , the recruitment age, between birth and recruitment. In a size-structured model, the time lag between birth and a fixed recruitment weight V can be variable, depending on how many years it takes a fish to reach the critical size. To be precise, suppose that k and K are the minimum and maximum age, respectively, at which a fish can reach a weight in the interval $[V, V']$. Let S_t^* be the spawning stock biomass in year t and assume that some function $F(S_t^*)$ can be used to calculate the total recruitment biomass in future years $(t+k, \dots, t+K)$ due to the stock biomass in year t . Assume further that the fraction π_a of this total recruitment is recruited at age a ($a = k, \dots, K$). Notice that the function $F(\cdot)$ and the fraction π_a are presumed independent of t , although these simplifying restrictions can easily be generalized. The above assumptions imply Walters' recruitment hypothesis for a weight-structured population (see footnote 1):

$$(1.26) \quad R_t^* = \sum_{a=k}^K \pi_a F(S_{t-a}^*).$$

The parameters π_a ($a = k, \dots, K$) are, of course, subject to the restrictions that they are fractions summing to 1:

$$(1.27a) \quad 0 < \pi_a \leq 1$$

$$(1.27b) \quad \sum_{a=k}^K \pi_a = 1.$$

In the special case that $k = K$, a weight-structured model reduces essentially to an age-structured one.

The assumption (1.26) differs slightly from a comparable assumption in Schnute (1985) where the number of recruits R_t , rather than the biomass R_t^* , is presumed dependent on an earlier stock size. Either choice, R_t or R_t^* , in (1.26) gives similar results, but slightly greater symmetry is achieved by choosing R_t^* . Another alternative to (1.26) might be

$$(1.28) \quad R_t^* = \sum_{a=k}^K \pi_a \sigma^{a-k} F(S_{t-a}^*)$$

where σ is a survival fraction. In (1.26), $F(S^*)$ represents the total biomass recruited to the fishery over a period of $K - k + 1$ yr. In (1.28), $F(S^*)$ is the biomass at age k destined to be recruited at an age between k and K . Natural mortality reduces this biomass by the fraction σ each year prior to actual recruitment. The two formulations (1.26) and (1.28) can be shown to give equivalent results, after suitably altering the definitions of various parameters. Although (1.28) is closer to the usual definition of recruitment in the context of cohort analysis, I use the simpler form (1.26) here.

Numerous forms for the recruitment functions $F(S^*)$ have been proposed in the literature, and in an earlier paper (Schnute 1985, equations (1.30)–(1.36), I suggested using

$$(1.29) \quad F(S^*) = \alpha S^* (1 - \beta \gamma S^*)^{1/\gamma},$$

a function that includes most historical alternatives, such as those of Ricker (1954, 1958), Schaefer (1954, 1957), Beverton and Holt (1957), and Pella and Tomlinson (1969). Unfortunately, all these models have the property that $F(0) = 0$; consequently, they do not extend continuously to the case of constant recruitment. Practical experience (Jacobson et al. 1987) shows that this can be a serious limitation. It is true, of course, that recruitment must be 0 when the stock is 0; however a curve through the available range of data need not extrapolate to the origin. This is precisely the traditional argument used in conjunction with von Bertalanffy growth (1.1): a useful growth model need not predict that a fish starts growing at age 0 with size 0. An extension of (1.29) along the lines of (1.1) is

$$(1.30) \quad F(S^*) = \alpha(S^* - \delta)[1 - \beta\gamma(S^* - \delta)]^{1/\gamma}$$

where δ is the extrapolated stock biomass at which $F = 0$, just as a_0 in (1.1) is the extrapolated age at size 0.

This modification of (1.29) preserves its desirable global properties. For example, by a proof similar to that in Schnute (1985, appendix B), (1.30) can be shown to be equivalent to

$$(1.31) \quad F(S^*) = G \frac{S^* - \delta}{H - \delta} \left[1 + \gamma \frac{H - S^*}{H - \delta} \right]^{(1/\gamma)}$$

where G and H are two parameters defined by

$$(1.32a) \quad G = \alpha\beta^{-1}(1 + \gamma)^{-(1+\gamma)/\gamma}$$

$$(1.32b) \quad H = \delta + [\beta(1 + \gamma)]^{-1}.$$

When $\gamma > -1$ in (1.31), $F(S^*)$ takes the maximum value G at $S^* = H$, and when $\gamma = 1$, (1.31) reduces to the constant recruitment function

$$(1.33) \quad F(S^*) = G.$$

Schnute (1985, fig. 3) illustrated the family of curves (1.31) when $\delta = 0$, and the possibility that $\delta \neq 0$ simply removes the restriction that the curves should pass through the origin by allowing translation to the right ($\delta > 0$) or left ($\delta < 0$). In many applications, $\delta < 0$ and $F(0) > 0$.

Each of the equivalent recruitment curves, (1.30) and (1.31),

has four parameters. Typically, it is impossible to estimate so many parameters, and some restriction is required. For example, when $\delta = 0$, the choices $\gamma = -1, 0$, or 1 in (1.30) correspond to the Beverton–Holt, Ricker, or Schaefer curves, respectively (Schnute 1985, section 1E). The curves described here are designed to accommodate both the historical alternatives and the practical limitations of real data sets.

1F. Summary

I have discussed the development of a weight-structured model in relation to more familiar age-structured assumptions. There are only three key assumptions in the new model. First, there is the growth equation (1.3), together with the concept of a more general growth law ($w \rightarrow w'$). Second, there is the dynamic equation (1.19), which is restated in differential form in (1.20). Finally, there is the recruitment hypothesis (1.26), which includes several time lags in the recruitment calculation. Although these three principles require some elaboration to become practically useful, they are adequate for deriving an interesting and useful general theory.

2. Difference Equations

A modified version of Schnute's (1985) methods can be used to derive difference equations similar to those of Deriso (1980) and Schnute (1985), based on the model hypotheses formulated above. A deeper perspective is possible, however, by generalizing the moment definitions (1.12)–(1.17) and applying a single method to obtain a complete set of moment equations. This approach parallels that of Fournier and Doonan (1987), although it leads in the present context to simpler results that can easily be interpreted biologically.

The essential distinction between the model here and that of Fournier and Doonan (1987) is the underlying structure variable. They used age, and I use size. To handle the problem of gear selectivity, they assumed that fish of a single age may belong to several groups with distinct vulnerabilities to the gear. I handle the problem differently, by assuming that selectivity relates directly to size; that is, that fish in a single weight interval are all equally vulnerable. Thus, they divided one age group into subgroups of differing vulnerability, while I do not similarly divide the fish within one size group. Since one of my size groups can include fish of several ages, these two analyses have something in common. My analysis is more rigid than theirs, however, because I apply my growth law (1.3) deterministically, while they assumed only that *mean* sizes at age follow a growth curve like (1.1). In my view, the model here is a compromise in favor of simplicity, although the greater complexity of their model may sometimes be required. Incidentally, the full significance of my selectivity hypothesis does not become clear until Section 4, where I derive generalized cohort analysis.

2A. Higher Order Moments

Notation presented so far has focussed on familiar population variables, such as numbers and biomass. As discussed above in connection with (1.12)–(1.17), these variables are moments of the underlying density $N(w, t)$. More generally, define n th-order moments as follows:

$$(2.1) \quad N_t^{[n]} = \int_v^{v_x} w^n N(w, t) dw$$

$$(2.2) \quad R_t^{[n]} = \int_V^{V'} w^n N(w, t) dw$$

$$(2.3) \quad P_t^{[n]} = \int_{V'}^{V_\infty} w^n N(w, t) dw.$$

For $n = 0$ or 1 , these are the usual measures of numbers and biomass, respectively. For example, $N_t^{[0]} = N_t$ and $N_t^{[1]} = N_t^*$; thus, the superscript "[0]" on N_t can be dropped and "[1]" can be replaced with "*". The quantities (2.1)–(2.3) represent *population moments about the origin* (Kendall and Stuart 1977, p. 57). Similarly, define *central moments about the mean* as follows:

$$(2.4) \quad N_t^{(n)} = \int_V^{V_\infty} (w - X_t)^n N(w, t) dw$$

$$(2.5) \quad R_t^{(n)} = \int_V^{V'} (w - Y_t)^n N(w, t) dw$$

$$(2.6) \quad P_t^{(n)} = \int_{V'}^{V_\infty} (w - Z_t)^n N(w, t) dw.$$

For $n = 0$, the central moments (2.4)–(2.6) are the same as (2.1)–(2.3), respectively. For $n = 1$, these moments are 0, as can be verified from the definitions (1.21)–(1.23) of X_t , Y_t , and Z_t . For $n \geq 2$, the moments (2.4)–(2.6) measure the dispersion of weights within the population. The average values,

$$(2.7) \quad X_t^{(n)} = N_t^{(n)} / N_t$$

$$(2.8) \quad Y_t^{(n)} = R_t^{(n)} / R_t$$

$$(2.9) \quad Z_t^{(n)} = P_t^{(n)} / P_t,$$

have straightforward biological interpretations. For example, $X_t^{(2)}$ is the weight variance in year t among fish with weight $w \geq V$, and $Z_t^{(2)}$ is the variance among fish with weight $w \geq V'$.

The average dispersions (2.7)–(2.9) all have units kg^n when weight is measured in kg. They can be estimated directly from a random sample of the catch. (Again, knife-edge selectivity above weight V implies that the catch has the same weight structure as the recruited population.) To be precise, suppose that a sample of M fish in year t includes the weights w_1, w_2, \dots, w_M . Then the sample mean \bar{w} provides an estimate for X_t , and an estimate for $X_t^{(n)}$ is

$$(2.10a) \quad \hat{X}_t^{(n)} = \frac{1}{M} \sum_{i=1}^M (w_i - \bar{w})^n.$$

Similar estimates for $Y_t^{(n)}$ and $Z_t^{(n)}$ are obtained by restricting the sample to fish with weights in the intervals $[V, V')$ and $[V', V_\infty)$, respectively. For example, suppose that M_z (with $M_z \leq M$) fish in the sample have weights at least V' . Denote these weights by z_i ($i = 1, \dots, M_z$), where $z_i \geq V'$. Then the subsample mean \bar{z} gives an estimate for Z_t , and an estimate for $Z_t^{(n)}$ is

$$(2.10b) \quad \hat{Z}_t^{(n)} = \frac{1}{M_z} \sum_{i=1}^{M_z} (z_i - \bar{z})^n.$$

It is important to notice that the means and sample sizes in (2.10a) and (2.10b) are different. Incidentally, estimates like (2.10a) and (2.10b) can be corrected for small sample bias, but a serious approach to this problem would involve the definitions of k -statistics and cumulants (Kendall and Stuart 1977, chap. 12 and 13). Such elaborate procedures are unnecessary here, given that reasonable sample sizes M are possible and that

other sources of error typically dominate the sample bias in (2.10a) and (2.10b).

2B. First Version of the Moment Equation

It is remarkably easy to derive a general dynamic equation for n th-order population moments, based on the model developed in Section 1. The key idea is to multiply the dynamic equation (1.20) by w'^n and then to integrate w from V to V_∞ . This gives

$$(2.11) \quad \int_V^{V_\infty} w'^n N(w', t + 1) \frac{dw'}{dw} dw = \tau_t \int_V^{V_\infty} w'^n N(w', t) dw.$$

In the left side of (2.11), the expression $(dw'/dw)dw$ reduces to dw' , and the integration variable can be converted from w to w' . The range of integration then goes from V' to V_∞ , since $V_\infty' = V_\infty$. Thus:

$$(2.12a) \quad \int_V^{V_\infty} w'^n N(w', t + 1) \frac{dw'}{dw} dw = \int_{V'}^{V_\infty} w'^n N(w', t + 1) dw'$$

$$(2.12b) \quad = P_{t+1}^{[n]}$$

where (2.12b) follows from the definition (2.3). The right side of (2.11) can be simplified using the fact that $w' = W + pw$; thus, by the binomial theorem:

$$(2.13) \quad w'^n = \sum_{i=0}^n \binom{n}{i} W^{n-i} p^i w^i$$

where $\binom{n}{i}$ denotes the usual binomial coefficient. Thus, the right side of (2.11) reduces essentially to a sum of integrals involving powers of w times $N(w, t)$, that is, moments of N about the origin. Combining (2.11)–(2.13) gives

$$(2.14) \quad P_{t+1}^{[n]} = \tau_t \sum_{i=0}^n \binom{n}{i} W^{n-i} p^i N_t^{[i]}.$$

I refer to (2.14) as the first version of the general moment equation of order n . A second version, which involves central population moments, is presented later.

Notice that (2.14) involves the population moments (2.1) and (2.3), the survival fraction τ_t , and the parameters W and p from the growth law. This result is based on only two assumptions, the dynamic law (1.20) and the growth law (1.3). Furthermore, (2.14) is easy to prove. Multiplying (1.20) by w'^n and integrating the result gives (2.11). This equation simplifies by changing the variable of integration from w to w' on the left and by applying the binomial theorem to w'^n on the right.

The expansion (2.13) demonstrates why binomial coefficients appear in the general moment equation, as first discovered by Fournier and Doonan (1987, equation (10.2) and theorems 2 and 4). In particular, these coefficients occur because of the linear growth law (1.3). They can, however, be eliminated from the analysis by reformulating (2.14) in terms of central moments. I explain this simplification in deriving the second version of the moment equation later.

From a biological point of view, (2.14) describes the transition of the entire recruited population in year t to the previously exploited population in year $t + 1$. Thus, moments $N_t^{[i]}$ ($i =$

0, ..., n) on the right side of (2.14) are used to compute $P_{t+1}^{[i]}$ on the left. Two processes, survival and growth, are involved in this transition. The factor τ_t accounts for survival, and the binomial expansion accounts for growth.

2C. Equations of Orders 0 and 1

To relate (2.14) to earlier work by Deriso (1980) and Schnute (1985), notice from definitions (2.1)–(2.3) that

$$(2.15) \quad P_t^{[n]} = N_t^{[n]} - R_t^{[n]}$$

for each n and t . In particular, by combining (2.14) and (2.15) when $n = 0$, we obtain the moment equation of order 0:

$$(2.16) \quad N_{t+1} - R_{t+1} = \tau_t N_t.$$

This has the obvious interpretation that the population in year $t + 1$, except for recruits, consists of survivals from the previous year t . Similarly, when $n = 1$, (2.14) reduces to

$$(2.17) \quad N_{t+1}^* - R_{t+1}^* = \tau_t (\rho N_t^* + W N_t),$$

the moment equation of order 1.

As it stands, the biological interpretation of (2.17) is not entirely clear. To obtain a more meaningful version, rewrite (2.17) in the form

$$N_{t+1}^* - R_{t+1}^* = \tau_t \left(\rho + \frac{W}{X_t} \right) N_t^*$$

using definition (1.21) for the average weight X_t of the recruited population. The growth law (1.3) implies that

$$\rho + \frac{W}{X_t} = \frac{W + \rho X_t}{X_t} = \frac{X'_t}{X_t},$$

and thus, (2.17) is equivalent to

$$(2.18) \quad N_{t+1}^* - R_{t+1}^* = \tau_t (X'_t / X_t) N_t^*.$$

This version of (2.17) has an interpretation analogous to that for (2.16). It states that the biomass in year $t + 1$, except for recruitment, consists of the biomass surviving from the previous year t , adjusted for growth by the factor X'_t / X_t . This adjustment factor is the key detail. It implies that biomass growth depends only on *average* weights; thus, the average weight X_t projects forward to an average weight X'_t determined by the growth law (1.3). I discuss this point further in developing the second version of the moment equation below.

Remarkably, fisheries literature has previously ignored (2.18). It is a simple first-order difference equation with a clear interpretation. Furthermore, if the average weight X_t were known for each year t , (2.18) could be used as the basis of a practical model similar to models proposed by Deriso (1980) or Schnute (1985). Their models, however, are based on *second-order* difference equations.

To understand the distinction between (2.18) and earlier models, notice that (2.16)–(2.17) involve both the biomass N^* and the population N at various times. These equations can be combined to give a single equation in biomasses alone. To achieve this, write a second version of (2.17) at time $t - 1$, multiply it by τ_t , and subtract the result from (2.17). This calculation gives

$$(2.19) \quad N_{t+1}^* - R_{t+1}^* - \tau_t (N_t^* - R_t^*) = \rho \tau_t (N_t^* - \tau_{t-1} N_{t-1}^*) + W \tau_t (N_t - \tau_{t-1} N_{t-1}).$$

From (2.16) at time $t - 1$, the expression $N_t - \tau_{t-1} N_{t-1}$

on the right side of (2.19) reduces to R_t . Furthermore, from (1.22):

$$R_t = R_t^* / Y_t$$

so that (2.19) is equivalent to

$$(2.20) \quad N_{t+1}^* - \tau_t N_t^* - R_{t+1}^* = \rho \tau_t \left[N_t^* - \tau_{t-1} N_{t-1}^* + \frac{1}{\rho} \left(\frac{W}{Y_t} - 1 \right) R_t^* \right].$$

The right side of (2.20) can be simplified using the calculation

$$\frac{1}{\rho} \left(\frac{W}{Y_t} - 1 \right) = \rho^{-1} (W - Y_t) / Y_t = -\tilde{Y}_t / Y_t$$

where \tilde{Y}_t is defined by (1.7)–(1.8). Consequently,

$$(2.21) \quad N_{t+1}^* - \tau_t N_t^* - R_{t+1}^* = \rho \tau_t [N_t^* - \tau_{t-1} N_{t-1}^* - (\tilde{Y}_t / Y_t) R_t^*].$$

This result is identical to equation (2.4) in Schnute (1985, p. 420) in the special case (1.24a) that $Y_t = V$; the symbol v in that paper has the same meaning as \tilde{Y} here. Indeed, the general size-structured model includes an age-structured one as a special case, by assuming that fish at each age have a fixed weight determined by the growth curve. Thus, the proof leading to (2.21) constitutes an alternative proof of the fundamental difference equations in Deriso (1980) and Schnute (1985).

The distinction between (2.18) and the Deriso–Schnute model (2.21) is now clear. The first-order moment equation (2.17) involves not only the biomass N_t^* but also the population N_t . There are two ways to eliminate N_t : either use a knowledge of the average weight X_t to obtain (2.18) or use both (2.16)–(2.17) to obtain (2.21). In brief, the modeler seems to be faced with two alternatives: either use the first-order difference equation (2.18) plus extra data or resort to the second-order difference equation (2.16). As I show later, there are better choices than either of these, but I include the next section to demonstrate that the Deriso–Schnute model (2.21) can be deceptive and should be used with extreme caution.

2D. Constant Average Weight

In an earlier work (Schnute 1985), I have stressed that the difference equations define a *class* of models for iterative model construction, as described by Box and Jenkins (1970). Thus, biologically meaningful special cases have considerable significance to the modeler. Unfortunately, the numerous cases outlined in Schnute (1985) omit an interesting possibility based on the new equation (2.18). To put this possibility into perspective, consider first the very simple case in which all fish have the same weight. This occurs if $W = 0$ and $\rho = 1$ in (1.3), since then $w' = w$ (i.e. the weight is constant). Making these choices for W and ρ in (2.17) gives

$$(2.22) \quad N_{t+1}^* - R_{t+1}^* = \tau_t N_t^*,$$

the biomass equation for a population with constant weight. This rather obvious result can also be obtained by multiplying both sides of (2.16) by the weight of a fish, presumed constant. In addition, (2.22) follows from (2.18) by noting that $X'_t = X_t$ in this case.

A much less restrictive assumption than constant weight for all fish is that only the *average* weight X_t of the recruited population is independent of the year t ; that is,

$$(2.23) \quad X_t = X$$

for all t . Then it follows from (2.18) that

$$(2.24) \quad N_{t+1}^* - R_{t+1}^* = \tau_t (X'/X) N_t^*.$$

The three biomass equations (2.22), (2.24), and (2.21) form a hierarchy of ascending complexity. The simplest possibility (2.22), cited earlier by Schnute (1985, model G3 in table 3), assumes that all fish in the population have the same weight. Equation (2.24) is only slightly more complicated than (2.22), yet it allows a full distribution of fish weights and assumes only that averages weights X_t are constant. The final possibility (2.21) involves no restrictive assumptions other than those that define the general model.

A simple analogy illustrates the problem with using the complex model (2.21) when (2.24) is adequate. Suppose that a time series x_t is generated by a noisy process in which the deterministic part is

$$(2.25) \quad x_{t+1} = bx_t.$$

It follows from (2.25) that for *any* value of c :

$$(2.26) \quad x_{t+1} - bx_t = c(x_t - bx_{t-1}).$$

If, however, we try to use the series x_t to estimate c in (2.26), two outcomes are inevitable: first, the estimate for c will be nonsense because the data have been generated independent of c , and second, the estimate for b will be prejudiced in some way. (For example, the loss of a degree of freedom for c will widen the confidence interval for b .) It turns out that if (2.24) applies, then the derivation of (2.21) is similar to the derivation of (2.26) from (2.25). This simple artifact may underlie many practical difficulties encountered in the use of models proposed by Deriso (1980) and Schnute (1985).

2E. Second Version of the Moment Equation

The principal result derived so far is the general moment equation (2.14), which follows from the dynamic equation (1.20) by the proof outlined in (2.11)–(2.13). Furthermore, when n is 0 or 1, (2.14) takes the form (2.16) or (2.18), respectively. These two special cases have particularly clear biological meaning: (2.16) describes the dynamics of population numbers, and (2.18) similarly describes biomass dynamics with the extra dimensionless factor X'_t/X_t to adjust for growth. It is reasonable to ask whether or not a counterpart of (2.18) exists for the general moment equation (2.14). In other words, is there an equation that expresses the dynamics of n th-order moments (with $n \geq 2$) in terms of survival and a dimensionless growth factor? The answer is yes, as long as we reformulate the problem in terms of the central moments (2.4) and (2.6).

The derivation begins with a simple conclusion from (2.16) and (2.18). Divide the latter by the former to obtain

$$(2.27) \quad \frac{P_{t+1}^*}{P_{t+1}} = \frac{X'_t}{X_t} \cdot \frac{N_t^*}{N_t},$$

a result based on the fact that the left sides of (2.16) and (2.18) are P_{t+1} and P_{t+1}^* , respectively. By (1.23), the left side of (2.27) is Z_{t+1} , and by (1.21), the right side is $(X'_t/X_t)X_t$, which reduces to X'_t . Thus, (2.27) implies that

$$(2.28) \quad Z_{t+1} = X'_t.$$

This conclusion has the simple interpretation that the average weight of previously exploited fish in year $t+1$ equals the aver-

TABLE 1. Two versions of the system of general moment equations. The system (A) for $n \geq 0$ is equivalent to (B0), (B1), and (B2) for $n \geq 2$. The first system involves moments about the origin, while the second is based on central moments. Equation (B0) describes survival from year t to $t+1$, and (B1) and (B2) relate to growth during year t . Specifically, (B1) and (B2) describe changes in mean and dispersion, respectively, of the underlying weight distribution. Figure 1 illustrates such changes for three values of ρ .

Label	Text No.	Equation
(A)	(2.14)	$P_{t+1}^{[n]} = \tau_t \sum_{i=0}^n \binom{n}{i} W^{n-i} \rho^i N_t^{[i]}$
(B0)	(2.16)	$P_{t+1} = \tau_t N_t$
(B1)	(2.28)	$Z_{t+1} = W + \rho X_t$
(B2)	(2.33)	$Z_{t+1}^{(n)} = \rho^n X_t^{(n)}$

age weight of the entire recruited population in year t projected forward by the growth law. Notice that the change in mean weights described by (2.28) is independent of mortality, a result consistent with the assumption that mortality is not selective for size.

The second version of the moment equation can be obtained by a proof similar to the first, with a modification that takes account of (2.28). The idea is to multiply the left side of the dynamic law (1.20) by $(w' - Z_{t+1})^n$ and the right side by $(w' - X'_t)^n$. By (2.28), both sides are thus multiplied by equal quantities. Integrating from V to V_∞ gives

$$(2.29) \quad \int_V^{V_\infty} (w' - Z_{t+1})^n N(w', t+1) \frac{dw'}{dw} dw = \tau_t \int_V^{V_\infty} (w' - X'_t)^n N(w, t) dw,$$

a result comparable with (2.11). The left side of (2.29) simplifies by the process applied in (2.12); that is, the integration variable can be converted from w to w' and the integration range is then the interval $[V', V_\infty)$. With reference to the definition (2.6), this proves that

$$(2.30) \quad \int_V^{V_\infty} (w' - Z_{t+1})^n N(w', t+1) \frac{dw'}{dw} dw = P_{t+1}^{(n)}.$$

To simplify the right side of (2.29), notice from the growth law (1.3) that

$$(w' - X'_t)^n = \rho^n (w - X_t)^n.$$

Consequently, with reference to the definition (2.4):

$$(2.31) \quad \int_V^{V_\infty} (w' - X'_t)^n N(w, t) dw = \rho^n N_t^{(n)}.$$

Combining (2.29)–(2.31) gives the second version of the general moment equation:

$$(2.32) \quad P_{t+1}^{(n)} = \rho^n \tau_t N_t^{(n)}.$$

Notice three key features of (2.32). First, it is a dynamic equation in central population moments. Second, it does not involve the binomial coefficients that appear in the first general moment equation (2.14); indeed, (2.32) is strikingly simpler than (2.14). Third, since central moments (for $n \geq 2$) measure dispersion, (2.32) has a simple biological interpretation. The dispersion of the previously exploited population in year $t+1$

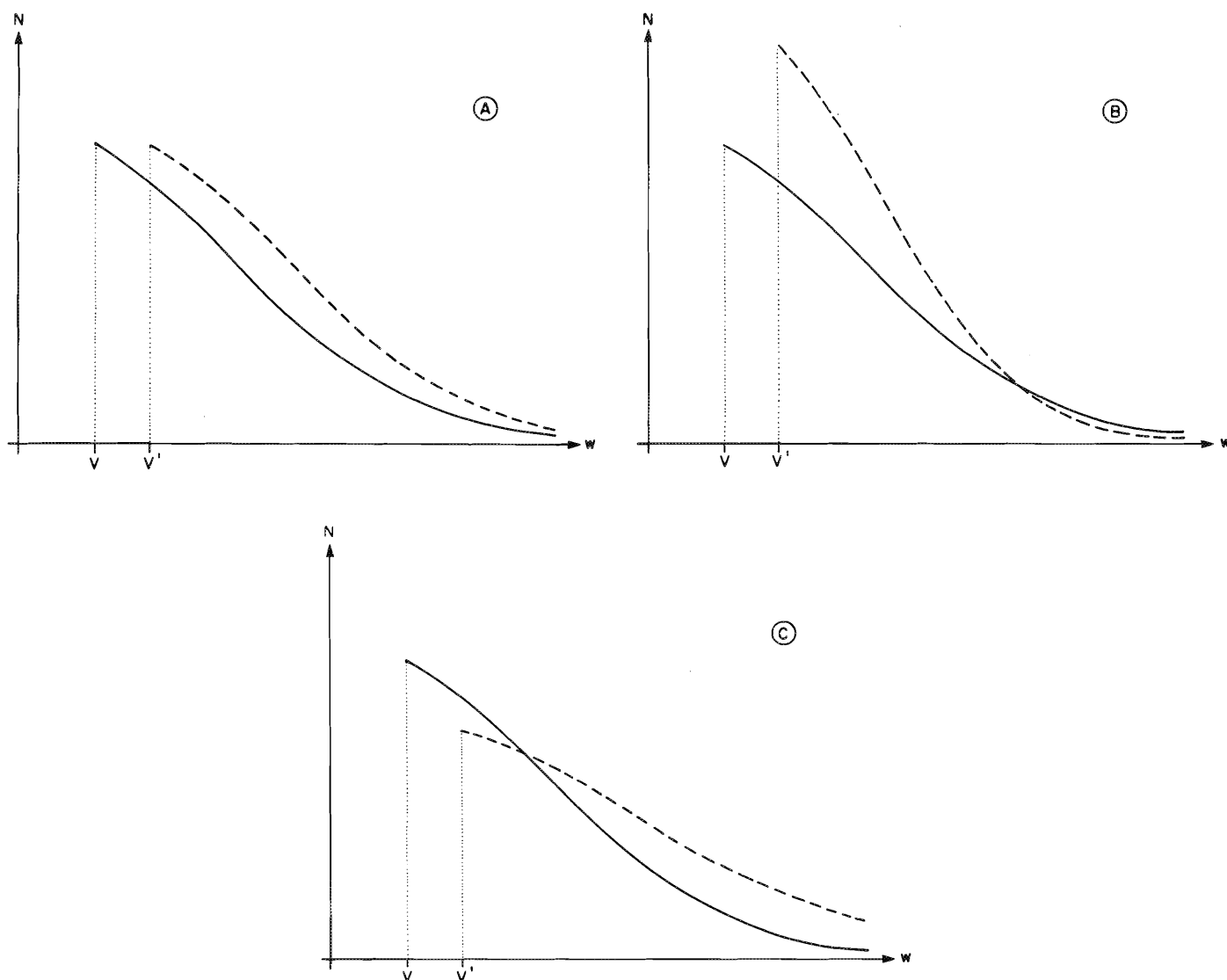


FIG. 1. Solid curve $N(w, t)$ with $w \geq V$, and broken curve $N(w, t + 1)$ with $w \geq V'$. The transition from time t to $t + 1$ is based on the dynamic law (1.19) or (1.20) with $\tau_t = 1$. (A) $\rho = 1$ and dispersion is unchanged; (B) $\rho < 1$ and dispersion is reduced; (C) $\rho > 1$ and dispersion is increased.

is a multiple of the dispersion of the recruited population in year t .

The moment equation (2.32) expresses a deep, yet simple consequence of the linear growth law (1.3). Divide (2.32) by (2.16) and use definitions (2.7) and (2.9) to show that

$$(2.33) \quad Z_{t+1}^{(n)} = \rho^n X_t^{(n)}.$$

As summarized in Table 1, this result is almost equivalent to the general moment equation. More precisely, the general equation (A) is equivalent to a set of dynamic equations: (B0) for population numbers, (B1) for mean weights, and (B2) for weight dispersions with $n \geq 2$. Figure 1 illustrates the significance of (B1) and (B2). In each panel, the solid curve represents $N(w, t)$ for $w \geq V$ and the broken curve represents $N(w, t + 1)$ for $w \geq V'$ after 1 yr of growth. For simplicity, the panels all assume that $\tau_t = 1$, since nonselective mortality has no effect on weight moments, as discussed earlier. Figure 1A represents the case when $\rho = 1$. In this case, all fish grow by a fixed increment, and the broken curve is simply a translation of the solid one. Such a translation is consistent with the predic-

tion from (B2) that the dispersion is identical for solid and broken curves when $\rho = 1$. In Fig. 1B, $\rho < 1$ so that small fish grow more rapidly than large fish. This causes the gap between small and large fish to be reduced. As a result, the broken curve is less dispersed than the solid one, just as (B2) predicts when $\rho < 1$. Similarly, Fig. 1C illustrates that when $\rho > 1$, large fish grow more rapidly than small fish. This increases the dispersion of weights within the population, as predicted by (B2) when $\rho > 1$. In all three panels, (B1) describes the shift to the right from solid to broken curves, corresponding to overall growth of the population.

The second version of the moment equation shows that moments of order 2 or higher relate to only one model parameter: ρ . Based on (2.33), a linear regression of $Z_{t+1}^{(n)}$ on $X_t^{(n)}$ constrained through the origin might give a slope estimate for ρ^n . However, in the framework of the model here, the modeler should not expect to improve estimates of other parameters by using moment equations with order $n \geq 2$. This means that the simple equation (2.18) is likely to play a dominant role in practical biomass models.

3. Model Development

The previous section describes how to obtain various difference equations for a size-structured population. To apply these equations in a specific case, the modeler requires further hypotheses related to the data available. In an earlier paper (Schnute 1985), I proposed one possible set of hypotheses in the context of catch and effort data for an age-structured population. To illustrate the flexibility of that model, I cited 24 cases of special interest. More recent experience suggests, however, that even this list is too narrow. Probably no single collection of additional hypotheses can ever prove adequate for all situations, and the modeler must always consider alternatives specific to the case under consideration. In this paper, the key assumptions used so far are the growth law (1.3) and the dynamic equation (1.19). The recruitment law (1.26) is also implicit in any difference equation involving the recruitment biomass R_t^* at some time t . Three aspects of the fishery remain to be included: the particulars of natural and fishing mortality, the process and timing of recruitment, and the means (such as catch per unit effort) whereby the population is indexed. In this section, I propose three further hypotheses and show how these can be used to develop a complete model for the available data.

3A. Model Details

The key mathematical object of the theory so far is a population density function $N(w, t)$. To develop a practical model, it is convenient to introduce three additional densities: $C(w, t)$ for the catch, $S(w, t)$ for the spawning stock, and $I(w, t)$ for the population index. These have interpretations similar to that for $N(w, t)$. For example,

$$\int_{w_1}^{w_2} C(w, t) dw$$

represents the number of fish caught during year t with weights between w_1 and w_2 . The population index might be a quantity like catch per unit effort, in which case the integral

$$\int_{w_1}^{w_2} I(w, t) dw$$

would be the number of fish in the weight interval $[w_1, w_2]$ caught per unit of effort in year t . The quantities C_t , C_t^* , S_t , S_t^* , I_t , and I_t^* can all be defined by analogy with the definitions (1.12)–(1.13) for N_t and N_t^* . Thus, for example, S_t and S_t^* represent number and biomass, respectively, of fish that spawn in year t .

The quantities C , S , and I are associated with processes that take place in the fishery: catching fish, spawning, and indexing the population. These processes have one feature in common: their significance depends on timing. Is the catch removed before, during, or after natural mortality? How much mortality occurs before spawning? Does the index apply to the population at the start of the year, or after some mortality has occurred? I address the question of timing in each case by introducing a timing parameter. Explicitly, let μ , ν , and θ be fractions defined as follows: μ = the fraction of catch removed prior to natural mortality; ν = the fraction of total mortality that occurs prior to spawning; θ = the fraction of total mortality that occurs prior to indexing the population. These parameters are built into the following three hypotheses for C , S , and I :

$$(3.1) \quad \tau_t N(w, t) = \sigma [N(w, t) - \mu C(w, t)] - (1 - \mu) C(w, t)$$

$$(3.2) \quad S(w, t) = (1 - \nu) N(w, t) + \nu \tau_t N(w, t)$$

$$(3.3) \quad I(w, t) = q[(1 - \theta) N(w, t) + \theta \tau_t N(w, t)].$$

These hypotheses have similar biological interpretations. In (3.1), σ represents survival from natural mortality. This equation assumes that the fraction μ of the catch C is first removed from N and then the survival fraction σ is applied to the difference $N - \mu C$. The remaining fraction $1 - \mu$ of the catch C is then removed to give the surviving population $\tau_t N$. Similarly, (3.2) assumes that the fraction $1 - \nu$ of the population N spawns before mortality and the remaining fraction ν spawns after mortality. In (3.3) the parameter q is a constant of proportionality between the actual population and the value of the index. The indexed population in (3.3) is assumed to be the sum of two parts, a fraction $1 - \theta$ of the population prior to mortality and the remaining fraction after mortality.

In practice, the timing parameters μ , ν , and θ would be specified by the modeler to conform with known circumstances in the fishery. For example, the choices

$$(3.4) \quad \mu = 1, \nu = 1, \theta = 0$$

imply that catch takes place prior to natural mortality (e.g. early in the year), that spawning occurs subsequent to all mortality (e.g. late in the year), and that the index $I(w, t)$ reflects the entire initial population prior to all mortality. Although these are perhaps the simplest choices, (3.1)–(3.3) are flexible enough to cover most practical circumstances. In some cases, it may be necessary to allow the timing parameters to vary from year to year. Nothing essential is lost, for example, by writing μ_t in place of μ , provided that μ_t is presumed known for each year t .

The approach taken in (3.1)–(3.3) differs somewhat from historical methods. In particular, an extensive set of alternatives exist for (3.1), based on the classical coefficients of fishing and natural mortality, F and M , respectively, where $\sigma = e^{-M}$ and $\tau = e^{-F-M}$. For example, assuming that fishing and natural mortality occur simultaneously throughout the year, it can be shown (Appendix B) that

$$(3.5) \quad \mu = \frac{F(1 - e^{-M}) - Me^{-M}(1 - e^{-F})}{F(1 - e^{-M})(1 - e^{-M-F})}.$$

This rather complex expression can be shown (Appendix B) to reduce to the simple approximation

$$(3.6) \quad \mu \cong \frac{1}{1 + \sqrt{\tau}}$$

when F and M are close. In particular, when fishing and natural mortality are equal ($F = M$ and $\tau = \sigma^2$), both (3.5) and (3.6) reduce to

$$(3.7) \quad \mu = \frac{1}{1 + \sigma}.$$

The results (3.5)–(3.7) are included here primarily to relate the new assumption (3.1) to classical theory. Something useful, however, comes from the comparison. Since $0 < \tau < 1$, (3.6) suggests that μ must lie between 0.5 and 1.0 if fishing and natural mortality occur together throughout the year. In some cases, it might be interesting to test the hypothesis that fishing and natural mortality are approximately equal, in which case (3.7) could be used to define a model in which the unknown parameter σ directly determines μ .

To apply assumptions (3.1)–(3.3) in a biomass model, it is

TABLE 2. A composite model for the data I_t^* , C_t^* , and X_t .

[A1]	$N_t^* = \frac{I_t^* + q\theta[1 - \mu(1 - \sigma)]C_t^*}{q[1 - \theta(1 - \sigma)]}$
[A2]	$S_t^* = [1 - \nu(1 - \sigma)]N_t^* - \nu[1 - \mu(1 - \sigma)]C_t^*$
[A3]	$R_{t+1}^* = \sum_{a=k}^K \pi_a F(S_{t+1-a}^*)$
[A4]	$N_{t+1}^* = R_{t+1}^* + \frac{X_t'}{X_t} [\sigma(N_t^* - \mu C_t^*) - (1 - \mu)C_t^*]$
[A5]	$I_{t+1}^* = q \left([1 - \theta(1 - \sigma)]N_{t+1}^* - \theta[1 - \mu(1 - \sigma)]C_{t+1}^* \right)$

necessary to convert them to biomass equations. Multiply each equation by w and integrate from V to V_∞ to obtain

$$(3.8) \quad \tau_t N_t^* = \sigma[N_t^* - \mu C_t^*] - (1 - \mu)C_t^*$$

$$(3.9) \quad S_t^* = (1 - \nu)N_t^* + \nu\tau_t N_t^*$$

$$(3.10) \quad I_t^* = q[(1 - \theta)N_t^* + \theta\tau_t N_t^*],$$

respectively, from (3.1)–(3.3). Using (3.8), one can eliminate τ_t from (3.9)–(3.10). This gives

$$(3.11) \quad S_t^* = [1 - \nu(1 - \sigma)]N_t^* - \nu[1 - \mu(1 - \sigma)]C_t^*$$

$$(3.12) \quad I_t^* = q \left([1 - \theta(1 - \sigma)]N_t^* - \theta[1 - \mu(1 - \sigma)]C_t^* \right),$$

respectively, from (3.9) and (3.10).

To summarize briefly, I have introduced the three assumptions (3.1)–(3.3) and derived several results. In particular, equations (3.8), (3.11), and (3.12) express τ_t , S_t^* , and I_t^* , respectively, in terms of N_t^* and C_t^* . These three equations, together with moment equations derived earlier, provide the basic components for a variety of possible fishery models.

3B. A Simple Composite Model

The first question to ask in constructing any model is: what data are available? Data complexity governs model complexity, and, in the present context, the simplest model is based on the availability of the following times series:

$$(3.13) \quad I_t^*, C_t^*, X_t.$$

For example, I_t^* and C_t^* could represent catch per unit effort and catch, respectively, where the mean fish weight X_t is also presumed known from historical catch samples. In cases where the time series X_t is not known, it may be adequate to make the assumption (2.23) that $X_t = X$, where X is a typical fish weight determined from practical experience with the fishery. In this sense, the constant X could even be treated as a parameter, and the model could be tested for sensitivity to the choice of X . Essentially, then, the data (3.13) are equivalent to traditional catch and effort data. Other interpretations are possible, however. For example, I_t^* might be a spawn index used as an indicator of adult biomass.

Table 2 presents a composite model for the data (3.13). The model's five equations are based on equations from this paper, as listed in Table 3. For example, [A2] and [A5] come from (3.11) and (3.12), respectively, that is, from the timing as-

TABLE 3. Text source(s), input, and output for each model equation in Table 2. The absence of a subscript on an input or output variable indicates a time prior to $t + 1$.

Model	Text source(s)	Input	Output
[A1]	(3.12)	I^*, C^*	$\rightarrow N^*$
[A2]	(3.11)	C^*, N^*	$\rightarrow S^*$
[A3]	(1.26)	S^*	$\rightarrow R_{t+1}^*$
[A4]	(2.18), (3.8)	X, C^*, N^*, R_{t+1}^*	$\rightarrow N_{t+1}^*$
[A5]	(3.12)	N_{t+1}^*, C_{t+1}^*	$\rightarrow I_{t+1}^*$

sumptions related to spawning and indexing. Similarly, [A1] comes from (3.12), where that equation is solved for N_t^* . [A3] is the recruitment hypothesis (1.26). The main theoretical result used in Table 2 is the first-order moment equation (2.18). This, together with the survival equation (3.8), leads to the key equation [A4].

Equations [A1]–[A5] are designed to predict I_{t+1}^* from C_{t+1}^* and data (3.13) at times prior to $t + 1$. Table 3 outlines the basis for this prediction by showing the input and output for each equation. Explicitly, the calculation would proceed as follows.

Step 1: Use [A1] and [A2] sequentially to compute S^* at times $t + 1 - K, t + 1 - (K - 1), \dots, t + 1 - k$.

Step 2: Use the results from step 1 in [A3] to compute R_{t+1}^* .

Step 3: Compute N_t^* from [A1]. Use this result and the value of R_{t+1}^* from step 2 to calculate N_{t+1}^* from [A4].

Step 4: Finally, substitute the result from step 3 into [A5] to predict I_{t+1}^* .

In biological terms, steps 1 and 2 predict the recruitment in year $t + 1$ from past population sizes. Step 3 calculates the biomass in year $t + 1$ as the predicted recruitment plus the surviving biomass from year t , where the latter is adjusted for growth by the factor X_t'/X_t . Finally, step 4 relates the biomass in year $t + 1$ to the index value, and thus gives the desired prediction for I_{t+1}^* .

The model in Table 2 involves the parameters

$$(3.14) \quad \mu, \nu, \theta, W, \rho, q, \sigma, G, H, \gamma, \delta, \pi_k, \dots, \pi_K.$$

The first three of these (μ, ν, θ) are timing parameters, prescribed by the modeler. The growth parameters W and ρ are used only to calculate X_t' in [A4], and these may be known from auxiliary growth data. Furthermore, if the assumption

(2.23) applies, then only the ratio X'/X enters the model, and this may be available from sources external to the model data. The recruitment parameters G , H , γ , and δ are used in [A3] if, say, the recruitment function (1.31) is adopted. These would usually be restricted in some way; for example, the choices $\gamma = 1$ and $\delta = 0$ correspond to the Schaefer model. Finally, the fractions π_a ($a = k, \dots, K$) are constrained by (1.27b); consequently, π_K , say, can be determined from the other π 's. In a typical case, then, the unknown parameters (3.14) would constitute a much shorter list, such as

$$(3.15) \quad q, \sigma, G, H, \pi_k, \dots, \pi_{K-1}.$$

Even this list could be further reduced by assuming that the π 's are restricted. For example, if the π 's are presumed equal, then

$$\pi_a = 1/(K - k + 1);$$

that is, each π_a is determined, and only four parameters (q, σ, G, H) remain unknown.

3C. A More Complex Model

The model in Table 2 includes only rudimentary size data, the average weight X_t for each year t . It is even possible to bypass this requirement through the simplifying assumption (2.23) that $X_t = X$. A more complex and informative model can be tailored to a richer data set consisting of the time series

$$(3.16) \quad I_t^*, C_t^*, X_t, Y_t, Z_t$$

together with higher moment data

$$(3.17) \quad X_t^{(n)}, Y_t^{(n)}, Z_t^{(n)}$$

for $n \geq 2$. As described in connection with (2.10a)–(2.10b), the size data in (3.16)–(3.17) can be compiled from annual fish samples taken from the catch. This involves dividing each sample into two weight intervals, $[V, V')$ and $[V', V_\infty)$; consequently, both V and V' must be known in advance. Typically, V would be a size adequate to indicate full gear selectivity. Fish smaller than V might even be eliminated from the catch, as indicated in the discussion following the definition (1.21). Once V is determined, V' can be computed directly from the growth law (1.3), based on prior knowledge of W and ρ . In summary, the data (3.16)–(3.17) can be compiled from historical samples, provided that values of

$$(3.18) \quad V, W, \rho$$

are known before compilation begins.

The estimated quantities (3.18) can, however, be checked. Equations (B1) and (B2) in Table 1 suggest that a regression of Z_{t+1} on X_t should have slope ρ and intercept W and that a regression, constrained through the origin, of $Z_{t+1}^{(n)}$ on $X_{t+1}^{(n)}$ should have slope ρ^n . Therefore, preliminary analysis of the data (3.16)–(3.17) should involve the scatter plots

$$A: Z_{t+1} \text{ vs. } X_t$$

$$B: Z_{t+1}^{(n)} \text{ vs. } X_{t+1}^{(n)} \text{ for, say, } n = 2 \text{ and } n = 3.$$

All plots should indicate a linear trend in the data, and the two plots B should suggest lines through the origin. Furthermore, using the prior values (3.18) for W and ρ , the line

$$Z = W + \rho X$$

should be drawn on plot A and the line

$$Z^{(n)} = \rho^n X^{(n)}$$

should be drawn on each plot B ($n = 2, 3$). If these lines do not appear to pass reasonably through the data, then it may be necessary to reestimate the values (3.18), recompile the data (3.16)–(3.17), and repeat the scatter plots A and B. When the parameters W and ρ are very poorly known, this entire procedure might be formalized numerically to give an algorithm for parameter estimation.

As explained at the end of Section 2, the higher moment data (3.17) are useful only to check or improve the estimate for ρ , and the data (3.16) are sufficient for a detailed parametric model. To build such a model, first define

$$(3.19) \quad \omega_t = R_t^*/N_t^*,$$

the fraction of total biomass in year t due to newly recruited fish. Since $N_t = R_t + P_t$, it follows from definitions (1.21)–(1.23) for the average weights X_t , Y_t , and Z_t that two equivalent expressions for the population N_t are

$$(3.20) \quad X_t^{-1}N_t^* = \omega_t Y_t^{-1}N_t^* + (1 - \omega_t)Z_t^{-1}N_t^*.$$

Solving for ω_t in (3.20) gives

$$(3.21) \quad \omega_t = \frac{Y_t Z_t - X_t}{X_t Z_t - Y_t}.$$

Thus, if the data (3.16) are known, then the time series ω_t is available. Incidentally, notice that

$$(3.22) \quad Y_t < X_t < Z_t,$$

since (1) newly recruited fish are smaller than previously exploited fish and (2) the population average lies between the averages for these two extreme populations. The inequalities (3.22) can be used in (3.21) to prove that $0 < \omega_t < 1$.

Table 4 presents a model for the data (3.16), where the text source for each model equation [B1]–[B5] is given in Table 5. The logic underlying Tables 4 and 5 is similar to that for Tables 3 and 4, except that the time series ω_t is now available. This makes it possible to obtain two predictions for I_{t+1}^* , based on the recruited biomass R_{t+1}^* and the previously exploited biomass P_{t+1}^* , respectively. As in the previous model, equations [B1]–[B3] predict R_{t+1}^* from earlier population biomasses. Similarly, [B4] predicts P_{t+1}^* from the survival and growth of biomass in year t . These two results give two independent predictions of N_{t+1}^* :

$$(3.23) \quad N_{t+1}^* = R_{t+1}^*/\omega_{t+1}$$

$$(3.24) \quad N_{t+1}^* = P_{t+1}^*/(1 - \omega_{t+1});$$

and these, in turn, give the two predictions [B5a] and [B5b] for I_{t+1}^* .

The essential feature of this model is that size-structure data make it possible to distinguish new recruits from previously exploited fish. This means that two biological processes can be distinguished in the data: recruitment [B3] from various earlier years and the combined effects [B4] of growth and survival from a previous year. Specifically, in [B4] the factor X'/X , accounts for growth and the expression in square brackets relates to survival. When using Table 4, the modeler can examine which prediction is better, that from [B5a] or [B5b]. This allows an objective assessment of which process, recruitment or combined survival/growth, is better defined by the data.

3D. Intuition

To be trustworthy, a model's results must appeal to common sense. An easy way to gain intuitive understanding is to exam-

TABLE 4. Composite model for the data I_t^* , C_t^* , X_t , Y_t , and Z_t . The time series ω_t is also presumed known, since it can be calculated from X_t , Y_t , and Z_t by (3.21).

$$\begin{aligned}
 \text{[B1]} \quad N_t^* &= \frac{I_t^* + q\theta[1 - \mu(1 - \sigma)]C_t^*}{q[1 - \theta(1 - \sigma)]} \\
 \text{[B2]} \quad S_t^* &= [1 - \nu(1 - \sigma)]N_t^* - \nu[1 - \mu(1 - \sigma)]C_t^* \\
 \text{[B3]} \quad R_{t+1}^* &= \sum_{a=k}^K \pi_a F(S_{t+1-a}^*) \\
 \text{[B4]} \quad P_{t+1}^* &= \frac{X_t'}{X_t} [\sigma(N_t^* - \mu C_t^*) - (1 - \mu)C_t^*] \\
 \text{[B5a]} \quad I_{t+1}^* &= q \left(\frac{1 - \theta(1 - \sigma)}{\omega_{t+1}} R_{t+1}^* - \theta[1 - \mu(1 - \sigma)]C_{t+1}^* \right) \\
 \text{[B5b]} \quad I_{t+1}^* &= q \left(\frac{1 - \theta(1 - \sigma)}{1 - \omega_{t+1}} P_{t+1}^* - \theta[1 - \mu(1 - \sigma)]C_{t+1}^* \right)
 \end{aligned}$$

TABLE 5. Text source(s), input, and output for each model equation in Table 4. The absence of a subscript on an input or output variable indicates a time prior to $t + 1$.

Model	Text source(s)	Input	Output
[B1]	(3.12)	I^*, C^*	$\rightarrow N^*$
[B2]	(3.11)	C^*, N^*	$\rightarrow S^*$
[B3]	(1.26)	S^*	$\rightarrow R_{t+1}^*$
[B4]	(2.18), (3.8)	X_t, C^*, N^*	$\rightarrow P_{t+1}^*$
[B5a]	(3.12), (3.23)	$C_{t+1}^*, R_{t+1}^*, \omega_{t+1}$	$\rightarrow I_{t+1}^*$
[B5b]	(3.12), (3.24)	$C_{t+1}^*, P_{t+1}^*, \omega_{t+1}$	$\rightarrow I_{t+1}^*$

ine special cases. The models in Tables 2 and 4 are particularly simple when the timing parameters are given by (3.4). In this case, the prediction [A5] for I_{t+1}^* reduces to the single formula

$$\begin{aligned}
 (3.25) \quad I_{t+1}^* &= q \sum_{a=k}^K \pi_a F \left[\frac{\sigma}{q} (I_{t+1-a}^* - qC_{t+1-a}^*) \right] \\
 &\quad + \sigma(X_t'/X_t)(I_t^* - qC_t^*).
 \end{aligned}$$

Similarly, assuming (3.4), the predictions [B5a] and [B5b] reduce to

$$(3.26) \quad I_{t+1}^* = \frac{q}{\omega_{t+1}} \sum_{a=k}^K \pi_a F \left[\frac{\sigma}{q} (I_{t+1-a}^* - qC_{t+1-a}^*) \right]$$

$$(3.27) \quad I_{t+1}^* = \sigma(X_t'/X_t)(I_t^* - qC_t^*)/(1 - \omega_{t+1}),$$

respectively, where ω_{t+1} is calculated from (3.21). Interpretations of these results are now familiar: (3.26) relates to recruitment, (3.27) to growth/survival, and (3.25) to both processes combined.

Equations (3.25) and (3.27) suggest that I_{t+1}^* should correlate positively with I_t^* and negatively with C_t^* . Biologically, a large stock in year t should survive to become a large stock in year $t + 1$, while a large catch in year t should reduce the stock in year $t + 1$. In real data sets, I_t^* and C_t^* are often positively correlated because fishermen tend to take a large catch in years with high catch per unit effort. Consequently, I_{t+1}^* may share a positive correlation with both I_t^* and C_t^* , suggesting a negative value for q in (3.25) or (3.27). This situation may easily occur if the catch represents a fairly minor component of the fish population. Since natural mortality is

highly variable, the catch in year t must have a significant negative effect on the available stock in year $t + 1$ if we are to distinguish fishing mortality from natural mortality. When the estimate for q turns out negative, it may be that the data show no evidence of stock reduction due to catch.

The above argument is incomplete, however, because the catch in year t influences the stock in two ways: through survival to year $t + 1$ and through recruitment to other future years. The model in Table 2 confounds these effects, while the more elaborate model in Table 4 has the potential to distinguish them. Since the effect of the catch is a fundamental issue in fishery management, there may be considerable value to the extra data needed to apply Table 4.

To gain even further insight into the models here, consider the case where (1) the fishery has little effect, that is, qC_t^* is small, (2) recruitment is constant ($F = G$), as in (1.33), and (3) the quantities X_t and ω_t are stable enough to be considered constants X and ω . Then, equations (3.25) and (3.27) reduce to

$$(3.28) \quad I_{t+1}^* = qG + \sigma(X'/X)I_t^*$$

$$(3.29) \quad I_{t+1}^* = \sigma(1 - \omega)^{-1}(X'/X)I_t^*,$$

respectively. These equations both suggest estimating the survival σ by regressing I_{t+1}^* on I_t^* . Essentially, (3.28) describes an autoregressive process, and the least squares slope estimator is known to be biased (Nahorski and Studzinski 1985; Walters 1985). By contrast, the regression (3.29) is *constrained through the origin*. Since I_t^* and I_{t+1}^* are approximately equal on average, (3.29) suggests that

$$(3.30) \quad \sigma(X'/X) = 1 - \omega.$$

The left side of (3.30) represents the usual survival and growth factors that govern the movement of the whole biomass into an exploited biomass one year later, and the right side is the fraction $1 - \omega$ of previously exploited biomass within the whole. This fraction reasonably relates directly to σ , as (3.30) suggests, because a population with high survival would typically have a large proportion of previously exploited fish. Thus, the time series ω_t is likely to be informative for the key parameter σ , and this suggests another potential value of the data needed to apply Table 4.

4. Generalized Cohort Analysis

The theory developed so far involves partitioning the population into two weight intervals, $[V, V')$ and $[V', V_\infty)$. These two groups of fish occur naturally in a model designed to capture the two processes of recruitment and survival. However, as discussed earlier in connection with the sequence of weights (1.10), the theory also suggests finer partitions of the population. The model can contemplate more processes as the number of groups increases. In particular, by increasing the number of distinct survival processes, the model can be designed to include size-dependent mortality.

The key idea for extending the theory here is to add weight intervals prior to $[V, V')$ and $[V', V_\infty)$. This requires a slight change of notation. Represent the weight of first recruitment by U , rather than V , and, by analogy with (1.10), define U_i recursively as follows:

$$(4.1a) \quad U_0 = U$$

$$(4.1b) \quad U_i = (U_{i-1})'$$

To include g weight intervals prior to $[V, V')$, define V by

$$(4.2) \quad V = U_g.$$

Then, the population can be divided into $g + 2$ groups of fish with weights in the intervals

$$(4.3a) \quad [U, U_1), \dots, [U_{g-1}, U_g), [V, V'), [V', V_\infty).$$

Surviving fish in group i grow into group $i + 1$ one year later, except for the final group of fish with weights above V' . These latter fish grow larger, of course, but remain in group $g + 2$. Incidentally, notice that if U_∞ is defined by letting i tend to ∞ in (4.1), then $U_\infty = V_\infty$, since $U_{i+g} = V_i$ (i.e. the two sequences agree beyond a certain point). Thus, the intervals (4.3a) can be written equivalently as

$$(4.3b) \quad [U, U_1), \dots, [U_{g-1}, U_g), [U_g, U_{g+1}), [U_{g+1}, U_{g+2})$$

where, for convenience, U_{g+2} is defined to be U_∞ .

Most of this paper has been devoted to the last two groups $g + 1$ and $g + 2$ in (4.3) because these have the common feature that both grow into group $g + 2$ one year later. The moment equations in Table 1 require the assumption that mortality is not size selective for fish in these groups (i.e. fish weighing V or more). However, each of the first g groups (4.3) grows exclusively into the next group one year later, and general moment equations for each group transition can be derived without assuming a common mortality for all groups. In short, the theory requires uniform mortality only for the last two groups, and this key feature distinguishes models like those of Deriso (1980) and Schnute (1985) from multigroup models, such as those used in cohort analysis.

To derive a generalized cohort model from the hypotheses here, I must extend the notation somewhat. As before, let $N(w, t)$ denote a population density, where the range of w is now $[U, U_\infty)$. The main hypothesis (1.20) is replaced by

$$(4.4) \quad N(w', t + 1) \frac{dw'}{dw} = \tau_i(w) N(w, t)$$

where $\tau_i(w)$ is the step function

$$(4.5) \quad \tau_i(w) = \begin{cases} \tau_{it} & \text{if } U_{i-1} \leq w < U_i \quad (i = 1, \dots, g) \\ \tau_i & \text{if } w \geq V. \end{cases}$$

Thus, survival τ_{it} from group i to group $i + 1$ during year t is indexed by both i and t , where $i = 1, \dots, g$; however, for fish with weight $w \geq V$, the survival is designated τ_i as before. Essentially, (4.5) allows a distinct survival for each group, except that the final two groups are presumed to share a common survival.

Define the population, biomass, and average weight of fish in group i as follows:

$$(4.6) \quad Q_{it} = \int_{U_{i-1}}^{U_i} N(w, t) dw$$

$$(4.7) \quad Q_{it}^* = \int_{U_{i-1}}^{U_i} w N(w, t) dw$$

$$(4.8) \quad Y_{it} = Q_{it}^* / Q_{it}.$$

Similarly, define the n th-order central moment and the corresponding average for fish in group i by

$$(4.9) \quad Q_{it}^{(n)} = \int_{U_{i-1}}^{U_i} (w - Y_{it})^n N(w, t) dw$$

$$(4.10) \quad Y_{it}^{(n)} = Q_{it}^{(n)} / Q_{it}.$$

Finally, define $N_i, N_i^*, X_i, X_i^{(n)}$ exactly as before, with reference to the weight interval $[V, V_\infty)$. Thus, these quantities apply only to the combination of groups $g + 1$ and $g + 2$ in (4.3), not to the whole population. In terms of the quantities just defined, the complete system of moment equations for all groups in the population turns out to be

$$(4.11) \quad Q_{i+1,t+1} = \tau_{it} Q_{it}$$

$$(4.12) \quad Y_{i+1,t+1} = W + \rho Y_{it}.$$

$$(4.13) \quad Y_{i+1,t+1}^{(n)} = \rho^n Y_{it}^{(n)}$$

for $i = 1, \dots, g$, and

$$(4.14) \quad Q_{g+2,t+1} = \tau_t N_t$$

$$(4.15) \quad Y_{g+2,t+1} = W + \rho X_t$$

$$(4.16) \quad Y_{g+2,t+1}^{(n)} = \rho^n X_t^{(n)}.$$

To understand this system of equations, notice first that the three equations (4.14)–(4.16) are identical to (B0)–(B2), respectively, in Table 1 with slightly altered notation. For example, $Y_{g+2,t+1}$ is the same as Z_{t+1} ; both correspond to the average weight of the population in the weight interval $[V', V_\infty)$. Thus, the three equations (4.14)–(4.16) have already been proved. The proofs of (4.11)–(4.13) are almost identical, except that the ranges of integration must be changed in steps of the proof similar to (2.11)–(2.12) and (2.29)–(2.30). Conceptually, (4.11)–(4.13) describe the transition of moments from group i to group $i + 1$, just as (4.14)–(4.16) describe the transition from the combined groups $g + 1$ and $g + 2$ into group $g + 2$. The intuitive argument suggested by Fig. 1 still applies, except that the solid and broken curves in each panel must be confined to the appropriate weight ranges for groups i and $i + 1$, respectively.

A complete dynamic model from (4.11)–(4.16) requires only one additional assumption. Since the equations describe all possible transitions from one group to the next, it remains only to account for the population in the first group, that is, recruitment. The needed assumption, then, is already stated in

(1.26), provided that R_i and R_i^* are redefined in relation to the interval $[U, U']$, rather than $[V, V']$ as in (1.14)–(1.15). In current notation the average recruitment weight is Y_{it} , rather than Y_i as before.

Readers familiar with cohort analysis will recognize in (4.11) the key equation of classical theory. If i represented age, then (4.11) would state that surviving fish of age i in year t reach age $i + 1$ in year $t + 1$. Here, the idea is generalized to refer to groups of fish with weights in the intervals (4.3). Indeed, the theory here includes age structure as a special case, because if the growth law is $w' = 1 + w$ (i.e. $W = 1$ and $\rho = 1$ in (1.3)), then w can be considered a measure of age.

Equations (4.11)–(4.16) tie together much existing theory. First, (4.11) generalizes cohort analysis with size-dependent mortality. Second, as proved in Section 2C, equations (4.14)–(4.15), which are equivalent to $\langle B0 \rangle$ – $\langle B1 \rangle$ in Table 1, imply the models of Deriso (1980) and Schnute (1985). Finally, the higher moment equations (4.13) and (4.16) correspond, although somewhat imprecisely, to equations derived by Fournier and Doonan (1987).

A complete model with size-dependent mortality would require data compiled in a manner similar to (3.16)–(3.17), including data for each group of fish. The hypotheses (3.1)–(3.3) would need further elaboration to account for size-dependent mortality. For example, τ_i , σ , and q might all be allowed to vary among groups. These details are, however, primarily technical. The essential features of such a model are already evident in Table 4.

In applying any model, it is important to consider its limitations. As discussed at the start of Section 2, the model here is somewhat rigid because it assumes deterministic growth (1.3). Since growth is typically variable, group i does not always grow precisely into group $i + 1$ during one year. Growth variability in this context can be compared with errors in aging fish for an age-structured model. Both sources of variation lead to the problem of appropriate group definition. For example, in the size-structured model here, slow growth could be interpreted as high mortality; that is, if some fish in group i fail to grow into group $i + 1$ the next year, their absence from group $i + 1$ might seem to indicate mortality. The model's validity depends on the assumption that such errors tend to cancel statistically over a sufficiently long time series.

This paper has focussed primarily on theoretical linkages among historical models, based on underlying population size structure. To restrict the paper's scope, I have not discussed likelihood functions or estimation methods, obviously important topics for practical application. By putting the available methods into perspective, I hope to clarify their possibilities and limitations. Simple arguments, such as those in Sections 2D and 3D, can often be used to assess a model's potential for parameter estimation. In the end, an effective model should lead to a coherent explanation of the salient features of the data. This goal guides the search for mathematical simplicity. The moment equations derived here can provide not only analytical, but also conceptual, tools for rational stock assessment.

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Appendix A. Notation

This appendix describes and summarizes alphabetically (with Greek letters following Latin letters) all notation used in the paper. Equation numbers refer to places in the text where the symbol is defined or used. The paper involves two types of models, a two-group model with knife-edged selectivity in Sections 1–3 and a multigroup model with nonuniform selectivity in Section 4. I refer to these models (in this appendix only) as types I and II, respectively. Where necessary, the definitions below distinguish between model types.

- a subscript for age in an age-structured model; (1.1), (1.18)
- a_0 parameter in the von Bertalanffy growth model (1.1) corresponding to theoretical age at weight 0
- b parameter in the autoregressive time series model (2.25)
- c constant in connection with the discussion (2.25)–(2.26) of autoregressive models
- C_t number of fish caught during year t
- C_t^* biomass of fish caught during year t ; (3.8)

$C(w, t)$	density of fish caught during year t at weight w ; (3.1)	R_t	number of newly recruited fish at the start of year t ; these have weights in the interval $[V, V']$ for a type I model or $[U, U']$ for a type II model; (1.14)
F	instantaneous fishing mortality; (3.5)	R_t^*	biomass of newly recruited fish at the start of year t ; (1.15), (1.26)
$f(w)$	function related to the distribution of weights in the fish population; (1.25)	$R_t^{[n]}$	n th-order weight moment about the origin for newly recruited fish at the start of year t ; (2.2)
$F(S^*)$	function defining the total biomass recruited from a stock biomass S^* ; (1.26), (1.29)–(1.31)	$R_t^{(n)}$	n th-order central weight moment for newly recruited fish at the start of year t ; (2.5)
g	number of groups prior to the last two in a type II model; thus, the total number of groups is $g + 2$; (4.3)	S_t	reproductive stock population in year t
G	parameter in the recruitment function corresponding to the maximum possible recruitment; (1.31)–(1.32)	S_t^*	reproductive stock biomass in year t ; (1.26), (3.9)
H	parameter in the recruitment function corresponding to the stock biomass at maximum recruitment; (1.31)–(1.32)	$S(w, t)$	reproductive stock density at weight w in year t ; (3.2)
i	index for a sequence of weights U_i or V_i ; group number in a type II model, where group i corresponds to fish in the weight interval $[U_{i-1}, U_i]$; (1.10), (4.1)	t	index for year t in a model; (1.12)–(1.20)
I_t	population index in year t	u	typical fish weight; see the description of w, w', \bar{w}
I_t^*	biomass index in year t ; (3.10)	U	weight at which fish are first selected by the gear in a type II model
$I(w, t)$	density index in year t for the population at weight w ; (3.3)	U_i	one of a sequence of weights defined by (4.1); in a type II model, group i is associated with fish in the weight interval $[U_{i-1}, U_i]$; (4.3)
k	youngest possible age of recruitment; (1.26)	U_∞	limit of the sequence U_i as $i \rightarrow \infty$; the same as V_∞ in a type II model; also denoted U_{g+2} for convenience in (4.3b)
K	<i>first meaning</i> : a parameter in the von Bertalanffy growth model (1.1); <i>second meaning</i> : oldest possible age of recruitment; (1.26)	V	weight (1.6) at which fish are recruited to the fishery and selected by the gear in a type I model; the same as U_g in a type II model
M	<i>first meaning</i> : number of fish in a sample; (2.10a); <i>second meaning</i> : instantaneous natural mortality; (3.1)	V_i	one of a sequence of weights defined by (1.10); see also (1.11)
M_z	number of fish sampled with weight at least V' ; (2.10b)	V_∞	limit of the sequence V_i as $i \rightarrow \infty$; equal to $W/(1 - \rho)$ if $\rho < 1$ or ∞ if $\rho \geq 1$
n	superscript indicating the order of a moment; (2.1)–(2.6)	w	typical fish weight
$\binom{n}{i}$	binomial coefficient; (2.14)	w'	weight of a fish one year after its weight was w ; (1.3)
N_{at}	number of fish aged a at the start of year t in an age-structured model; (1.18)	\bar{w}	weight of a fish one year prior to having weight w ; (1.7)–(1.8)
N_t	number of fish with weight $w \geq V$ at the start of year t ; (1.12)	w_a	weight at age a ; (1.1)
N_t^*	biomass of fish with weight $w \geq V$ at the start of year t ; (1.13)	w_i, \bar{w}	weight of a single fish and average weight of all fish in a sample; (2.10a)
$N_t^{[n]}$	n th-order weight moment about the origin for fish with weight $w \geq V$ at the start of year t ; (2.1)	W	parameter in the growth model $w \rightarrow w'$; (1.3)–(1.4)
$N_t^{(n)}$	n th-order central weight moment for fish with weight $w \geq V$ at the start of year t ; (2.4)	W_∞	parameter in the von Bertalanffy growth model (1.1), corresponding to asymptotic fish weight
$N(w, t)$	density of fish with weight w at the start of year t ; (1.12)–(1.17), (1.19)–(1.20)	x_t	observation in the autoregressive process (2.25)
P_t	number of previously exploited fish with weight $w \geq V'$ at the start of year t ; (1.16)	X	possible constant value for X_t below; (2.23)
P_t^*	biomass of previously exploited fish with weight $w \geq V'$ at the start of year t ; (1.17)	X_t	average weight of fish in the fully recruited population with weight $w \geq V$ during year t ; (1.21)
$P_t^{[n]}$	n th-order weight moment about the origin for fish with weight $w \geq V'$ at the start of year t ; (2.3)	$X_t^{(n)}$	average value of the n th central weight moment for fish with weight $w \geq V$ during year t ; (2.7)
$P_t^{(n)}$	n th-order central weight moment for fish with weight $w \geq V'$ at the start of year t ; (2.6)	$\hat{X}_t^{(n)}$	sample estimate for $X_t^{(n)}$; (2.10a)
q	parameter, essentially a constant of proportionality, in the indexing equation (3.3)	Y_t	average weight of fish in the newly recruited population with weight in the interval $[V, V']$ during year t ; (1.22)
Q_{it}	number of fish in group i at the start of year t for a type II model; (4.6)	$Y_t^{(n)}$	average value of the n th central weight moment for fish with weight in the interval $[V, V']$ during year t ; (2.8)
Q_{it}^*	biomass of fish in group i at the start of year t for a type II model; (4.7)	Y_{it}	average weight of fish in group i at the start of year t for a type II model; (4.8)
$Q_{it}^{(n)}$	n th-order central weight moment in group i at the start of year t for a type II model; (4.9)	$Y_{it}^{(n)}$	average n th-order central weight moment in group i at the start of year t for a type II model; (4.10)
		z_i, \bar{z}	see w_i, \bar{w} above; (2.10b)
		Z_t	average weight of fish in the previously exploited population with weight $w \geq V'$ during year t ; (1.23)
		$Z_t^{(n)}$	average value of the n th central weight moment for fish with weight $w \geq V'$ during year t ; (2.9)
		$\hat{Z}_t^{(n)}$	sample estimate for $Z_t^{(n)}$; (2.10b)

α, β, γ	parameters in the recruitment function (1.29)
δ	recruitment parameter included to remove the requirement that $F(0) = 0$; extrapolated stock at zero recruitment; (1.30)–(1.31)
θ	fraction of total mortality that occurs prior to indexing the fish population; (3.3), (3.10)
μ	fraction of the catch removed prior to natural mortality; (3.1), (3.8)
ν	fraction of total mortality that occurs prior to spawning; (3.2), (3.9)
π_a	fraction of total recruitment from a single brood year that is newly recruited at age a , where new recruits have weights in the interval $[V, V']$; (1.26)–(1.27)
ρ	parameter in the growth model $w \rightarrow w'$; (1.3)–(1.4)
σ	fraction of the fish population that survives mortality by natural causes; (3.1), (3.8)
τ_{it}	in a type II model, fraction of the population in group i that survives all mortality (fishing and natural) during year t ; (4.5), (4.11)
τ_t	fraction of the population that survives all mortality (fishing and natural) during year t ; (1.19)–(1.20), (3.1), (3.8); in a type II model, τ_t applies only to the population in the weight interval $[V, V_\infty]$; (4.5), (4.14)
$\tau_t(w)$	total survival fraction in a type II model, for which mortality is size dependent; (4.5)
ω_t	fraction of the total biomass in year t due to newly recruited fish; (3.19)–(3.21)

Appendix B. Proofs of (3.5)–(3.6)

In this appendix only, let t be a continuous variable ranging from 0 to 1, where t denotes time during the course of one year. Let $A(t)$ and $B(t)$ represent the population and catch, respectively, at time t resulting from an initial population N at time 0. If F and M are the coefficients of concurrent fishing and natural mortality, respectively, then $A(t)$ and $B(t)$ are governed by the system of equations

$$(B.1a) \quad dA/dt = -(F + M)A$$

$$(B.1b) \quad dB/dt = FA$$

$$(B.1c) \quad A(0) = N$$

$$(B.1d) \quad B(0) = 0.$$

Solving the system (B.1) for $A(t)$ and $B(t)$ gives

$$(B.2) \quad A(t) = Ne^{-(F+M)t}$$

$$(B.3) \quad B(t) = \frac{FN}{F+M} [1 - e^{-(F+M)t}].$$

If (3.1) is integrated with respect to w from V to V_∞ , the result is

$$(B.4) \quad A(1) = \sigma[N - \mu B(1)] - (1 - \mu)B(1)$$

in the notation here, since N is the initial population, $A(1)$ is the surviving population τN , and $B(1)$ is the catch for one year. Substitute (B.2)–(B.3) with $t = 1$ into (B.4) and then solve the result for μ to complete the proof of (3.5). Also, notice from (B.2) that since $\tau = A(1)/N$,

$$(B.5) \quad \tau = e^{-F-M}.$$

To prove the approximate result (3.6), rewrite (3.5) as

$$(B.6) \quad \mu = \frac{1}{1 - e^{-M-F}} \left[1 - \frac{Me^{-M}}{F} \frac{1 - e^{-F}}{1 - e^{-M}} \right].$$

Schnute (1977, equation (37)) cited essentially the following approximation:

$$(B.7) \quad \frac{M}{F} \frac{1 - e^{-F}}{1 - e^{-M}} \cong e^{(M-F)/2}$$

when M and F are close. Taking account of (B.5), substitute (B.7) into (B.6) to obtain the approximate result

$$\begin{aligned} \mu &\cong \frac{1}{1 - \tau} [1 - e^{-(M+F)/2}] \\ &= \frac{1 - \sqrt{\tau}}{1 - \tau} \\ &= (1 + \sqrt{\tau})^{-1}. \end{aligned}$$

This proves (3.6).