

Recruitment stability and survival – simple size-specific theory with examples from the early life dynamics of marine fish

Jan E. Beyer

Danish Institute for Fisheries and Marine Research,
Charlottenlund Castle, DK-2920 Charlottenlund, Denmark

Abstract

Recruitment is treated here as the result of the development of a year-class through a series of particular stages. The basis of classical fish population dynamics is, therefore, presented in terms of age-specific and size-specific survival. The simple theory is extended to account for the fact that natural mortality exhibits a decreasing relationship with the size of the fish. With these ingredients, focus is placed on density-dependent growth and the relationship between classical recruitment curves and size-specific recruitment curves is clarified. The analysis draws upon a number of existing models and their modifications. Two concepts of critical points on the size-specific recruitment curve are introduced. Several examples are included to elucidate the dramatic effects of a consistent amount of food on the shape of the recruitment curve. The result of food and size specific recruitment is a stabilization of the recruitment curve against variations in the mortality rate at medium to high levels of initial numbers of first feeding larvae. It is, theoretically, possible that the year-class strength is already fixed during the first months of active life during which the individual fish larvae gain a factor of 100 in weight and are completely dependent on the production of copepod nauplii as food. Good year-classes can be explained by a combination of high food availability and low mortality in the present theory.

The focal point of the paper is ten elements of simple but general theory. Each theory block is explained by a *Comment* and an associated *Example* on how to use the theory. The size-based theory makes recruitment studies part of overall fishery population dynamics. Several new mortality concepts are introduced with implications for e.g. length-based fish stock assessment.

Contents

Introduction	47
Age-specific survival	51
Size-specific survival	54
Density-dependent growth and classical recruitment curves	58
Food competition theory and recruitment stability	61
Conclusions	64
Acknowledgements	72
References	72
Notation	74

continued next page

Examples	78
Example 1: Mean age, longevity and age-specific survival	78
Example 2: Multiplicative aspects of survival to age	80
2.1. The power rule	81
Example 3: The Ricker type and the Beverton & Holt type of recruitment curves	82
Example 4: Mean size, Beverton & Holt theory and size-specific survival	83
4.1. Mean-size and B&H theory in length	84
4.2. B&H theory in weight	85
4.3. Mortality inversely proportional to length	86
4.4. B&H theory and early life dynamics	88
Example 5: Recruitment variations in size-specific theory	90
Example 6: The effects of changes in the rate of growth on survival	91
6.1. The effect of the power-rule for a change in growth	92
6.2. Survival to size with age-dependent mortality	93
6.3. Survival to age with size-dependent mortality	95
Example 7: Further considerations following Beverton & Holt (1957) on the Ricker & Foerster (1948) suggestion	97
7.1. First interpretation of B&H on R&F	97
7.2. The general case of several predators	101
7.3. Decreasing mortality with increasing size	104
7.4. Second interpretation of B&H on R&F	107
7.5. Conclusions and implications for improved models	110
Example 8: On the Shepherd & Cushing (1980) suggestion	112
8.1. Growth and recruitment in the S&C model	112
8.2. Generalized size-dependent vital rates	117
8.3. Generalized density-dependent vital rates	120
8.4. Discussion and conclusions	121
Example 9: Size-specific recruitment to meet a food-consumption requirement in the Shepherd & Cushing (1980) model	123
9.1. Biomass account	123
9.2. Critical recruitment points	126
9.3. The recruitment curve	128
9.4. Discussion and conclusions	131
Example 10: A simple allometric model of growth and mortality of larval fish	135
10.1. Model basis	135
10.2. Critical points and food criterion	138
10.3. Recruitment to meet a constant average rate of food consumption	142
10.4. Discussion and conclusions	144

Introduction

A stock and recruitment relationship is most often identified with either the Ricker (1954) type or the Beverton & Holt (1957) type of recruitment curve. The concept of recruitment is usually related to the abundance at some age of first capture obtained from a VPA. The variability in recruitment is considered the key issue in most recruitment research. The decimation of a year-class takes place at a constant rate of mortality.

These statements are but four examples of attitudes and beliefs or concepts and mathematical relationships that fisheries research gradually has accepted as parts of the traditional treatment of fish populations. This, of course, is not without reason. The classical concepts of age-specific year-class dynamics (B&H, *op. cit.*) are simple and useful in particular as a basis for fish stock assessment in temperate waters. But, it is possible that the traditional way of thinking may be less useful for sustained progress in recruitment research, and a major reason for the fact that fisheries research after one century still has not been able, for even the most intensively studied stocks worldwide, in just one case to predict year-class strength in one single year (Rothschild, 1986). Then, as the very first step, it is not only useful but necessary to stop for a moment and reconsider the classical concepts. With such a critical attitude in mind we return to the four initial statements concerning:

- (i) Classical recruitment curves
- (ii) The concept of recruitment
- (iii) Recruitment variability
- (iv) Exponential decay of numbers at age.

The Ricker curve and the B&H recruitment curve are rather widely used, partly because of theoretical considerations as to how compensatory mortality might work, but mainly, I fear, just because they are simple. These are the precise words of Ricker (1973, p. 337) and he doubts 'if ever data are abundant enough to provide a definite clue as to the expected shape' of the recruitment curve. This is but another way of expressing the need for theory development. We only obtain one recruitment domain per year. The term domain is used here to indicate that the concept of a recruitment point is an artefact (apart from extinction at the origin). Considerable uncertainty may be attached to total catch-at-age data (the input to VPA) for various reasons. Furthermore, the procedure of VPA in itself is not an estimation technique but rather, a technique for backcalculating numbers at age based on questionable mortality assumptions. This point will not be pursued further in the present paper but, taking all the uncertainties into account, the outcome of a VPA should really be represented by a stock and recruitment plot of patches and not points. Data from young fish (trawl or acoustic) surveys may, of course, reduce the uncertainty but whatever sensors the future fosters, the basic task in fisheries research and stock assessment will always be one of extracting information from imperfect data (compared, say, to various branches of physics) (see discussion by Rothschild, 1986). Theory on the underlying biological-physical processes governing recruitment is needed (Bakun, 1985) to help extracting

information from abundance data on e.g. the shape of the recruitment curve (Beyer, 1981).

There are really only two possibilities for dealing with the concept of a recruitment curve at present. If the purpose simply is to obtain an empirical relationship, one can use an arbitrary mathematical relationship that is capable of producing a sufficient spectrum of various shapes of recruitment curves. The cost involved, compared to the classical recruitment curves, is represented by an increase in the number of parameters to be estimated (i.e. at least a three parameter system is required). A sensible choice is suggested by Shepherd (1982). However, if the purpose is one of increasing our understanding, the recruitment curves must represent the logical consequences of hypotheses on the vital rates as stated above. This latter point in combination with Ricker's fear or his indirect advice not to exclude a recruitment curve because of a more complex mathematical relationship constitutes the first beginning point of the present study.

The second statement refers to the definition of the concept of recruitment. Recruitment has (for good reasons) been considered as an external factor or input to the traditional assessment models. Apparently (but very likely incorrectly) there has been no need for a more precise definition of the term. However, dealing with recruitment as part of fish population dynamics immediately puts focus on this need. Recruitment to the size at beginning metamorphosis, to arrival on the fishing ground, to the age of first capture, to the 50%-retention length, to the size of first maturity, to the age of massive maturation or whatever represents the outcome of a complex growing-up process and it is necessary to define precisely the beginning as well as the end of each of the stages this process is considered to comprise. In the present study, recruitment is regarded as the outcome of the development of a year-class through a particular stage. For example, this stage may be defined as a specific age interval or a specific size interval. It is of particular importance to note that recruitment represents the outcome of a conditional process, i.e. the number of survivors with a specific property (the end criterion) given an initial number of fish with properties according to the beginning criterion. The term 'recruitment' can never stand alone. It must be accompanied by a term specifying the particular stage we are dealing with. If not specified, the initial condition is tacitly assumed to be represented by the parental stock. This definition of recruitment in terms of stage-specific survivorships constitutes the second beginning point of the present study.

The third statement concerns recruitment variations as the focal point of recruitment research. It is clear that the unexpected – a sudden departure from the expected trend – has greatest economical impact. It is perhaps also clear that the effect of specific variations in year-class strengths on the stock and, hence, on the fishery increases as the mean age of the population decreases. However, looking back on past efforts in recruitment research, it is less clear that studies of the millions of events that affect recruitment variability will bring us much closer to an understanding of the causes of good and bad year-classes unless we receive some guidance as to what to look for and how to set priorities in this research. To clarify one aspect of this problem, Fig. 1 shows three types of recruitment patterns (for

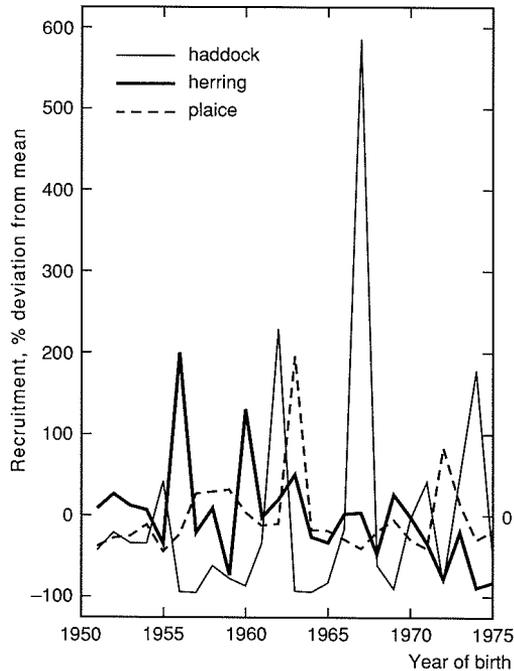


Fig. 1. Percentage deviation in recruitment at one year of age (for North Sea herring, haddock and plaice) from long-term means. Data from VPA, subsequently adjusted to one year of age using standard mortality assumptions according to Garrod (1982). Note that the size (length or weight) using this measure of recruitment may change considerably from one year to the next.

more, see Rothschild, 1986). The figure focuses on the most reliable information obtained from the VPAs, i.e. the relative changes in abundance.

Recruitment to the stock of North Sea plaice shows an impressive degree of stability. Apart from the good 1963 year-class, which is almost three times the mean (i.e. mean plus almost 200%), and the somewhat smaller 1972 year-class, the variations are so small that the question is if recruitment varies at all (Ursin, 1982). This recruitment pattern is typical for North Sea plaice and cod. Good year-classes are rare. The strongest year-classes are about 5 times the size of the weakest classes. North Sea herring shows a recruitment variation of about a factor of 10. However, recruitment to North Sea haddock varies by a factor of about 100.

Fig. 1 and similar examinations of other stocks (e.g. Ursin, 1982, Rothschild, 1986) show that recruitment usually involves year-to-year fluctuations of 25%-50% from the long-term mean. Once in a while, the unexpected occurs – good or bad year-classes. However, strong year-classes do not occur very often, say, on average for 25 stocks once every 11 years, see Rothschild (*op. cit.*). The general situation for an arbitrary stock thus seems to reflect a factor of 10-20 in recruitment variation. We do not know the causes of this variation. Some stocks, like North Sea plaice exhibit smaller variations. Relatively few stocks, such as North Sea haddock, vary by more than a factor of 50. The question is whether it should be surprising that recruitment varies so much? Suppose that an average year-class of say, North Sea cod represents a survival of one egg out of ten million for the development to the size of maturity (in order to account for the generation replacement). Then deviations of $\pm 10\%$ in the vital rates from average conditions imply that re-

recruitment should vary by a factor of almost 700! (see also Ex. 5 and Houde, 1987). Changes of $\pm 20\%$ in growth and mortality would imply that the recruitment to the adult stock should vary by a factor on the order of 700 000! Thus what immediately appears very variable (Fig. 1) in reality represents an amazing degree of stability. There is, thus, reason to believe that we may obtain some guidance as to how to explain the causes of recruitment variability by first trying to understand the normal situation, i.e. the disguised but fundamental stability of marine life and its causes (Ursin, 1982). This switch in attention from the apparent variability to the underlying stability represents the third beginning point of the present study.

The fourth statement concerns the convenient perception of the rate of natural mortality being constant in classical age-specific theory. The fact that predation mortality, the single most important known cause of natural mortality in juvenile life, bears a decreasing relationship to body-size (e.g. Ursin, 1967; Ware, 1975; Peterson & Wroblewski, 1984 and Anon. 1988) seems to enter the circles of stock assessment at a slow rate. Second, why do we only treat the development of a year-class as a function of age? The importance of body-size in describing ecosystem properties was recognised already in the 1920s (Platt, 1985). Haldane (1928) considered the size of an organism as the single most significant attribute. Replacing chronological age with a measure of physiological age such as body length or body weight represents an interesting alternative to classical fish population dynamics. In view of the importance of sizes for understanding the predation process (e.g. Andersen & Ursin, 1977; Beyer, 1981) and in general for the vital rates (see reviews by Werner & Gilliam, 1984 and Anderson, 1988), it is likely that a switch from a description in chronological age to physiological age (e.g. length-based theory) also will be useful for the integration of recruitment studies with overall population dynamics and fish stock assessment.

These critical comments (related to the initial four statements) immediately raise a number of questions to basic theory: Everybody knows the exponential decay of numbers with age because it is part of basic training in fish population dynamics. But what is the equivalent relationship for numbers at length? Why is this not part of basic training? How do these relationships change when the mortality rate is, say, inversely proportional to length? What are the implications for length-based fish stock assessment? In more generalized terms, what is the major difference between age-specific and size-specific survival? Which types of multiplicative rules can be applied in size-based theory? For example, when is a change in the rate of growth going to affect the rate of mortality? What is the connection between the classical recruitment curves and density-dependent growth? What is the principal difference between the shapes of age- and size-specific recruitment curves? Does density-dependent growth stabilize recruitment against fluctuations in the rate of mortality? How can the relationship of density-dependent growth be derived from food competition? Does the shape of the recruitment curve and its stability depend on the available amount of food for the stage-specific development of the year-class? Can recruitment really be stabilized within the first couple of months? The purpose of this study is to provide a simple theoretical basis for answering such questions.

Comment

In an attempt to enhance readability and to focus on basic principles, this paper is built up in ten small theoretical blocks with a minimum of mathematics. Although the entire paper deals only with the most simple classical theory (considering the year-class to comprise identical fish) the interpretation or the logical consequences of the theory are not always that simple. These matters are thoroughly explained in *Comments 1 to 10* in the text and in *Examples 1 to 10* collected at the end of the paper. A list of notation is also included. Each *Comment* refers to the particular theory block with which it is placed and also to the *Example* with the same number. The idea is that a *Comment* contains remarks on general principles and also, to a certain degree, the conclusion from the more thorough examinations in the associated *Example*. The first three blocks/comments/examples deal with age-specific theory and the next series of three provides the basis of size-specific theory. *Examples 7 to 10* deal with density-dependent growth and the effect of food competition. These *Examples* are more comprehensive and, therefore, set up as individual papers each containing an introduction and a conclusion. *Examples* are crossed referenced but self-contained in the sense that they can be read independently of each other (with few references to the main text). It should, thus, be possible to read the paper in different ways. The cost of this procedure is, of course, a certain amount of overlap but, perhaps, it is useful that certain points are explained in different ways since we are trying to deal with a synthesis of some basic principles in recruitment related fish population dynamics.

The purpose of this paper is not to consider species specific recruitment dynamics or assessment but rather to present some elements of size-based theory which may be useful in such species specific investigations.

Age-specific survival

We are considering the decimation of a year-class during a period of time, $\tau = t_1 - t_0$, starting with N_0 fish of age t_0 . Let $M(t)$ denote the instantaneous rate of mortality at age t , i.e. the decay in numbers $N(t)$ is governed by

$$\frac{dN(t)}{dt} = -M(t)N(t) \quad (1)$$

or, by the survivorship

$$S(t_1, t_0) = \frac{N(t_1)}{N(t_0)} = \exp \left\{ - \int_{t_0}^{t_1} M(x) dx \right\} \quad (2)$$

Multiplying the start number by this age-specific survival gives N_1 , the number of fish alive at age t_1 , i.e.

$$N_1 = N_0 S \quad (3)$$

This constitutes the fundamental basis of traditional fish population dynamics. The year-class is considered to be comprised of identical fish and the entire question of survival and recruitment becomes one of specifying the fishes' mortality rate and, in particular, how mortality changes with time or age.

Comment 1

It is mathematically convenient to operate with $M(t)$, the rate of mortality at age t . However, as an instantaneous rate $M(t)$ is a non-observable quantity which can only be measured and understood in terms of its cumulative effect across a smaller (dt) or larger interval of time, i.e. when integrated into a cumulative mortality. In this deterministic description, the significance of a low or a high value of $M(t)$ is most easily interpreted by considering situations in which the rate of mortality is assumed to attain low or high values for certain periods of time. Suppose the cohort is exposed to M in τ_0 units of time and put $M\tau_0 = -\ln S_0$. The survivorship $S_0 = 1/e = 0.368$ is achieved with a cumulative mortality of one, i.e. $M\tau_0 = 1$ or $\tau_0 = 1/M$. For example, $M = 0.1 \text{ yr}^{-1}$ means that 36.8% of the population would still be alive if this rate of mortality had been operating for 10 yrs. If $M = 0.1 \text{ d}^{-1}$ (or 36.5 yr^{-1}) then 36.8% of the fish larvae would survive ten days. In this situation, we often (incorrectly) say that the mortality rate is 10% per day. However, the exact daily mortality factor is one minus the survivorship on a daily basis, i.e. $1 - \exp(-0.1)$ or 9.52%.

Fish stock assessment is usually based on an assumption of a constant and low rate of natural mortality for all age groups. In lack of anything better, it is simply Beverton & Holt's (1957) estimation of $M = 0.1 \text{ yr}^{-1}$ for adult plaice and $M = 0.2 \text{ yr}^{-1}$ for adult haddock in the North Sea that has been adopted in the VPAs. This mortality figure for plaice was partly based on an estimate of the survival from age 5 yrs in pre-war samples to age 13 yrs in post-war samples (of very few old fish). There was no direct estimation of M available for the younger age groups. However, the survivorship to maturity must be about $10^{-6} = \exp(-13.8)$. To explain such a cumulative mortality of 13.8 to age, say 3-4 yrs, $M(t)$ must increase considerably from the older to the younger age groups. For a simple treatment of this situation, suppose the rate of natural mortality is inversely proportional to age, $M(t) = a/t$. Then, from Eq.(2), the survivorship from age t_0 to t_1 becomes $(t_1/t_0)^{-a}$. The survivorship for an increase in age by a factor of ten ($t_1 = 10t_0$) is simply 10^{-a} . Thus, the survivorship from the onset of feeding at age, say 2 weeks to 20 weeks of age (4.6 months or 0.38 year) is 10^{-a} and equals the survivorship from 0.38 yr to 3.8 yrs of age. If $a = 3$, then the survivorship from the onset of feeding to maturation is about 10^{-6} . The mortality at first feeding in this description is 78 yr^{-1} (0.21 d^{-1}) but diminishes by one half in the course of two weeks. Perhaps such a high larval mortality may be considered sensible since we have not accounted for mortality during the egg and yolk-sac stages. However, the mortality at three years of age is 1 yr^{-1} or five times the standard value of 0.2. Such simple considerations indicate that juvenile mortalities are grossly underestimated in traditional fish stock assessment.

The multiplicative nature of the survivorship in Eq. (2) has some important consequences that are valid independently of the actual course of mortality during the time-period considered.

If the time-period considered is divided into consecutive sub-periods, then the total survivorship equals the product of the individual survivorships.

If the mortality rate is changed by a factor which is constant over the time-period considered, then the new survivorship becomes the old one to the power of this constant factor. For example, a doubling in mortality results in the square of the initial survivorship. Independent causes of mortality give rise to multiplicative survivorships, i.e. additive mortalities $M_1 + M_2 + M_3 \dots = M$ produce the survivorship $S_1 S_2 S_3 \dots = S$. In general, we can say that a linear combination of mortalities, $bM_1 + cM_2$ produces a power factorial survivorship, $S_1^b S_2^c$.

Comment 2

The multiplicative rules enable us to calculate the relative effect on recruitment of relative changes in cumulative mortality without knowing the exact course of mortality. Suppose S denotes the survivorship under average conditions during some part of pre-recruit life. If mortality in one year happens to be, say, 10% higher than usual for this phase then the recruitment to any later age will change by a factor of $S^{0.10}$. Hence, the ratio of year-class strength will vary by a factor of $S^{-0.20}$ due to $\pm 10\%$ changes in mortality. If the survivorship in the larval stage is 0.01, then year-to-year variations in larval mortality of $\pm 10\%$ will cause a good year-class to be 2.5 times stronger than a bad year-class. If these changes in mortality occur during a juvenile phase which is characterized by $S = 0.0001$, then recruitment will vary by a factor of 6.3 (or 2.5^2). Changes in mortality of $\pm 10\%$ during all juvenile stages (i.e. $S \approx 10^{-6}$) will result in a factor 16 (or 2.5^3) variation in the recruitment to the adult stock. This variation will be reduced to a factor of 4 (or $16^{1/2}$) if mortality only changes by $\pm 5\%$.

In classical stock and recruitment models, the integral period of time in Eq. (2) denotes the entire pre-recruit period, i.e. we are considering the decimation of the year-class from when egg-production takes place, $N_0 = E$ eggs at age t_0 , until R fish at age t_r are recruited to the fishery. The choice of age zero is arbitrary. Usually, hatching is considered age zero in which case t_0 is negative. Recruitment is obtained as egg-production multiplied by the age-specific survivorship for the pre-recruit period,

$$R = E S(t_r, t_0) \tag{4}$$

The survivorship must be derived from Eq. (1) based on a mortality theory yielding $M(t)$. This theory must involve some sort of density-dependent regulation of the cumulative mortality in order to account for the observed stability of recruitment.

Comment 3

The traditional recruitment curves are derived from basic principles. If $M(t)$ is a linear function of E , then by applying the multiplicative rules we may write Eq.(4) using the Ricker form,

$$R = E S_1 S_2^E = S_1 E \exp(-aE), \quad a = -\ln S_2; \quad M(t) = M_1(t) + E M_2(t)$$

where S_i is the survivorship through (t_0, t_r) when the mortality coefficient, $M_i(t)$ is operating as the only source of mortality. This is the generalization of the Ricker (1954) model in the sense that a Ricker curve is obtained for age-specific recruitment for whatever continuous functions, $M_1(t)$ and $M_2(t)$, we may propose.

The mortality coefficient, $M_2(t)$, is explained by cannibalism in the Ricker formulation. Beverton & Holt (1957) replaced E by $N(t)$ so that the rate of natural mortality is, instead, a linear function of the size of the year-class at the same instant in time. In this formulation, B&H used the mortality coefficient, $M_2(t)$, to describe the effect of severe competition among young fish for food. Note that the survivorship is not given by Eq.(2) because M now is a function of $N(t)$ and not just an explicit function of age, t . It is necessary to go back to the starting point and obtain numbers at age by solving Eq.(1).

The Ricker and the Beverton & Holt recruitment curves will reappear in equivalent cases of the size-specific theory. We shall use N_0 rather than E to designate the number

at t_0 , the beginning of the age-interval. This is because we do not consider the process of spawning or the number of eggs as creating the initial condition in the present recruitment study. The beginning is simply described by N_0 fish of weight w_0 at age t_0 and the theory does not depend on whether this instant in time coincides with the onset of feeding or some later development stage. Of course, the interpretation of the theory may depend on this choice. Situations of the Ricker type in which the vital rates depend on the initial number are referred to as start-density dependent in contrast with density-dependent processes formed by the B&H type of situations (cf. the discrimination made by Harris (1975)).

Instead of relating the effect of food competition to a density-dependent rate of mortality (which in the first approximation produces the B&H type of recruitment curve), it seems sensible and in agreement with Beverton and Holt's (1957) belief to derive the effect on the survival directly from the changes in growth rates that must result from severe competition for food. This is in accordance with the Ricker & Foerster (1948) suggestion that when the larval density is low, individuals may grow more rapidly through a critical period and, thus, suffer smaller losses from predation than when the density is high. To describe directly such effects of changes in the growth rate on the cumulative mortality we need to express the survival as a function of both growth and mortality.

Size-specific survival

We are considering the decimation of a year-class during the period of time (τ_1) in which the fish increases its body-weight from w_0 to w_1 . Let $\mu(w)$ denote the instantaneous rate of mortality at size w , i.e.

$$\frac{dN(w)}{dt} = -\mu(w)N(w); \quad w = f(t) \quad (5)$$

where $N(w)$ is the number of fish in the year-class of size w at time t . The year-class is considered to comprise a population of identical fish starting with N_0 fish of size w_0 at time t_0 . It is the growth rate $g(w)$ i.e.

$$\frac{dw}{dt} = g(w) \quad \text{and} \quad w_0 = f(t_0) \quad (6)$$

which, in this simple theory, determines a one-to-one relationship between size and age and enable us to express the mortality rate as a function of weight, $\mu(w)$, instead of age, $M(t)$, or *vice versa*. Dividing Eq.(5) by Eq.(6) yields

$$\frac{dN(w)}{dw} = -\frac{\mu(w)}{g(w)} N(w) \quad (7)$$

or, the weight-specific survivorship (van Sickle, 1977),

$$l(w_1, w_0) = \frac{N(w_1)}{N(w_0)} = \exp \left\{ - \int_{w_0}^{w_1} \frac{\mu(x)}{g(x)} dx \right\} \quad (8)$$

Multiplying the initial number of fish of size w_0 by this survival gives the number of fish still alive at size w_1 :

$$N_1 = N_0 l(w_1, w_0) \quad (9)$$

The associated period of time, τ_1 , required to grow from w_0 to w_1 , is obtained by integrating the reciprocal of the growth rate:

$$\tau(w_1, w_0) = \int_{w_0}^{w_1} \frac{dx}{g(x)} = t_1 - t_0 = \tau_1 \quad (10)$$

Comment 4

Characteristics of the body-size distribution may be derived from the survivorship in Eq.(8). For example, the mean size-at-death is simply obtained by integrating the survivorship. The formulas above are valid whether we use weight or, say, length to specify size. The essential point is that the 'new' rate-variable, g , denotes the rate of increase in the physiological attribute of the fish that has been chosen in the description of the year-class.

Notice that $N(w)$ designates numbers-at-weight. The number at age t is, therefore, $N(f(t))$ which (incorrectly from a mathematical point of view) also is called $N(t)$ in the previous section. A mathematically correct notation would be, for example, $N_{\text{age}}(t)$, $N_{\text{weight}}(w)$ and $N_{\text{length}}(L)$, respectively for numbers at age, weight and length. With this in mind the more simple N -notation is maintained. It should not cause confusion because mortalities and survivorships are designated by different symbols at age and at size.

The important variable in determining the survival to a certain size w_1 is NOT the rate of mortality BUT μ/g , the rate-ratio of mortality to growth. If this ratio is constant then we obtain an exponential size-specific survivorship,

$$l(w_1, w_0) = \exp(-(\mu/g)(w_1 - w_0)); \quad \mu/g \text{ constant}$$

Suppose the rates of mortality and growth decrease in exactly the same manner with increasing size, then μ/g , the constant of proportionality, determines the exponential decimation of numbers at size in the year-class. If μ and g are constants, then $(w_1 - w_0)/g$ is the time required to grow through the size interval. The dimension of μ/g is 1/SIZE.

We obtain the dimensionless rate-ratio, μ/G , by introducing the instantaneous rate of growth, $G(w) = g(w)/w$. If this instantaneous rate-ratio is constant, then Eq.(8) produces a power function,

$$l(w_1, w_0) = (w_1/w_0)^{-\mu/G}; \quad \mu/G \text{ constant.}$$

A special case arises if the ratio is one, $\mu = G$. Then the biomass of the year-class remains constant and the survivorship becomes simply w_0/w_1 . Suppose $w_1/w_0=100$. The survival in this situation is 1% if $\mu = G$ but increases to 1.6% if the rate of mortality is reduced by 10% to $\mu = 0.9G$ in which case the biomass increases by a factor of 1.6. If the rate of mortality is half the specific growth rate, $\mu = 1/2G$, then 10% of the fish are able to gain a factor of 100 in weight thereby increasing the biomass of the year-class by a factor of 10. Note, again, that it is the constant of proportionality, μ/G , which appears in the power of the survivorship equation. It is, thus, a delicate balance between high rates of growth and high rates of mortality that determines the increase of year-class biomass, in particular during the larval stage (Jones, 1973).

Maximum survival across a small size interval, dw , occurs at that size where $\mu(w)/g(w)$ attains its minimum value. In the simple Beverton & Holt (1957) theory with constant mortality, $\mu = M$, and the von Bertalanffy growth equation, $g(w) = Hw^{2/3} - kw$, $W_\infty = (H/k)^3$, this minimum is attained at $W_m = 8/27W_\infty$, the point of inflexion of the growth curve. The maximum biomass is achieved at $W_b = W_\infty/(1+M/k)^3$. If $M = 0.5k = 1.5K$, then the size at maximum biomass coincides with $0.296W_\infty$, the size at minimum

M/g . With a more realistic mortality model, $\mu(w) = M_\infty(W_\infty/w)^{1/3}$, taking into account that predation mortality decreases with increasing size, the minimum of μ/g is attained at $W_m = 27/64 W_\infty$. Maximum biomass occurs at $W_b = W_\infty(1 - M_\infty/k)^3$ which is identical to the former size if $M_\infty = 0.25k = 0.75K$. The rate of mortality at $W_m = W_b = 0.422 W_\infty$ for this situation is equal to K .

At first sight, the size-specific survivorship in Eq. (8) appears very much different from the age-specific survivorship in Eq. (2) but it is not! We are, in both cases, describing the fate of a cohort of fish under the same conditions. The survivorships simply express survival as a function of cumulative mortality:

$$\text{survivorship} = \exp(-\text{cumulative mortality})$$

where

$$\text{cumulative mortality} = \int_{t_0} M(t)dt = \int_{w_0} \frac{\mu(w)}{g(w)} dw$$

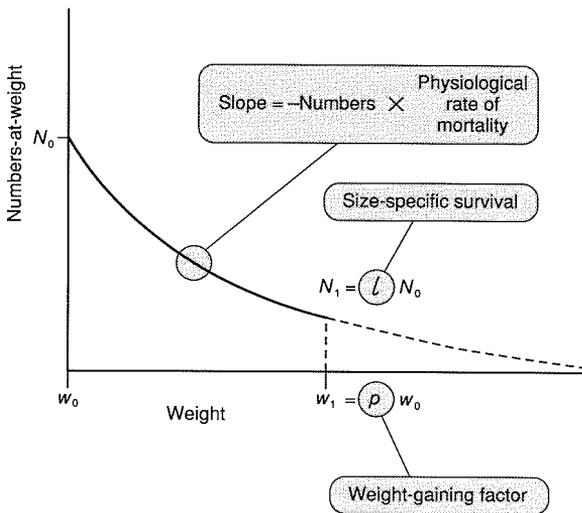


Fig. 2. Basic concepts in size-specific theory. Chronological age is replaced by a physiological age measured as body-size. The physiological rate of mortality equals the rate-ratio of mortality to growth. The weight-gaining factor, $p = w_1/w_0$, occurs in the applications as the most important factor in specifying the size-interval. Once p is specified and the physiological rate of mortality expressed as a function of size, then the survivorship (l) may be derived. The survivorship always refers to numbers. But since we consider numbers at size, a simple p -scaling of the graph gives biomass, i.e. $B_1 = B_0 lp$, or the ratio of biomass increase equals the survivorship multiplied with the weight-gaining factor.

The shift from a description in age to a description in size is here merely one of changing integral variable. Note that $1/g(w)$ is a measure of the time spent at size w and $\mu(w)/g(w)$, thus, represents the instantaneous ‘physiological rate’ of mortality at size w which also is expressed by Eq.(7) (see Fig. 2). The number-at-age, $N(t)$, calculated from the survivorship in Eq.(2), will be the same as the number-at-size, $N(w)$, obtained from Eq. (9) if w is the size at age t .

Comment 5

For most applications, we want to compute the recruitment to a certain age or the survival across a certain size interval and then age-specific and size-specific survival may respond differently to changes in the environment. For example, if special environmental conditions cause the growth rate at any age (size) to change by a constant factor b com-

pared to 'normal years' then recruitment to age, say, one year, will not change IF the rate of mortality is unchanged. However, the size-at-age will have changed according to the constant factor ($b < 1$ describing a growth reduction). The time required to grow through any dw has increased by a factor of $1/b$. Thus, the cumulative mortality to a certain size has increased by a factor of $1/b$ causing the survival to change by a power of $1/b$:

$$\begin{aligned} \text{survivorship}_* &= \exp(-\text{cumulative mortality}/b) \\ &= [\exp(-\text{cumulative mortality})]^{1/b} \\ &= (\text{survivorship})^{1/b} \end{aligned}$$

This is but another example of the multiplicative aspects of the survivorship. Suppose the rate of mortality in the same year also happens to change by a factor of c . The survivorship for this situation equals the normal survivorship (for $b = c = 1$) to the power of c/b . A change in the environmental conditions involving opposite changes in growth and mortality thus increases its effect on the survivorship. Annual changes in the vital rates of only a few per cent during early life (where the survivorship is small) can explain that recruitment to a certain size varies within 25-50% of the long-term mean!

The effect of simultaneous and independent changes in growth and mortality rates on stage duration and survival can be expressed as follows (Werner & Gilliam, 1984):

$$g_* = b g ; \quad b \text{ and } c \text{ constants}$$

$$\mu_* = c \mu ; \quad w_0 \leq w \leq w_1$$

produce

$$\begin{aligned} \tau_* &= \tau/b \\ l_* &= l^{c/b} \end{aligned} \tag{11}$$

It is a straightforward matter to apply these multiplicative rules to additive mortalities or situations that require a splitting up of the size interval.

Comment 6

The multiplicative rules with respect to the effects of changes in the rate of a density-independent mortality are generally valid for survivorships to specific size or age. In some situations, however, the multiplicative rule in Eq.(11) with respect to growth is NOT valid because the rate of mortality is affected by a change in the growth rate. The issue here is entirely one of how mortality depends on age and size.

Suppose the rate of mortality exhibits a decreasing relationship to age. In this situation, the survival to a specific age is not affected by a change in growth. A growth increase, however, implies that a specific size is attained at an earlier age causing the rate of mortality at size to increase as well. The size-specific survival will, therefore, not fully increase to 'the $1/b$ -power', i.e. $S_* = S$ and $l < l_* < l^{1/b}$; $b > 1$.

The size-specific survival will obey Eq.(11) if the rate of mortality depends only on size. In this situation, however, the age-specific survival also changes because mortality-at-age now depends on size-at-age. Exactly how S will change depends, of course, on the formulation of the rates of growth and mortality as functions of size. But compared to the $1/b$ -power rule for changes in size-specific survival or in recruitment-at-size (for constant initial number), the changes in recruitment-at-age are moderated, i.e. in the case of a growth increase ($b > 1$), recruitment increases according to $l_* = l^{1/b}$ and $S < S_* < S^{1/b}$

when the situation is one of decreasing mortality with increasing size. Assume that it happens occasionally that larger fish larvae are exposed to a higher mortality than the smaller larvae. In this situation of increasing mortality with increasing size, recruitment-at-size will increase as above due to a growth increase but recruitment-at-age will decrease, i.e., $l_* = l^{1/b} > l$ and $S_* < S$; $b > 1$. A growth reduction will cause recruitment-at-age to increase but recruitment-at-size to decrease, i.e., $l_* = l^{1/b} < l$ and $S_* > S$; $b < 1$!

We are now ready to consider the causes of changes in the rate of growth. Instead of describing a growth change by a constant factor b , we need to incorporate a description of how this factor depends on the number of fish and the amount of food available.

Density-dependent growth and classical recruitment curves

We are considering simple ways of quantifying the suggestion of Ricker & Foerster (1948) that density-dependent growth affects cumulative mortality and, hence, recruitment. Suppose N_0 fish of size w_0 compete for food until size w_1 is attained. The most simple treatment of the R&F idea is to express the rate of growth as a function of size multiplied by a function of N_0 , the initial number of fish in the cohort or the start-density. If A denotes a food-measure of the carrying capacity and

$$g(w, N_0) = g_0(w) / (1 + N_0 / A); \quad w_0 \leq w \leq w_1; \quad N_0 = N(w_0) \quad (12)$$

then growth takes place at the density-independent rate $g_0(w)$ if the start-density is low ($N_0 \ll A$), precisely half the g_0 -rate if $N_0 = A$ and, at a rate inversely proportional to N_0 , $Ag_0(w)/N_0$ at high start-densities ($N_0 \gg A$). Noting that the N_0 -term in Eq.(12) represents a growth reduction compared to density-independent growth (i.e. $b = 1/(1+N_0/A)$ in Eq.(11)), the survivorship across the size interval (w_0, w_1) as a function of N_0 follows directly from the multiplicative rule,

$$l_1 = l_0^{1+N_0/A} = a_1 \exp(-a_2 N_0); \quad a_1 = l_0, \quad a_2 = -A^{-1} \ln l_0 \quad (13)$$

where l_0 denotes the maximum survival in the case of density-independent growth, i.e. when growth and mortality are determined by $g_0(w)$ and $\mu_0(w)$, the size-specific vital rates. Hence, recruitment at size w_1 , $N_1 = N_0 l_1$ is described by the Ricker type of curve for any choice of the size-specific vital rates. If the rate of mortality is changed by a constant factor c , then the survival changes according to Eq.(11), i.e. the first Ricker coefficient is changed to a_1^c and the second to ca_2 . The survival to size is, therefore, very sensitive to fluctuations in A or μ . In other words, the type of start-density dependent growth in Eq.(12) does not stabilize recruitment against fluctuations in the vital rates.

Comment 7

It is not surprising that Eq.(12) leads to the Ricker type of recruitment curve. The survival depends only on the rate ratio, μ/g , and the start-density-dependent growth in Eq.(12) will therefore produce exactly the same effect as a start-density-dependent mortality, $\mu(w, N_0) = \mu_0(w)(1+N_0/A)$, as long as we are only concerned about recruitment at a specific size.

Recruitment at a specific age generally does not follow a Ricker type of curve. The shape of the age-specific recruitment curve depends on the age of recruitment and the size-specific vital rates. The curve may reach a local maximum and a local minimum but will, ultimately, approach an asymptote (in case of density-independent mortality). If the rate of mortality is constant, then recruitment will always increase in proportion to N_0 , whether or not the growth rate is density-dependent:

$$R = N(t_r) = N_0 S \quad ; \quad S = \exp(-M(t_r - t_0)) \quad ; \quad M \text{ constant}$$

Suppose the pre-recruit period consists of a period with high, size-dependent mortality, $M + \mu_0(w)$, and a subsequent period with low, approximately constant mortality, M . If the additional mortality, $\mu_0(w)$, operates in the size interval (w_0, w_1) in combination with the start-density-dependent growth described by Eq.(12), then it follows directly from the multiplicative rules that the recruitment above for constant M is reduced by the survivorship in Eq.(13), i.e.

$$R = N_0 S a_1 \exp(-a_2 N_0) \quad ; \quad \text{if } t_1(N_0) < t_r$$

where $t_1(N_0)$ is the age at size w_1 . This is the generalization of Beverton & Holt's (1957) quantification of the R&F suggestion. The size-specific recruitment curve is simply copied to age and for whatever continuous functions, $g_0(w)$ and $\mu_0(w)$, we propose, recruitment at age t_r is described by a Ricker curve if the rate of mortality becomes constant before this age is attained.

Alternatively, one may replace the initial number N_0 in Eq.(12) with $N(w)$, the number of live fish of size w (Shepherd & Cushing, 1980):

$$g(w, N) = g_0(w) / (1 + N(w)/A) \quad ; \quad w_0 \leq w \leq w_1 \tag{14}$$

As a consequence, the larvae start to grow at a rate determined by Eq.(12) and then gradually achieve a growth rate that approaches the density-independent level of $g_0(w)$ as the year-class diminishes. This leads to the Beverton & Holt (1957) type of recruitment curve,

$$l_1 = \frac{l_0}{1 + (1 - l_0) N_0/A} \quad ; \quad N_1 = N_0 l_1 \tag{15}$$

where l_0 denotes the maximum survival at low initial numbers ($N_0 \ll A$) determined by the size-specific vital rates. The survival is still sensitive to changes in A and μ but the effect is somewhat moderated compared to the power-rule in Eq.(11). If μ is changed by a constant factor, c , then it is only the maximum survival that will change to the c th power of its initial value. Hence, the new survivorship l_{1*} is obtained by Eq.(15) with l_0 replaced by l_0^c . In the case of a mortality reduction ($c < 1$), the survival thus increases but not quite to the c th power of its initial value (i.e. $l_{1*} < l_1^c$). The increase in survival that occurs as a direct consequence of the mortality reduction gives rise to a growth reduction (through density-dependent regulation of the growth rate) which partly counteracts the mortality reduction. This counteractive effect of mortality on growth is relatively weak in the present model and we may conclude that density-dependent growth as formulated by Eq.(14) does not stabilize recruitment against fluctuations in the vital rates (Shepherd & Cushing, 1980).

Comment 8

Shepherd & Cushing (1980) considered the special case of exponential growth, $g_0(w) = Hw$, and exponential decay of the cohort, $\mu_0(w) = M$. The result in Eq.(15), however, is valid for any continuous functions, $g_0(w)$ and $\mu_0(w)$, specifying density-independent growth and mortality as functions of size in the interval considered. The B&H type of curve for size-specific recruitment is simply always obtained if the rate-ratio of mortality to growth can be separated into a size-dependent factor and a linear density-dependent factor. For these reasons, Eq.(15) represents a generalization of the S&C model or simply, the size-version of the B&H recruitment curve.

Age-specific recruitment, in general, is not described by the B&H type of curve. The shape of the curve depends on the age of recruitment and on the size-specific vital rates. The actual shape of the curve is moderated compared to the case of start-density dependent growth because of the counteractive effect of mortality on growth. Note that the situation considered by B&H in their treatment of the R&F suggestion applies equally well to any case of density-dependent vital rates: The size-specific recruitment curve is copied to recruitment at a specific age as long as the larvae grow through the critical size range and reach a constant rate of mortality before or at this age of recruitment.

From a mass point of view there is a major difference between a situation of N_1 recruits at size w_1 and the situation of R recruits at age t_r . The biomass is merely a scaling of size-specific recruitment, $B_1 = N_1 w_1$, but the biomass at age-specific recruitment, $B(t_r) = R w(t_r)$, depends on the decreasing relationship between weight, $w(t_r)$, and N_0 , the initial number of fish. In the most simple case of a constant rate of mortality, the straight line of age-specific recruitment in the S&C model represents a complex curve for biomass. The shape of the biomass curve depends on the age of recruitment and may reach a local maximum followed by a local minimum prior to the asymptotic behaviour. The same type of biomass curve (with an even more pronounced max-min amplitude) is obtained in the equivalent case of start-density dependent growth.

The rates $g = g_0 / (1 + N/A)$ and $\mu = \mu_0$ produce the same size-specific survivorship as the rates $g = g_0$ and $\mu = (1 + N/A)\mu_0$ but, as already indicated, there is a major difference in the interpretation of the two situations. The latter does not reflect the R&F suggestion but rather the extreme case of larval death from starvation or indirectly from debility due to insufficient food. Other interpretations of density-dependent mortality such as predator switching are, of course, also possible but are not dealt with in the present study. The important point here is that a linear model can be interpreted as providing a first approximation to the description of density-dependent mortality irrespective of the underlying causes. This is not really the case with the models of density-dependent growth in Eqs.(12) and (14). The inverse linear relationship takes the form of a hyperbola which is difficult to interpret as a general first order approximation to some rationale of studying the effect of competition for food. These models (constructed to represent the growth counterpart to the classical mortality considerations of age-specific stock and recruitment) are, nevertheless, mathematically convenient and useful for gaining some insight into the effect of density-dependent growth.

Food competition theory and recruitment stability

In creating a rational framework for investigating the effects of competition for food on recruitment, the mechanism of density-dependent growth must be derived from basic principles with the cost of losing the mathematical tractability inherent in the traditional approaches here represented by Eqs (12) and (14). For a simple treatment of the R&F idea in this direction, suppose that the rate of growth is described by a function, $g(w, N, H(N_0))$, of weight, numbers-at-weight and of some parameter, which represents an unknown function of the initial number, N_0 . The mortality rate is considered to be adequately described by some function of size, $\mu(w)$. We shall consider the size-specific survivorship, $l_1 = l(pw_0, w_0)$, to gain a factor of p in weight. This survival will be a function of the parameter H and we may describe p -stage specific recruitment as follows:

$$N_1 = N_0 l_1(H(N_0)) ; \quad p = w_1/w_0$$

Suppose H takes a constant value, $H(N_0) = A$, then the recruitment curve is specified (see Fig. 3, top).

We further introduce the maximum rate of growth, $H_{\max} g_0(w)$, at size w as a physiologically determined concept. The maximum growth rate puts an upper limit on the survival which appears as a straight line on the recruitment plot (see C-line in Fig. 3). The minimum rate of growth is assumed to be determined by the survival, $l_{\min} = 1/p$, of *status quo* in biomass (see B-line in Fig. 3). The interpretation of the situation in Fig. 3 (mid-part) is as follows. The grey upper triangle represents an unattainable zone for physiological reasons. The lower grey triangle represents a reduction in biomass in the sense that the biomass of the recruits (sized pw_0), $B_1 = B_0 l_1 p$, is smaller than the initial biomass (B_0). This zone of very few, relatively old (very slow growing) recruits is considered unattainable mainly because of evolutionary reasons (assuming a sufficiently high value of p , the weight gaining factor).

The rate of food consumption by the year-class, $C(t)$, is determined by $N(w)i(w)$ where $i(w) = GGE^{-1} dw/dt$ denotes the individual rate of food consumption at size w , and GGE, the gross growth efficiency. The total amount of food consumed through p -stage recruitment, F_p , is obtained by integrating $C(t)$ through $\tau_1 = t_1 - t_0$, the time required to grow from size w_0 to size pw_0 . That is, replacing number at size w , $N(w)$, with $N_0 l(w, w_0)$,

$$F_p = \int_{t_0}^{t_1} C(t) dt = N_0 \int_{w_0}^{pw_0} GGE^{-1} l(w, w_0) dw \quad (16)$$

Let us assume that F_p is constant from one year to the next. We can then use Eq. (16) as the criterion for determining $H(N_0)$ and, hence, F_p -specific recruitment (see Fig. 3, bottom part).

Comment 9

It is, of course, necessary to specify the vital rates in order to obtain the survivorship, $l(w, w_0)$, before the integral in the F_p -criterion can be evaluated. If the survivorship in Eq. (15) for the S&C type of density-dependent growth in Eq. (14) is used in connection with

a generalized allometric model of larval growth and mortality, $g_0(w) \propto w^{1-m}$ and $\mu(w) \propto w^{-m}$, then the result shows resemblance to the situation in Fig. 3. The B&H p -stage specific recruitment curve is reversed into a concave shape F_p -specific recruitment curve. The procedure is simply to replace the constant A in the S&C density-dependent growth coefficient with the parameter $H(N_0)$ which, then, is obtained from the food criterion. The F_p -curve, thus, results from a combination of density-dependent growth and start-density dependent growth where the latter is determined from the F_p -requirement. Note that H also becomes a function of the rate of mortality. It is competition for food among young fish that creates a strong mortality-to-growth effect through the F_p -criterion. This stabilizes F_p -specific recruitment against variations in the rate of mortality.

The food-competition situation may be interpreted in relation to various size domains of larval and juvenile life but the F_p -formulation has been adopted with particular reference to early life. Assume that $p = w_1/w_0 \approx 100$ is the ratio of larval size to prey size and that the year-class comprises N_0 larvae at the onset of feeding. In this interpretation the larvae depend entirely on the production of copepod nauplii as food while growing through the size interval. Larvae that reach size w_1 , have a much broader food-spectrum available including the standing crop of the smallest copepods. The cohort considered eats, of course, nauplii in competition with other predators and F_p refers to the fraction of the total copepod production that is consumed by the cohort. The model above with constant F_p clearly represents a very simple treatment of a complex and dynamic situation of food competition but there is no need for a more elaborated treatment in the present context.

The lower limit of the recruitment window (determined by the B-line) is not a demand for increasing biomass from the onset of feeding. The biomass may bear a decreasing relationship to size as is actually the case in the S&C model, but the reduction must be regained before or at recruitment.

The most simple treatment of the R&F suggestion, then, is to resume at the beginning point in Eq. (12) and specify the growth rate by $H(N_0, F_p, \mu)g_0(w)$. The dependency of F_p and μ indicates that the food criterion also makes H a function of environmental conditions specified by the amount of food consumed (F_p) and the mortality rate (μ). In this model, the survivorship in the integrand of Eq. (16) can be replaced with

$$l(w, w_0) = l_0(w, w_0)^{1/H} \quad (17)$$

and it follows that the F_p -criterion stabilizes recruitment. For example, a reduction in spawning biomass (most likely) implies a reduction in N_0 , and H will, consequently, increase to meet the balance in Eq. (16). This improves survival and thus stabilizes recruitment against variations in the spawning stock. If N_0 is constant but favourable environmental conditions in one year cause a reduction in mortality, then H must decrease as well to meet the balance. If GGE is (approximately) independent of H , then it actually follows from Eqs (16) and (17) that recruitment is (approximately) constant independent of the rate of mortality. The argument is based on the multiplicative rule,

$$l_*(w, w_0) = l_0(w, w_0)^{c/H_*}; \quad \mu_*(w) = c\mu(w)$$

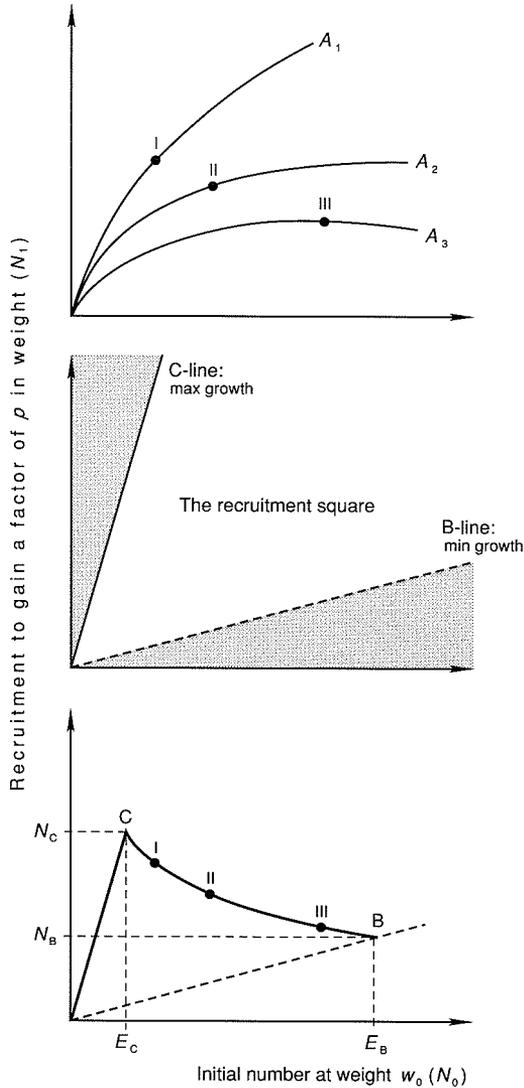


Fig. 3. Illustrates the principle in the derivation of the food-and-size-specific recruitment curve. Size-specific recruitment to gain a factor of p in weight (i.e. p -stage specific) is known except for the constant A which is related to the food supply (top part). The B and C lines of min. growth (i.e. *status quo* in biomass) and max. growth define a potential recruitment square or window (mid-part). For a particular initial situation, N_0 fish of size w_0 , the value of $H(N_0) = A$ is obtained by requiring that a constant amount of food, F_p , is available for the p -stage specific development of the year-class. The intersection between the vertical N_0 -line and the p -stage specific curve for $H(N_0) = A$ represents a F_p -specific point (cf. points I, II and III). The F_p -specific recruitment curve is obtained by continuing this procedure (bottom part). The initial part of the recruitment curve is specified by the maximum survivorship, i.e. the C-line for max. growth (for low initial numbers at which the F_p -criterion no longer constitutes a limiting factor for recruitment).

The exponent, c/H_* , must remain constant to meet the F_p -balance and hence, $H_* = cH$ as a result of the change in the mortality rate by a factor of c . Food competition as formulated by Eq. (16) thus stabilizes size-specific recruitment against fluctuations in the mortality rate. Since F_p is proportional to N_0 , it also follows from Eq. (16) that fluctuations in the amount of food consumed (F_p) will cause recruitment to fluctuate by exactly the same mechanism that provides recruitment stability against fluctuations in N_0 in the case of constant F_p .

The same procedure can be used to elucidate the point C dynamics of the F_p -recruitment curve. The only difference from the situation described above is that H

remains constant (H_{\max}) at this critical point occurring at $N_0 = E_C$. Recruitment at point C is

$$N_C = E_C l_0(pw_0, w_0)^{1/H_{\max}} \quad \text{C: Point of max. growth rate} \quad (18)$$

and it follows from Eq. (16) that E_C increases but N_C decreases as the rate of mortality increases. The C-line for maximum (and density-independent) survival and the position of the critical point are, thus, sensitive to changes in mortality as would be expected.

Comment 10

The allometric model with start-density dependent growth derived from the F_p -criterion, $g_0(w, N_0) = H(N_0)w^{1-m}$, $\mu(w) = qw^{-m}$ and hence, $l(w, w_0) = (w/w_0)^{-q/H}$, produces a steeper descending F_p -recruitment curve than in the S&C case. The dynamics of point C are the same in the two situations. We expect that GGE, the gross growth efficiency increases only slightly when H increases from q (point B) to H_{\max} (point C) because the rate of fasting metabolism is small compared to the growth rate for larval fish. Recruitment at a specific initial number (fixed N_0) is, therefore, almost constant when the rate of mortality changes as it is only moderate changes in $GGE(H)$ that will cause q/H to change slightly to meet the food requirement in Eq. (16). However, it turns out that the mortality-to-growth effect is so strong that F_p -recruitment actually increases somewhat when the mortality rate increases!

Eq. (16) represents but one consistent and simple way of expressing the effect of food competition. If it is not so much the total amount of food eaten as C_p , the average rate of food consumption, that is likely to remain constant, then the situation changes. The C_p -specific recruitment curve is raised at the B-end compared to the F_p -curve because there is more food, $F_p(N_0) = C_p \tau_1(N_0)$, available at low growth rates. The C_p -criterion also stabilizes recruitment against variations in mortality. The response to a change in mortality is (now reversed to) the expected one: recruitment increases (slightly) with a reduction in mortality and *vice versa*. Yet another criterion would be to consider the amount of food eaten during a specific time to be constant. Age-specific recruitment to meet this food criterion bears an increasing relationship to the initial number!

Conclusions

The general principles of size based theory are quite simple. The decimation of numbers at size is determined by the physiological rate of mortality which equals the rate ratio of mortality to growth. Integrating the physiological mortality rate gives the size-specific cumulative mortality. The survivorship is obtained in the usual manner, taking the exponential of minus the cumulative mortality. If the mortality rate increases by a factor, c , the cumulative mortality increases with the same factor and hence, age-specific survival (see Ex. 2) and size-specific survival (in the case of unchanged (or density-independent) growth) change to the c th power of their initial values. If the mortality rate is constant then the exponential decay in numbers at age has nothing to do with the rate of growth. However, a decrease in the growth rate will have the same effect as an increase in the mortality rate on the physiological rate and hence, on the size-specific survival (see Ex. 6.1). These useful multiplicative rules for the size-specific survival (e.g. Ex. 5) are ex-

pressed in Eq. (11). However, some care is required because a change in the growth rate may affect the rate of mortality. This is because the shift from a description in age to size, or from size to age is determined by the growth curve. Suppose that mortality is described as a function of age (Ex. 1), $M(\text{age})$, then the mortality at size depends on the growth rate (Ex. 6.2). In the more realistic case, mortality is described by a (decreasing) function of size, $\mu(\text{size})$, and mortality at age consequently depends on the growth rate (Ex. 6.3). These concepts of size based theory can be applied to any formulation of the vital rates. Two types of growth models are considered in the present paper, VBGE (Ex. 4) and the allometric model (Exs 7 to 10).

In the classical (assessment) model with a constant rate of total mortality, Z , and VBGE, $dL/dt = K(L_\infty - L)$, numbers at length become (Ex. 4.1),

$$N(L) = N(L_0) \left[\frac{L_\infty - L}{L_\infty - L_0} \right]^{Z/K}; \quad Z: \text{constant total mortality} \quad (19)$$

Hence, numbers bear a linear relationship to length when the total rate of mortality equals the growth coefficient, K . This curve for numbers at length actually changes from a convex shape when $Z < K$ to a concave shape for $Z > K$. The in between situation, the straight line for $Z = K$, represents a balance in the physiological rate of mortality between the effect of constant rate of mortality and the effect of decreasing growth rate with increasing length. The dimension of physiological mortality is LENGTH^{-1} . If weight is used instead to describe size (Ex. 4.2) then, even though Z is constant, the physiological rate of mortality changes (because the growth rate in weight is different from the growth rate in length) and its dimension becomes WEIGHT^{-1} . In Eq. (19), K appears in the denominator of the exponent in the size-specific survival because the growth rate is directly proportional to K . This consequence of the multiplicative rule is very important. It explains why it is the coefficients of the vital rates (here Z and K) that play the most significant role in size based theory because these coefficients end up in the exponent.

Comment

Length based theory is not part of basic training because size (incorrectly) never really was considered to be of great importance for (age-specific) stock assessment and population dynamics in temperate waters (with the otoliths age-reading technique available). For example, the Beverton & Holt (1956) Z -equation (Ex. 4.1) for estimating the ratio Z/K from the mean length in the catch was first rediscovered in the 1970s by Munro (1974, 1983) in his important work on portable fish trap based assessment which actually caused an opening for tropical fish stock assessment. Introductions to length-based (or length converted) methods are available today (Pauly, 1984; Sparre *et al.*, 1989) but it is important to note that methods for estimating Z , such as the length converted catch curve, can be derived directly from length based theory without reference to age.

For clarification, suppose that the population in the sea (which usually consists of several age-groups) is in a steady state (obtained after some years with constant annual recruitment pattern to the fishery (at size, $L_0 = L_t$) and constant coefficients of vital rates; see e.g. Beyer, 1981), then Eq. (19) still describes numbers at length (for this pseudo-cohort situation). Using standard notation, the fishing mortality and the catch are denoted

by F and C , respectively (but only in this and the next *Comment*). The catch rate, $dC/dt = FN$, divided by the growth rate gives the length-based beginning point,

$$\frac{dC}{dL} = \frac{F}{K(L_\infty - L)} N(L); \quad N(L) = N(L_t) l(L, L_t)$$

Considering this physiological catch rate at the mid-point, $L_{12} = (L_1 + L_2)/2$, of a length class to equal $C(L_1, L_2)/\Delta L$, the total catch from that length class divided by the class length (ΔL), inserting numbers from Eq. (19), and taking logarithms gives the length based linearized catch curve,

$$\ln[C(L_1, L_2)/\Delta L] \approx \text{constant} + (Z/K - 1) \ln(L_\infty - L_{12})$$

from which Z/K can be estimated by the linear regression technique. Integrating the physiological catch rate gives the fundamental (classical) catch equation,

$$C(L_1, L_2) = \frac{F}{Z} N(L_1) [1 - l(L_2, L_1)]; \quad N(L_1) = N(L_t) l(L_1, L_t)$$

or, the exact (linearized) length based catch curve,

$$\ln[C(L_1, L_2)/(1 - l(L_2, L_1))] = a + \frac{Z}{K} \ln(L_\infty - L_1); \quad l(L_2, L_1) = \left[\frac{L_\infty - L_2}{L_\infty - L_1} \right]^{Z/K}$$

which, however, can only be used in an iterative way. The first estimate of Z must be used to evaluate the survivorship, $l(L_2, L_1)$, on the left hand side and then, an improved estimate of Z is obtained from the slope of the regression line (assuming K to be known, of course). Putting $L_2 = L_\infty$ or $l(L_\infty, L_1) = l(\infty, L_1) = 0$ gives the Jones & van Zalinge (1981) equation for the length based cumulated catch curve,

$$\ln C(L_1, L_\infty) = a + \frac{Z}{K} \ln(L_\infty - L_1); \quad a = \text{constant}$$

This formulation is also useful for comparing the two approaches because the right hand sides of both the catch curve and the cumulated catch curve are identical.

Eq. (19) describes the decimation of numbers at length of one year-class according to the classical assumptions. In a more realistic case, the rate of natural mortality is inversely proportional to length, $M_\infty (L_\infty/L)$, (but the fishing mortality remains constant) and we obtain from Exs 4.1 and 4.3, using the multiplicative rule,

$$N(L) = N(L_0) \left[\frac{L_\infty - L}{L_\infty - L_0} \right]^{Z_\infty/K} \left[\frac{L_0}{L} \right]^{M_\infty/K}; \quad M_\infty: \text{natural mortality} \quad (20)$$

(of infinitely old fish)

where Z_∞ denotes the total mortality of infinitely old fish, i.e. the fishing mortality plus M_∞ . The age-specific survival is obtained by inserting length-at-age from the von Bertalanffy growth curve (see e.g. Ex. 4.4) in Eq. (20). If there is no fishing, then Z_∞ can be replaced by M_∞ in Eq. (20). The physiological rate of mortality attains a minimum at some length because it reaches high values for small fish (due to high mortality) as well as for large fish (due to slow growth). For larval and juvenile fish a simple, allometric growth model seems more appropriate because of the problem with a very rapid decrease in the specific growth rate according to VBGE. Considering the specific rate of food consumption as a measure of natural mortality (Ex. 10.1) is one way of avoiding estimating the weight-exponent in the mortality relationship.

Comment

The minimum of the physiological rate of mortality occurs at $L_m = L_\infty / (1 + \sqrt{1 + F/M_\infty})$ where F denotes the fishing mortality. L_m thus specifies the length class through which the cohort suffers smallest cumulative losses (i.e. maximum survival). Comparing Eq. (20) with Eq. (19) shows that the major effect of introducing this size-dependent mortality model, $Z = F + M_\infty (L_\infty/L)$, is determined by the last factor in Eq. (20). The implications for stock assessment, thus, depend on the size-gaining factor (from the size at which the fish can be considered fully recruited to the fishery to L -infinity) and on the ratio of M -infinity to K in the exponent. In some cases there may be a considerable effect on estimates of gear-selection parameters from catch curve analysis. However, we shall not go further into stock assessment problems in the present context. The main point here is, rather, that we can consider eggs, larval fish and small juveniles on one side (recruitment studies) and adult fish on the other side (classical population dynamics) but within the same mortality model!

The concept of M being inversely proportional to L is in agreement with the results of Ex. 10.1 in that we may expect to find a tendency to proportionality between M and the specific rate of food consumption (i.e. $Hw^{-1/3}$ in VBGE). In the allometric model (Ex. 10) we considered $m = 0.25$ as the weight exponent instead of the $m = 0.33$ considered here (Ex. 4.3, Ex. 7). A $m = 0.25$ may still be consistent with the simple idea of mortality being inversely proportional to length because the exponent in the weight-length relationship for larval fish often seems to be closer to 4 than to 3. But whether or not it is possible to distinguish between, say, $1/4$ and $1/3$ for the weight exponent in the mortality relationship, depends on a critical examination of available data, in particular the bias and uncertainty involved. It may be worthwhile to compile existing data on the matter. For example, Pauly's (1980) empirical M -formula, based on data from 175 different fish stocks,

$$M = 0.9849 L_\infty^{-0.279} K^{0.6543} \text{TEMP}^{0.463}; \quad \text{DIM: } M(\text{yr}^{-1}), L_\infty(\text{cm}), K(\text{yr}^{-1}), \text{TEMP}(\text{°C})$$

in combination with the Pauly & Munro (1984) empirical formula, $K \propto L_\infty^{-2}$, (where the coefficient of proportionality is almost constant within closely related fish species), is perhaps applicable for M_∞ . It also depends on to which degree existing data on natural mortality reflects the situation of M_∞ (rather than a higher M for a smaller size). B&H's classical estimate of natural mortality of North Sea plaice refers to fish between 5 and 13 years of age and actually gives $M_\infty = 0.06 \text{ yr}^{-1}$ (Ex. 4.4). Note that it makes sense to express M as a function of the sea temperature. We expect that solar energy, and hence, the water temperature determines the speed of the overall rate of food turnover and hence, M (cf. Ex. 10.1). It is most likely that more refined models of natural mortality will involve different constants of proportionality if not different slopes (for different groups of animals).

The allometric model has been used as a basis for the examination of age-specific and size-specific recruitment situations with various types of density-dependent vital rates (Exs 7 to 10).

The classical recruitment curves represent the result of a first order approximation to (generalized) density-dependent mortality (Ex. 3). Thus, if mortality is a linear function of the start-density (but otherwise density-independent) then age-specific as well as size-specific recruitment become Ricker curves. The size-specific Ricker curve is maintained if the linear density-function (as a mortality coefficient)

instead is moved to the denominator of the growth rate (as a reciprocal coefficient of growth) because this operation does not change the physiological rate of mortality. Note that the size-specific recruitment curve is always copied to age if the rate of mortality reaches a constant value at or before the age of recruitment (Ex. 7). These results are valid if the terms 'start-density' and 'Ricker curve' are replaced with 'density-dependent' and 'B&H curve' (Ex. 8). Note that all of these results are also valid for whatever functions we propose to describe the size-dependent part of the vital rates. However, age-specific recruitment (in the case of density-dependent growth) depends very much on the relationship that mortality has to size. Even in the most simple case, with natural mortality inversely proportional to length, the shape of the age-specific recruitment curve changes dramatically as the age of recruitment increases. From showing a steadily increasing trend, through the B&H type of curve, to a max-min type of curve, the age-specific curve ends up showing resemblance to the Ricker type of curve (see Fig. 7.4).

The major difference between the recruitment situations for start-density dependent growth and for density dependent growth is as follows. Density-dependency creates a mortality-to-growth effect (which tends to moderate changes and stabilize recruitment against variations in initial numbers) in contrast to the independent vital rates in the case of start-density dependency. It is, thus, this effect that is responsible for raising the right (descending) limb of the Ricker size-specific curve to the stable level in the B&H type of size-dependent recruitment (Fig. 8.2). However, the effect of S&C-density-dependent growth is not strong enough to stabilize recruitment against fluctuations in the rate of mortality.

There is a major difference between size-specific and age-specific recruitment. Size-specific recruitment is simply proportional to the biomass of the recruits. Age-specific recruitment may consist of many but very small fish. For example, in the S&C model, the rate of mortality is constant and age-specific recruitment, consequently, follows a straight line. However, the biomass of equally aged recruits (which is more appropriate to compare with size-specific recruitment) shows a much more complicated relationship to the initial number (see Fig. 8.1).

The most simple size-specific model of the vital rates that appears to explain present knowledge on early life dynamics is the following allometric model (Ex. 9.4 and Ex. 10),

$$\begin{aligned} g(w) &= H w^{1-m} && : \text{rate of growth } (dw/dt) \text{ at size} \\ \mu(w) &= q w^{-m} && : \text{instantaneous rate of mortality at size} \end{aligned} \quad (21)$$

where H , q and m are constants. The physiological rate of mortality is, thus, inversely proportional to weight and q/H denotes the constant of proportionality. The size-specific survivorship is independent of the initial weight, w_0 , and the exponent, m ,

$$l_p = p^{-q/H} \quad : p\text{-stage specific survivorship (from size } w_0 \text{ to size } pw_0) \quad (22)$$

Note that the traditional model of constant mortality is obtained for $m = 0$ in which special case growth becomes exponential, i.e. the basis (the density-independent part) of the S&C model.

Comment

The weight gaining factor (p) is the most important factor in specifying the size interval. The theory, of course, can be applied to any selection of consecutive size intervals but two alternative definitions of p are of particular interest for early life studies. The first relates to physiological reasonably well-defined stages e.g.

$$p = \frac{\text{weight at metamorphosis}}{\text{weight at onset of feeding}} \approx 200$$

The second relates to the size ratio between larvae and their prey,

$$p = \frac{\text{weight of predator}}{\text{weight of prey}} \approx 100 \text{ (larval fish as predators)}$$

Examples on the use of both types of definitions are given in Ex. 10. The interpretation of the effect of food competition on the recruitment curve (as illustrated in Fig. 4) relates to the second definition.

In specifying the allometric model, it has already been noted that a sensible value of the exponent m appears to be about $1/4$ (Ex. 10). However, the p -stage specific survivorship is completely determined by the exponent q/H , the instantaneous rate-ratio of mortality to growth. The disappearance of m from the survivorship is, again, a simple consequence of the fact that it is not the mortality rate but the physiological rate (or the dimensionless, instantaneous rate ratio q/H) which determines the size-specific situation. The model in Eq. (21), elaborated by multiplying the vital rates with the same but arbitrary size-dependent function is, therefore, still governed by the survivorship in Eq. (22). That is a straight line of p -stage specific recruitment in the case of a density-independent (constant) value of the ratio q/H .

If the growth coefficient, H , is inversely proportional to the initial number (or a linear function of N_0), the p -stage specific recruitment curve becomes a Ricker curve which is replaced by a B&H curve in the case of the equivalent situations of density-dependent growth. However, these curves bear no direct relationship to the available food supply or the amount of food eaten. Fig. 4 illustrates the dramatic change in the recruitment curve that occurs when the total consumption of food is constant for the stage-specific development of the year-class. The curve shows resemblance to the case of S&C-density-dependent growth considered in Fig. 9.2. The right part or the B-end is more compressed in case of start-density dependency (see Fig. 10.2).

The two most important aspects of food and size specific recruitment are the stability of the recruitment curve in the regime of medium initial numbers and the dynamics of the three domains. The food criterion stabilizes recruitment against variations in the rate of mortality. In the case considered in Ex. 9.4, the variations in recruitment (domain II) due to $\pm 50\%$ changes in mortality were reduced by a factor of about 10 compared to the situation of density-independent (max) growth in domain I. The position of point C (max. growth) is very sensitive to fluctuations in the mortality rate. Domain I becomes narrower when mortality decreases (E_C decreases) but point C moves up (N_C increases). The movements of point B for *status quo* in biomass are more restricted because the slope of the B-line (i.e. p^{-1}) is independent of changes in the mortality rate. Point B represents the transition to domain III where other causes of natural mortality than predation (such as starva-

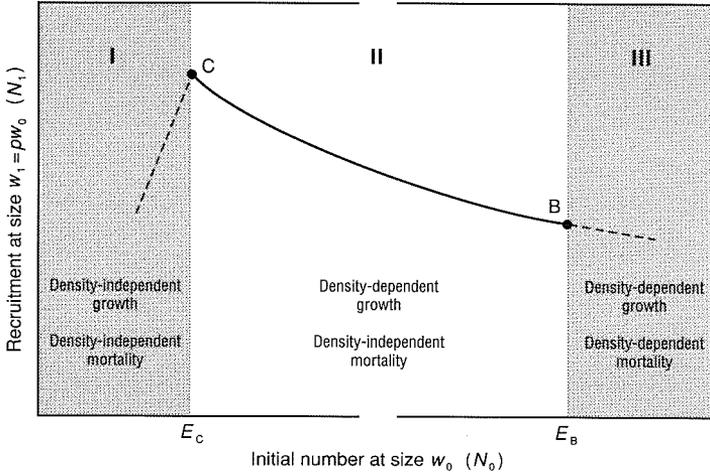


Fig. 4. Illustration of size- and food-specific recruitment curve. Point C denotes the critical point of max. growth rate. Point B represents *status quo* in biomass. The opening on mid- N_0 axis indicates that domain II represents a large intermediate range of stock-sizes ($E_B/E_C \approx 10$) while the extreme range of variation in recruitment is less than, say, a factor of 2. Note that the position of the critical points, in particular point C, depend on the amount of food available, the mortality rate and the p -stage considered.

tion) also are considered to play an important role. The dynamics of the recruitment curve in domain III are perhaps, less interesting and beyond the scope of the present work (and the models considered). The shape and the stability of the recruitment curve also depend on the type of food criterion that is applied (see Fig. 10.2 and Ex. 10.4).

The basic point of these considerations is that the degree of long-term stability in recruitment that many stocks appear to show can be explained by what happens during the first months of life during which the larvae gain a factor of 100 in weight (while depending entirely on the production of copepod nauplii as food). Recruitment at medium to high initial numbers is, furthermore, almost unaffected by even considerable year-to-year fluctuations in the rate of mortality (say, $\pm 50\%$). Deviations from stable conditions due to year-to-year variations in the copepod nauplii production *available* as larval food (causes here presumably also include variations in hydrographic conditions such as stability of fronts and turbulence-dependent contact rates) and other causes that temporarily will change or cause a breakdown of the overall degree of competition among young fish and invertebrates for pelagic food can (in combination with mortality fluctuations) easily explain the magnitude of observed variability in recruitment for most stocks.

The present strategy for explaining the stock and recruitment problem seems useful and promising because it is based exclusively on a synthesis of the think tank provided by the grand old men of fisheries during almost a century. This includes Hjort (1914), Ricker & Foerster (1948), Ricker (1954), Beverton & Holt (1957) and Cushing (1975).

Comment

The models considered in this paper are very simple and hence, represent a high level of abstraction. For example, we do not deal with actual encounters between predators, larvae and prey organisms or between aggregations (patches) of these 'particles' but only with the average outcome of millions of events for the entire sea per time unit. The only but most important problem is that it is difficult to deal with the 'average' without knowing the underlying probability distributions. The ultimate approach must be a stochastic one.

The model considerations show the necessity for a precise and consistent account of the mechanisms governing food consumption and predation. This really requires a multispecies approach (e.g. Beyer, 1981). Furthermore, we do not really deal with food competition. Competition must imply that some members get little while others get more of the limited resource. This is another drawback with the present account – a general and fundamental inconsistency of the discrete models used in classical fish population dynamics – which we need to deal with first: the members of a year-class are not identical. We may, in particular, expect that the heterogeneous composition of a year-class of larval fish affects its dynamics. This requires a continuous approach and Fig. 10.1 introduces the very first step.

Fig. 10.1 is stimulated by empirical evidence which suggests the usefulness of allometric equations in describing the biomass spectrum of the pelagic ecosystem. On a logarithmic body-weight scale, the biomass spectrum should decrease slightly for the smaller plankton with increasing size (e.g. Sheldon *et al.*, 1972, 1973). Note that the ordinate in Fig. 10.1 (incorrectly) refers to numbers. It should be a number density. This point often causes confusion. For clarification, suppose $\eta(w)$ is the number density, i.e. $\eta(w)dw$ denotes the number of fish with sizes in the interval $(w, w + dw)$. The biomass density is thus $w\eta(w)$. In a continuous approach we may write, for numbers and biomass in the small weight interval,

$$\begin{aligned} \text{numbers} &= \eta(w)dw &= \eta(w)w \, d\ln(w) \\ \text{biomass} &= w \text{ numbers} &= \eta(w)w^2 \, d\ln(w) \end{aligned}$$

It is $\eta(w)w^2$ that is called the biomass spectrum and if this spectrum only decreases slightly it means that the absolute slope of the line for number density in Fig. 10.1 is a little more than two! In the present context, Fig. 10.1 merely serves to illustrate a point but note that the conclusion, i.e. that mortality rate is proportional to specific rate of food consumption still holds if a more elaborate log-normal like preference function (Andersen & Ursin, 1977) is applied. Biologists usually prefer to use the biomass spectrum because it is volume or biomass that is measured. However, in dealing with the concept of mortalities, it is more convenient to work with the number density. It was here that the present work actually began but the continuous approach is not included here.

One question from the introduction still remains to be answered: How can the relationship of density-dependent growth be derived from food competition? It cannot! At least not based on the present type of approach. We have only been able to obtain H as a function of the initial number based on the food criterion (Ex. 10). In the S&C type of model, the density-dependency was assumed to be of the B&H type and we could only determine the food measure, A , as a function of the initial number based on the food criterion (Ex. 9). The present investigations, at best, give some ideas on the expected effect of food competition. The theory presented is entirely based on classical theory and a sort of beginning point.

What is needed is theory development to cope with the biological-physical mechanisms (e.g. the Rothschild & Osborne (1988) hypothesis) governing, for example, rates of encounter and food consumption in the sea. This task of theory development is a tremendous one (Rothschild, 1986). It must be done in an iterative procedure. At present much can be done based entirely on historical data after re-assessing according to size etc. All we need to know is probably there somewhere! Many of the examinations in this study could be continued but then, as a second step, it is more interesting to apply the present elements of theory to specific cases.

Acknowledgements

Nobody said it was going to be easy to return to research but, I thought I had chosen an easy little piece of work as a starter. I want to thank my colleagues, Jørgen Møller Christensen, Thomas Kiørboe and, in particular, Knud P. Andersen for moral support. The stimulating response at the ICES working group meeting of larval fish ecology in Aberdeen, July 1989, on some of my thoughts was very helpful.

Discussions with Mike Sinclair, Brian Rothschild, Daniel Pauly and others on the need for size-based theory in recruitment and fisheries research have stimulated the present work. In particular, I thank Ray J.H. Beverton for his persistency in urging me to contribute to the story on size-based theory. The study here represents at least a beginning. Katherine Richardson proof-read the entire manuscript for language on short notice up to Christmas and I'm most grateful for this and her many useful suggestions. Time, unfortunately did not permit peer review.

This work could not have been completed in 1989 without the professional incredible assistance and flexibility of the printers, Olsen & Olsen.

References

- Anon., 1988. Report of the multispecies assessment working group. – ICES C.M. 1988/Assess: 23.
- Andersen, K.P. & E. Ursin, 1977: A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. – Meddr Danm. Fisk.- og Havunders. N.S. 7: 319-435.
- Anderson, J.T., 1988: A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. – J. Northw. Atl. Fish. Sci. 8: 55-66.
- Bakun, A., 1985: Comparative Studies and the Recruitment Problem: Searching for Generalizations. – CalCOFI Rep., Vol. XXVI: 30-40.
- Beverton, R.J.H., 1962: Long-term dynamics of certain North Sea fish populations. – In Cren & Holdgate (eds): The exploitation of natural animal populations, pp. 242-259. Blackwell, Oxford.
- Beverton, R.J.H. & S.J. Holt, 1956: A review of methods for estimating mortality rates in exploited fish populations, with special reference to source of bias in catch sampling. – Rapp. P.-v. Réun. Ciem. 140: 67-83.
- Beverton, R.J.H. & S.J. Holt, 1957: On the dynamics of exploited fish populations. – Fish. Invest. Minist. Agric. Fish. Food G.B. (2 Sea Fish.) 19. 533 pp.
- Beverton, R.J.H. & S.J. Holt, 1959: A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. – In G.E.W. Wolstenholme & M. O'Connor (eds): The lifespan of animals, pp. 142-180. CIBA Foundation, colloquia on ageing, Vol. 5. Churchill, London.
- Beyer, J.E., 1981: Aquatic ecosystems – An operational research approach. – Univ. Wash. Press, Seattle and London. 315 pp.
- Cushing, D.H., 1975: Marine ecology and fisheries. – Cambridge Univ. Press, Cambridge and New York. 278 pp.
- Fenchel, T., 1974: Intrinsic rate of natural increase: the relationship with body size. – Oecologia 14: 317-326.
- Fry, F.E.J., 1949: Statistics of a lake trout fishery. – Biometrics 5: 27-67.

- Garrod, D.J., 1982: Stock and recruitment – again. – Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft, 68: 22 pp.
- Gulland, J.A., 1965: Estimation of mortality rates. Annex to Arctic fisheries working group report. – ICES C.M.Doc. 3 (mimeo).
- Haldane, J.B.S., 1928: On being the right size. – reprinted in H. Shapely, S. Raffort & H. Wright (eds): A treasure of science, pp. 321-325. Harper, New York, 1946.
- Harris, J.G.K., 1975: The effect of density-dependent mortality on the shape of the stock and recruitment curve. – J. Cons. int. Explor. Mer 36(2): 144-149.
- Hemmingsen, A.M., 1960: Energy metabolism as related to body size and respiratory surfaces, and its evolution. – Rep. Steno Memorial Hospital, 9(2): 110 pp.
- Hjort, J., 1914: Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research. – ICES Rapp. Proc.-Verb. 20: 1-228.
- Houde, E., 1987: Fish early life dynamics and recruitment variability. – Am. Fish. Soc. Symp. 2: 17-29.
- Jones, R., 1973: Density dependent regulation of the number of cod and haddock. – Rapp. P.-v. Réunion. Cons. int. Explor. Mer 164: 156-173.
- Jones, R., 1984: Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). – FAO Fish. Tech. Pap. 256: 118 pp.
- Jones, R. & N.P. van Zalinge, 1981: Estimates of mortality rate and population size for shrimp in Kuwait waters. – Kuwait Bull. Mar. Sci. 2: 273-288.
- Kjørboe, T., 1989: Growth in fish larvae: are they particularly efficient? – Rapp. P.-v. Réunion. Cons. int. Explor. Mer 191: in press.
- Kjørboe, T., P. Munk & K. Richardson, 1987: Respiration and growth of larval herring *Clupea harengus*: relations between specific dynamic action and growth efficiency. – Mar. Ecol. Prog. Ser. 40: 1-10.
- Kjørboe, T., P. Munk, K. Richardson, V. Christensen & H. Paulsen, 1988: Plankton dynamics and herring larval growth, drift and survival in a frontal area. – Mar. Ecol. Prog. Ser. 44: 205-219.
- Munro, J.L., 1974: The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. – J. Cons. CIEM 35(3): 337-350.
- Munro, J.L., (ed.), 1983: Caribbean coral reef fishery resources. – ICLARM Stud. Rev. 7: 276 pp.
- Parker, R.R. & P.A. Larkin, 1959: A concept of growth in fishes. – J. Fish. Res. Bd Can. 16: 721-745.
- Paulik, G.J., 1973: Studies of the possible form of the stock-recruitment curve. – Rapp. P.-v. Réunion. Cons. int. Explor. Mer 164: 303-315.
- Pauly, D., 1980: On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. – J. Cons. CIEM 39(2): 175-192.
- Pauly, D., 1984: Fish population dynamics in tropical waters: a manual for use with programmable calculators. – ICLARM Stud. Rev. 8: 325 pp.
- Pauly, D. & J.L. Munro, 1984: Once more on the comparison of growth in fish and invertebrates. – ICLARM Fishbyte 2(1): 21.
- Peterson, I. & J.S. Wroblewski, 1984: Mortality rate of fishes in the pelagic ecosystem. – Can. J. Fish. Aquat. Sci. 41: 1117-1120.
- Platt, T., 1985: Structure of the Marine Ecosystem: Its Allometric Basis. – Can. Bull. Fish. and Aquat. Sci. 213: 55-64.
- Ricker, W.E., 1954: Stock and recruitment. – J. Fish. Res. Bd. Can. 11: 559-623.
- Ricker, W.E., 1973: Critical statistics from two reproduction curves. – Rapp. P.-v. Réunion. Cons. int. Explor. Mer 164: 333-340.
- Ricker, W.E. & R.E. Foerster, 1948: Computation of fish production. – Bull. Bingham oceanogr. Coll. 11: 173-211.
- Rothschild, B., 1986: Dynamics of Marine Fish Populations. – Harvard Univ. Press, Cambridge, Mass. & London, England. 277 pp.
- Rothschild, B. & T. Osborn, 1988: Small-scale turbulence and plankton contact rates. – J. Plank. Res. 10(3): 465-474.
- Sheldon, R.W., A. Prakash & W.H. Sutcliffe, Jr., 1972: The size distribution of particles in the ocean. – Limnol. Oceanogr. 17: 327-340.
- Sheldon, R.W., W.H. Sutcliffe Jr. & A. Prakash, 1973: The production of particles in the surface waters of the ocean with particular reference in the Sargasso Sea. – Limnol. Oceanogr. 18: 719-733.

- Shepherd, J.G.*, 1982: A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. – J. Cons. int. Explor. Mer 40: 67-75.
- Shepherd, J.G. & D.H. Cushing*, 1980: A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. – J. Cons. int. Explor. Mer 39(2): 160-167.
- Silvert, W. & T. Platt*, 1980: Dynamic energy-flow model of the particles size distribution in pelagic ecosystems. – In W.C. Kerfoot (ed.): Evolution and ecology of zooplankton communities, pp. 754-763. Univ. Press of New England, Hannover, NH.
- Sparre, P., E. Ursin & S.V. Venema*, 1989: Introduction to tropical fish stock assessment, Part A – Manual. – FAO Fish. Tech. Pap. 306(1): 337 pp.
- Theilacker, G.H.*, 1986: Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. – U.S. National Marine Fisheries Service Bulletin 84: 1-17.
- Ursin, E.*, 1967: A mathematical model of some aspects of fish growth, respiration, and mortality. – J. Fish. Res. Bd Can. 24: 2355-2453.
- Ursin, E.*, 1973: On the prey size preferences of cod and dab. – Meddr Danm. Fisk.- og Havunders., N.S. 7: 85-98.
- Ursin, E.*, 1979: Principles of growth in fishes. – Symp. zool. Soc. Lond. 44: 63-87.
- Ursin, E.*, 1982: Stability and variability in the marine ecosystem. – Dana 2: 51-67.
- van Sickle, J.*, 1977: Analysis of a distributed-parameter population model based on physiological age. – J. theor. Biol. 64: 571-586.
- Ware, D.M.*, 1975: Relation between egg size, growth and natural mortality of larval fish. – J. Fish. Res. Bd. Can. 32: 2503-2512.
- Werner, E.E. & J.F. Gilliam*, 1984: The ontogenetic niche and species interaction in size-structured populations. – Ann. Rev. Ecol. Syst. 15: 393-425.

Notation

a	constant
A	population size at half max S&C-growth-coefficient
A_B	A at critical recruitment point B
b	constant; change in growth rate
B	biomass of year-class (usually specified by index)
B-line	lower limit of recruitment square (window) designating minimum survivorship
B-point	critical recruitment point of <i>status quo</i> in biomass
B_0	initial biomass of year-class (at age t_0 , weight w_0)
B_1	biomass of year-class at size-specific recruitment
B_∞	biomass of infinitely old year-class
$B(t)$	biomass of year-class at age t
B&H	Beverton & Holt (1957) (BH as index)
c	constant; change in mortality rate
C	rate of food consumption by year-class
C-line	upper limit of recruitment square (window) designating maximum survivorship
C-point	critical recruitment point of max growth rate
C_0	cumulative mortality to age-specific recruitment with constant mortality rate ($= \mu_0 \tau_r$)
C_p	average rate of food consumption by the year-class to size-specific recruitment

$C(t)$	rate of food consumption at age t by year-class
$C(w)$	rate of food consumption at size w by year-class
CUMT	age-specific cumulative mortality
CUMW	weight-specific cumulative mortality
CR-point	critical recruitment point in B&H on R&F
e	base of natural logarithm;
e	egg-index
E	initial number of eggs
E_B	initial number at point B
E_C	initial number at point C
E_{C0}	minimum value of E_C (at zero mortality)
E_{CG}	maximum value of E_C ($= E_B$)
E_{CR}	initial number at point CR
E_m	initial number at local recruitment max
E_{max}	initial number at max recruitment
$E_{1/2}$	initial number at half asymptotic max recruitment
$f(t)$	growth curve: weight at age
$f^{-1}(w)$	inverse growth curve: age at weight
$f_1(t)$	growth curve: length at age
$f_1^{-1}(L)$	inverse growth curve: age at length
F_p	total amount of food consumed by year-class to size-specific recruitment
F_τ	total amount of food consumed by year-class to age-specific recruitment
$g(w,.)$	rate of growth in weight (vital rate): $g(w)$, $g(w, N)$, etc.
$g_0(w)$	density-independent rate of growth in weight
$g_1(L)$	rate of growth in length
$G(w)$	weight-specific rate of growth at weight w (specific growth rate, instantaneous growth rate)
$G(t)$	weight-specific rate of growth at age t (specific growth rate, instantaneous vital rate)
GGE	gross growth efficiency ($= g(w)/i(w)$)
h	coefficient of anabolism in allometric model
H	coefficient of anabolism in VBGE; coefficient of growth in allometric model
$i(w)$	rate of food consumption at weight w
$I(t)$	specific rate of food consumption at age t
$I(w)$	specific rate of food consumption at weight w
k	coefficient of fasting metabolism
K	curvature parameter in VBGE curve in length ($= k/3$)
$l(w, w_0)$	weight-specific survival from w_0 to w (survivorship)
$l_1(L, L_0)$	length-specific survival from L_0 to L (survivorship)
l_1	short for p -specific survivorship ($= l(pw_0, w_0)$)
l_0	short for density-independent survivorship
l_{max}	max size-specific survival (survivorship)

l_{\min}	min size-specific survival (survivorship)
L	length (total body-length)
L_0	body-length at beginning of size-interval (stage): initial length
L_{∞}	length of infinitely old fish
\bar{L}	mean length-at-death above initial length
m	numerical value of weight exponent in allometric model for the instantaneous vital rates
M	constant instantaneous rate of natural mortality
$M(t)$	instantaneous rate of mortality at age (natural mortality or mortality rate or mortality coefficient or vital rate)
M_{∞}	mortality rate of infinitely old fish
$N(t)$	numbers at age (abundance or number of survivors in the year-class at age t)
$N(w)$	numbers at weight (abundance or number of survivors in the year-class at weight w)
N_a	size-specific recruitment (at asymptotic recruitment)
N_A	relative initial number ($= N_0/A(N_0)$)
N_B	size-specific recruitment at point B
N_C	size-specific recruitment at point C
N_{C0}	minimum value of N_C at zero mortality
N_{CG}	maximum value of N_C
N_0	initial number of fish in the year-class at age t_0 and weight w_0
N_1	size-specific recruitment at weight $w_1 = pw_0$
N_{\max}	max size-specific recruitment
p	weight gaining factor ($= w_1/w_0$)
P	short for biomass lost in predation;
P	P-point
$P(t, t_0)$	biomass removed during (t_0, t) due to predation
psd	particle size distribution
q	coefficient of size-specific mortality
$Q(t, t_0)$	cumulated total excretion (loss) during (t_0, t)
R	age-specific recruitment
R_B	age-specific recruitment at point B
R_C	age-specific recruitment at point C
R_m	local maximum of age-specific recruitment
R_{CR}	critical age-specific recruitment in B&H on R&F
R&F	Ricker & Foerster (1948)
$S(t, t_0)$	age-specific survivorship from t_0 to t
S_{\max}	max age-specific survival (survivorship)
S_{\min}	min age-specific survival (survivorship)
S_{∞}	age-specific survival at asymptotic high initial numbers (asymptotic survivorship)
S&C	Shepherd & Cushing (1980)
t	age
t_0	age at w_0 (initial age)

t_1	age at w_1
t_r	age at (age-specific) recruitment
$\bar{i}(t_0)$	mean age-at-death above age t_0
T	age of maturation
T_0	age at zero length in VBGE (t -zero auxilliary in assessment terminology)
$U(N)$	generalized density-dependent mortality coefficient
VBGE	the von Bertalanffy growth equation
VPA	virtual population analysis (developed by Fry (1949), applied by Gulland (1965), reviewed by e.g. Jones (1984))
w	weight
$w(t)$	weight at age t
w_0	weight at beginning of size-interval or stage considered (initial weight)
w_1	weight at (size-specific) recruitment
w_e	egg weight
$\bar{w}(w_0)$	mean weight-at-death above w_0
W_b	weight at max biomass
W_m	weight at min physiological mortality rate
W_∞	weight of infinitely old fish
x	variable (auxilliary)
Z	total instantaneous rate of mortality (total mortality coefficient, total mortality rate, total mortality)
Z_∞	total mortality rate of infinitely old fish
α	fraction of absorbed food lost (in sda etc.)
β	fraction of food absorbed
γ	assimilation efficiency
δ	numerical value of N -exponent in density-dependent growth
$\mu(w)$	instantaneous rate of mortality at size w (mortality or mortality rate or mortality coefficient or vital rate)
$\mu_1(L)$	instantaneous rate of mortality at length L
τ	time measured from initial age (time interval $t - t_0$)
τ_1	time required to grow to size-specific recruitment (or, to gain a factor of p in weight)
τ_r	time to (age-specific) recruitment (time interval $t_r - t_0$)

Note: This list of symbols is not complete. Several parameters and variables are specified by indices such as i (inflexion point), c (critical), s (saddle-point), ref (reference point), max (maximum), min (minimum) and * (new value after a change in vital rates).

Examples

Example 1: Mean age, longevity and age-specific survival

The survivorship $S(t, t_0)$ gives the fraction of fish at age t_0 that is still alive at age t . We, therefore, obtain a general formula for the mean age-at-death of fish above age t_0 by integrating the survivorship, i.e.

$$\bar{i}(t_0) = t_0 + \int_{t_0}^{\infty} S(x, t_0) dx$$

In the special but often considered case of a constant rate of mortality, M , we obtain an exponential life-time distribution, $S(t, t_0) = \exp(-M(t - t_0))$ and, the conditional mean age-at-death becomes $\bar{i}(t_0) = t_0 + 1/M$ or $M = 1/(\bar{i}(t_0) - t_0)$ as shown by Beverton & Holt (1956). Note that it is 'the lack of memory' (Markovian) property of the exponential distribution which ensures that the expected future life-span is constant and independent of the past. Whether we consider, say, two week old fish larvae, one year old juveniles or ten year old adults then – on average – their life will terminate after $1/M$ units of time if M is constant. We may consider fractiles of the life-time distribution as measures of the longevity of the fish. The mean age-at-death of the fish in the year-class, $\bar{i}(0) = 1/M$, corresponds to a survivorship of $\exp(-1)$ or the 36.8% fractile. The age at which only 1% of the cohort is alive (i.e. the 1% fractile) equals the mean age-at-death multiplied by $-\ln 0.01$ or 4.61. However, in describing the early life dynamics and the process of recruitment we are dealing with much smaller survival.

Suppose $T = 3$ years is the age of (massive) maturation. We know that the survival to maturation is on the order of $10^{-6} = \exp(-13.8)$ for many species (cf. Ex. 5) because, on average, only two eggs of the total number of eggs produced by an adult fish survive and develop into two mature fish. The cumulative mortality through the first three years of life must, then, be about 13.8, i.e.

$$\int_0^T M(t) dt = -\ln S(3, 0) = 13.8 ; \quad T = 3 \text{ yr} ; \quad S(3, 0) = 10^{-6}$$

If the rate of natural mortality remains constant throughout life, then the mortality level required to explain the one in a million survival must be $M = 4.6 \text{ yr}^{-1}$ ($1.3\% \text{ d}^{-1}$) giving a mean age of 79 days and an annual survival rate of $\exp(-4.6)$ or 1%. A more realistic distribution of natural mortality should involve a proportionally higher cumulative mortality in early life than in the later juvenile stages. Suppose for a simple treatment of this situation, that the rate of mortality decreases inversely with age according to

$$M(t) = b/(1 + ct)$$

We then obtain the following survival and mean age,

$$S(t, 0) = (1 + ct)^{-b/c} ; \quad \bar{i}(t_0) = t_0 + \frac{1 + ct_0}{b - c} ; \quad b > c$$

One interpretation of this model is that the rate of mortality is inversely proportional to the length of the fish and that growth in length takes place at a constant rate. The constant, c , then denotes the specific growth rate in length at age zero.

We tentatively set $c = 9.125 \text{ yr}^{-1}$ (2.5% d⁻¹) and $b = 4c = 36.5 \text{ yr}^{-1}$ (10% d⁻¹) for the rate of mortality at age zero. The mean age-at-death of the fish in the year-class is less than two weeks ($1/(b-c) = 13.3 \text{ d}$). However, 31.6% of the cohort is alive at this mean age and the rate of mortality has dropped to $b-c$ or 7.5% d⁻¹. The survival to three years of age is $1.5 \cdot 10^{-6}$ at which time the mortality is 1.29 yr^{-1} . Three year old fish will on average just survive their fourth birthday ($\bar{i}(3) = 4.04 \text{ yr}$).

Table 1.1. Rate of mortality, cumulative mortality and survivorship at age in a simple model of age-dependent mortality: $M(t) = b/(1 + ct)$ with $b = 4c = 36.5 \text{ yr}^{-1}$.

Age t yr	Rate of mortality $M(t)$ yr ⁻¹ d ⁻¹		Cumulative mortality CUMT($t,0$) = $-\ln S(t,0)$ (dimensionless)	Survivorship $S(t,0)$ (dimensionless)
0	36.5	10.0%	0	1.00
1/12	20.7	5.6%	2.3	0.10
2/12	14.5	4.0%	3.7	0.025
3/12	11.1	3.0%	4.8	0.0086
0.5	6.56	1.8%	6.9	$1.0 \cdot 10^{-3}$
1	3.60	0.99%	9.3	$9.5 \cdot 10^{-5}$
2	1.90	0.52%	11.8	$7.3 \cdot 10^{-6}$
3	1.29	0.35%	13.4	$1.5 \cdot 10^{-6}$
5	0.78	0.21%	15.4	$2.1 \cdot 10^{-7}$
10	0.40	0.11%	18.1	$1.4 \cdot 10^{-8}$
20	0.20	0.055%	20.8	$8.8 \cdot 10^{-10}$

Table 1.1 gives a more detailed picture of the course of mortality. The cumulative mortality is 6.9 during the first six months and 6.5 during the following 2.5 years. Considering that much stock assessment in temperate waters is still based on an assumption of a natural mortality of 0.2 yr^{-1} in the exploited phase, a mortality of 1.3 yr^{-1} seems high for a three year old fish. However, since we still have to explain a cumulative mortality of about 13 at the age of three years, the rate of mortality for fish older than, say, half a year can only be reduced at the expense of increasing the rate of mortality in early life. If the rates of mortalities in early life are higher than suggested in Table 1.1, then they are likely to exceed the specific growth rate in weight of larval fish and the biomass of the year-class will begin to decrease already in early life!

It is this delicate balance between the vital rates that determines the changes in the biomass of the year-class (Jones, 1973). We can hardly expect to gain much new insight into this important mass-balance for early life by elaborating on empirical based age-specific models such as the one presented here. There is a need for developing rational models to describe the early life dynamics of marine fish. The present paper advocates that such models are likely to be size-specific rather than age-specific. It is, apparently, not known at which life-history stage the biomass of a year-class is likely to begin to increase. We know only that the biomass is decreasing during the egg- and yolk-sac stages. A sensible criterion could be that the biomass at metamorphosis (when the larvae have gained, say, a factor of 200 in weight) should

exceed the biomass at the onset of feeding. These criteria are considered in Exs. 9 and 10 after introducing size-specific models in Ex. 4 and going through the few existing elements of size-specific recruitment theory in Exs. 7 and 8.

Example 2: Multiplicative aspects of survival to age

The purpose of this example is to recapitulate the usefulness of the basic properties of age-specific survivorships. Changes in the age-specific survival, however, are not always that simple to quantify. One example is the change in the age-specific survival that will occur due to a change in the rate of growth in the case of a size-dependent rate of mortality (see Ex. 6.3). Other, even more complicated, situations may arise in the case of density-dependent vital rates. For a simple treatment of such a situation, assume that the rate of mortality is a linear function of density,

$$M(t) = M_1 + M_2 N(t)$$

and denote the survivorship from, say, age zero to age t by S . If the mortality coefficients are changed by a constant factor, $M_{1*} = c M_1$ and $M_{2*} = c M_2$, then the new survivorship does NOT equal S^c ! The initial rate of mortality, $M(0)$, is changed by a factor of c but this subsequently changes numbers-at-age (compared to the situation before the change) and the new rate of mortality at age t is, therefore, not simply the old one multiplied by c . The mathematical treatment of this linear mortality assumption underlying the Beverton and Holt recruitment curve (see Ex. 3) is well-known and we obtain (cf. the equivalent size-specific procedure in Ex. 8.2),

$$S = N(t)/E = S_0 / (1 + (1 - S_0)EM_2/M_1) ; \quad S_0 = \exp(-M_1 t)$$

where E is the initial number at age zero (hatching). Note that S_0 is the survivorship in the absence of density-dependent mortality (i.e. $M_2 = 0$). With the factor- c change of the coefficients of mortality, it is only the survivorship, S_0 , that will change to the c th power: $S_{0*} = S_0^c$. In the case of a mortality increase ($c > 1$), the survivorship thus decreases but not quite to the c th power of its initial value (i.e. $S^c < S_* < S$, cf. equivalent sensitivity analysis in Ex. 8.2). Replacing the number $N(t)$ with SE gives the rate of mortality as an explicit function of age,

$$M(t) = M(0) / (1 + (1 - S_0)E M_2/M_1) ; \quad M(0) = M_1 + M_2 E$$

and it follows directly that the increase in M_1 and M_2 by a factor of c leads to a smaller relative change in $M(t)$ because of an increase in the denominator (S_0 decreases).

The fact that $S_* \neq S^c$ in the case of density-dependent mortality does not mean that the power-rule is not valid but rather that it is difficult to create two situations in which the rate ratio of mortality is constant throughout the entire age-interval considered. With this in mind, we can proceed to consider the applications of the power-rule in simple cases of constant mortalities or situations in which the rate of mortality is described by, e.g., an explicit function of age (or time) such as in Ex. 1.

2.1. *The power rule*

Suppose for a species such as the Atlantic herring (*Clupea harengus harengus*) that one egg in 100 develops into a juvenile fish under ‘normal environmental conditions’. Favourable survival conditions in one year may, perhaps, reduce the normal mortality rate by, say, 25% thereby increasing the survival from $S_1 = 0.01$ to $S_1^{0.75} = 0.0316$. In another year, mortality may be 25% higher than usual producing a survivorship of $S_1^{1.25} = 0.00316$. Thus, year-to-year variations in mortality of $\pm 25\%$ in the egg and larval stage alone will cause recruitment to vary by a factor of 10 (cf. Houde, 1987). If the survival from the (ca. 9 month) juvenile stage until age one year is 2% under normal conditions (i.e. $S_2 = 0.02$), then the survival from egg to one year of age becomes $S = S_1 S_2 = 0.0002$. Recruitment will vary by a factor of more than 70 (i.e. $S^{-0.50}$) due to year-to-year variations of $\pm 25\%$ in the mortality rate during the first year of life. If fishing or a new predatory species affects the juvenile stage by a mortality rate of, say, 1.2 per year then the survivorship until one year of age will decrease by a factor of $\exp(-1.2 \cdot 0.75) = 0.41$ (9 months = 0.75 year).

The classical assumption of a rate of natural mortality of about 0.2 per year gives an annual survival on the order of 80%. Raising the mortality on age group one to about 1 yr⁻¹ (as has been recently done in the stock assessment of North Sea herring) reduces annual survival to ca. 36% (see Fig. 2.1). Recruitment as calculated by VPA, therefore, more than doubles because we still need to explain the same spawning stock size as with the low rate of mortality. The long-term mean of ca. $8 \cdot 10^9$ one year old North Sea herring before the collapse of the stock in the mid-seventies (e.g. Beyer, 1981) is actually increased by 10^{10} recruits due to this change in juvenile mortality. Fig. 2.1 also illustrates the multiplicative rule with a fishing mortality of about 0.3 yr⁻¹ (simulating fishing during mid-recovery in the early eighties). The effect in terms of absolute reduction in survival is small in the $M = 1$ case because most of the fish ending in the trawl would had suffered natural mortality in any case.

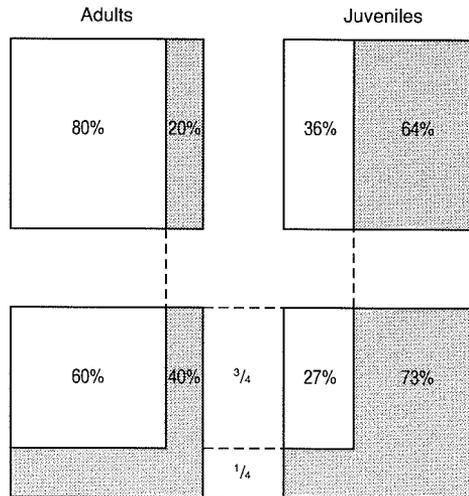


Fig. 2.1. Annual percentage survival and mortality (dark area) for adult and juvenile without fishery (top part) and with a fishery that by itself would remove 1/4 of the population.

The general rule of the effect of a change in mortality is that $x\%$ increase in the rate of mortality causes the survivorship to change by a factor equal to the initial survivorship to the power of $x/100$, i.e.

$$M_*/M = 1 + x/100 \text{ produces } S_*/S = S^{x/100}$$

where the star-index again denotes the change. In Ex. 1, we considered $M(t) = 0.10/(1 + 0.025t)$ where t denotes the age in days. If the constant 0.10 is changed by $\pm 25\%$, then the survivorships to three months, one year and three years of age will vary by factors of 11, 103 and 816, respectively. If age zero denotes hatching, then in stock and recruitment considerations, the survivorships in Ex.1 should be multiplied by the survivorship through the egg stage, say, $\exp(-0.10 \cdot 14)$ or 0.25 for two weeks with a daily mortality of 10%.

The power-rule applied to size-specific survivorships is considered in Ex. 5. Ex. 6 deals with the effects of changes in the rate of growth on the survivorships.

Example 3: The Ricker type and the Beverton & Holt type of recruitment curves
Ricker(1954) proposed that the instantaneous rate of mortality was constant in time and could be expressed as a linear function of E , i.e.

$$M(t) = M_1 + M_2 E ; \quad t_0 \leq t \leq t_r ; \quad \tau_r = t_r - t_0$$

where the egg-density dependent term accounts for cannibalism of young by adults or for predation when the abundance of predators can be considered proportional to E , the egg-production of one of its prey. The survival becomes $\exp(-M_1 \tau_r - M_2 \tau_r E)$ which gives rise to the dome-shaped Ricker type of recruitment curve:

$$R = c_1 E \exp(-c_2 E)$$

where $c_1 = \exp(-M_1 \tau_r)$, the survival in the absence of cannibalism ($M_2 = 0$) determines the steepness of the ascending left limb. Maximum recruitment of $0.368c_1/c_2$ occurs at an egg-production of $1/c_2$ and $c_2 = M_2 \tau_r$ also determines the steepness of the descending right limb. The inflexion point occurs at $E = 2/c_2$ or at twice the egg-production of maximum recruitment and recruitment is reduced to 0.736 of maximum recruitment (i.e. 26.4% reduction).

Cannibalism is a very direct population-regulating mechanism and it is quite apt to exist undetected (Ricker, op. cit. p. 613). Ricker's opinion was that cannibalism would prove to be important in only a minority of populations. However, the Ricker recruitment curve may also appear under quite different assumptions as will be discussed in Ex. 7.

Beverton & Holt (1957) proposed an egg, larval and juvenile mortality rate varying linearly with density,

$$M(t) = M_1(t) + M_2(t)N(t) ; \quad t_0 \leq t \leq t_r$$

and they considered the pre-recruit phase to be split into any number of stages during which the mortality coefficients (M_{1j}, M_{2j}) are constants. Deriving the survivorship produces the Beverton and Holt type of recruitment curve:

$$R = 1/(b_1 + b_2/E)$$

where $1/b_2$ is the survival in the absence of the density dependent mortality ($M_2(t) = 0$). The curve rises to an asymptotic level of $1/b_1$ which depends on all the M_1 s and the M_2 s (see B&H op. cit. p.49). The mortality coefficient, M_1 , relates to predation and factors such as temperature, wind and currents. If, for example, the number of predators is changed by a factor of c , then, in a first approximation, b_1 is unchanged but b_2 is changed to b_2^c .

Beverton and Holt considered severe competition for food among young fish to be the most likely candidate of compensatory mortality and the idea was to express this effect by the M_2 s. It is to be expected that competition for food ultimately may lead to death either directly from starvation or indirectly from debility due to insufficient food. These types of starvation events are particularly likely to occur during the early larval stages (e.g. Hjort, 1914; Jones, 1973 and Theilacker, 1986). Clearly, it is practical that a larval fish, which is constructed to grow at an enormous rate, is poorly adapted to situations in which fast growth is impossible (Jones, 1973). However, although larval deaths due to insufficient food undoubtedly occur frequently in the sea, it is less obvious that a starvation-induced mortality in early life should always play the major role in regulating year-class strength. It seems much more obvious to begin the investigation of the possible causes of recruitment stability by considering the immediate effects of competition for food in terms of density-dependent growth. This idea goes back to Ricker & Foerster (1948) and its quantification requires another model approach using body-size instead of age as the key variable. We shall deal with this type of size-structured analysis in the following examples and in Ex. 8, how the B&H recruitment curve may occur under quite different assumptions is discussed. The basic point here is that density-dependent mortality caused by starvation may be considered as the extreme outcome of density-dependent or food-limited growth.

Example 4: Mean size, Beverton & Holt theory and size-specific survival

The simple Beverton & Holt (1957) theory of fishing with constant parameters still constitutes the fundamental element of most fish stock assessment. It seems sensible to use this theory as a general starting point in illustrating the effects of considering the survival to length (Section 4.1) or weight (Section 4.2) rather than to age. However, the assumption of a constant rate of natural mortality throughout life appears basically wrong particularly in juvenile life and the suggestion is made that predation mortality is inversely proportional to the length of the fish (Section 4.3). This amendment to the classical theory must be accompanied by a change of the power in the metabolic growth model (Section 4.4) in order to create a simple and more promising beginning point for modelling growth and mortality in the early life of marine fishes.

4.1. Mean-size and B&H theory in length

The weight-specific survivorship gives the fraction of fish at size w_0 that attains size w . The mean size-at-death of these fish above size w_0 is obtained by integrating the survivorship,

$$\bar{w}(w_0) = w_0 + \int_{w_0}^{\infty} l(x, w_0) dx$$

For a steady state situation, $\bar{i}(t_0)$ in Ex. 1 and $\bar{w}(w_0)$ also express the mean age above age t_0 and the mean size above size w_0 in the total population.

Suppose the dynamics of the year-class are described by the B&H (cohort) model. The fundamental elements of this model are a constant rate of mortality and the von Bertalanffy growth equation, i.e. using length as the measure of size,

$$\begin{aligned} \mu_1(L) &= M \\ g_1(L) &= K(L_{\infty} - L) \end{aligned}$$

and we obtain the length-specific survivorship from Eq.(8), replacing w by L ,

$$l_1(L, L_0) = \left[\frac{L_{\infty} - L}{L_{\infty} - L_0} \right]^{M/K}; \quad L_0 \leq L < L_{\infty}$$

The mean length-at-death above L_0 is

$$\bar{L} = L_0 + \int_{L_0}^{\infty} l_1(x, L_0) dx = L_0 + \frac{L_{\infty} - L_0}{1 + M/K}$$

or, $M/K = (L_{\infty} - \bar{L})/(\bar{L} - L_0)$. This is the famous Beverton & Holt (1956) equation used in tropical fish stock assessment for a steady state population to estimate total mortality in units of K from the mean length above L_0 in the annual catch. In this application, L_0 denotes a size at which the fish can be considered fully recruited to the fishery in question.

The interpretation of the formula is that the average length depends on the potential growth span ($L_{\infty} - L_0$) and on how fast the fish grow (K) relative to the rate of mortality (M). The survivorship to the mean length-at-death becomes independent of L_0 ,

$$l_1(\bar{L}, L_0) = \left(\frac{M/K}{1 + M/K} \right)^{M/K} = (1 + K/M)^{-M/K}$$

and it decreases towards a minimum of $\exp(-1)$ or 36.8% for increasing values of M/K . As an example, we may consider North Sea plaice. B&H (1957) estimated $K = 0.095 \text{ yr}^{-1}$ and $L_{\infty} = 68.5 \text{ cm}$ from size-at-age of adult plaice. Fish of length 10 cm (ca. 1 year of age) will, on average, attain a size of 28.5 cm if $M = 0.1 \text{ yr}^{-1}$ but only 15 cm if $M = 1 \text{ yr}^{-1}$. The survival to the mean length-at-death is 50% if $M = 0.1$, 38.5% if $M = 1$ and 36.8% if $M = 36.5$ (10% d⁻¹). Larvae of length 5 mm will obtain a mean length-at-death of only 6.77 mm with a daily mortality of 10%.

4.2. B&H theory in weight

Now returning to weight, the von Bertalanffy growth equation (VBGE) reads

$$g(w) = Hw^{2/3} - kw = 3Kw^{2/3} (W_\infty^{1/3} - w^{1/3}) ; \quad K = k/3 ; \quad W_\infty = (H/k)^3$$

and we obtain the weight-specific survivorship from Eq.(8),

$$l(w_1, w_0) = \left[\frac{H - kw_1^{1/3}}{H - kw_0^{1/3}} \right]^{3M/k} = \left[\frac{W_\infty^{1/3} - w_1^{1/3}}{W_\infty^{1/3} - w_0^{1/3}} \right]^{M/K} = \left[\frac{G(w_1)}{G(w_0)} \right]^{3M/k} \left(\frac{w_1}{w_0} \right)^{M/k}$$

where G denotes the specific or instantaneous rate of growth, i.e.

$$G(w) = Hw^{-1/3} - k = k [(W_\infty/w)^{1/3} - 1]$$

Note that, since body-weight is considered to be proportional to the cube of body-length in the B&H theory, results in weight may be directly translated into results in length or *vice versa*. Age-at-size, $t = f^{-1}(w)$, is obtained from Eq.(10), integrating $1/g(w)$,

$$\tau = t - t_0 = -\frac{1}{K} \ln \left(\frac{W_\infty^{1/3} - w^{1/3}}{W_\infty^{1/3} - w_0^{1/3}} \right) = -\frac{3}{k} \ln \left(\frac{H - kw^{1/3}}{H - kw_0^{1/3}} \right)$$

In the case of North Sea plaice, B&H estimated $k = 0.285 \text{ yr}^{-1}$ and $H = 4.05 \text{ g}^{1/3} \text{ yr}^{-1}$ ($W_\infty = 2870 \text{ g}$). Suppose $w_0 = 0.5 \text{ mg}$ at the onset of feeding. According to this model, it takes the plaice larva 106 days to grow to a size of 0.1 g hereby increasing its body-weight by a factor of 200. Suppose the rate of mortality is about 11 yr^{-1} or 3% per day. The survival across the size interval is then 4.15%. The specific growth rate decreases from 14% at first feeding to 2.3% per day at weight $200w_0$. With a mortality rate of about 3% per day, the biomass of the year-class begins to decline at a body-weight, W_b , of about 0.05 g,

$$W_b = W_\infty / (1 + M/k)^3 ; \quad G(W_b) = M \text{ in B\&H theory}$$

Thus, the specific growth rate drops to the level of natural mortality already at a weight of ca. $100w_0$ which is more than 62000 times smaller than W_∞ . One of the problems here is that the mortality rate is not likely to remain constant when the plaice larvae increase in weight by a factor of 200 in the course of about 100 days (see below and Ex. 7.3). We note that the growth rate continues to increase until the fish has attained a weight W_m which is only about 2.5 times smaller than W_∞ ,

$$W_m = {}^{8/27} W_\infty ; \quad \text{MAX } g(w) \text{ or MIN } (M/g) \text{ at } W_m \text{ in B\&H theory}$$

If $M = k/2$ or 0.143 yr^{-1} in the case of adult plaice, then $W_b = W_m$ and the biomass of the year-class attains its maximum at body-size $0.30W_\infty$ or 850 g, the point of inflexion at the sigmoidal growth curve.

Note that W_m occurs at $2/3 L_\infty$ and designates the weight at maximum survival across a small weight interval because $\mu(w)/g(w)$, the physiological rate of mortality, here attains its minimum value. If length is used as the measure of size, then the physiological rate of mortality does not attain its minimum value at $2/3 L_\infty$! The convex shape of the von Bertalanffy growth curve in length creates a concave

shape of the physiological rate of mortality at length. The maximum survivorship across a small length interval with VBGE, thus, occurs at the smallest length.

4.3. Mortality inversely proportional to length

Suppose natural mortality decreases with increasing body-size. There is empirical evidence to support such an effect and a power function of size seems to produce the trend (e.g. Peterson and Wroblewsky, 1984). Empirical evidence also indicates that G and M are closely related in early life (Ware, 1975). Mass balance considerations for the pelagic ecosystem further indicate that predation mortality in a first approximation may be considered to be proportional to the specific rate of food consumption (see Ex. 10). This suggests the following extension of the B&H theory:

$$\mu(w) = qw^{-1/3} = M_\infty(W_\infty/w)^{1/3}; \quad M_\infty = q/W_\infty^{1/3} = qk/H$$

where q is a constant and M_∞ denotes the rate of natural mortality at size W_∞ . That is, that the rate of mortality of very old fish is considered to be inversely proportional to $W_\infty^{1/3} = H/k$ or to L_∞ . Now the biomass of the year-class is maximised at a body-weight of

$$W_b = ((H - q)/k)^3 = W_\infty (1 - M_\infty/k)^3; \quad G(W_b) = \mu(W_b)$$

where G denotes the specific rate of growth in VBGE. The physiological rate of mortality, μ/g , attains its minimum value at (see Fig. 4.1)

$$W_m = {}^{27/64}W_\infty; \quad \text{MIN}(\mu/g) \text{ at } W_m$$

Suppose $M_\infty \approx 0.5k$. Then for plaice, $M_\infty = 0.14 \text{ yr}^{-1}$ and $q = 2.0 \text{ g}^{1/3} \text{ yr}^{-1}$ and the mortality rate decreases from 6.9% at first feeding ($G = 14\%$) to 1.2% per day ($G = 2.3\%$) when the plaice larva has gained a factor of 200 in weight. Thus, the specific growth rate is about twice the rate of mortality in early life and will gradually approach mortality until the rates become equal at size $W_b = W_\infty/8 = 360 \text{ g}$. The survival to size w is obtained from Eq.(8) by integration,

$$l(w, w_0) = \left[\frac{Hw^{-1/3} - k}{Hw_0^{-1/3} - k} \right]^{3M_\infty/k} = \left[\frac{w^{-1/3} - W_\infty^{-1/3}}{w_0^{-1/3} - W_\infty^{-1/3}} \right]^{M_\infty/K} = \left(\frac{G(w)}{G(w_0)} \right)^{3q/H}$$

Note the three different ways of expressing the power. With $q = 2$ and w_0 denoting the size at first feeding the survival to $w_1 = 200w_0$ becomes 7%. The effect of introducing the size-dependent mortality is most easily interpreted by expressing $\mu(w)$ by the form

$$\mu(w) = (q/H) G(w) + M_\infty; \quad q/H = M_\infty/k$$

Now, it follows directly from the multiplicative rules that the survival to age t is

$$S(t, t_0) = l(f(t), w_0) = (w/w_0)^{-q/H} \exp(-M_\infty(t - t_0))$$

where $w = f(t)$ is the weight-at-age obtained by VBGE and the initial conditions $w_0 = f(t_0)$. If mortality is constant and equal to M_∞ , then the survival to age equals the exponential factor and the survival to size is given by the expressions for l in

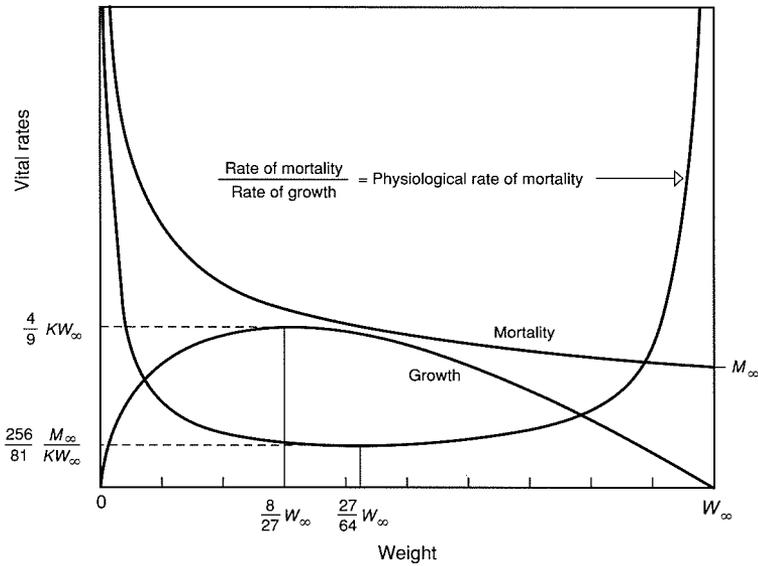


Fig. 4.1. Vital rates at weight when the rate of mortality is inversely proportional to length in the classical B&H model. The rate of growth (VBGE) attains a maximum at size $0.296 W_{\infty}$, the point of inflexion at the sigmoidal growth curve. Mortality approaches a minimum value denoted by M_{∞} . The physiological rate of mortality attains a minimum at weight $0.422 W_{\infty}$, the weight of maximum survival across a small weight interval. An example of parameter values for this size-structured extension of classical theory is $K \approx 0.1 \text{ yr}^{-1}$, $M \approx 0.1 \text{ yr}^{-1}$ and $W_{\infty} \approx 3 \text{ kg}$ for North Sea plaice. The very high size-specific vital rates for the early life stages are included in the same picture although they are not visible in this figure. Actually, the entire first year of life with body-weights from ca. 0.5 mg to 10 g ‘disappears’ from the graph and is virtually represented by the y -axis in this figure.

the preceding section with $M = M_{\infty}$. With mortality inversely proportional to length, the survivorships are reduced by the weight-gaining-factor to the power of $-q/H$. In the example with North Sea plaice, $q/H \approx 1/2$ and the survival to gain, say, a factor of 100 in weight is reduced to $1/10$ of the survival in the case of constant mortality.

Note that W_m occurs at $3/4 L_{\infty}$ and thus determines the size at maximum survival across dw . If length is used instead as the measure of size then the physiological rate of mortality attains its minimum value at $1/2 L_{\infty}$!

In case of North Sea plaice, $W_m = 1210 \text{ g}$ and the maximum biomass occurs at a smaller weight W_b if $M_{\infty}/K > 3/4$. Perhaps $M_{\infty}/K = 1.5$ used above may be regarded as a qualified guess since Beverton and Holt (1959) found values between 1.5 and 2.5 for the ratio of natural mortality to K . Suppose, however, $M_{\infty}/K = 3/4$, then the specific rate of growth continues to exceed the rate of mortality until the fish attains the size $W_b = W_m$. For plaice, we then obtain $M_{\infty} = 0.07 \text{ yr}^{-1}$ (or $q = 1$) and the mortality at size $W_0 = 0.0005 \text{ g}$ is reduced to 3.4% per day. After gaining

a factor of 200 in weight, this rate of mortality is further reduced by a factor of $200^{-1/3}$ to 0.6% per day. The critical power $q/H = M_\infty / k = 1/3 M_\infty / K$ is reduced by a factor of two to $1/4$ and the fish must gain a factor of $100^2 = 10000$ in weight for this weaker size-dependent mortality to reduce the survival to $1/10$ of the value obtained in the case of size-independent mortality, $M = M_\infty$.

4.4. B&H theory and early life dynamics

The major problem with applying the von Bertalanffy growth equation to larval fish appears to be the rapid decrease in specific growth rate. The estimation of the growth parameters is usually based on mature fish and the later juvenile stages. For North Sea haddock, B&H (1957) obtained $k = 0.60$ and $H = 6.39$ ($W_\infty = 1209$ g) which gives a haddock larva of 0.2 mg wet weight a specific growth rate of 30% d^{-1} at the onset of feeding. When the larva has increased its weight by a factor of 1000, the specific growth rate has dropped to 2.8% d^{-1} . North Sea herring, assuming $k = 1.38$ and $H = 8.83$ (Ursin, 1979) at the onset of feeding ($w_0 = 1/2$ mg), should also start to grow by 30% d^{-1} decreasing by more than a factor of six to 4.8% d^{-1} at $200w_0$ according to the VBGE. However, larval herring in the North Sea and in the laboratory are reported to grow by 10% d^{-1} at the most (Kjørboe *et.al.* 1987, 1988). This problem cannot be solved by selecting another set of (H, k) -parameters for early life since it is the weight-gaining-factor to the power of $-1/3$ that causes the rapid decrease in the specific rate of growth.

The second problem consists of determining where the growth curve should start. The displacement of the growth curve that provides the best fit to size-at-age data for larger fish usually gives quite meaningless sizes for the fish larvae. B&H obtained in this way the weight at birth to be 1.19 g for plaice and 8.64 g for haddock and such weights give specific growth rates of less than 1% d^{-1} . Although the VBGE is useful for illustrating various aspects of size-structured population dynamics, these problems show the need for another metabolic model in describing growth in early life.

The constant rate of mortality constitutes another problem in applying the B&H theory to the juvenile stages. The assumption of mortality being inversely proportional to body length appears to be a step in the right direction. To illustrate the situation from a mortality point of view, we may again use North Sea plaice as an example. First, we consider the adult phase and Beverton and Holt's (1957) estimate of a cumulative mortality of 0.8 from age 5 to 13 years.

The cumulative mortality, CUMW, across a size-interval (w_1, w_2) is obtained from the size-specific survivorship:

$$\text{CUMW}(w_2, w_1) = -\ln l(w_2, w_1) = \frac{M_\infty}{K} \ln \left(\frac{w_1^{-1/3} - W_\infty^{-1/3}}{w_2^{-1/3} - W_\infty^{-1/3}} \right)$$

and inserting $w = f(t)$ using the standard T_0 -notation in fish stock assessment:

$$w^{1/3} = W_\infty^{1/3}(1 - \exp(-K(t - T_0))) ; \quad L \propto w^{1/3} ; \quad L = w = 0 \text{ for } t = T_0$$

gives the cumulative mortality, CUMT through the age-interval (t_1, t_2)

$$\text{CUMT}(t_2, t_1) = -\ln S(t_2, t_1) = \frac{M_\infty}{K} \ln \left(\frac{\exp(K(t_2 - T_0)) - 1}{\exp(K(t_1 - T_0)) - 1} \right)$$

from which we obtain $M_\infty = 0.06 \text{ yr}^{-1}$ using the B&H estimates of $K = 0.095 \text{ yr}^{-1}$, $T_0 = -0.815 \text{ yr}$ and $\text{CUMT}(13, 5) = 0.8$. Note that this estimate, $M_\infty/K = 0.6$, is close to $M_\infty/K = 3/4$ which produces maximum year-class biomass at the size of minimum physiological rate of mortality.

Now, suppose this combined VBGE and size-dependent mortality model of $\mu = 0.06(2867/w)^{1/3} = 0.85w^{-1/3}$ is valid for the juvenile stages. Then, the rate of mortality at the onset of feeding (0.5 mg) is $179M_\infty$ or 11 yr^{-1} and decreases to $6.6M_\infty$ or 0.4 yr^{-1} at size 10 g which is attained at about one year of age according to the growth curve above used by B&H. The rate of mortality is reduced to $2.4M_\infty$ or 0.15 yr^{-1} when the fish become fully mature, say at size 200 g or at almost 5 years of age according to the adult growth curve. However, the cumulative mortality for the juvenile stages apart from the egg- and yolk-sac stages is only $3 = \text{CUMW}(200, 0.0005)$. That is, 5% of first feeding larvae become mature fish! But we know that the cumulative mortality must be about 13 to explain the survival of one in a million.

Note that the age-interpretation of the size-specific cumulative mortality requires a specification of the growth curve. If feeding commences at, say, age two weeks, then the growth curve must be displaced to give weight $w_0 = 0.0005 \text{ g}$ at age $t_0 = 0.0385 \text{ yr}$:

$$w^{1/3} = W_\infty^{1/3} - (W_\infty^{1/3} - w_0^{1/3}) \exp(-K(t - t_0))$$

Thus, $\text{CUMW} = 3$ equals the cumulative mortality to age ca. 5.5 years, the time required to grow to size 200 g according to this growth curve. With the growth curve for adult fish ($w_0 = 0$ and $t_0 = T_0$), the cumulative mortality to age 4.8 years or size 200 g is only 1.3! This is but another illustration of the importance of applying an accurate description of growth particularly for the juvenile stages because of size-dependent growth. The displacement of the growth curve by ca. $3/4$ year along the age-axis to fit adult growth causes the weight at birth to increase to 1.19 g at which size the rate of mortality has dropped to 0.8 yr^{-1} and $\text{CUMW}(200, 1.19) = 1.3$.

The critical factor in determining the cumulative mortality is q/H . In order to see this, it is convenient to use the mixed size-age expression for the survivorship from the preceding section. That is

$$\text{CUMW}(w_1, w_0) = \text{CUMT}(t_1, t_0) = \frac{q}{H} \ln \frac{w_1}{w_0} + M_\infty(t_1 - t_0)$$

where the first term determines the contribution due to the size-dependent part of mortality. The second much smaller term represents the contribution from M_∞ , the size-independent part of mortality. During the first year of life, the logarithmic weight-gaining-factor for plaice is ca. $\ln 20000 = 9.9$ and q/H must be on the order of 0.8 to 0.9 to explain a cumulative mortality of about 9. This gives $M_\infty/K \approx 2.5$ and $M_\infty \approx 0.25$ for plaice ($K = 0.095$). If $K = 0.20$ as for North Sea haddock, then

$M_\infty \approx 0.5$. A $K = 0.46$ as for North Sea herring gives $M_\infty \approx 1.2$! The critical ratio, q/H , can be interpreted here as the instantaneous rate ratio of mortality to growth:

$$\frac{q}{H} = \frac{1}{3} \frac{M_\infty}{K} = \frac{\mu(w)}{G(w)} [1 - (w/W_\infty)^{1/3}]$$

Example 5: Recruitment variations in size-specific theory

A cod spawns between half a million and five million eggs per year. Let us say (following Ursin (1982)) that a mature female on the average lays two million eggs in its short lifetime under heavy fishing pressure and that the number is forty million eggs under light exploitation. The number surviving until maturity in both situations is around two, say from one to ten. Let's say, for this example, that a strong year-class of North Sea cod is achieved when one fish in one million survives to maturity. The same order of survival probability, $l = 10^{-6}$, governs North Sea plaice (Beverton, 1962). If the growth rate decreases by 10% (i.e. $b = 0.9$ in Eq.(11)), then it takes the fish 11% more time to reach the size of maturity with a reduced chance of survival of $0.215 \cdot 10^{-6}$ assuming an unchanged rate of mortality (i.e. $c = 1$ in Eq.(11)). This weak year-class is, thus, a factor of 4.6 smaller than the strong year-class. If, instead, growth is only reduced by 5% but happens to coincide with a simultaneous increase in mortality of 5% (i.e. $b = 0.95$ and $c = 1.05$), then the ratio of year-class strengths becomes 4.3. Hence, variations in growth and mortality rates on the order of a few percent during the juvenile stages can explain a five fold variation in year-class strength which is the order of magnitude observed for North Sea plaice and cod.

In this cod example, we have considered the variations in recruitment to the adult stock that would arise from small but persistent changes in growth and mortality when the cod is gaining a factor 10^6 or 10^7 in weight during the first ca. three years of life. Clearly, the effect of annual changes in growth and mortality rates on the recruitment variations will be smaller if these changes only are considered to take place at some part of the juvenile stages. According to the multiplicative rules, it becomes entirely a question about the magnitude of the survival. The smaller the survival, the greater the effect of changes in the vital rates on recruitment variations. Houde (1987) gives some examples along these lines and it may be of interest to give a simple but general formula for calculating the recruitment variations. It follows from Eq. (11) that recruitment to a certain size will vary by a factor of

$$\text{Ratio of year-class strength at size} = [\text{Size-specific survivorship}]^{\frac{-400x}{(100+x)(100-x)}}$$

where x denotes the percentage (opposite) changes in growth and mortality rates that are considered to produce good and bad year-classes. For example, if $x = 5\%$ then the ratio of a good year-class ($b = 1.05$ and $c = 0.95$) to a bad year-class ($b = 0.95$ and $c = 1.05$) becomes the survival to the power of $-2000/(105 \cdot 95) = -0.2005$. In the case of a survivorship of 0.01 for the larval stage of Atlantic herring (cf. Ex.2), recruitment to metamorphosis will vary by a factor of 2.5 due to $\pm 5\%$ changes in the vital rates from the onset of feeding. If these changes occur

during the entire first year of life and if the herring, under normal conditions, attains a length of, say, 10 cm at one year of age ($l \approx 0.0001$), then recruitment to this size will vary by a factor of 6.3. Table 5.1 gives some further results.

Table 5.1. Ratio of year-class strength at size due to $\pm 5\%$ to $\pm 25\%$ changes in the unknown growth and mortality rates that produce a given size-specific survivorship.

Size-specific survivorship	Ratio of year-class strength due to a percentage change in vital rates				
	$\pm 5\%$	$\pm 10\%$	$\pm 15\%$	$\pm 20\%$	$\pm 25\%$
0.1	1.6	2.5	4.1	6.8	12
0.01	2.5	6.4	17	46	136
0.001	4.0	16	69	320	1600
0.0001	6.3	41	290	2200	18000
0.00001	10	105	1200	15000	215000
0.000001	16	270	4800	100000	2500000
0.0000001	25	670	20000	680000	29000000

Recruitment to North Sea haddock varies by a factor of 100 but that could be explained alone by occasional 20-25% annual changes in the vital rates during a period in early life that under normal growth and mortality conditions is characterised by a size-specific survivorship of 0.01. It could also be explained by a 10% change in the vital rates from first feeding to that juvenile size at which only one in 100,000 survives under average conditions. However, North Sea haddock present an extreme example of recruitment variations. Very few commercially important fish stocks worldwide vary by a factor of more than 50 in recruitment (Rothschild, 1986). The usual situation is that recruitment to the age one year varies within 25-50% of the long-term mean – see also Fig. 1. This corresponds to a factor of only 2-3 in normal annual recruitment variation. It appears from Table 5.1 that we have more reason to be astounded at the stability of recruitment than at its variability.

Example 6: The effects of changes in the rate of growth on survival

The question of whether or not a change in growth may affect mortality needs some consideration. As a basis, we first illustrate the fundamental impact of a change in the rate of growth on the size-specific survivorship – created by the related change in the time required to grow through the size interval considered. Thus, the changes in the survival considered in Section 6.1 are caused solely by changes in growth and not by simultaneous changes in the rate of mortality (but see Table 5.1 for clarification of the intensive effect of simultaneous and opposite changes in the vital rates). Section 6.2, then, deals with the additional effect on the survival that are caused by mortality changes at size induced by growth changes in the case of an age-dependent rate of mortality. The opposite situation dealing with the effect of mortality changes at age caused by growth changes in

the case of a size-dependent rate of mortality is described in Section 6.3. These simple situations indicate that the sensitivity of size or age-specific recruitment to changes in the growth rate during the larval stage is very much related to the particular way in which the rate of mortality depends on the characteristics of the fish (e.g. size, growth rate or age). The situation is even more complicated when the vital rates depend on the number of fish in the year-class (see Ex. 7 and Ex. 8).

6.1. *The effect of the power-rule for a change in growth*

The relative effect of a change in the growth rate on the survival through a size interval increases with decreasing survival. The percentage change in survival is according to Eq. (11):

$$(l_*/l - 1)100 = (l^{(1/b)-1} - 1)100 = (l^{-1/(1+100/x)} - 1)100$$

where $b = 1 + x/100$ denotes the constant factor of change in growth rate throughout the size interval in question. For example, a survival of 0.1 would increase by 58% if growth increases by 25% but a survival of, say, 0.01 would increase by 150%, and $l = 0.001$ would increase by almost 300%! Table 6.1 gives such percentage changes in recruitment to a certain size as a function of the original survivorship for various percentage changes (x) in the growth rate.

Table 6.1. Percentage changes in recruitment at size due to -25% to +25% changes in the unknown rate of growth that produces a certain size-specific survivorship assuming the unknown rate of mortality is unchanged.

Survivorship	Percentage change in survivorship due to a percentage change in the rate of growth					
	-25%	-10%	-5%	5%	10%	25%
0.15	-47%	-19%	-9.5%	9.5%	19%	46%
0.10	-54%	-23%	-11%	12%	23%	58%
0.05	-63%	-28%	-15%	15%	31%	82%
0.01	-78%	-40%	-22%	25%	52%	150%
0.005	-83%	-44%	-24%	29%	62%	190%
0.001	-90%	-54%	-30%	39%	87%	300%
0.0001	-95%	-64%	-38%	55%	130%	530%

In case of a growth reduction of, say, 25%, the recruitment to a certain size will decrease by 54%, 78% or 90% if the survival to that size before the growth reduction was 0.1, 0.01 or 0.001 respectively.

The survival during the early life history stage from size at first feeding to size at metamorphosis is believed to be in the order of a few percent for many marine fish (Houde, 1987). Thus, the survival that is characteristic for larval fish may be 1, 5 or 10%. The percentage change in such a size-specific survivorship against x (the percentage change in growth) is given by a row in the table and represents a sigmoidal curve. Each of these curves starts at -100% (i.e. $l_* = 0$) when growth is zero and approaches an asymptote of $(1/l - 1)100\%$ (i.e. $l_* = 1$) at very high

growth rates. The point of inflexion occurs at $b_i = -1/2 \ln l$ or $x_i = -100 - 50 \ln l$. The curve based on a survival of $l = \exp(-2)$ or 13.5% has, therefore, its inflexion point exactly at $x_i = 0\%$ (or $b_i = 1$). Since the domain of inflexion determines the part of the curve with maximum slope, we may say that $x_i = 0\%$ characterizes the most sensitive part of a 13.5% survival curve with respect to the impact of changes in growth on relative recruitment. Curves based on survival greater than 13.5% exhibit inflexion at a growth reduction (i.e. $b_i < 1$ or $x_i < 0\%$). Survival less than 13.5% produce curves with inflexion occurring at a growth increase. For the 10% curve which is represented by the second row in Table 6.1, the point of inflexion has moved to $x_i = 15\%$ and the effect of a small percentage growth increase is slightly higher than the numerical effect of the same percentage growth reduction. For the 5% and 1% curves (represented by the third and fourth rows), inflexion occurs at growth increases of 50% and 130%, respectively. As a rule of thumb, the percentage change in survival is $-x \ln l$ where x denotes a small percentage change in growth. This linear approximation to the rows in Table 6.1 in the neighbourhood of $x = 0\%$ is, of course, best for $l \approx 13.5\%$, i.e. when the point of inflexion is $x = 0\%$. If, for example, $l = 0.01$ then the slope of the curve at $x = 0\%$ is $-\ln l = 4.605$ but the maximum slope at $x_i = 130\%$ is almost three times higher (11.75) and the approximation, thus, underestimates the increase in survivorship in the case of a growth increase.

We note again that the relative changes in the size-specific survival considered in Table 6.1 are caused only by relative changes in the unknown rate of growth and not by direct or indirect changes in the unknown rate of mortality at size.

6.2. Survival to size with age-dependent mortality

If the rate of mortality is an explicit function of age, $M(t)$, then the survival to a certain age remains constant independent of changes in growth. However, the impact of a change in growth on the survival to size is not described by Eq. (11) or Table 6.1 in this case because $\mu(w)$ will change as well! To investigate this point further, we consider the rate of mortality at size w before and after the change in growth

$$\begin{aligned} \mu(w) &= M(f^{-1}(w)) ; & t &= f^{-1}(w) & df^{-1}/dw &= 1/g(w) \\ \mu_*(w) &= M(f_*^{-1}(w)) ; & t_* &= f_*^{-1}(w) ; & df_*^{-1}/dw &= 1/g_*(w) \end{aligned}$$

Here f^{-1} denotes the inverse function. That is $\tau_1 = t_1 - t_0 = f^{-1}(w_1) - f^{-1}(w_0)$ is the time required to grow through the size interval (w_0, w_1) as given by Eq. (10). The star designates the change. A growth increase, $g_*(w) > g(w)$, implies that size w is attained at an earlier age, $f_*^{-1}(w) < f^{-1}(w)$, and the rate of mortality at size w becomes greater than the initial, $\mu_*(w) > \mu(w)$, if $M(t)$ is a decreasing function of age. The physiological rate of mortality, $-\ln N/dw = \mu(w)/g(w)$ will, therefore, not decrease by a factor of $1/b$ due to an increase in growth rate by a factor b because the simultaneous increase in $\mu(w)$ provides a compensatory effect. The combined effect, however, must be that the survival to a certain size will increase because that size now is reached at an earlier age at the profit of a smaller cumulative mortality.

Suppose the rate of growth in length is constant and mortality decreases inverse-proportional to a linear function of age as in Ex. 1. That is

$$M(t) = ac/(1 + ct) \quad \text{or} \quad S(t,0) = (1 + ct)^{-a}; \quad t_0 = 0$$

$$g_1(L) = H_1 \quad \text{or} \quad L = f_1(t) = L_0 + H_1 t; \quad t = f_1^{-1}(L) = (L - L_0)/H_1$$

The size-specific mortality and survival become

$$\mu_1(L) = M(f_1^{-1}(L)) = \frac{ac}{1 + c(L - L_0)/H_1}$$

$$l_1(L, L_0) = S(f_1^{-1}(L), 0) = (1 + c(L - L_0)/H_1)^{-a}$$

Suppose $c = H_1/L_0 = 0.05 \text{ d}^{-1}$ and $a = 2$. That is, the larvae begin to grow in length with 5% per day while exposed to a mortality rate of 10% per day. After $t_1 = 20$ days, the surviving larvae have gained a factor of 2 in length and the specific rates of growth in length and mortality have been reduced to half their initial values. The survival is

$$l_1(2L_0, L_0) = S(20, 0) = (1 + 1)^{-2} = 0.25; \quad a = 2, \quad c = 0.05, \quad H_1 = 0.05L_0$$

Now, suppose the rate of growth increases by 25%. That is $H_{1*} = 1.25H_1$ without changing a and c , the constants of age-dependent mortality. Then the survival to the age of 20 days will not change, $S_* = S$, but the length-specific survival will increase because the doubling in length now is achieved already after $t_{1*} = t_1/1.25$ or 16 days:

$$l_{1*}(2L_0, L_0) = S(16, 0) = (1 + 1/1.25)^{-2} = 0.309; \quad H_{1*} = 1.25H_1$$

Using the multiplicative rule, $S(20, 0) = S(16, 0)S(20, 16)$, it follows that the length-specific survival increases by a factor of $1/S(20, 16)$. Thus,

$$l_{1*} = l_1 \left[\frac{1 + ct_1}{1 + ct_{1*}} \right]^a = l_1 (2/1.8)^2 = 1.235 l_1$$

and l_1 increases by 23.5% or less than the 32% as in the case of unchanged mortality at size ($l^{(1/b)-1} = 1.32$; $l = 0.25$, $b = 1.25$; see preceding section).

Returning to weight, the general situation may be described as follows: Let CUMW and CUMT denote cumulative mortality in weight and age. Then, by changing the integral variable from w to $t = f^{-1}(w)$,

$$\text{CUMW}(w_1, w_0) = \int_{w_0}^{w_1} \frac{\mu(w)}{g(w)} dw = \int_{f^{-1}(w_0)}^{f^{-1}(w_1)} M(t) dt = \text{CUMT}(f^{-1}(w_1), t_0)$$

and, in the same way, we obtain after the growth increase that

$$\text{CUMW}_*(w_1, w_0) = \text{CUMT}(t_{1*}, t_0); \quad t_{1*} = f_*^{-1}(w_1)$$

Since the age-at-size decreases, $t_{1*} < t_1$, CUMW_* will be smaller than CUMW and the size-specific survival will, consequently, increase. It follows that

$$\text{CUMT}(t_1, t_0) = \text{CUMT}(t_{1*}, t_0) + \text{CUMT}(t_1, t_{1*}) \text{ or}$$

$$S(t_1, t_0) = S(t_{1*}, t_0) S(t_1, t_{1*}) \text{ or } l(w_1, w_0) = l_*(w_1, w_0) S(t_1, t_{1*})$$

The time required to grow to size w_1 decreases by a factor of $1/b$ when growth increases by b :

$$t_{1*} - t_0 = (t_1 - t_0)/b$$

However, the cumulative mortality in the age interval (t_0, t_{1*}) is greater than $1/b$ of the cumulative mortality in the b times larger age interval, (t_0, t_1) , because mortality here is considered to decrease with increasing age. The cumulative mortality through the size interval (w_0, w_1) simply decreases by the cumulative mortality across the age interval (t_{1*}, t_1) and this is why $l_* = l/S(t_1, t_{1*})$ expresses the impact of the growth increase.

6.3. Survival to age with size-dependent mortality

If the rate of mortality is an explicit function of size, $\mu(w)$, then the impact of changes in growth on the survival through a certain size interval is still exemplified by the b -rule in Eq. (11) or Table 6.1 because $\mu(w)$ is not affected by a change in the growth rate. The survival to a specific age t_1 , however, is now depending on the rate of growth. We proceed as before and consider the rate of mortality at time t before and after the change in growth

$$M(t) = \mu(f(t)) ; \quad w = f(t), \quad df/dt = g(w)$$

$$M_*(t) = \mu(f_*(t)) ; \quad w_* = f_*(t), \quad df_*/dt = g_*(w)$$

Here, f again denotes the particular growth curve defined by the initial conditions: size w_0 at age t_0 . If, for example, $\mu(w)$ is a decreasing function of size and we consider a growth increase (i.e. $b > 1$) then the fish has attained a greater weight at age t after the change, $f_*(t) > f(t)$, and the rate of mortality at time t is, thus, smaller than the initial, $M_*(t) < M(t)$. Then the cumulative mortality to age t_1 also becomes smaller than the initial and survival to age t_1 increases.

Suppose the rate of growth in length is constant as in the previous example and the rate of mortality is inversely proportional to length. That is

$$\mu_1(L) = q_1/L \quad \text{and} \quad g_1(L) = H_1 \quad \text{or} \quad L = f_1(t) = L_0 + H_1 t ; \quad t_0 = 0$$

and the size-specific survival becomes

$$l_1(L, L_0) = (L/L_0)^{-q_1/H_1}$$

from which we obtain the age-dependent mortality and survivorship,

$$M(t) = \mu_1(f_1(t)) = q_1/(L_0 + H_1 t)$$

$$S(t, 0) = l_1(f_1(t), L_0) = (1 + H_1 t/L_0)^{-q_1/H_1}$$

Note that $H_1/L_0 = c = 0.05 \text{ d}^{-1}$ and $q_1/H_1 = a = 2$ in the terminology of the previous example with age-dependent mortality. Thus, these values produce the same initial survival as before:

$$S(20, 0) = l_1(2L_0, L_0) = 0.25 ; \quad H_1 = 0.05L_0$$

If $H_{1*} = 1.25H_1$ then the survival to doubling in length increases according to the $b = 1.25$ rule because the size-dependent mortality remains constant (and length $2L_0$ is attained after 16 days):

$$l_{1*}(2L_0, L_0) = [l_1(2L_0, L_0)]^{1/1.25} = 0.33 \quad ; \quad H_{1*} = 1.25H_1$$

After 20 days length $2.25L_0$ is attained and the age-specific survival becomes

$$S_*(20, 0) = l_{1*}(2.25L_0, L_0) = 2.25^{-2/1.25} = 0.27 \quad ; \quad H_{1*} = 1.25H_1$$

The relationship between S_* and l_{1*} follows directly from the multiplicative rule:

$$l_{1*}(2.25L_0, L_0) = l_{1*}(2L_0, L_0) l_{1*}(2.25L_0, 2L_0) \quad \text{or}$$

$$S_* = l_1^{1/1.25} l_{1*}(2.25L_0, 2L_0) = S^{1/1.25} (2.25/2)^{-2/1.25} = 0.33 \cdot 0.828$$

The important point is that the age-dependent mortality now changes with changes in the rate of growth. The above results are obtained with the age-dependent mortality model of the previous example, $M(t) = M(0)/(1 + ct)$, if the mortality change, $c_* = bc$, accompanies the growth change, $H_{1*} = bH_1$ (and if $M(0) = ac = q_1/L_0$ is kept constant).

Returning to weight, the general situation may be treated as follows: Before the growth increase, $w_1 = f(t_1)$ and the survivorships are equal

$$l(w_1, w_0) = S(t_1, t_0) \quad \text{or} \quad \text{CUMW}(w_1, w_0) = \text{CUMT}(t_1, t_0) \quad ; \quad w_0 = f(t_0)$$

After the growth increase, the size-specific survival increases according to the b -rule, $l_* = l^{1/b} = S^{1/b}$, but $w_{1*} = f_*(t_1) > w_1$ and we obtain

$$\text{or} \quad \text{CUMT}_*(t_1, t_0) = \text{CUMW}_*(w_{1*}, w_0) = \text{CUMW}_*(w_1, w_0) + \text{CUMW}_*(w_{1*}, w_1)$$

$$S_*(t_1, t_0) = (S(t_1, t_0))^{1/b} l_*(w_{1*}, w_1) \quad ; \quad b > 1$$

Hence, $S_* < S^{1/b}$ in the case of a growth increase and it was shown above that $S_* > S$ if mortality decreases with increasing size. Thus, in this mortality situation which is the most realistic one, a growth increase will lead to an improved survival (at recruitment) whether recruitment is measured at a specific size or at a specific age. This does not mean that recruitment (in terms of numbers) also will increase (see Ex. 7.3) unless, of course, the initial number remains constant.

If the rate of mortality in some year should happen to increase with increasing size through a certain range, then a growth increase will still improve the size-specific survival but age-specific survival will diminish:

$$S_* < S < S^{1/b} = l_* \quad ; \quad M_*(t) > M(t) \quad ; \quad b > 1$$

Suppose mortality in the example above increases proportionally to length. That is

$$\mu_1(L) = q_0 L \quad \text{and} \quad g_1(L) = H_1 \quad ; \quad H_1/L_0 = q_0 L_0 = 0.05 \text{ d}^{-1}$$

and μ_1 doubles from 5% to 10% per day when length increases from L_0 to $2L_0$ during the first 20 days. The survivorships are

$$l(L, L_0) = [\exp(-1/2 q_0 (L^2 - L_0^2))]^{1/H_1} \quad ; \quad L = 2L_0$$

$$S(t, 0) = \exp(-q_0 L_0 t) [\exp(-1/2 q_0 t^2)]^{H_1} \quad ; \quad t = 20 \text{ days}$$

and equal 0.223. A growth increase of 25% causes the size-specific survival to increase by 35% to $l_* = l^{1/1.25} = 0.301$ but the age-specific survival to decrease by 11.7% to $S_* = 0.197$. However, the latter recruits are of size $2.25L_0$ or 12.5% longer than $2L_0$.

Example 7: Further considerations following Beverton & Holt (1957) on the Ricker & Foerster (1948) suggestion

In their computation of production for the young sockeye salmon of Cultus Lake, British Columbia, Ricker & Foerster (1948) noted that predation apparently represents the major cause of mortality. R&F (p.174) write 'the mortality rate is greatest while the sockeye are very small, and the prolongation of this period of small size (hence greater vulnerability) in years when many fry are present appears to be a part of the mechanism whereby the total size of the population is regulated'. R&F, observing the small amount of food eaten by the very small sockeye in May, further suggested with some reservation that 'in years of very large populations some might even succumb to starvation'. This is but a logical consequence of the first hypothesis.

The R&F suggestion constitutes the biological basis of the present paper and the remaining examples are devoted to simple quantifications of this regulatory mechanism. Stimulated by Beverton & Holt's (1957) brief but very interesting considerations of the R&F suggestion, the aim of the present example is to elucidate the effect of start-density dependent growth on recruitment to size and age. The term start-density means that the growth rate depends on the initial numbers and not on the present numbers as would be the case in density-dependent growth (see Ex. 8). It is important to make this discrimination between stock and density dependent processes (Harris, 1975). The designation start-density is here preferred to stock because the processes that lead to the initial number of N_0 fish of body-weight w_0 at age t_0 are not considered. It should be noted that the rate of mortality is considered to be density independent throughout this example (but see the closing Section 7.5). The initial condition is interpreted as the onset of feeding in the present context but the theory does not depend on this choice. The example represents a continuation of Exs 4 and 6 with the changes in the rate of growth explained in the simplest possible way by year-to-year changes in numbers. The intention is to provide a basis for more consistent studies of the possible effects of food-competition on recruitment.

7.1. First interpretation of B&H on R&F

The very first quantification of the R&F suggestion and its impact on recruitment was provided by Beverton & Holt (1957, p. 55) using the von Bertalanffy growth equation as a starting point,

$$g(w) = Hw^{2/3} - kw \quad ; \quad W_\infty = (H/k)^3$$

Suppose the larvae begin feeding at age t_0 and weight w_0 . Following B&H, let us further suppose that the larvae are grazed by a predator until they reach a specific

size w_c at a certain age t_c , after which they are too large to be eaten by the predator. We assume that the predator exerts a mortality M_1 in addition to M_0 , the mortality of other causes, i.e. the total rate of mortality in the size range of the predator field ('the window'), $M_1 + M_0$, drops to M_0 from size w_c onwards. The survivorship to t_r , the age of recruitment becomes, using the multiplicative rules,

$$S(t_r, t_0) = \exp(-M_0(t_r - t_0)) \exp(-M_1 \tau_c) ; \quad \tau_c = t_c - t_0$$

where τ_c is the time required to grow through the width of the predator window, $\Delta w = w_c - w_0$. Now, if there is competition for food among the larvae then the rate of food consumption by each larva or H , the coefficient of net anabolism will depend on N_0 , the number of first feeding larvae. For a first approximation, B&H in reality regard H (or $W_\infty^{1/3}$) as being inversely proportional to N (see Section 7.4 for discussion). At low weights (i.e. $w_0^{1/3} \ll W_\infty^{1/3}$) and over a short period of time (i.e. $\tau_c \ll 3/k$), we also find that τ_c is inversely proportional to H (see below). These relationships give

$$\tau_c \propto \frac{1}{H} \propto [\text{rate of food consumption}]^{-1} \propto N_0$$

so the critical survival factor becomes

$$\exp(-M_1 \tau_c) = \exp(-N_0 \text{ constant})$$

which leads to the Ricker type (Ex. 3) of recruitment curve,

$$R = N_0 S(t_r, t_0) \propto N_0 \exp(-N_0 \text{ constant}) ; \quad t_c(N_0) < t_r$$

The first approximation, $\tau_c \propto 1/H$, underlying these early considerations of the R&F suggestion is obtained by neglecting the k -term of the growth equation, i.e. putting

$$g(w) = Hw^{2/3} \quad \text{or} \quad G(w) = Hw^{-1/3}$$

which, with a constant rate of mortality, M , through Eqs (11) and (13) leads to the survivorship,

$$l(w, w_0) = \exp(-(w^{1/3} - w_0^{1/3})3M/H) = \exp(-M\tau)$$

and the time required to grow to size w ,

$$\tau = (w^{1/3} - w_0^{1/3})3/H$$

This is a good approximation to the age-at-size obtained by the von Bertalanffy growth equation (VBGE). Suppose the predator window or the critical size range is specified by $w_c/w_0 = 200$ and put $H = 4.05 \text{ g}^{1/3} \text{ yr}^{-1}$, $k = 0.285 \text{ yr}^{-1}$ and $w_0 = 0.5 \text{ mg}$ as in Ex. 4 for North Sea plaice. The critical period of 106 days in the case of VBGE becomes 104 days using the above formula. The reduction of 2 days is due to faster growth because the k -term or the rate of fasting metabolism has been neglected. In the approximation, the specific growth rate decreases from 14.0% at the onset of feeding to 2.4% at the end of the critical period. Compared to these percentages, the specific growth rate in VBGE is reduced by $k = 0.00078 \text{ d}^{-1}$ or 0.08% per day.

Recalling from Ex. 4.4 that VBGE is not the best starting point for describing larval growth, it seems more appropriate to interpret $g(w) = Hw^{2/3}$ as a ‘new model’ rather than to regard the B&H considerations as based on an approximation to VBGE. With one amendment, this growth model seems to constitute a promising and simple starting point for describing growth at least in early life. In combining anabolism and catabolism in one single term we expect (based on traditional physiological considerations) that the exponent should take a value between $2/3$ and 1. This will reduce the fall of specific growth rate during early life compared to the situation considered above with a power of $2/3$. This type of a general allometric growth model is considered in Ex. 10. In the present context of B&H on R&F, the power of $2/3$ is maintained but generalizations are straight forward (see also Section 7.5).

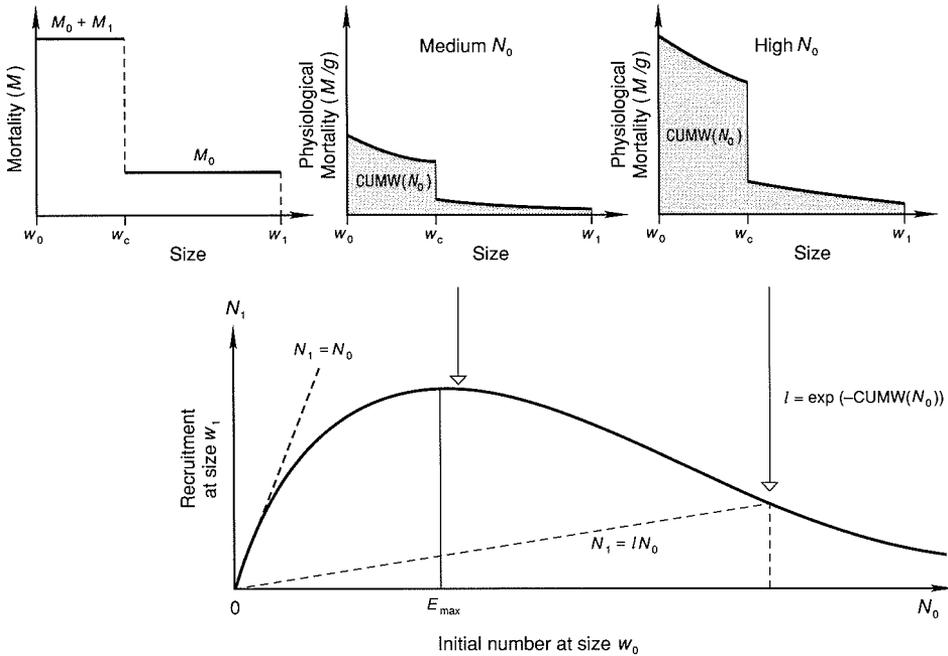


Fig 7.1. Illustration of the Ricker curve for recruitment at size (bottom fig.) in the B&H one predator situation described by an extra mortality coefficient M_1 in the size-window (w_0, w_c) (top left fig). The time required to grow to a certain size and hence CUMW, the size-specific cumulative mortality increases in proportion to the initial number, N_0 fish sized w_0 , because the rate of growth is considered inversely proportional to N_0 .

The second approximative relationship states that H , the coefficient in the allometric growth model, is inversely proportional to the start density:

$$H(N_0) = H_1/N_0$$

Fig 7.1 illustrates that this assumption leads to a Ricker curve for recruitment to a specific size, w_1 . The cumulative mortality across the size-interval from w_0 to

w_1 becomes proportional to N_0 and we can write

$$\text{CUMW}(N_0) = N_0/E_{\max} ; \quad E_{\max} = [M_0\tau_0(1) + M_1\tau_c(1)]^{-1}$$

where $E_{\max}^{-1} = \text{CUMW}(1)$ denotes the cumulative mortality in case of $N_0 = 1$ calculated as the sum of the contributions from M_0 and M_1 . The time-units to grow to the critical size w_c and to the size of recruitment can be expressed as functions of weight using the age-to-weight formula above:

$$\tau_c(1) = (w_c^{1/3} - w_0^{1/3})3/H_1 \quad \text{and} \quad \tau_1(1) = (w_1^{1/3} - w_0^{1/3})3/H_1$$

The equation for the recruitment curve in Fig. 7.1 can now be written as

$$N_1 = N_0 \exp(-\text{CUMW}(N_0)) = N_0 \exp(-N_0/E_{\max})$$

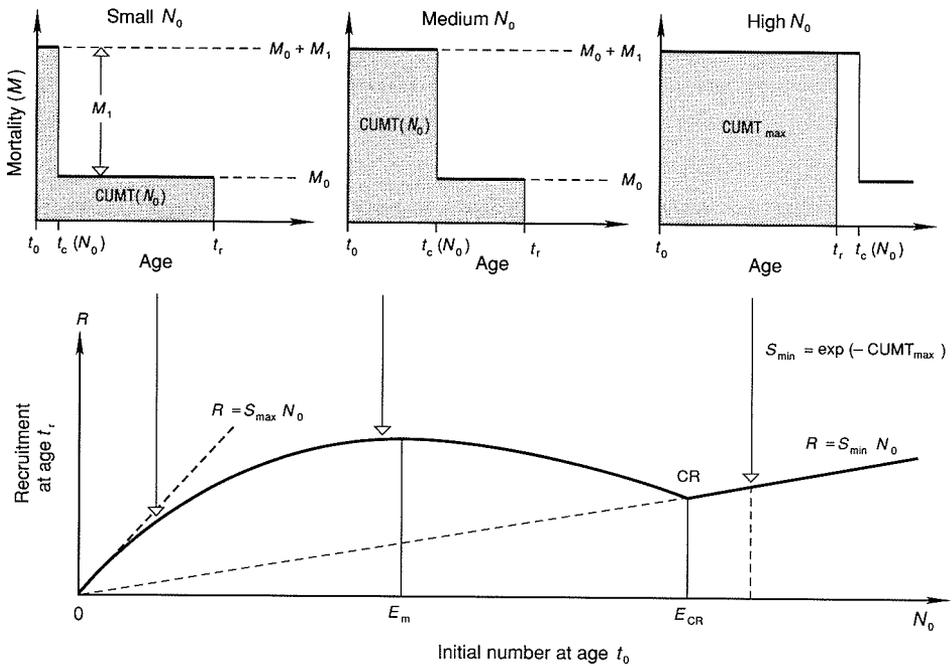


Fig 7.2. Illustration of recruitment at a specific age in B&H on the R&F suggestion. This is the age equivalent to the size version shown in Fig. 7.1. When the initial number of larvae, N_0 is small, the larvae grow quickly through the predator field ($t_c - t_0$ is small in top left fig.) and recruitment is almost entirely determined by the cumulative mortality of other causes (S_{\max} -line in bottom fig.). As N_0 increases (top mid-fig.), the critical time, $\tau_c = t_c - t_0$, increases in proportion to N_0 and recruitment follows a Ricker curve. At $N_0 = E_{CR}$, the rate of growth has been reduced to such a low level that surviving larvae leave the predator field exactly at the age of recruitment (critical point CR). The cumulative mortality has reached its maximum and the recruitment graph is transformed into a straight line (the S_{\min} -line) for $N_0 > E_{CR}$ (top right fig.).

The situation for recruitment at age is shown in Fig. 7.2. The time required to grow through the predator field increases proportionally to N_0 :

$$\tau_c(N_0) = t_c(N_0) - t_0 = N_0 \tau_c(1)$$

Thus, the cumulative mortality to recruitment is

$$\text{CUMT}(N_0) = M_0 \tau_r + M_1 \tau_c(N_0) ; \quad \tau_r = t_r - t_0 , \quad \tau_c(N_0) \leq \tau_r$$

and recruitment takes the form

$$R = \begin{cases} N_0 S_{\max} \exp(-N_0/E_m) ; & N_0 \leq E_{\text{CR}} \\ N_0 S_{\min} & ; \quad N_0 \geq E_{\text{CR}} \end{cases}$$

where the maximum and minimum survival are

$$S_{\max} = \exp(-M_0 \tau_r) \quad \text{and} \quad S_{\min} = S_{\max} \exp(-M_1 \tau_r)$$

Maximum recruitment of the Ricker part of the curve is specified by

$$R_m = S_{\max} E_m \exp(-1) ; \quad E_m = [M_1 \tau_c(1)]^{-1} = \frac{H_1}{3M_1 (w_c^{1/3} - w_0^{1/3})}$$

and the transition to the S_{\min} -recruitment line occurs at

$$R_{\text{CR}} = S_{\min} E_{\text{CR}} ; \quad E_{\text{CR}} = \tau_r / \tau_c(1) = \frac{H_1 \tau_r}{3(w_c^{1/3} - w_0^{1/3})}$$

The ratio of recruitment for these two points becomes

$$\frac{R_{\text{CR}}}{R_m} = \frac{E_{\text{CR}}}{E_m} \cdot \frac{S_{\min}}{S_{\max}} e = M_1 \tau_r \exp(1 - M_1 \tau_r) ; \quad \frac{E_{\text{CR}}}{E_m} = M_1 \tau_r$$

It is, thus, $M_1 \tau_r$, the cumulative mortality to the age of recruitment with the predator mortality acting alone that specifies the relative position of the two points. If $M_1 \tau_r = 1$ then $E_{\text{CR}} = E_m$ and the Ricker part of the recruitment graph is terminated already at the maximum point after which recruitment continues to increase but in direct proportion to N_0 . If $M = 20 \text{ yr}^{-1}$ and $\tau_r = 1/4 \text{ yr}$ (3 months), then $E_{\text{CR}} = 5 E_m$ and most of the Ricker curve is maintained (the critical recruitment point, CR occurring at less than 1/10 of the maximum Ricker level). If the age of recruitment is, instead, about one year ($\tau_r = 1 \text{ yr}$), then the critical point occurs at $20 E_m$ and recruitment is described by a Ricker curve for all relevant values of initial stock sizes.

7.2. The general case of several predators

Suppose the larvae are grazed not by one but by several predators each of which is characterized by a specific size-window. These more or less overlapping size-windows determine a consecutive series of critical size intervals that the larvae must succeed to grow through in order to become recruits. The time spent in the j th size interval is $\tau_j = (w_j - w_{j-1})3/H_j$ with a survival factor of $\exp(-M_j \tau_j)$ where M_j denotes the total predation mortality from the types of predators that contain (w_{j-1}, w_j) in their size-window. This creates a situation of stepwise constant rates of predation

mortality-at-size in excess of M_0 , the constant level of mortality of other causes. If H_j is inversely proportional to N_{j-1} or some other measure of the size of the year-class in the j th interval, then the calculation of the recruitment curves becomes more complex. Ex. 8 deals with this type of true density-dependency in a continuous case. If all the H_j s are inversely proportional to N_0 , then the Ricker type of curve for recruitment at age is maintained irrespective of the number and the character of the predatory species provided that the surviving larvae grow through the entire predator field before the age of recruitment.

For a treatment of this general situation, we can write the vital rates in the following form:

$$g(w, N_0) = H(N_0) g_0(w) ; \quad H(N_0) = H_1/N_0$$

$$\mu(w) = \begin{cases} M_0 + \mu_0(w) & , \quad w_0 \leq w \leq w_c \\ M_0 & , \quad w \geq w_c \end{cases}$$

where $g_0(w)$ and $\mu_0(w)$ (with the condition $\mu_0(w_c) = 0$) denote two arbitrary, positive and continuous functions. Recruitment to size w_1 is, then, described by the following Ricker curve:

$$N_1 = N_0 \exp(-N_0/E_{\max}) \quad \text{with} \quad E_{\max} = \left[\int_{w_0}^{w_1} \frac{\mu(w)dw}{H_1 g_0(w)} \right]^{-1}$$

The cumulative mortality to the age of recruitment becomes a linear function of the start density:

$$\text{CUMT}(N_0) = M_0 \tau_r + N_0/E_m ; \quad E_m = \left[\int_{w_0}^{w_c} \frac{\mu_0(w)dw}{H_1 g_0(w)} \right]^{-1}$$

and we obtain part of a Ricker curve (see Fig 7.3):

$$R = N_0 S_{\max} \exp(-N_0/E_m) ; \quad N_0 \leq E_{CR}$$

where the critical start density is determined as

$$E_{CR} = \tau_r / \tau_c(1) ; \quad \tau_c(1) = \int_{w_0}^{w_c} \frac{dw}{H_1 g_0(w)}$$

The shape of the recruitment curve beyond this critical point depends on $g_0(w)$ and $\mu_0(w)$ but recruitment will ultimately increase towards the asymptote for the constant mortality rate achieved at zero growth rate, i.e.

$$R = S_{\infty} N_0 ; \quad S_{\infty} = \exp(-(M_0 + \mu_0(w_0))\tau_r) = S_{\max} \exp(-\mu_0(w_0)\tau_r)$$

In order to illustrate that part of a Ricker curve is obtained for any formulation of the size-dependent rates of growth and mortality, a rather sophisticated M -shape of size-dependent mortality is used in Fig 7.3. Notice that these and all other calculations of the effects of start-density-dependent growth simply represent applications of the multiplicative rule for a change in the rate of growth. For recruitment at age, the constant part of mortality (M_0) contributes with a constant factor of S_{\max} . The contribution to recruitment-at-age from the size-dependent part of

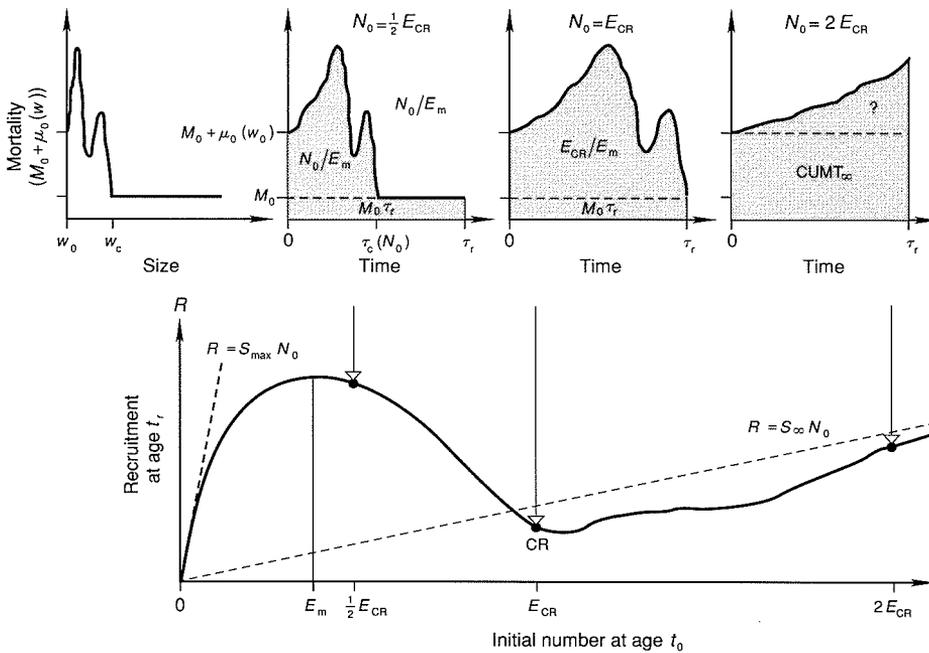


Fig 7.3. Illustration of the generalization of B&C on the R&F suggestion. The rate of mortality is described by an arbitrary continuous function, $\mu_0(w)$, in the size-window (w_0, w_c) in excess of M_0 , the constant level of mortality (top left fig.). The cumulative mortality to age-at- w_c , generated by $\mu_0(w)$ alone, becomes proportional to N_0 because the rate of growth is considered to be inversely proportional to N_0 . Consequently recruitment at age t_r follows a Ricker curve until $N_0 = E_{CR}$ at which point (CR) the critical weight w_c is achieved at age t_r . For $N_0 > E_{CR}$, the mortality function at age is further stretched (top right fig.) and recruitment will follow a complex curve determined by the shapes of the size-dependent rates of mortality and growth. Recruitment ultimately increases towards an asymptote with slope $S_\infty = \exp(-CUMT_\infty)$ determined by the rate of mortality at size w_0 (age t_0). The figure is merely an illustration of the principles but the allometric $2/3$ -power growth model with $w_1 = 200w_0$ was used to draw (by hand) the mortality-at-age curves (top fig.).

mortality ($\mu_0(w)$) follows the multiplicative rule and creates the Ricker curve because here the real age considered ($t_c(N_0) = t_*$ in the terminology of Ex. 6) is not constant but changes with changes in the rate of growth in order to continue to represent the age-at-the critical size (w_c). When this age-at- w_c exceeds the chosen age of recruitment, then the multiplicative rule is no longer valid for the survival to t_r and the second part of the recruitment curve (for $N_0 > E_{CR}$) will be located above the continuation of the Ricker curve. In Fig. 7.3, the rate of mortality starts by an increasing relationship to size and hence, the recruitment curve will ultimately approach the asymptote from below. A growth reduction caused by an increase in N_0 here leads to an increase in the age-specific survivorship but a decrease in the size-specific survivorship (cf. the Ricker curve) – see also Ex. 6.3.

7.3. Decreasing mortality with increasing size

Suppose the total effect of all the different causes of natural mortality operating on the juvenile stages is a general trend of decreasing mortality with increasing body-size. How will this change the shape of the age-specific recruitment curve? We already know, from the considerations of Fig. 7.3, that recruitment ultimately will increase and approach an asymptote from above if the rate of mortality bears any decreasing relationship to size but will the first part of the recruitment curve still be part of a Ricker curve?

Following Ex. 4.3, a simple treatment of this situation is obtained by considering mortality as being inversely proportional to weight to the power of $1/3$. That is,

$$\mu(w) = qw^{-1/3} \text{ and } g(w, N_0) = H(N_0)w^{2/3} ; \quad H(N_0) = H_1/N_0$$

which gives rise to the following survivorship and weight-at-age:

$$l(w, w_0) = S(t, t_0) = (w/w_0)^{-q/H(N_0)} ; \quad w = [w_0^{1/3} + (t - t_0)H(N_0)/3]^3$$

In the plaice example, we used $w_0 = 0.0005$ g and $q = 2 \text{ g}^{1/3} \text{ yr}^{-1}$ so $q/H = 0.494$ and the survival during the first 104 days becomes $l = 200^{-0.494}$ or 7.3%. Halving the rate of food consumption doubles the duration of the critical period. That is, with $H/2$, the larvae use 208 days to gain a factor of 200 in weight and the survivorship is $l^2 = 200^{-0.988}$ or 0.53%. After 104 days, the larvae have only gained a factor of 40 in weight (20mg), so the survival to this age has only decreased to $S = 40^{-0.988}$ or 2.6%. Recruitment at age t_r is given by

$$R = N_0 S(t_r, t_0) = N_0 [1 + w_0^{-1/3}(t_r - t_0)H(N_0)/3]^{-3q/H(N_0)}$$

or, since $H(N_0)$ is inversely proportional to N_0 ,

$$R = N_0 (1 + C_0 E_1/N_0)^{-N_0/E_1} = N_0 \exp[(-N_0/E_1)\ln(1 + C_0 E_1/N_0)]$$

where

$$C_0 = \text{CUMT}_{\max} = \mu_0 \tau_r ; \quad \mu_0 = qw_0^{-1/3} ; \quad E_1 = H_1/3q$$

Due to the logarithmic factor in the exponent, recruitment at age does not represent a Ricker curve but, as we shall see below, the shape of the recruitment curve will have a strong resemblance to the Ricker curve for sufficiently high values of C_0 . First, we consider the extremes. At very low initial numbers, N_0 , growth is extremely fast and the cumulative mortality to the age of recruitment approaches zero. The slope of the recruitment curve at $N_0 = 0$ is $S_{\max} = 1$ (or 100%). At very high initial numbers, growth is extremely slow and the cumulative mortality approaches a maximum of C_0 . Hence, as noted above, recruitment ultimately increases towards an asymptote:

$$R = S_{\min} N_0 ; \quad S_{\min} = \exp(-C_0)$$

Fig. 7.4 illustrates how the constant C_0 or S_{\min} determines the shape of the recruitment curve. Note that the other constant, E_1 , represents the initial number at which the survival is $(1 + C_0)^{-1}$.

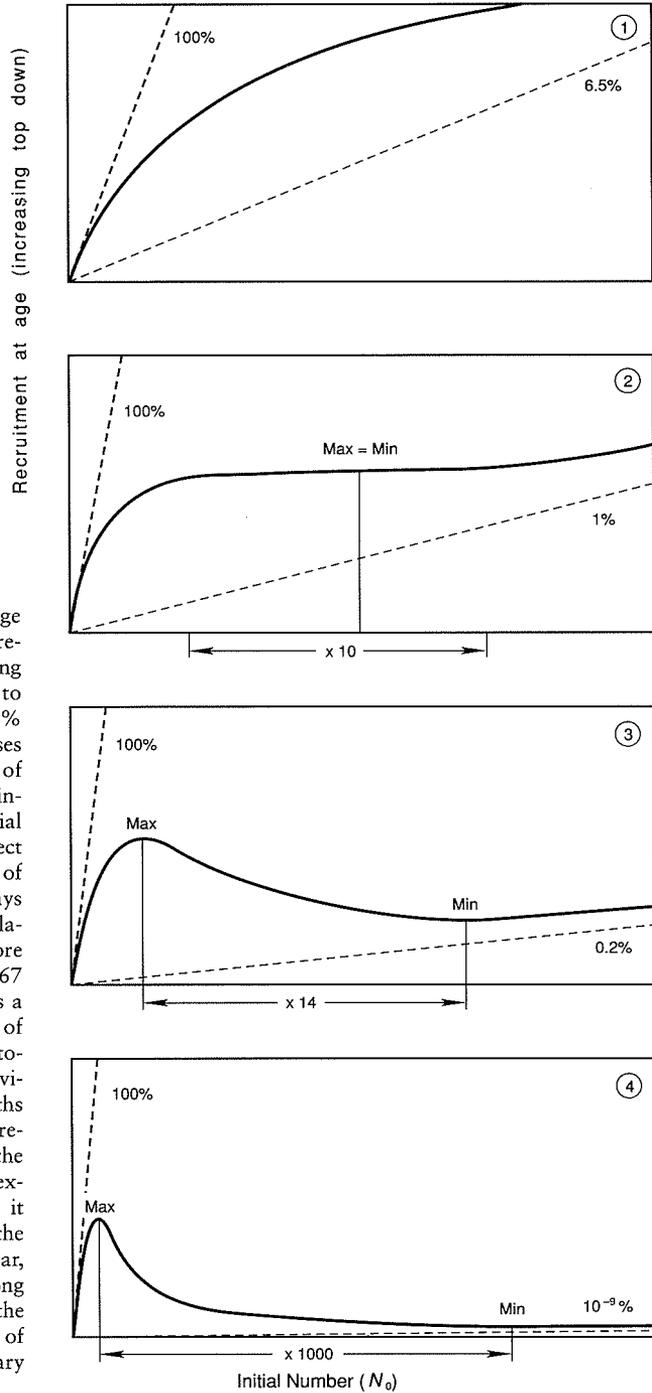


Fig. 7.4. Illustration of the change in the shape of the age-specific recruitment curve with increasing age of recruitment from case 1 to 4. The initial mortality rate is 7% per day and it thereafter decreases in inverse ratio to the cubic root of weight. The rate of growth is inversely proportional to the initial number (N_0) but increases in direct proportion to the $2/3$ -power of weight. Recruitment after 40 days (case 1) bears an increasing relationship to N_0 . When a little more than two months have elapsed (67 days in case 2), recruitment has a resemblance to the B&H type of curve but continues to increase towards the asymptote of 1% survival at high N_0 . After three months (case 3), the first part of the recruitment graph is shaped like the Ricker curve but recruitment exhibits a local minimum before it starts to raise slowly towards the 0.2%-asymptote. After one year, (case 4) recruitment has a strong resemblance to a Ricker curve, the minimum and asymptote being of no practical importance (arbitrary scales).

Fig 7.4 again refers to the plaice example ($q = 2$, $w_0 = 0.0005$ and, $H = 4.05$ now valid for $N_0 = 10^{10}$, i.e. $H_1 = 4.05 \cdot 10^{10}$). The initial rate of mortality becomes $\mu_0 = 25.2 \text{ yr}^{-1}$ (or 6.9% per day) and we get

$$C_0 = 25.2 \tau_r \quad \text{and} \quad E_1 = 6.75 \cdot 10^9$$

If τ_r , the time to recruitment is $1/25.2 \text{ yr}$ or about two weeks then $C_0 = 1$ (or $S_{\min} = \exp(-1)$) and recruitment will increase rapidly towards the steep 37%-survival asymptote. As the age of recruitment and, hence, C_0 increase, S_{\min} , the slope of the asymptote will decrease and the shape of the recruitment curve will gradually change exhibiting a local maximum and a local minimum (see Fig. 7.4). The initial numbers for these Max and Min points are found by differentiating R with respect to N_0 and setting equal to zero, i.e. obtaining the roots of the following transcendental equation:

$$x - 1 + C_0(1 - 1/x - \ln x) = 0 ; \quad N_0 = C_0 E_1 / (x - 1) ; \quad x > 1$$

Setting the second derivative also equal to zero (i.e. the inflexion point becomes a saddle point), gives the additional condition:

$$2x = C_0 + \sqrt{C_0(C_0 - 4)}$$

and we obtain $C_0 = 4.625$. This is how the basic shape of the recruitment curve is determined by $C_0 = \mu_0 \tau_r$, the cumulative mortality to age of recruitment with a constant rate of mortality equal to initial mortality. If C_0 takes a smaller value than 4.625, recruitment increases with stock throughout the range and there is no maximum on the curve at all. However, if C_0 exceeds 4.625, there will be a maximum as well as a minimum before the asymptotic increase. In the present example, the intermediate saddle-situation is achieved when we consider recruitment at $\tau_r = 4.625/25.2 \text{ yr}$ or after 67 days (case 2 in Fig. 7.4). Specification and characteristics of the four cases are given in Table 7.1. It may be noted that the local max-to-min ratio of recruitment increases from 1.8 in case 3 ($\tau_r = 3$ months) to 8.2 million in case 4 ($\tau_r = 1$ year).

Fig 7.5 shows the initial part of the four age-specific recruitment curves on the same scale together with the Ricker curve for recruitment to gain a factor of 200 in weight. All size-specific recruitment curves become Ricker curves with the global maximum located on the line for 37% survival ($N_{\max} = E_{\max} \exp(-1)$):

$$N_1 = N_0 l(w_1, w_0) = N_0 \exp(-N_0/E_{\max})$$

where

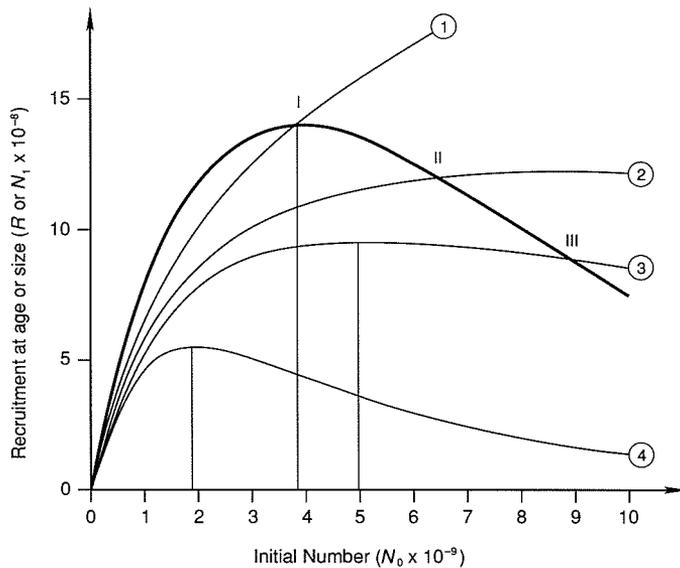
$$E_{\max} = \frac{H_{\text{ref}}}{q \ln(w_1/w_0)} E_{\text{ref}} ; \quad H_1 = H_{\text{ref}} E_{\text{ref}}$$

In the present case with $q = 2$, $w_1/w_0 = 200$ and a reference growth coefficient of $H_{\text{ref}} = 4.05$, maximum recruitment occurs at an initial number of $0.382 E_{\text{ref}} = E_{\max}$. $E_{\text{ref}} = 10^{10}$ is a random choice. Note that the age-specific recruitment curve in case 1 is selected to intersect the Ricker curve at its maximum ($N_{\max} = 1.406 \cdot 10^9$ at $E_{\max} = 3.822 \cdot 10^9$).

Table 7.1. Time to recruitment (τ_r) and characteristics of the four cases considered in Figs 7.4 and 7.5. $C_0 = 25.2 \tau_r$ and is the maximum cumulative mortality. R_m is the local recruitment maximum occurring at $N_0 = E_m$. $E_{200} = 35.08 \cdot 10^9 \tau_r$ and is the initial number (N_0) at which recruits have gained a factor of 200 in weight (points I to IV on Fig. 7.5).

Case	$\tau_r(\text{yr})$	C_0	S_{\min}	$R_m \cdot 10^{-9}$	$E_m \cdot 10^{-9}$	$E_{200} \cdot 10^{-9}$
1	0.1089	2.738	0.065	—	—	3.8
2	0.1835	4.625	0.010	1.2	14	6.4
3	0.25	6.30	0.0018	0.94	4.9	8.8
4	1	25.2	$1.2 \cdot 10^{-11}$	0.53	1.9	35

Fig 7.5. The size-continuous equivalent to B&H on the R&F suggestion. The rate of mortality bears a decreasing relationship to body-weight. Curves 1 to 4 represent recruitment at increasing age. Table 7.1 gives some characteristics. Fig. 7.4 shows the shape of the curves over the entire range. The heavy outlined curve is the Ricker recruitment curve to gain a factor of 200 in weight. The points of intersection are denoted by I (40 days), II (67 days), III (3 months) and IV (1 year), the latter occurring outside the graph at an initial number of $3.5 \cdot 10^{10}$.



7.4. Second interpretation of B&H on R&F

The correct approximation between the time required to grow through a weight range and H or $W_\infty^{1/3}$ is (Section 7.1)

$$\tau_c \propto \frac{1}{H} \propto \frac{1}{W_\infty^{1/3}}$$

However B&H somewhat misleadingly used $\tau_c \propto 1/W_\infty$ (see also comments by Harris (1975)) and, in order to obtain the same Ricker type of results as B&H, we have so far assumed H to be inversely proportional to N_0 (i.e. the first interpretation). B&H, instead, suggest that it is the amount of food eaten by each larva that is inversely proportional to N_0 and for a first approximation, they considered the food eaten to be proportional to W_∞ :

$$H \propto \text{Rate of Food Consumption} \propto \frac{1}{N_0} \quad (1. \text{ interpretation})$$

$$W_\infty \propto \text{Food eaten per larva} \propto \frac{1}{N_0} \quad (2. \text{ interpretation})$$

We shall here consider the quantification of this second interpretation within the case of continuous decreasing mortality with the size of the fish as described in the previous section. That is

$$g(w, N_0) = H(N_0)w^{2/3}; \quad H(N_0) = H_2/N_0^{1/3}$$

$$\mu(w) = qw^{-1/3} = \mu_0(w_0/w)^{1/3}; \quad \mu_0 = \mu_0(w) = qw_0^{-1/3}$$

Recruitment to size w_1 becomes

$$N_1 = N_0 \exp(-N_0^{1/3}/E_0); \quad E_0 = H_2/(q \ln(w_1/w_0))$$

We shall in the following refer to this recruitment relationship as the cube-root-Ricker type of curve. It bears a resemblance to the shape of the Ricker curve (Paulik, 1973 and Harris, 1975) but it is more flat – see Fig. 7.6. The survival at maximum recruitment is only 5%,

$$N_{\max}/E_{\max} = \exp(-3) = 0.0498; \quad E_{\max} = (3E_0)^3$$

and at the inflexion point, occurring at more than twice E_{\max} , recruitment is only reduced by a factor of 0.87,

$$N_i/N_{\max} = (E_i/E_{\max}) \exp(-1) = 0.872; \quad E_i/E_{\max} = 64/27 = 2.37.$$

To illustrate the stabilization in recruitment against changes in initial numbers, we may compare recruitment at $8E_{\max}$ with the maximum. Recruitment is reduced by a factor of $8\exp(-7)$ or to 0.73% of the maximum in the Ricker case but only by $8\exp(-3)$ or to 40% in the cube-root-Ricker case. On the Ricker curve, the survival is simply reduced from $\exp(-1)$ (point Max_1 on Fig. 7.6) to $\exp(-8)$ because the rate of growth is reduced by a factor of 8. In the cube-root-Ricker case, however, the rate of growth is only halved and the survivorship decreases from $\exp(-3)$ (point Max_2) to $\exp(-6)$. It is this damping of the variations in the rate of growth at size that, from a cause and effect point of view, makes the cube-root-Ricker curve a tractable alternative to the Ricker curve.

The constants producing Fig 7.6 are the same as before i.e., $q = 2$ and $w_1 = 200w_0$. The location of the recruitment curve is determined by H_{ref} , the reference value of the coefficient of growth:

$$E_{\max} = \left(\frac{3H_{\text{ref}}}{q \ln(w_1/w_0)} \right)^3 E_{\text{ref}}; \quad H_2 = H_{\text{ref}} E_{\text{ref}}^{1/3}$$

If $H_{\text{ref}} = 4.05$ then $E_{\max} = 1.507 E_{\text{ref}}$ or $15.07 \cdot 10^9$ with $E_{\text{ref}} = 10^{10}$. Instead H_{ref} has been chosen so that the maximum of the cube-root-Ricker curve also occurs at $E_{\max} = 3.822 \cdot 10^9$, the maximum of the Ricker curve. That is, from

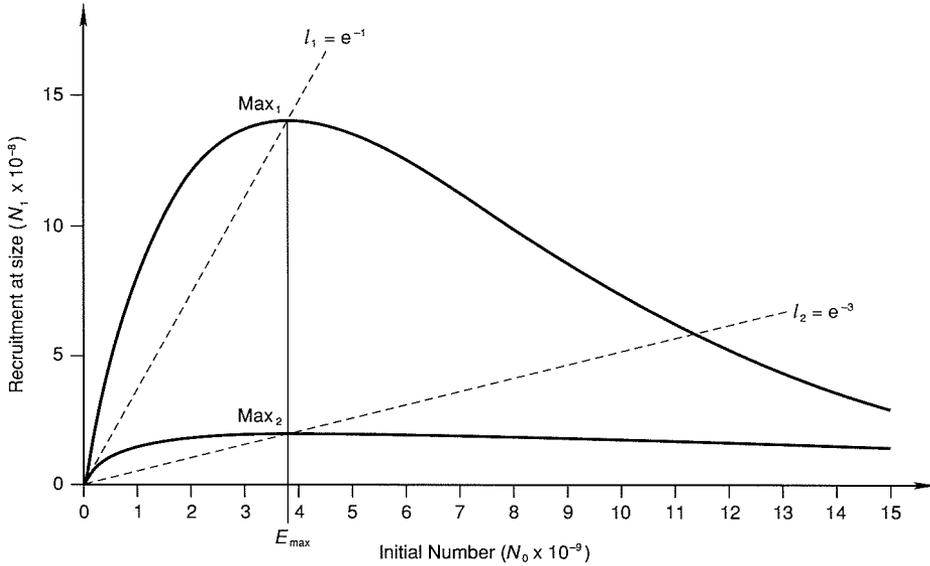


Fig 7.6. Recruitment to gain a factor of 200 in weight when the rate of mortality is inversely proportional to the cube root of weight and the rate of growth is proportional to the cube root of weight squared. The top curve is the Ricker curve in the first interpretation of B&H on R&F with H , the growth coefficient being inversely proportional to N_0 (same curve as in Fig 7.5). The flat curve is the cube-root-Ricker curve in the second interpretation of B&H in which H is inversely proportional to $N_0^{1/3}$. The point of intersection ($H = 2.04$ at $N_0 = 2 \cdot 10^{10}$) was selected in such a way that the maxima occur at an initial number of $3.82 \cdot 10^9$. At the maximum Max_1 ($H = 10.6$), the rate of growth is three times greater than in Max_2 ($H = 3.53$) because the survivorship in Max_2 (5%) equals the survivorship in Max_1 (37%) cubed.

$$H_{ref} = \frac{1}{3\sqrt{3}} q \ln(w_1/w_0) = 2.039 ; \quad E_{max} = E_{ref}/(3\sqrt{3}) = 0.1925 E_{ref}$$

we obtain $E_{ref} = 1.986 \cdot 10^{10}$ and, hence, $H_2 = 5523$ or $E_0 = 521.2$.

Recruitment at age t_r is described by the following relationship (cf. Section 7.3):

$$R = N_0(1 + C_0 E_2 / N_0^{1/3})^{-N_0^{1/3} / E_2} ; \quad C_0 = \mu_0 \tau_r ; \quad E_2 = \frac{H_2}{3q}$$

and the asymptote is still determined by $S_{min} = \exp(-C_0)$. Note that E_2^3 determines the initial number at which the survival is reduced to $(1 + C_0)^{-1}$. $E_2 = 920.5$ in the example. The development in the shapes of these cube-root recruitment curves with increasing age of recruitment follows an equivalent pattern to the situation depicted in Fig. 7.4. However, C_0 is replaced by $C_0/3$ in the x -equation for the determination of local Max and Min, i.e.

$$x - 1 + (C_0/3)(1 - 1/x - \ln x) = 0 ; \quad N_0 = [C_0 E_2 / (x - 1)]^3$$

and the saddle-point situation occurs at $C_0/3 = 4.625$ or at $C_0 = 13.875$, a three times greater μ_0 -generated cumulative mortality. Thus, in the previous example

with $\mu_0 = 25.2 \text{ yr}^{-1}$ (i.e. $w_0 = 0.5 \text{ mg}$), the saddle-point situation after 67 days in Fig. 7.4 (case 2) is now occurring after 201 days ($\tau_r = 0.55 \text{ yr}$), a three times longer recruitment period. At the same time, the asymptotic survival is cubed hereby; being reduced from 1% in Fig. 7.4 to about one in a million. This is but another way of expressing that one effect of the cube-root recruitment is to lengthen the right part of the curve. The cube-root recruitment curve, therefore, in reality bears more resemblance to a B&H shaped curve than to a Ricker curve for $C_0 \geq 13.875$. For example, after one year ($C_0 = 25.2$), recruitment at maximum ($R_m = 3.51 \cdot 10^7$ for $E_m = 3.16 \cdot 10^9$ ($x = 16.8$)) is only reduced by 38% when the initial number increases by a factor of 10. The equivalent situation in Fig. 7.4 (case 4) is a 26 factor of reduction in recruitment!

Recruitment after less than 201 days bears an increasing relationship to the start-density. Fig. 7.7 depicts the situation with $\tau_r = 1/4 \text{ yr}$.

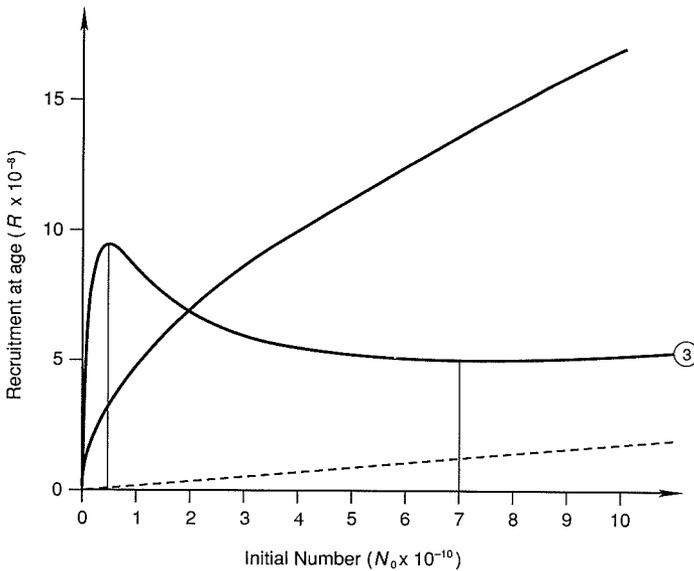


Fig 7.7. Recruitment after three months corresponding to the size-specific situation considered in Fig. 7.6. The initial rate of mortality is 7% per day producing a critical cumulative mortality of $C_0 = 6.3$. There is a maximum and a minimum on the curve when the growth coefficient is inversely proportional to N_0 (case 3 of Figs 7.4 – 7.5 and Table 7.1). However, in the cube-root case, recruitment increases with N_0 and there is no maximum on the curve at all. The point of intersection is selected to occur at $N_0 = 2 \cdot 10^{10}$. Both curves ultimately approach the shown asymptotic line for the $\exp(-6.3)$ or 0.18% survival.

7.5. Conclusions and implications for improved models

The basic results may be summarized as follows: Whatever continuous functions we propose for describing the size-dependency of the vital rates, recruitment at any specific size follows a Ricker curve if the growth coefficient is inversely propor-

tional to the start-density. In the more general case of growth being inversely proportional to the start-density in some power, δ , we obtain a δ -power-Ricker curve (see also Ex.8.3):

$$N_1 = N_0 \exp(-a_1 N_0^\delta) ; \quad \text{Rate of growth} \propto N_0^{-\delta}$$

Note that, due to the power-rule, the same type of relationship still holds if the rate of mortality is also proportional to the start-density in some power. For example, if the growth rate is inversely proportional to $N_0^{1/3}$ and the mortality rate is proportional to $N_0^{2/3}$, then the combined effect is a size-specific recruitment curve with $\delta = 1/3 + 2/3$ i.e. a Ricker curve. In the cube-root case ($\delta = 1/3$), the curve is stretched out and, in fact, bears more resemblance to a B&H curve than to a Ricker curve (see Fig. 7.6). Because of the power-rule, the curves are sensitive to changes in the vital rates (as indicated by the selection of the reference values) and the maxima will move respectively on the $\exp(-1)$ and $\exp(-3)$ survival-lines in the two cases considered.

The shape of the age-specific recruitment curve depends on the age of recruitment, the size-specific vital rates and, of course, on δ . Even in a simple case of a size-independent instantaneous-rate-ratio of mortality to growth (i.e. $\mu(w)/G(w) \propto N_0$), the first part of the recruitment curve changes from a mode of steady increase through the B&H shape of curve to the Ricker type of curve as the age of recruitment increases (see Fig. 7.4 in a case of density-independent mortality and $\delta = 1$). The second part of the recruitment curve always exhibits an increasing relationship to N_0 and, ultimately, approaches the survival-line determined by the initial rate of mortality. If, however, the rate of mortality (in the examples considered) is also proportional to the start-density in some (positive) power, then age-specific recruitment will reach a maximum and be reduced for high initial numbers (because C_0 , the asymptotic cumulative mortality is now proportional to N_0 in that power). Only in the special case of $\mu(w)$ being proportional to N_0 and $g(w)$ being independent of N_0 will recruitment at age follow a Ricker curve.

However, in the situation considered by B&H in their treatment of the R&F suggestion, the shape of the size-specific recruitment curve is copied to recruitment at a specific age as long as the larvae grow through the critical size range and reach the constant level of mortality before or at this age of recruitment. Thus, age-specific recruitment in Figs 7.2 and 7.3 will follow the first part of cube-root-Ricker curves if the rate of growth is inversely proportional to the cubic root of N_0 .

B&H, in reality, use the $2/3$ -power allometric growth model, $g(w) = Hw^{2/3}$, which is the first step towards a more appropriate growth model for larval fish than the von Bertalanffy growth equation (see Exs 4 and 7.1). B&H need only to assume this growth model to apply in (w_0, w_c) , the critical size range, because the age-specific survivorship from w_c onwards is determined by the constant rate of mortality and is, thus, independent of the rate of growth. The time required to grow through the critical range is inversely proportional to H , the coefficient of growth which again is related in some way to N_0 because B&H consider the individual food supply to be restricted due to the high density of fish (see excellent discussion on p. 147 in Harris, 1975 but disregard his general statement). In the first

interpretation (i.e., the Ricker case), it is the total rate of food consumption that is considered to be constant ($\sim N_0 H$) and the individual rate of growth becomes very sensitive to changes in N_0 . This sensitivity is considerably moderated in the second interpretation or the cube-root Ricker case in which the total amount of food eaten is considered to be constant ($\sim N_0 H^3$). Two further improvements stand to reason.

First, it is necessary to impose limits on the rate of growth. At low initial numbers, the growth rate increases beyond any sensible maximum in the models considered here. Conversely, at high initial numbers the growth rate becomes extremely small and actually approaches zero in the asymptotic behaviour. Introducing max and min limits on the rate of growth corresponds to considering only a certain central part of the recruitment curves. This is done in Ex. 9 but a max limit is already considered in Ex. 8.

Secondly, deviating from the constant rate of mortality in B&H on R&F creates, in particular, a need for introducing a consistent biomass account of food consumption in describing density-dependent growth. The rate of growth must, in some consistent way, depend on the numbers-at-age or the rate of mortality and not only on the initial number. Ex. 8 gives an introduction to density-dependent growth models in continuation of the present example. A simple approach to incorporate the effect of mortality on the rate of growth is then described in Ex. 10 with the attempt of dealing with both types of improvements in a general, allometric model of growth and mortality of larval fish.

Example 8: On the Shepherd & Cushing (1980) suggestion

This example deals with some simple cases of density-dependent vital rates stimulated by the Shepherd & Cushing (1980) model. In each case, the respective situation of density-dependency will be compared to the equivalent situation of start-density dependency as introduced in Ex. 7. Even the most simple situations of density-dependent growth result in complicated dynamics and it is instructive to begin by considering the behaviour of the S&C model in time (or age) before dealing directly with numbers at size.

8.1. *Growth and recruitment in the S&C model*

Shepherd & Cushing (1980) use the classical assumption of a constant rate of mortality, i.e. an exponential decay in numbers:

$$N(t) = N_0 \exp(-M(t - t_0)) ; \quad \frac{dN(t)}{dt} = -MN(t)$$

Age-specific recruitment, consequently, follows a straight line:

$$R = N_0 S_0 ; \quad S_0 = \exp(-M(t_r - t_0))$$

S&C consider the specific rate of growth to be inversely proportional to a linear function of the population density at the same instant in time. That is a growth rate,

$$\frac{dw(t)}{dt} = G(t)w(t)$$

with $G(t)$, the specific rate of growth:

$$G(t) = \frac{G_{\max}}{1 + N(t)/A} = \frac{G_{\max}}{1 + N_0 \exp(-M(t - t_0))/A}$$

and by integrating we obtain the mortality dependent weight-at-age,

$$w(t) = w_0 \left(\frac{N_0/A}{1 + N_0/A} + \frac{\exp(M(t - t_0))}{1 + N_0/A} \right)^{G_{\max}/M}$$

S&C note that the constant A is related to the abundance of food. If $N_0 = A$, then the (specific) rate of growth increases from $G_{\max}/2$ at age t_0 towards G_{\max} as the year-class diminishes, the result of which is the following weight-at-age:

$$w(t) = w_0 [1/2 + 1/2 \exp(M(t - t_0))]^{G_{\max}/M} ; \quad N_0 = A$$

Suppose for this situation that the maximum growth rate is 10% per day, i.e. $G_{\max} = 0.10 \text{ d}^{-1}$. If the rate of mortality is as high as 10% per day then the growth rate of the survivors increases rapidly with age (reduced numbers). After 6 days the rate of growth has increased from the initial 50% to 65% of the maximum and, after 60 days, it has virtually reached the maximum (99.8%) at which time the larvae have gained a factor of 202 in weight. Maximum growth at $M = \infty$ is about twice this $M = G_{\max}$ case and results in $\exp(G_{\max} 60)$ or a theoretical increase in weight by a factor of 403 (but no larvae survive). At a mortality rate of 5% per day, the larvae gain a factor of 111 in weight in the course of the 60 days. This factor is reduced to 31 with a mortality rate of 1% per day in which case the rate of growth increases to only 65% of the maximum after the 60 days.

The equivalent situation with start-density dependent growth is,

$$\frac{dw(t)}{dt} = \frac{G_{\max}}{1 + N_0/A} w(t) \quad \text{or} \quad w(t) = w_0 \exp\left(\frac{G_{\max}(t - t_0)}{1 + N_0/A}\right)$$

and, with $G_{\max} = 0.10 \text{ d}^{-1}$, the larvae grow 5% per day and the weight consequently increases by a factor of 20 during 60 days irregardless of mortality (but with an initial number of $N_0 = A$ larvae). This is the minimum growth achieved in the S&C model at zero rate of mortality. Thus, an important consequence of the S&C model is that the specific rate of growth bears an increasing relationship to the rate of mortality with G_{\max} as the asymptotic maximum.

The time required to grow to a specific size (w_1) is derived by inverting the relationship for weight-at-age and we obtain,

$$\tau_1 = t_1 - t_0 = -\frac{1}{M} \ln\left(\frac{l_0}{1 + (1 - l_0)N_0/A}\right) ; \quad l_0 = (w_1/w_0)^{-M/G_{\max}}$$

where the bracket, the argument of the logarithm equals $\exp(-M\tau_1)$ and, thus, designates the survival to gain a factor of $p = w_1/w_0$ in weight. That is, size-specific recruitment follows a Beverton and Holt type of curve:

$$N_1 = N_0 \frac{p^{-M/G_{\max}}}{1 + (1 - p^{-M/G_{\max}})N_0/A} ; \quad p = w_1/w_0$$

This recruitment curve and its derivation is considered in the next section in a more general context. The asymptotic maximum of recruitment becomes

$$N_a = A / (p^{M/G_{\max}} - 1) ; \quad N_0 \gg A$$

In order to illustrate the important difference between age and size-specific recruitment, suppose that the rate of mortality is 5% per day. The survival to 60 days is then $\exp(-3)$ or 5% and independent of N_0 . However, size-at-age depends on N_0 . If $N_0 = A$, then the weight-gaining factor is $p_{60} = 111$ in the case of $G_{\max} = 0.10$ as noted above. However, if the initial number is multiplied by 100 then $p_{60} = 1.41$. That is only an increase of 41% in body-weight which is achieved during the 60 days for the 5% survivors. The time required to gain a factor of 111 in weight has increased to ca. 137 days with the cost of a reduction in the survival from 0.05 to 0.001. This reduction by a factor of 50 in the survival for a 100-fold increase in initial numbers implies a doubling in recruitment from $0.05A$ to $N_a = 0.10A$. Recruitment to $p = 111$ is virtually constant for further increases in N_0 because the survival decreases almost in an inverse ratio to N_0 as growth ceases. This type of calculation indicates the need for considering the biomass as well, in order to make a sensible comparison between size-specific and age-specific recruitment.

The instantaneous rate of biomass-increase equals the difference between the instantaneous rates of growth and mortality:

$$\frac{dB(t)}{dt} = B(t)(G(t) - M) ; \quad B(t) = N(t)w(t)$$

Fig. 8.1. Biomass and recruitment characteristics of the Shepherd & Cushing (1980) model in the case of 10% max-growth and 5% mortality per day.

The top part depicts biomass at size and age with $N_0 = 10^{13}$ or 5000 metric tons of larvae ($w_0 = 0.0005$ g) beginning to grow at 1.6% per day at the onset of feeding (time zero). The minimum of ca. 2700 tons is reached after ca. 33 days when the numbers are reduced to $A = 1.9476 \cdot 10^{12}$ and the body-weight has increased by a factor of $p = 2.80$. The growth rate at the minimum is 5% per day and reaches 9.2% on day 81 (time 80.58) when the $1.78 \cdot 10^{11}$ survivors have obtained a 100-fold increase in weight. The cost of increasing the biomass by a factor of 1.78 to 8900 tons at point P has been a survival of 1.78% and a total food-consumption of almost 43000 tons copepod nauplii (assuming an assimilation efficiency of 0.7 and a starving metabolism of 3% per day, see point P on Fig. 9.2).

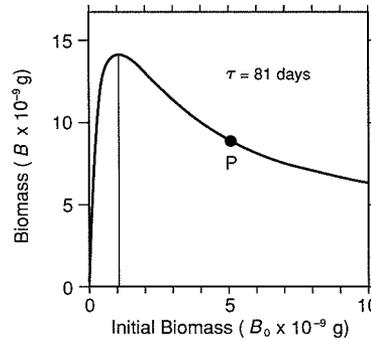
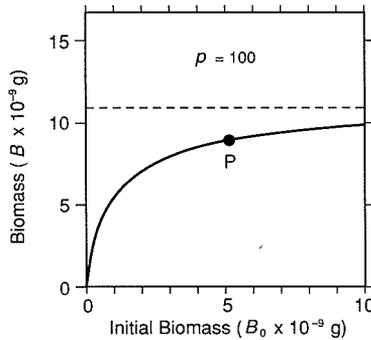
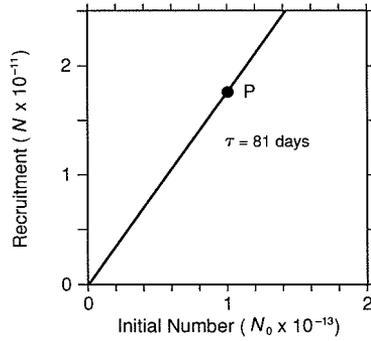
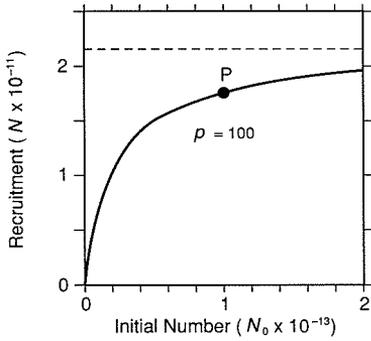
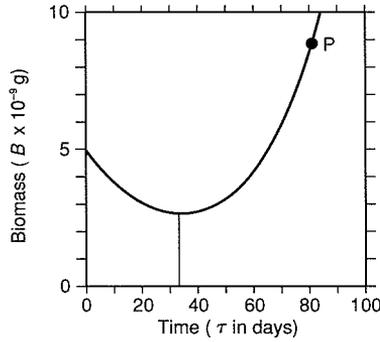
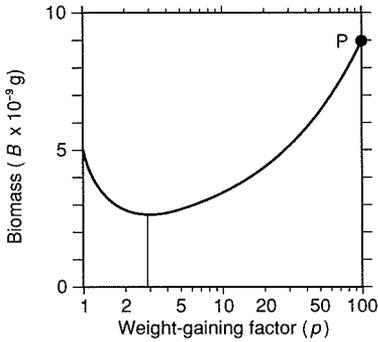
The mid-part shows the B&H curve for recruitment at weight 0.050 g ($p = 100$) and the straight line of 1.78% survival for recruitment after 81 days. The asymptotic maximum of $2.16 \cdot 10^{11}$ 1/20-gram-larvae produces an asymptotic maximum of 10800 tons in the B&H curve for biomass at $p = 100$ recruitment (bottom left). The initial slope of the B&H curve increases by a factor of p from 0.10 in numbers to 10 in biomass. The initial slope of the curve for biomass after 81 days (bottom right) is ca. 56. The curve reaches a maximum of 14200 tons at an initial biomass of 1050 tons ($N_0 = 0.21 \cdot 10^{13}$). Thus, the $0.37 \cdot 10^{11}$ surviving larvae (1.78%) at the maximum have gained a factor of 760 in weight in the course of the 81 days. Their initial growth rate was 4.8% and exceeded the critical 5% already during the second day.

Note that the bottom right figure only shows the first part of the curve. The biomass reaches a minimum of ca. 3750 tons at an initial biomass of ca. 50800 tons after which the biomass increases and approaches the recruitment line of slope 0.0178 for zero growth. One may also note that the food consumption for the (local) maximum situation only has increased by 30% compared to the P-situation. The biomass of the fewer recruits at the max exceeds the P-biomass by 60%. Food consumption for the min situation ($p = 4.16$) has also increased (44%) because of ca. 10 times as many (but smaller) fish than in the P-situation.

Hence, the biomass bears a decreasing relationship to age or size if M is greater than or equal to G_{\max} but, an increasing relationship if M is less than or equal to $G_0 = G_{\max}/(1 + N_0/A)$. In the in-between mortality situation, $G_0 < M < G_{\max}$, the biomass ultimately increases but reaches a minimum at that age (or size) at which the specific rate of growth has increased to M . The time required to reach this minimum is $M^{-1} \ln((N_0/A)/(G_{\max}/M - 1))$ at which τ -age the numbers have been reduced to $A(G_{\max}/M - 1)$ and the body-weight has increased by a p -factor of $(1 + A/N_0)(1 - M/G_{\max})$ to the power of $-G_{\max}/M$. Fig. 8.1 (top) depicts such a situation for the $G_{\max}/M = 2$ case above.

SIZE-SPECIFIC

AGE-SPECIFIC



Biomass represents a proportional scaling of size-specific recruitment ($N_1 = lN_0$) and $B_1 = B_0lp$ depicted against B_0 (for constant p) is still a B&H curve (Fig. 8.1 bottom left). However, biomass represents a non-linear (weight-at-age) scaling of age-specific recruitment ($R = S_0N_0$) and $B = B_0S_0 w(t_r)/w_0$ depicted against B_0 (for constant t_r and hence, constant S_0) is not a straight line but follows a rather complicated curve (Fig. 8.1 bottom right) with resemblance to Fig. 7.4:

$$B = N_0 w_0 S_0 \left[\frac{N_0/A + 1/S_0}{N_0/A + 1} \right]^{G_{\max}/M}; \quad B_0 = N_0 w_0; \quad S_0 = \exp(-M\tau_r)$$

The initial slope of this B vs B_0 curve is $p_{\max} = \exp(G_{\max} \tau_r)$ (for max growth) multiplied by S_0 , the slope of the recruitment line which becomes the asymptote for very high initial biomass ($p_{\min} = 1$ for zero growth). If the rate of mortality is greater than or equal to G_{\max} , then the biomass at any specific age of recruitment increases with N_0 (or B_0) and there is no maximum or minimum on the curve. This situation of a steady increase towards the asymptote is maintained for $M < G_{\max}$ but only if the τ -age of recruitment is smaller than τ_s , a certain mortality-dependent age:

$$\tau_s = \frac{2}{M} \ln \left(\frac{G_{\max} + M}{G_{\max} - M} \right); \quad S_s = \exp(-M\tau_s) = \left(\frac{G_{\max} - M}{G_{\max} + M} \right)^2; \quad 0 \leq M \leq G_{\max}$$

When the age of recruitment equals τ_s , the curve has a saddle-point of B_s occurring at an initial biomass B_{0s} :

$$B_s = A w_0 \left(\frac{G_{\max} + M}{G_{\max} - M} \right)^{(G_{\max}/M) - 1}; \quad B_{0s} = A w_0 \frac{G_{\max} + M}{G_{\max} - M}; \quad \tau_r = \tau_s$$

In the special case, $G_{\max} = 2M$, the saddle-point situation occurs at a survival of $S_s = 1/9$ and the biomass at the saddle-point equals the initial biomass $3A w_0$. With $M = 0.05 \text{ d}^{-1}$ as in Fig. 8.1, this situation of an extended plateau occurs for $\tau_s = 40 \ln 3$ which means that the first (important) part of the curve for biomass at ca. 44-days-recruitment bears a resemblance to the B&H curve for biomass at $p = 9$.

Suppose that the age of recruitment exceeds τ_s as in Fig. 8.1. Then the biomass curve reaches a local maximum at a certain initial biomass B_{01} followed by a local minimum at B_{02} after which the curve slowly rises towards the S_0 -asymptotic line. The important part of the biomass-recruitment curve bears now a resemblance to a Ricker type of curve with a moderate descending right limb. The maximum biomass B_{m1} occurs at the initial number,

$$B_{01} = A w_0 (X - \sqrt{X^2 - S_0^{-1}}) \text{ where } X = 1/2 [(S_0^{-1} - 1)(G_{\max}/M) - (S_0^{-1} + 1)]$$

and the following max-min relationships are valid:

$$B_{01} B_{02} = (A w_0)^2 \exp(M\tau_r); \quad S_0^{-1} = \exp(M\tau_r)$$

$$B_{m1} B_{m2} = (A w_0)^2 \exp((G_{\max} - M)\tau_r)$$

where B_{m2} denotes the biomass at the local minimum.

The equivalent situation with start-density dependent growth produces the

same straight line of age-specific recruitment with slope S_0 and the biomass becomes,

$$B = N_0 w_0 S_0 \exp(G_{\max} \tau_r / (1 + N_0/A))$$

It follows by differentiation (or from the expressions above for density-dependent growth in the case of zero mortality) that the local maximum and minimum situations occur at

$$\left. \begin{matrix} B_{01} \\ B_{02} \end{matrix} \right\} = 1/2 Aw_0 [(G_{\max} \tau_r - 2) \mp \sqrt{G_{\max} \tau_r (G_{\max} \tau_r - 4)}]$$

In particular, the saddle-point situation is achieved for $\tau_s = 4/G_{\max}$ producing the biomass $B_s = Aw_0 \exp(2(1 - 2M/G_{\max}))$ for $B_{0s} = Aw_0$. Thus, in the case of $G_{\max} = 2M$, we obtain for $\tau_s = 2/M$, $B_s = B_{0s} = Aw_0$ or exactly one third of the corresponding biomass in the saddle-point situation of density-dependent growth for $\tau_s = 2.20/M$. For the equivalent situation to Fig. 8.1 (bottom right), the maximum biomass is reduced by a factor of five and it occurs at a correspondingly smaller initial biomass ($B_{m1} = 2885$ tons at $B_{01} = 165$ tons and $B_{m2} = 329$ tons at $B_{02} = 5730$ tons). The asymptote is unchanged.

8.2. Generalized size-dependent vital rates

We are considering a generalized version of the S&C model in the sense that the rates of changes in size and numbers are described by

$$\frac{dw}{dt} = \frac{g_0(w)}{1 + N(w)/A}; \quad \frac{dN(w)}{dt} = -N(w)\mu_0(w)$$

where $g_0(w)$ and $\mu_0(w)$ are continuous functions that can be selected in any way we choose to describe the size-dependency of growth and mortality. It is shown below that size-specific recruitment in this model will always follow the B&H type of curve.

The shape of the age-specific recruitment curve depends on the particular choice in functions but, as discussed in Ex. 7, the curve must, ultimately, increase towards the asymptote specified by the initial rate of mortality, i.e. the line through origin with slope $S_\infty = \exp(-\mu_0(w_0)\tau_r)$. The curve may reach a local maximum but then there must also be a local minimum. The shape of the curve will change as the age of recruitment increases and, hence, as the slope of the asymptote decreases (cf. Fig. 7.4). Again, it is possible to copy the size-specific curve to age using the principles in B&H on the R&F suggestion. Suppose that $\mu_0(w)$ operates as an additional source of mortality on the larvae but only in the size interval (w_0, w_c) . If the rate of mortality otherwise may be considered to be constant then the first part of the age-specific recruitment curve will be replaced by a B&H curve. The second part of the recruitment curve is unchanged except for a multiplicative factor equal to the constant survivorship generated by the constant mortality of other causes (cf. Fig. 7.3).

The physiological rate of mortality is derived from the rates above,

$$-\frac{1}{N(w)} \frac{dN(w)}{dw} = \frac{\mu_0(w)}{g_0(w)} (1 + N(w)/A)$$

and by integration, utilizing the fractional expansion,

$$\frac{1}{N(1 + N/A)} = \frac{1}{N} - \frac{1}{N + A}$$

we obtain the maximum survival,

$$l_0 = \exp \left\{ - \int_{w_0}^{w_1} \frac{\mu_0(w)}{g_0(w)} dw \right\} = \frac{N_1}{N_0} \cdot \frac{N_0 + A}{N_1 + A}$$

or the B&H recruitment curve,

$$N_1 = \frac{l_0 N_0}{1 + (1 - l_0) N_0 / A} = \frac{l_0 E_{1/2}}{1 + E_{1/2} / N_0} ; \quad E_{1/2} = A / (1 - l_0)$$

where $E_{1/2}$ denotes the initial number which results in half of the asymptotic maximum of recruitment. This maximum equals the initial slope l_0 multiplied by $E_{1/2}$, $N_a = l_0 E_{1/2}$.

The equivalent case of start-density dependent growth is obtained by replacing $N(w)$ by N_0 in the growth rate and produces a Ricker curve with initial slope l_0 ,

$$N_1 = N_0 l_0^{1 + N_0/A} = N_0 l_0 \exp(-N_0/E_{\max}) ; \quad E_{\max} = -A/\ln l_0$$

It follows that the ratio of maximum recruitment in the B&H curve to the Ricker curve increases as the maximum survival l_0 decreases,

$$N_a/N_{\max} = e E_{1/2}/E_{\max} = -e \ln l_0 / (1 - l_0) \geq e = 2.72$$

The ratio is 12.6 for a survival of 1% and 6.95 for a survival of 10%. The minimum value is obtained with zero mortality ($\mu_0(w) = 0$ gives $l_0 = 1$) in which case both recruitment curves degenerate into the $N_1 = N_0$ line. Note that $E_{1/2}$ exceeds E_{\max} . Fig. 8.2 depicts the situation in which E_{\max} equals A obtained for $l_0 = 1/e = 0.368$.

In order to illustrate the sensitivity of recruitment to changes in the vital rates, denote the survival N_1/N_0 by l_{BH} and l_{R} in the two cases. Suppose that the rate of mortality is changed by a constant factor, $\mu_* = c\mu$. The maximum survival changes to the c th power of its initial value. The Ricker survival, thus, changes according to the power rule but changes in the B&H case are somewhat moderated compare to the power rule,

$$l_{\text{BH}*} = \frac{l_0^c}{1 + (1 - l_0^c) N_0 / A}$$

and $l_{\text{BH}*} > l_{\text{BH}}^c$ in the case of a mortality increase ($c > 1$). For example, the B&H recruitment at $N_0 = A$ in Fig. 8.2 (22.5% survival) is reduced by 26% and not 31% as prescribed by the power rule in the case of a 25% increase in the rate of mortality. Of course, the effect of this dampening of recruitment variations against changes in the rate of mortality becomes more pronounced when the survival is low. The B&H survival of 5% at recruitment for $N_0 = 10A$ in Fig. 8.2 is reduced by 30% due to the 25% increase in mortality. The reduction would have been 53% if there was no counteractive effect of mortality on growth (i.e. the power-rule).

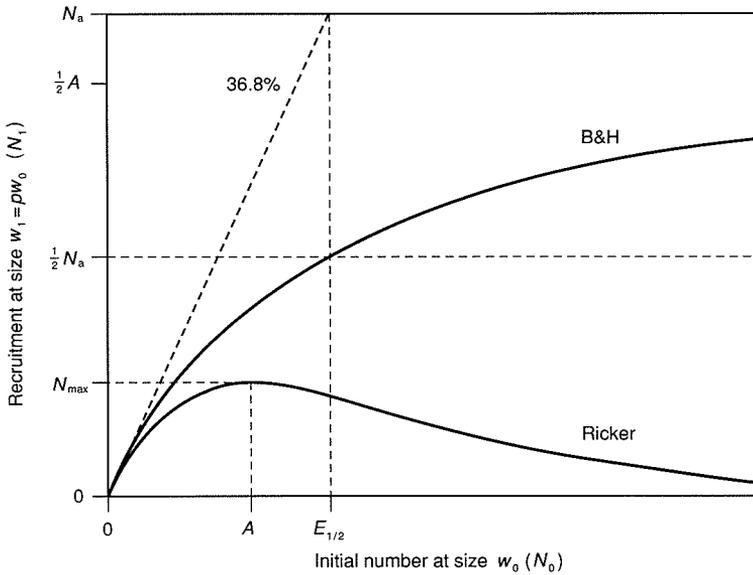


Fig. 8.2. Size-specific types of recruitment curves in the case of simple density-dependency for whatever continuous functions we propose in describing size-dependent vital rates. It is assumed that the size dependency, in itself, generates a cumulative mortality of one across the size-interval considered. This leads to the straight line of recruitment with slope 0.368. The line is transformed into a B&H curve if the rate of growth at size is inversely proportional to a linear function of density, $1+N(w)/A$ (or, if the rate of mortality is instead proportional to the same density function). The constant A denotes the number of fish that causes a 50% reduction in the rate of growth at size (or, alternatively, a doubling in the rate of mortality at size). The equivalent situation of start-density dependency, obtained by replacing $N(w)$ with N_0 produces the Ricker type of curve. The ratio between the asymptotic recruitment in the B&H curve and the maximum of the Ricker curve, N_a/N_{max} , is 4.30 in the present case.

The difference between the B&H and the Ricker curve in Fig. 8.2 represents another aspect of the counteractive effect of mortality on growth. The initial conditions are exactly the same in the two situations; N_0 fish of size w_0 growing at rate $g_0(w_0)/(1 + N_0/A)$. However, the growth rate at recruitment (size w_1) in the B&H situation becomes

$$\frac{g_0(w_1)}{1 + N_1/A} = \frac{g_0(w_1)}{1 + N_0/A} \cdot (1 + (1 - I_0)N_0/A)$$

where the first factor is the growth rate at recruitment in the Ricker situation. The growth rate at recruitment for the B&H case in Fig. 8.2 thus exceeds the growth rate for the Ricker case by a factor of $1 + 0.632N_0/A$ or 7.32 for $N_0 = 10A$. It is the cumulative effect of such differences in growth rates that causes a smaller size-specific recruitment in the Ricker case. The effect is greatest for small initial growth rates and, hence, for high initial numbers. The B&H recruitment at $N_0 = 10A$ in Fig. 8.2 exceeds the Ricker recruitment by a factor of 3000.

8.3. Generalized density-dependent vital rates

Suppose the rates of change in size and numbers are described by

$$\frac{dw}{dt} = g_0(w)H(N(w)) ; \quad \frac{dN(w)}{dt} = -N(w)\mu_0(w)U(N(w))$$

where the continuous functions $H(N)$ and $U(N)$ specify density-dependent growth and mortality. We shall first see that size-specific recruitment always bears an increasing relationship to initial number. Proceeding as in Section 8.2, we obtain

$$\int_{N_0}^{N_1} \frac{dN}{N U(N)/H(N)} = - \int_{w_0}^{w_1} \frac{\mu_0(w)}{g_0(w)} dw = -\text{CUMW}_0 = \text{constant}$$

which, by differentiation with respect to N_0 , gives

$$\frac{1}{N_1 U(N_1)/H(N_1)} \cdot \frac{dN_1}{dN_0} - \frac{1}{N_0 U(N_0)/H(N_0)} = 0$$

or the positive slope,

$$\frac{dN_1}{dN_0} = \frac{N_1 U(N_1) H(N_0)}{N_0 U(N_0) H(N_1)} > 0$$

and it follows that recruitment at a specific size follows an increasing curve such as the B&H type for any choice of the four functions in describing size and density-dependent growth and mortality. For example, in the case of density-independent mortality, $U(N) = 1$, and density-dependent growth according to $H(N) = H_0/N^\delta$, we obtain $dN_1/dN_0 = (N_1/N_0)^{1+\delta}$. That is that the slope of the recruitment curve equals the survivorship to the power of $1+\delta$. The initial slope must be one and the curve resembles the B&H type with an asymptotic maximum for any description of growth and mortality as a function of size. Exactly the same result would be obtained if the rate of growth is instead density-independent, $H(N) = 1$, but the rate of mortality is proportional to numbers in the power of δ . Evaluating the integral gives the equation for the recruitment curve (Harris, 1975),

$$N_1 = \frac{N_0}{[1 + (N_0/N_a)^\delta]^{1/\delta}} ; \quad N_a = (\delta \cdot \text{CUMW}_0)^{-1/\delta}$$

This is the δ -power-B&H curve. The equivalent start-density dependent situation produces the δ -power-Ricker curve which was considered in Ex. 7 in the special case of $\delta = 1/3$,

$$N_1 = N_0 \exp(-\delta^{-1}(N_0/E_{\max})^\delta) ; \quad E_{\max} = N_a$$

Note that maximum recruitment, $N_{\max} = E_{\max} \exp(-1/\delta)$ occurs at an initial number (E_{\max}) that is equal to the asymptotic maximum (N_a) in the δ -power B&H curve. The considerations in Section 8.2 for a $\delta = 1$ case also apply to this more general situation. Recruitment at the δ -power B&H curve exceeds recruitment at the δ -power Ricker case. The difference in recruitment increases with increasing initial numbers.

The slope of the age-specific recruitment curve is obtained in a similar way. From

$$\int_{N_0}^R \frac{dN}{U(N)N} = - \int_{t_0}^{t_r} \mu_0(w) dt$$

we obtain by differentiation with respect to N_0 ,

$$\frac{1}{U(R)R} \frac{dR}{dN_0} - \frac{1}{U(N_0)N_0} = - \int_{t_0}^{t_r} \frac{d\mu_0(w)}{dN_0} dt$$

or

$$\frac{dR}{dN_0} = U(R)R \left[\frac{1}{U(N_0)N_0} - \int_{t_0}^{t_r} \frac{d\mu_0(w)}{dw} \cdot \frac{dw(t)}{dN_0} dt \right]$$

where the integrand is positive in the situations of interest because $d\mu_0(w)/dw$ is negative and so is dw/dN_0 since we expect a greater N_0 to imply smaller size-at-age. The slope, dR/dN_0 may, therefore, very well become zero and recruitment may reach a maximum and perhaps also a minimum. If the growth rate approaches zero for asymptotic high initial values such as in the δ -power case for density-independent mortality, $U(N) = 1$, then recruitment ultimately approaches an asymptote. Note that in the case of size-independent mortality, $\mu_0(w) = 1$, the integral in the above expression for the recruitment slope vanishes and we obtain the simplified situation for density-dependent mortality with positive recruitment slope as considered by Harris (1975).

8.4. Discussion and conclusions

The basic results of Ex. 8 may be summarized as follows. Whatever continuous functions we propose in describing the size-dependency of the vital rates, recruitment at any specific size follows a Beverton and Holt curve if the growth coefficient is inversely proportional to a linear function of density. In the more general case of growth being inversely proportional to the density in some power, δ , we obtain a δ -power B&H curve (see Section 8.3) which bears a close resemblance to a B&H curve ($\delta = 1$). The important point is that the result of size-specific recruitment always is a B&H curve if the rate-ratio of mortality to growth (the physiological rate of mortality) can be separated into a size-dependent factor and a linear density-dependent factor. For example, the result is still a B&H curve if the growth rate is inversely proportional to the square root of a linear function of density but the rate of mortality increases with density in direct proportion to the square root of the same linear function. In the case of a general density-dependent factor and a general size-dependent factor of the physiological rate of mortality, size-specific recruitment still bears an increasing relationship to the initial density.

The weight-gaining factor ($p = w_1/w_0$) is used for specifying the size interval. The conversion from numbers at size to biomass always represents a constant weight-scaling: $B_1/B_0 = lp$, i.e. the ratio of biomass increase equals the size-specific survivorship multiplied by the constant weight-gaining factor. The biomass curve, therefore, has exactly the same shape as the curve for size-specific recruitment.

This is not the case for the biomass at age-specific recruitment. In the most simple case of a constant rate of mortality, the straight line of age-specific recruitment in the S&C model is converted into the age-of-recruitment dependent max-min-asymptote type of curve for biomass (Fig. 8.1 bottom right but see also Fig. 7.4). Weight at age represents the conversion factor from numbers at age to biomass. It is, thus, the body-weight at the age of recruitment as a function of the initial number (or $p = w(t_r)/w_0$ as a function of N_0 for fixed t_r) that is basically responsible for the complicated behaviour of age-specific biomass in the S&C model. For these reasons, we also obtain the same shape of biomass curve in the equivalent case of start-density dependent growth. The initial slope and the asymptotic line are unchanged but the entire curve is compressed compared to the S&C situation. This is but another example on the effect of independent vital rates in the case of start-density dependent growth. For clarification, let us consider the situation for a certain initial number (or biomass). Since the rate of mortality is constant, exactly the same number of fish will attain the age of recruitment in the two cases. However, the specific growth rate remains constant at the low initial level throughout the pre-recruit period in the case of start-density dependent growth. The recruits in the S&C model have gained more in weight because their specific growth rate has increased throughout the same pre-recruit period. It is this same effect that is responsible for the compression of the B&H size-specific recruitment curve into a Ricker curve in the case of start-density dependent growth (Fig. 8.2). The time required to reach the size of recruitment and, hence, the cost in cumulative mortality is inversely proportional to the rate of growth.

If the rate of mortality in the S&C model depends on weight in a simple way such as a power function, then the max-min-asymptotic type of curve is obtained for age-specific recruitment but the max-to-min descending part will be moderated compared to the case of start-density dependent growth (Fig. 7.4). Such moderations are caused by the counteractive effect of mortality on growth in situations of density-dependent growth. Recruitment in the S&C model is, therefore, less sensitive to changes in the vital rates than recruitment in the equivalent case of start-density dependent growth.

Note that the first part of the size-specific recruitment curve is copied to age under the assumptions used by B&H in their treatment of the R&F suggestion (cf. Ex. 7). The Ricker curve in Fig. 7.3 will, therefore, be replaced by a B&H curve in the equivalent case of density-dependent growth.

The S&C model introduces the concept of a physiological mechanism that limits the specific growth rate to G_{\max} even when food is superabundant. If this maximum limit on the rate of growth is removed, then weight-at-age and, hence, the first part of the biomass curve at age-specific recruitment will change drastically. Suppose for a treatment of this situation that we remove the number 1 in the denominator of S&C's $G(t) = G_{\max}/(1 + N(t)/A)$ and, instead, consider the specific rate of growth to be inversely proportional to the density in some power, i.e.

$$\frac{dw(t)}{dt} = H_0(N(t))^{-\delta} w(t) ; \quad N(t) = N_0 \exp(-M(t - t_0))$$

We already know that size-specific recruitment follows the δ -power B&H curve (Section 8.3), which changes to the δ -power Ricker curve in the equivalent case of start-density dependent growth (Section 7.5). Age-specific recruitment is the same as in the S&C model, $R = N_0 S_0$. The new weight-at-age is obtained by integrating the growth rate and we obtain a double-exponential relationship:

$$w(t) = w_0 \exp \left\{ \frac{H_0 N_0^{-\delta}}{\delta M} [\exp(\delta M(t - t_0)) - 1] \right\} ; \quad p(t) = w(t)/w_0$$

Evaluating $B(t_r) = B_0 S_0 p(t_r)$, the biomass at the age of recruitment produces a curve that (for any positive value of the power δ) reaches a minimum and then rises towards the asymptote with slope S_0 for very high initial biomass ($p(t_r) = 1$). The curve does not reach a local maximum as in the S&C situation (Fig. 8.1 bottom right) because the growth rate and, hence, the weight of the extremely few recruits increases beyond any limit when the initial number approaches zero. This unrealistic situation again (Section 7.5) illustrates the need for incorporating a consistent account of food consumption in the models (see Ex. 9).

Example 9: Size-specific recruitment to meet a food-consumption requirement in the Shepherd & Cushing (1980) model

The basic idea in a quantification of the Ricker & Foerster (1948) suggestion is that the reduction in the rate of growth at higher densities is caused by competition for food. A balance between the amount of food available and the actual rate of food consumption should, therefore, constitute a basic requirement for any treatment of the R&F suggestion. It is important to note that such a requirement for a consistent amount of food represents a new dimension to the classical recruitment curves derived from density-dependent growth (Exs 7 and 8).

The purpose of this example is first to put focus on the biomass account using the S&C quantification of the R&F suggestion as an example. The next step is to quantify the food situation during the period of time required for the individual larva to gain a factor of p in weight in the S&C model. We shall do this in the simplest possible way by assuming that the total amount of food consumed by the year-class is constant under average environmental conditions. The second aim of this example is then to illustrate the dramatic change in the shape and the stability of the recruitment curve that will occur as a result of such a requirement for a consistent food consumption.

9.1. Biomass account

Let $I(t)$ denote the specific rate of food consumption and k the specific rate of fast-ing metabolism, i.e.

$$I(t) = \gamma^{-1}(k + G(t)) \quad \text{or} \quad G(t) = \gamma I(t) - k$$

where γ is the assimilation efficiency and G is the specific rate of growth in the S&C model:

$$G(t) = G_{\max}/(1 + N(t)/A) ; \quad G_0 = G_{\max}/(1 + N_0/A) , \quad N(t) = N_0 \exp(-M\tau)$$

Age t is replaced by time $\tau = t - t_0$ whenever it is convenient for keeping a short notation. With these amendments to the S&C model, we obtain the rate of food consumption by the year-class,

$$C(t) = B(t)I(t) = \gamma^{-1}B(t)(k + G(t))$$

which, by inserting the expression for biomass (cf. Ex. 8.1),

$$B(t) = N(t)w(t) = B_0 \exp((G_{\max} - M)\tau) [G_0/G(t)]^{G_{\max}/M}$$

takes the form,

$$C(t) = \gamma^{-1}B_0 G_0 \exp((G_{\max} - M)\tau) (1 + k/G(t)) [G_0/G(t)]^{(G_{\max}/M) - 1}$$

In the particular case of $M = G_{\max}$, the (total) rate of food consumption, $C(t)$, exhibits a decreasing relationship to age (cf. Section 9.3). If the rate of mortality is smaller than the maximum specific growth rate, $C(t)$ may still initially decrease but will reach a minimum at an age t_{\min} , after which the rate of food consumption increases (ultimately exponential) with age. The age t_{\min} can be derived from the following requirement obtained by differentiation,

$$G(t_{\min}) = 2M / (1 + [1 + (1 - M/G_{\max})4M/k]) \quad : \text{Min } C \text{ at age } t_{\min}.$$

Table 9.1 gives an example of the case of $M = G_{\max}/2$. The assimilation efficiency is set to 70% for larval fish (cf. Ex. 10) and the rate of fasting metabolism is put to 3% per day. The year-class is assumed to comprise 10^{13} larvae of weight 0.5 mg (i.e. a biomass of 5000 tons) at the onset of feeding. The biomass reaches a minimum after ca. 33 days when the specific growth rate has increased to $M = 0.05 \text{ d}^{-1}$ (see also the graph in Fig. 8.1, top right). However, the rate of food consumption, C , reaches a minimum after 18 days when $G(t_{\min}) = 0.0324$ or $N(t_{\min})/A = 2.08$. This minimum occurs because the fish cannot lose weight in the S&C model. At very high initial numbers, $G_0 \approx 0$ and the specific rate of food intake is initially equal to the maintenance rate, $\gamma^{-1}k$ or 4.3% per day. The total food consumption will, therefore, decrease with the decimation of the year class as long as the effect of increasing food consumption per larva is small. If the initial number is smaller than $2.08A$ (or $4.05 \cdot 10^{12}$ in the present example), such a minimum will not occur.

The amount of food eaten is obtained by integrating $C(t)$, i.e.

$$F(t, t_0) = \int_{t_0}^t C(x) dx = \gamma^{-1} \int_{t_0}^t B(x)(k + G(x)) dx$$

The part of the food consumed that is not used for growth (i.e. specific dynamic action, fasting metabolism and defecation) is excreted one way or another and constitutes a loss of biomass. The total rate of excretion thus becomes $dQ/dt = B(I - G)$ and the cumulated loss is obtained by integration,

$$Q(t, t_0) = \int_{t_0}^t B(x)(I(x) - G(x)) dx = F(t, t_0) - \int_{t_0}^t B(x)G(x) dx$$

Natural mortality constitutes the second loss term. The rate of biomass lost in predation (or due to other possible causes of natural mortality) is $dP/dt = MB$ and the cumulated loss becomes,

$$P(t, t_0) = M \int_{t_0}^t B(x) dx$$

Table 9.1. Example of biomass account in the S&C model with an assimilation efficiency of $\gamma = 0.7$ and a specific rate of fasting metabolism of $k = 0.03 \text{ d}^{-1}$. Note that time 80.6 d represents the P-situation in Figs 8.1 and 9.2. The formulas for the population characteristics are given at the bottom of the table for this $M = 1/2 G_{\max}$ case ($N_0 = 10^{13}$, $w_0 = 0.5 \text{ mg}$, $A = 1.9476 \cdot 10^{12}$, $M = 0.05 \text{ d}^{-1}$).

Time τ d	Number N 10^{11}	Specific growth rate G $\% \text{ d}^{-1}$	Weight gaining factor p	Biomass B 10^9 g	Rate of food consumption C 10^9 g d^{-1}	Food eaten F 10^9 g	Losses	
							Mortality P 10^9 g	Excretion Q 10^9 g
0	100	1.6	1.0	5.0	0.33	0	0	0
10	61	2.4	1.2	3.7	0.29	3.1	2.1	2.2
20	37	3.5	1.6	3.0	0.28	5.9	3.8	4.0
30	22	4.7	2.5	2.7	0.30	8.7	5.2	5.8
40	14	5.9	4.2	2.8	0.36	12	6.6	7.6
50	8.2	7.0	8.0	3.3	0.47	16	8.1	9.7
60	5.0	8.0	17	4.2	0.66	22	10	12
70	3.0	8.7	39	5.9	0.98	30	12	16
80	1.8	9.1	95	8.7	1.5	42	16	22
90	1.1	9.5	240	13	2.4	61	21	31
100	0.67	9.7	630	21	3.8	91	30	45

Notation for $G_{\max} = 2M$ case: $S = \exp(-M\tau)$, $B_A = B_0/(1 + N_0/A)^2$, $N_A = N_0/A$

$$N = N_0 S ; \quad G = 2M/(1 + N_A S) ; \quad p = [(N_A + S^{-1})/(N_A + 1)]^2$$

$$B = B_A[S^{-1} + N_A^2 S + 2 N_A]$$

$$C = \gamma^{-1} B_A [(2M + k) S^{-1} + k N_A^2 S + 2(M + k) N_A]$$

$$F = \gamma^{-1} B_A [(2 + k/M) S^{-1} + 2(M + k) N_A \tau - (k/M) N_A^2 S - 2 + (N_A^2 - 1)k/M]$$

$$P = B_A [S^{-1} + 2M N_A \tau - N_A^2 S + N_A^2 - 1]$$

$$Q = F - 2B_A [S^{-1} + M N_A \tau - 1]$$

In the special case, $G_{\max} = 2M$, the integrals are easy to evaluate analytically (see Table 9.1 bottom). Table 9.1 gives an example of the development in F , P and Q for the first 100 days. The biomass account can be expressed as $B = B_0 + F - P - Q$ or

Food eaten = Biomass increase + Mortality loss + Excretion

For example, after 30 days, $F = 8728$ tons, $P = 5230$ tons and $Q = 5757$ tons which gives a biomass reduction of 2259 tons. This, of course, does not mean that there has been no production. The population comprises 22.31 10^{11} larvae after 30 days. Their biomass has increased from $B_{01} = 1115$ tons ($w_0 = 0.5 \text{ mg}$; $p = 1$) to $B = 2741$ tons ($w = 1.23 \text{ mg}$; $p = 2.457$) during this month. The remaining 77.69 10^{11} larvae of initial biomass $B_{02} = 3885$ tons have all suffered natural mortality during these 30 days. Their total weight at death equals $P = 5230$ tons. We may, therefore, alternatively write the biomass account in terms of production as

$F = (B - B_{01}) + (P - B_{02}) + Q$, or

Production (retained) ($B - B_{01}$):	2741 - 1115	=	1626 tons (19%)
Production loss ($P - B_{02}$):	5230 - 3885	=	1345 tons (15%)
Excretion loss:			5757 tons (66%)

Food eaten (during 30 days): 8728 tons (100%)

The biomass account after 80.582 days when the live larvae (1.78%) have gained a factor of $p = 100$ in weight (referred to as point P in Figs 8.1 and 9.2) has changed to the following,

Biomass increase ($B - B_0$):	8895 - 5000	=	2895 tons (9%)
Predation loss (P):			16273 tons (38%)
Excretion loss (Q):			22592 tons (53%)

Food eaten (F_{100}): 42760 tons (100%)

The biomass has increased by only ca. 2900 tons at the cost of ca. 43000 tons copepod nauplii (or other types of food organisms). The alternative representation below more clearly states that the gross production efficiency is ca. 47% and that the actual biomass (taking mortality into account) represents a production efficiency of 21%:

Production (retained):	8895 - 88.95	=	8806 tons (21%)
Production loss:	16273 - 4911	=	11362 tons (27%)
Excretion loss:			22592 tons (53%)

Food eaten (during ca. 81 days) (F_{100}): 42760 tons (100%)

Note the dramatic increase in food consumption and biomass from day 80 to 100 in Table 9.1. This is because the population has been reduced to such a low level that food consumption and growth almost take place at the maximum rates. The maximum specific rate of food consumption is $I_{\max} = \gamma^{-1}(k + G_{\max}) = 0.13/0.7$ or 0.186 of which 53% is used for growth and 46% is excreted. The initial rate of food consumption is almost three times less, $I_0 = \gamma^{-1}(k + G_0) = 0.0657$ and only 24% is used for growth while 76% is excreted.

9.2 Critical recruitment points

Focus is now placed on the B&H type of recruitment to gain a factor of p in weight with the additional requirement that the amount of food eaten must equal a certain value, F_p . In Table 9.1 and Fig. 8.1 with $p = 100$ and $N_0 = 10^{13}$, point P represents such a point if $F_{100} = 42760$ tons. The resulting recruitment curve formed by such points is dealt with in the next section. We are here interested in obtaining the critical points that represent the boundary of the new recruitment curve.

The first critical point, C, is obtained when growth takes place at the maximum rate. This situation occurs when $A = \infty$ and the B&H curve degenerates into the straight line,

$$N_1 = N_0 \exp(-M\tau_1) = N_0 p^{-M/G_{\max}} ; \quad A = \infty$$

We seek that particular point $(N_0, N_1) = (E_C, N_C)$ on the line at which the food eaten equals F_p . The rate of food consumption is obtained from the expression given in the preceding section by inserting $G(t) = G_0 = G_{\max}$ for the present case of exponential growth. That is,

$$C(t) = \gamma^{-1} B_0 (G_{\max} + k) \exp((G_{\max} - M)\tau)$$

and the food eaten is obtained by integration,

$$F_p = \gamma^{-1} E_C w_0 \frac{G_{\max} + k}{G_{\max} - M} [p^{1-M/G_{\max}} - 1]$$

or

$$E_C = \frac{\gamma F_p}{w_0} \cdot \frac{G_{\max} - M}{G_{\max} + k} / [p^{1-M/G_{\max}} - 1] ; \quad N_C = E_C p^{-M/G_{\max}}$$

The interpretation of the E_C -situation is as follows. If the initial number equals E_C , the larvae take in food at the maximum rate, $I_{\max} = \gamma^{-1}(k + G_{\max})$, and consume the total amount, F_p , during $\tau_1 = G_{\max}^{-1} \ln p$, the time required for gaining a factor p in weight. If $N_0 < E_C$, the amount eaten will be less than F_p since the larvae cannot grow faster and recruitment will be determined by the straight line connecting point C with the origin.

Note that E_C exhibits an increasing relationship to M . At zero mortality, E_C takes on its minimum value,

$$E_{C0} = \frac{\gamma F_p}{w_0} \cdot \frac{G_{\max}}{G_{\max} + k} / (p - 1) , \quad N_{C0} = E_{C0} ; \quad M = 0$$

Since we are not concerned with mortality-situations in which the biomass of the year-class cannot increase, the maximum limit of E_C is considered to occur in case of $M = G_{\max}$,

$$E_{CG} = \frac{\gamma F_p}{w_0} \cdot \frac{G_{\max}}{G_{\max} + k} / \ln p , \quad N_{CG} = E_{CG} / p ; \quad M = G_{\max}$$

The ratio of critical initial numbers for these two extreme situations of mortality, therefore, becomes

$$\frac{E_{CG}}{E_{C0}} = \frac{p - 1}{\ln p} = \begin{cases} 21.5 , & p = 100 \\ 37.6 , & p = 200 \end{cases}$$

and the corresponding ratio of critical recruitment is

$$\frac{N_{CG}}{N_{C0}} = \frac{E_{CG}}{E_{C0}} \cdot \frac{1}{p} = \begin{cases} 0.215 , & p = 100 \\ 0.188 , & p = 200 \end{cases}$$

This is but one way of illustrating the effect of the food criterion on the stabilization of recruitment against variations in the rate of mortality. When the rate of mortality increases from zero to the physiological maximum of the specific growth rate, the critical initial number (for point C) increases by more than a factor of 20 in the case of $p = 100$ but the recruitment reduction is less than a factor of 5.

The second critical point, B, is determined by E_B , the (high) initial number at which the biomass of the surviving larvae is equal to the initial biomass. This *status quo* situation occurs at the point of intersection between the B&H curve and the line representing a survival of p^{-1} . We obtain the relationship,

$$E_B/A_B = \frac{p - p^{M/G_{\max}}}{p^{M/G_{\max}} - 1} \quad , \quad N_B = E_B/p$$

where A_B denotes that particular value of the constant A in the S&C model which is consistent with the requirement for food consumption. Note that point B coincides with point C in case of $M = G_{\max}$.

9.3. The recruitment curve

The starting point for obtaining the food-specific recruitment curve connecting the critical points C and B is the size-specific recruitment curve for constant A in the S&C model, i.e. the B&H curve described by the equation (cf. Ex. 8.1-8.2),

$$N_1 = N_0 \frac{p^{-M/G_{\max}}}{1 + (1 - p^{-M/G_{\max}})N_0/A(N_0)} \quad ; \quad N_A = N_0/A(N_0)$$

With the additional food-criterion to size-specific recruitment, A is no longer a constant but depends on the initial condition (N_0 and w_0), the size at recruitment (p), the amount of food (F_p) and the specification of the vital rates (γ, k, G_{\max}, M). Suppose that the entire model is specified by constants, then A becomes a function of N_0 and the equation above will describe the food-specific recruitment curve. To see how this procedure works, we first consider the simplest possible case of $M = G_{\max}$. The biomass decreases from B_0 towards B_∞ as time elapses,

$$B(t) = B_\infty [1 + N_A \exp(-M\tau)] \quad ; \quad B_\infty = B_0/(1 + N_A) \quad , \quad G_{\max} = M$$

and the rate of food consumption by the year-class will consequently also decrease towards a constant, $I_{\max} B_\infty$,

$$C(t) = \gamma^{-1} B_\infty [M + k + k N_A \exp(-M\tau)] \quad , \quad G_{\max} = M$$

Integrating over the time required to gain a factor of p in weight, τ_1 , yields the food-criterion,

$$F_p = \gamma^{-1} B_\infty \{ (M+k)\tau_1 + (k/M)N_A [1 - \exp(-M\tau_1)] \} \quad ; \quad \tau_1 = -M^{-1} \ln(N_1/N_0), \quad G_{\max} = M$$

It appears from this equation that it is not possible to obtain an analytical expression for A as a function of N_0 . However, we may express A or N_A as a function of N_0 and N_1 based on the food criterion. Inserting this expression into the B&H equation above yields the following transcendental equation:

$$0 = N_0/N_1 - p - (p-1) \left[\frac{(1+k/M)\ln(N_1/N_0) + \gamma F_p/(N_0 w_0)}{(k/M)(1-N_1/N_0) - \gamma F_p/(N_0 w_0)} \right], \quad G_{\max} = M$$

This is the equation for food-and-size-specific recruitment in the S&C model in case of $M = G_{\max}$. One cannot obtain N_1 directly. For an initial number, N_0 , recruitment, N_1 , must be obtained as the zero of the equation by iteration. Alternatively,

one can rearrange this recruitment equation to express the initial number as a function of the survivorship, $l = N_1/N_0$. This gives N_0 for a selected l and hence, $N_1 = lN_0$. The calculation of N_0 has, of course, no meaning for $N_0 < E_C$ (or $l > 1/p$) because $A(N_0)$ then becomes negative (i.e. the specific growth rate exceeds G_{\max}).

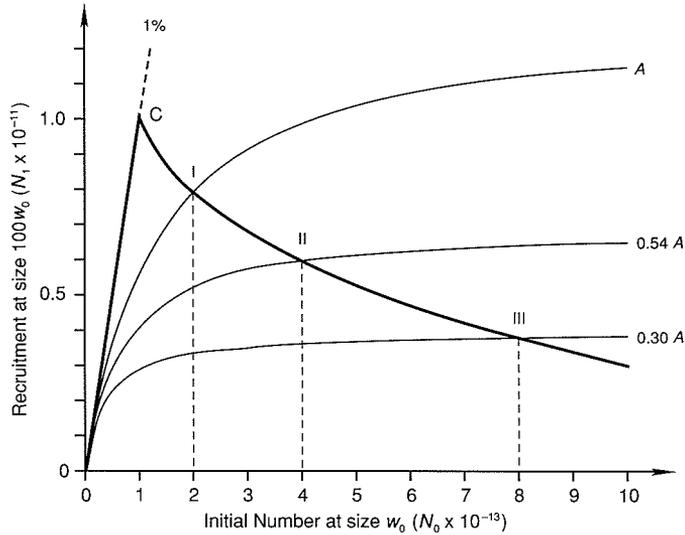


Fig. 9.1. The food-and-size-specific recruitment curve (heavy outlined) for $F_{100} = 42762$ tons and $M = G_{\max} = 0.10 \text{ d}^{-1}$ in the S&C model elaborated to account for an assimilation efficiency of 70% and a specific rate of fasting metabolism of 3% per day. N_0 denotes the number of first feeding larvae with body-weight 0.5 mg. The maximum survival is $1/p$ or 1%. The critical point of max growth (i.e. 10% per day from onset of feeding until point C is reached ca. 46 days later) also represents the *status quo* point (B) for biomass. Three B&H curves for recruitment to weight $1/20 \text{ g}$ ($p = 100$) are also shown ($A = 1.28 \cdot 10^{13}$). The amount of food eaten is equal to 42762 tons only at the points of intersection denoted respectively by I (55 days), II (65 days) and III (77 days). At point I, the initial $2E_C$ larvae begin to grow with 3.9% per day. A redoubling in initial numbers to $4E_C$ at point II reduces the initial growth rate to 1.5% (and to 0.5% at point III). The growth rate at recruitment is ca. 9.9% in all three cases.

Fig. 9.1 shows the recruitment graph in the case of $p = 100$. The food-criterion was simply determined in this example by requiring that $E_C = 10^{13}$, i.e. from the point-C-equation in section 9.2 or from the F_p -equation above putting $N_A = 0$ ($A = \infty$),

$$F_p = \gamma^{-1} w_0 E_C (1 + k/M) \ln p = 42762 \text{ tons} ; \quad \tau_{IC} = M^{-1} \ln p , \quad G_{\max} = M$$

This case of $M = G_{\max}$ is not so interesting from a recruitment point of view because the biomass cannot increase. The situation changes when the rate of mortality is smaller than the maximum specific rate of growth. The C and B lines will

separate and open a potential recruitment window of biomass increase. For the most simple treatment of this situation, suppose that $G_{\max} = 2M$. The survivorship for the B&H recruitment situation becomes,

$$N_1/N_0 = \exp(-M\tau_1) = p^{-1/2}/(1 + (1 - p^{-1/2})N_A) , \quad G_{\max} = 2M$$

and the F_p -criterion is obtained from Table 9.1, inserting $\tau = \tau_1$,

$$\gamma F_p(1 + N_A)^2 = N_0 w_0 [(2 + k/M)(N_0/N_1 - 1) - 2(1 + k/M)N_A \ln(N_1/N_0) + (k/M)N_A^2(1 - N_1/N_0)]$$

The transcendental equation for food-specific recruitment is obtained by eliminating N_A from the two equations above. This is a straight forward procedure and the details are omitted here. Fig. 9.2 shows the recruitment curve in the same ($p = 100$) case considered in Fig. 9.1, the only difference being that the rate of natural mortality is reduced from 10% to 5% per day.

The equation for the critical point C becomes,

$$E_C = (\gamma F_p / w_0) / [(2 + k/M)(p^{1/2} - 1)] ; \quad N_C = E_C p^{1/2} , \quad G_{\max} = 2M$$

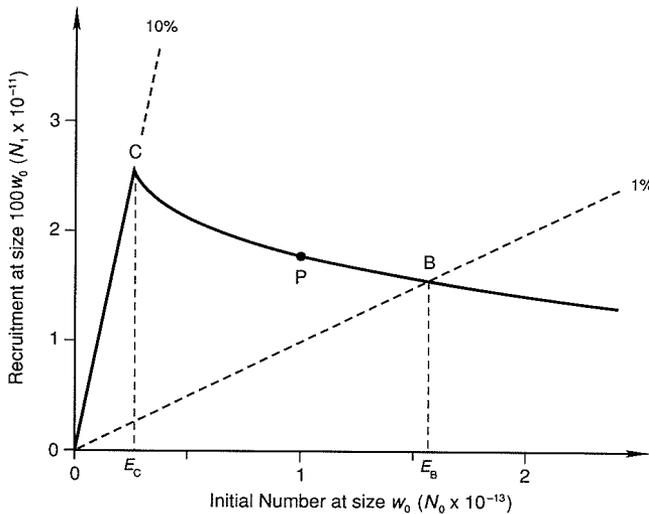


Fig. 9.2. The food-and-size-specific recruitment curve for $F_{100} = 42762$ tons and $M = 1/2 G_{\max} = 0.05 \text{ d}^{-1}$ in the same specification of the elaborated S&C model as in Fig. 9.1. Biomass and recruitment characteristics underlying point P are shown in Fig. 8.1 (see also the discussion of the biomass account based on Table 9.1). C is the critical point of maximum growth which represents a factor of $p^{1/2} = 10$ in biomass increase. Point B, representing *status quo* in biomass, occurs at an initial number, $E_B = 1.56 \cdot 10^{13}$, which is 6.1 times higher than $E_C = 2.56 \cdot 10^{12}$. However, point B represents a recruitment reduction of only 39% compared to maximum recruitment at point C (i.e. $N_B = 0.61 N_C$).

The equation for *status quo* in biomass (point B) is obtained by replacing N_A with $p^{1/2}$, and N_1/N_0 with p^{-1} in the F_p -equation, i.e.

$$E_B = \frac{\gamma F_p}{2w_0} \cdot \frac{M}{M+k} \cdot \frac{(p^{1/2} + 1)^2}{p-1 + p^{1/2} \ln p} ; \quad N_B = E_B p , \quad G_{\max} = 2M$$

Hence, the ratio of E_B to E_C is independent of the amount of food eaten, the assimilation efficiency and the initial body weight (i.e. F_p , γ and w_0),

$$E_B/E_C = [(M+k/2)/(M+k)](p^{1/2} + 1)(p-1)/(p-1 + p^{1/2} \ln p) , \quad G_{\max} = 2M$$

The corresponding extreme in recruitment variation is also exclusively determined by p , k and the $G_{\max} = 2M$ level,

$$N_B/N_C = p^{-1/2} E_B/E_C , \quad G_{\max} = 2M$$

In the present example with $M = 0.05$ and $k = 0.03$ per day, the E -ratio increases from ca. 6 in the $p = 100$ situation to ca. 22 in the $p = 1000$ situation. However, the recruitment or the N -ratio increases only from 0.61 to 0.69. That is a C to B reduction in recruitment of about 35%. These results (for a ten-fold variation in the weight gaining factor, p) are rather insensitive to changes in the specific rate of fasting metabolism (k). When k increases from 0 to 5%, the C to B recruitment reduction increases from ca. 20% to 40%.

9.4. Discussion and conclusions

Introducing the F_p -criterion completely changes the shape of the size-specific recruitment curve. The convex shape of the B&H recruitment curve for constant A in the S&C model is reversed into a curve of concave shape (in the recruitment window determined by the critical B and C lines) when A is interpreted as a parameter related to the abundance of food through the F_p -criterion. Such a concave shape is, perhaps, to be expected because the food consumption requirement makes A a function of N_0 (when the model otherwise is specified). We are, therefore, really dealing with a combined case of density and start-density dependent growth and the curve shape in Fig. 9.2 may, indeed, be interpreted as something in between the B&H and the Ricker type of curves. This does not mean that the Ricker type of curve (created by start-density dependent growth, see Ex. 7) is maintained completely when the F_p -criterion is introduced. The F_p -criterion creates an important mortality-dependent effect on growth and the result can, therefore, also in this case be interpreted as a combination of start-density and density dependent growth (see Ex. 10).

The fact that the food-criterion makes A a function of the rate of mortality has some important consequences for recruitment stability. We may, for example, consider the situation with an initial number of $2 \cdot 10^{13}$ larvae in Fig. 9.1 (i.e. point I). The rate of mortality is 0.10 d^{-1} and the situation is described by $A = 1.28 \cdot 10^{13}$ in the S&C model as indicated by the shown B&H curve. The survival is ca. 0.4% and the question is by how much this survival will increase when the rate of mortality is halved. If mortality had no effect on growth, the change in survival would follow the power-rule, $0.004^{1/2}$ and, hence, increase survival to 6.3%. In the S&C

model (cf. Ex. 8.2), the effect of density-dependent growth is a modification of the increase and the survival becomes 4.2% (with half the rate of mortality but with unchanged A). However, the F_p -criterion changes A to $0.138 \cdot 10^{13}$ and the survival will only increase to 0.7% (see $N_0 = 2 \cdot 10^{13}$ situation in Fig. 9.2). In other words, the survival increases by a factor of 16 if growth is independent of mortality. This factor is reduced to 11 in the S&C model but becomes less than 2 with the present requirement for a consistent amount of food. It can be concluded that the requirement for a constant amount of food eaten stabilizes recruitment against fluctuations in the rate of mortality.

The investigation of the recruitment ratio for the critical points in the $M = 1/2 G_{\max}$ case elucidates the other aspect of stability. A 10-20 fold increase in initial number (depending on the choice of p) implies only a 30-40% reduction in recruitment.

This also means that the dynamics of the recruitment situation can be understood by considering the critical points. The choice of p will be discussed later. For the moment, we shall consider the situation for a specific p . The slope of the B-line for *status quo* in biomass is $1/p$ and, thus, independent of the vital rates. The slope of the C-line (which constitutes the first part of the recruitment curve) equals the slope of the B-line to the power of the instantaneous rate ratio of mortality to maximum growth (i.e. $p^{-M/G_{\max}}$). The recruitment window is, therefore, closed when $M = G_{\max}$ (B and C line coincides, see Fig. 9.1) and gradually opens when M decreases (see Fig. 9.2 for a $M = 1/2 G_{\max}$ situation). The maximum opening (or recruitment square) is obtained at zero mortality, in which case the slope of the C-line is one. Note that this window dynamic, including the position of the C-point, will be exactly the same in the equivalent case of start-density dependent growth because point C is specified by the maximum growth rate.

Now, for constant vital rates, points B and C will move along the respective lines in direct proportion to F_p , the amount of food eaten. This offers one possible beginning point for explaining fluctuations in recruitment. As an example, we consider Fig. 9.2 which represents a recruitment situation with $F_{100} = 42762$ tons. With an initial population of 10^{13} fish (see point P representing a survival of 1.78%), recruitment will increase by a factor of 5.6 (i.e. $10/1.78$) if the food available increases by a factor of 3.9 (because point P moves up and becomes the new C-point when $F_{100} = 167143$ tons). However, recruitment at initial numbers below $E_C \approx 1/4 \cdot 10^{13}$ is not affected by an increase in the amount of food available. But if the rate of mortality is halved (from 5% to 2.5% per day), then the slope of the C-line increases by a factor of 3.2. Recruitment in the density-independent domain (the collapse zone below E_C) will, therefore, increase by a factor of 3.2 if the mortality reduction is accompanied by an increase in food. If the amount of food remains constant (i.e. 42762 tons), then the mortality reduction causes a reduction in E_C as well and recruitment will increase (but only by a factor of 3.2 for initial numbers below the new $E_C = 1.1 \cdot 10^{12}$).

One consequence of food-and-size-specific recruitment is, therefore, that fluctuations in year-class strength at medium to high initial numbers mainly are determined by fluctuations in the amount of food available. The chance of the oc-

currence of a good year-class is considerably reduced at low initial numbers because the survival is high (for $N_0 \leq E_C$) and unaffected by an increase in food availability.

The interpretation of p and the F_p -criterion remain to be considered. The beginning of the size interval has been interpreted as the weight at the onset of feeding. This does not mean that the onset of feeding necessarily must be considered the beginning of a critical period. Focus is rather placed on the end of a critical period in the sense that the biomass of the year-class at some body-weight must exceed the initial biomass at the onset of feeding. This is not a demand for increasing biomass right from the onset of feeding. The biomass may bear a decreasing relationship to age or size initially (cf. the P-situation in Fig. 8.1 and Table 9.1) but the reduction must be regained before size pw_0 is reached. It seems sensible that this increase in biomass must have taken place at or before the occurrence of metamorphosis (say, at $p \approx 200$). In the present considerations, we have used typical parameter values for larval fish in temperate waters such as for North Sea herring (with relatively big eggs). The choice $p = 100$ represents a qualified guess of the minimum ratio of larval size to prey size. In this interpretation, p designates a critical period during which the larvae depend entirely on the production of copepod nauplii as food. The part of this production that is available as food for the year-class has here been treated as a constant, F_p , to represent the average situation. These points are discussed in more detail elsewhere. The basic point, however, is that the incorporation of an account of food consumption (Section 9.1) enables us to compare different recruitment situations in a consistent way from a mass point of view. At an initial number, E_C , the biomass increases by a factor of $p^{1-M/G_{\max}}$. This factor gradually decreases as the initial number increases until the *status quo* situation is reached at E_B . The cost of recruiting this biomass of fish sized pw_0 is, in every case, a food consumption of F_p . Other types of density-dependent mechanisms (such as mortality caused by starvation) are likely to play a major role in regulating recruitment at initial number in excess of E_B . This domain of very high initial numbers is not dealt with in the present model.

The above considerations represent but one interpretation of the model. Other food-criteria can be used (see Ex. 10.3). Density-dependent growth in other stages of larval or juvenile life can be considered instead or at the same time in a consecutive application of the model. However, the argument may be raised that the exponential basis of the S&C growth model provides an unrealistic description of growth for most species in particular for the juvenile stages. One could also argue that the assumption of a constant rate of natural mortality in the S&C model is unacceptable except perhaps for adult life. Apart from the usefulness of simple models and the fact that statements such as unrealistic or unacceptable models must be related to the aim of modelling in each particular case, it is important to note that the food-and-size-specific recruitment curves obtained in this example also are valid for a much broader class of growth and mortality models than exponential growth and constant mortality.

For clarification, we consider generalized size-specific vital rates, $g_0(w)$ and $\mu_0(w)$, producing the size-specific survivorship $l_0(x)$, $x = w/w_0$. The final formu-

lation of the rate of growth is obtained by multiplying $g_0(w)$ with the S&C density-dependent factor, i.e.

$$g(w, N) = g_0(w)/(1 + N/A)$$

Size-specific recruitment in this model is also described by the B&H curve (see Ex. 8.2) and inserting the B&H survivorship in the size-version of the food-equation (see Eq. (16)) gives the F_p -criterion,

$$F_p = B_0 \int_1^p (\text{GGE}(x))^{-1} l_0(x)/[1 + (1 - l_0(x))N_0/A] dx$$

where GGE is the gross growth efficiency. Suppose that the rate of fasting metabolism is proportional to $g_0(w)$. The relationship for the reciprocal gross growth efficiency becomes,

$$\text{GGE}(x)^{-1} = \gamma^{-1}(1 + k_1 g_0(w)/g(w, N)) = \gamma^{-1} \left(1 + k_1 \frac{1 + N_0/A}{1 + (1 - l_0(x))N_0/A} \right)$$

implying that F_p is completely specified by the survivorship $l_0(x)$. For example, in the allometric model considered in Ex. 10 (with $k_1 = k/H_{\max}$),

$$g_0(w) = H_{\max} w^{1-m} \quad \text{and} \quad \mu_0(w) = qw^{-m}$$

the survival becomes independent of the value of the exponent m ,

$$l_0(x) = x^{-q/H_{\max}} \quad ; \quad x = w/w_0$$

This actually means that whether we consider the S&C model with $m = 0$ (and $G_{\max} = H_{\max}$, $M = q$) or some other situation such as $m = 1/4$ (see Ex. 10), the B&H recruitment curve (Section 9.3) and $A(N_0)$ obtained from the F_p -requirement remain unchanged because they are based on one and the same survivorship l_0 . Figs 9.1 and 9.2 represent, therefore, food-and-size-specific recruitment curves for the general allometric model. The vital rates may even be multiplied by some arbitrary size-specific function. The size-specific recruitment curves do not change as long as the instantaneous rate ratio of mortality to growth remains constant.

It is interesting to note that the specific rate of growth in the generalized allometric version of the S&C model, $G(w, N) = H_{\max} w^{-m}/(1 + N/A)$, will not necessarily increase as the year-class diminishes because of the factor w^{-m} . The final point concerns age-specific recruitment which is constant and, thus, independent of any food-criteria in the S&C model. This is not the case for the general allometric model (see Ex. 8.4). It is only numbers at size that remain unchanged for different versions of the allometric model. Weight at age and hence, numbers and biomass at age depend on the specification of the allometric model (i.e. on m). The food-and-age-specific recruitment curve will, therefore, depend on the exponent m (see also Ex. 10). An investigation of these matters calls for a numerical evaluation of the integrals. It is only in very few cases of density and start-density dependent growth such as those considered in the present example that analytical expressions for recruitment can be evaluated.

Example 10: A simple allometric model of growth and mortality of larval fish

The B&H theory with constant rate of mortality and the von Bertalanffy growth equation (VBGE) constituted the beginning point for quantifying the vital rates of larval and juvenile life in Ex. 4. It was necessary to take into account that the rate of mortality bears a decreasing relationship to the size of the fish. The situation was treated by considering $\mu(w)$ to be inversely proportional to length or to the cube root of weight (Ex. 4.3). It was also recognized that $G(w)$, the specific rate of growth, exhibits a close relationship to mortality (Ware, 1975). However, the consequence of $G(w) \propto w^{-1/3}$ is a rapid reduction in the specific rate of growth during the first months of life which seems to be in conflict with present knowledge on early life dynamics (Ex. 4.4). In the considerations of B&H on the R&F suggestion, the situation of instantaneous vital rates being proportional to $w^{-1/3}$ was also considered (Ex. 7.3) and it was mentioned that a power less than one third would reduce the fall in G . It is the need for such a more general allometric model that constitutes the beginning point in the present example.

The basis of the allometric model (Ware, 1975) is derived directly from mass balance in the general predation process of the pelagic ecosystem using simple particle-size distribution (psd) theory (Section 10.1). As an example, the larval model is used on Atlantic herring and cod. However, the main application of the allometric model in the present context is the continuation of the treatment of the R&F suggestion with start-density dependent growth in Ex. 7. The purpose is to examine the effect of requirements for a consistent amount of food consumption on size-specific recruitment. Section 10.2 deals with the F_p -requirement to the amount of food eaten by the year-class that is considered in Ex. 9 in the case of the same allometric model but with the S&C density-dependent growth factor. In Section 10.3, the food criterion is changed to a constant average rate of food consumption during the time required to gain a factor of p in weight. Some comments on age-specific recruitment to meet the F_p -criterion and an F_{τ} -criterion are included in the discussion (Section 10.4).

10.1. Model basis

First, we consider the situation in which the abundance-at-size of all organisms in the sea, in the first approximation, can be described by an allometric model (see Fig. 10.1). Assume that the natural mortality in this system is caused mainly by predation and that a predator eats prey of a specific fraction, $1/p$, of its own size. Mass balance in this predation process must at any size express that the rate of prey-biomass removed by predation equals the rate of food consumption by the predators (see the consumption arrow in Fig. 10.1). That is

$$w\mu(w) \cdot \text{Prey Number} = i(pw) \cdot \text{Predator Number}$$

where $i(pw)$ denotes the rate of food consumption (of prey sized w) by a predator of size pw .

The abundance ratio of predator to prey is constant in this allometric model (equalling the size ratio of predator to prey, p , to the power of one plus the slope

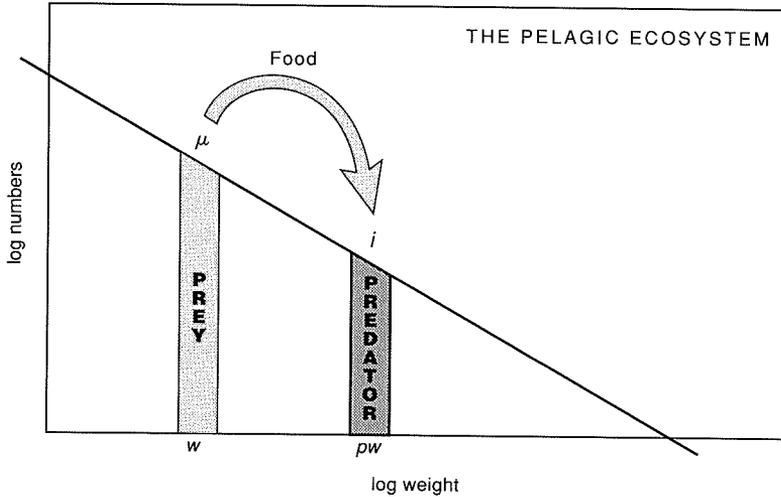


Fig. 10.1. The predation mortality (μ) or the food consumption (i) process in the pelagic ecosystem described by an allometric model for abundance at size (for all species combined). In this interpretation, the weight-gaining factor, p , describes the size-ratio of predator to prey. The food-arrow shows the basic requirement for mass balance in the predation process at any size and through any interval of time: Organisms suffering predation mortality constitute the food consumption of the predators. Furthermore, in metabolic growth models, the rate of food consumption is proportional to the body-weight in some power. The requirement for mass balance then implies proportionality between $I(w)$ and $\mu(w)$, the instantaneous rates of food consumption and mortality. This constitutes the basis for using the same exponent in describing growth and mortality as allometric processes in the present example.

of the line in Fig. 10.1). The numbers in the equation above for mass balance may, therefore, be replaced by a constant of proportionality and we can write

$$w\mu(w) \propto i(pw)$$

The rate of food consumption is usually considered to be proportional to the weight in some power. We put

$$i(w) = hw^{1-m} \quad \text{or} \quad I(w) = hw^{-m}$$

It now follows from the relation of mass balance that the instantaneous rate of predation mortality is proportional to the specific (instantaneous) rate of food consumption, $I = i/w$, i.e.

$$\mu(w) = \text{constant} \cdot I(w) = qw^{-m}$$

where the constant of proportionality has been denoted q/h .

The next step is to calculate the growth rate from the rate of food consumption and the requirements for metabolism. Let β denote the fraction of food that is absorbed and α the fraction of absorbed food that is lost in specific dynamic action etc. That is, the fraction $\gamma = (1 - \alpha)\beta$ of the food is assimilated. Let further kw^{1-m} denote the rate of fasting metabolism. The coefficient of growth becomes,

$$H = \gamma h - k ; \quad \gamma = (1 - \alpha)\beta$$

and the allometric model of growth and mortality of larval fish takes the final form,

$$g(w) = Hw^{1-m}$$

$$\mu(w) = qw^{-m}$$

It is this model with H , q and m as (stage-specific) constants that is used throughout this example. The gross growth efficiency, $GGE = g(w)/i(w)$, is determined by γ , the assimilation efficiency, and H and k , the coefficients of growth and fasting metabolism:

$$GGE = H/h = \gamma H/(k + H) ; \quad h = \gamma^{-1}(k + H)$$

Some consequences and applications of the allometric model will briefly be considered. The time required to grow through the size interval, beginning at weight w_0 and ending at weight $w_1 = pw_0$, becomes

$$\tau_1 = \tau(w_1, w_0) = \begin{cases} \frac{w_0^m}{mH} (p^m - 1) ; & m \neq 0 \\ \frac{1}{H} \ln p & ; \quad m = 0 \end{cases}$$

and the survivorship is independent of the choice of power m :

$$l_1 = l(w_1, w_0) = p^{-q/H} ; \quad p = w_1/w_0$$

Note that the dimension of q or H is $\text{MASS}^m \text{TIME}^{-1}$. These formulas are valid for any positive value of p because here p simply denotes an auxiliary used to specify the weight interval considered. In the present example, the beginning of the weight interval is related to the onset of feeding.

The model may also be applied to the egg and yolk-sac stages. During these stages, we assume a maximum efficiency of energy transfer. That is, yolk is completely absorbed ($\beta_{\max} = 1$) with the minimum cost of conversion into tissue ($\alpha_{\min} = 0.1$, cf. Kiørboe 1989). This gives a maximum assimilation efficiency of $\gamma_{\max} = 0.9$. The rate of weight loss is, in a first approximation, equal to $g(w) - i(w)$ and the reduction in weight during the egg and yolk-sac stages is, therefore, described by the allometric model with a negative value for H , i.e. the survivorship becomes

$$l_e = l(w_0, w_e) = (w_0/w_e)^{-q/H_e} ; \quad H_e = -[(1 - \gamma_{\max})h_e + k]$$

where w_e denotes the egg weight and index e otherwise refers to the egg and yolk-sac stage. Note that the weight-gaining factor, $p = w_0/w_e$, here is less than one.

As an example, we consider a larval model with $m = 1/4$, $H_e = -0.09$ ($\mu\text{g dry wt})^{0.25} \text{d}^{-1}$ during the egg and yolk-sac stages, $H = 0.25$ ($\mu\text{g dry wt})^{0.25} \text{d}^{-1}$ from the onset of feeding and $q = 0.15$ ($\mu\text{g dry wt})^{0.25} \text{d}^{-1}$ for all stages. The value of H_e is obtained by assuming $h = h_e$, $k = 0.05$ ($\mu\text{g dry wt})^{0.25} \text{d}^{-1}$ and a general value of $\beta = 0.8$ for the fraction of food absorbed (Andersen & Ursin, 1977). Putting $\alpha \approx 0.12$ gives an assimilation efficiency of $\gamma = 0.7$ and $h = 0.43$ ($\mu\text{g dry wt})^{0.25} \text{d}^{-1}$. If a 30% reduction in weight is adopted as the death-criterion of starvation, then

$k = 0.05$ means that a larva of 100 μg dry-weight can sustain starvation for about three weeks whereas a 25 μg dry-weight larva only can sustain starvation for about two weeks (obtained by using τ -formula with $H = -0.05$ and $p = 0.70$).

The model cannot be rejected immediately as the following example will show. Using the values quoted above for m , H and q and body-weight data in μg dry weight on Atlantic herring and Atlantic cod from Houde (1987), we obtain the following results. A herring egg of weight $w_e = 225$ develops into a first feeding larva of weight $w_0 = 135$ in 21 days and the survival is 0.43 (i.e. a loss in numbers of 57%). The specific growth rate at the onset of feeding is 0.07 per day and the instantaneous rate of mortality is 0.04 per day. Only 4.4% of these larvae reach the beginning of the juvenile stage (weight 24472 = 181 w_0) during the next 145 days and the mortality rate has dropped to 0.012 per day and the specific growth rate to 0.02 per day. The total survival from the egg to the juvenile stage is 2% in the course of 166 days. These stage specific growth and mortality rates are all in good agreement with the data (Houde, 1987) deduced from published size-at-age data. The same parameter values seems to work equally well on Atlantic cod. 30.5% of the cod eggs of weight $w_e = 50$ results in first feeding larvae of weight $w_0 = 24.5$ after 19 days. These larvae begin to grow at a rate of 11% per day suffering a mortality rate of 6.7% per day. The 3.5% survivors reach the weight of 269 $w_0 = 6600$ after another 109 days and daily growth and mortality have dropped to respectively, 2.8% and 1.7%. The survival over the 128 days from spawning to metamorphosis is 1%, i.e. one egg of 50 μg dry weight has, on average, developed into 6600 \cdot 0.01 or 66 μg dry weight (32% increase in biomass).

10.2. Critical points and food criterion

The decimation of a year-class during the time-period required for the individual fish to gain a factor of p in weight and for the year-class to consume a specific amount of food, F_p , is being considered here. The rates of growth and mortality are described by the allometric model, i.e.

$$g(w, H) = H(N_0, q, p, F_p) w^{1-m} ; \quad q \leq H(N_0, q, p, F) \leq H_{\max}$$

$$\mu(w) = qw^{-m}$$

where H no longer is a constant but depends on the initial condition (N_0 and w_0), the relative size at recruitment (p), the amount of food (F_p) and the specification of the rates of food consumption and mortality (γ , k , H_{\max} and q). However, the weight at onset of feeding (w_0), the coefficient of starving metabolism (k), the assimilation efficiency (γ) and the maximum coefficient of growth (H_{\max}) can be regarded as species-specific constants. Furthermore, specifying p as the size-ratio of larvae to their prey (or, alternatively, defining p according to a physiological well-defined stage (size) such as the onset of metamorphosis), makes H a function of the predation pressure (q), the food situation (F_p) and the initial number (N_0). Secondly, considering steady state conditions, in the sense that the environmental conditions (i.e. q and F_p) remain the same from one year to the next, then H becomes a function of the initial numbers only.

The situation $N_0 = E_C$ defines the critical point C on the recruitment curve at which growth takes place at the maximum rate, $H(E_C) = H_{\max}$ (cf. Ex. 9.2). The other extreme situation, occurring at a high initial number, $N_0 = E_B$, defines point B of *status quo* in biomass obtained at (what we here consider to be) the minimum rate of growth, $H(E_B) = q$. Note that H is independent of the choice of the exponent, m , because the size-specific survivorship in the allometric model (see Section 10.1), l_1 , is independent of m . Hence, size-specific recruitment is expressed as,

$$N_1 = N_0 p^{-q/H(N_0)} ; \quad q/H_{\max} \leq q/H(N_0) \leq 1 , \quad p = w_1/w_0$$

In particular, we obtain the recruitment relationships for the two critical points,

$$N_B = E_B/p \quad ; \quad \text{B: Point of zero biomass increase, } H(E_B) = q$$

$$N_C = E_C p^{-q/H_{\max}} ; \quad \text{C: Point of maximum rate of growth, } H(E_C) = H_{\max}$$

Note, in passing, that the p -specific recruitment curve without the requirement for a consistent amount of food consumption (i.e. $H(N_0)$ is constant) simply becomes the straight line with slope l_1 . Returning to the present situation with the F_p -requirement, the first step in obtaining the recruitment curve, connecting the critical points, is to insert the survivorship of the allometric model in Eq. (16) for F_p . Hence, we obtain the following requirement for food balance,

$$F_p = \frac{N_0 w_0}{\text{GGE}(H(N_0))} \int_1^p x^{-q/H(N_0)} dx = \begin{cases} \frac{N_0 w_0}{\text{GGE}(H(N_0))} \cdot \frac{p^{1-q/H(N_0)} - 1}{1 - q/H(N_0)} ; & H(N_0) \neq q \\ \frac{N_0 w_0}{\text{GGE}(H(N_0))} \cdot \ln p & ; H(N_0) = q \end{cases}$$

from which the initial numbers for the critical points may be derived:

$$E_B = \frac{F_p \cdot \text{GGE}(q)}{w_0 \ln p} ; \quad H(E_B) = q (= H_{\min})$$

$$E_C = \frac{F_p \cdot \text{GGE}(H_{\max})}{w_0} \cdot \frac{1 - q/H_{\max}}{p^{1-q/H_{\max}} - 1} ; \quad H(E_C) = H_{\max}$$

or the ratio,

$$\frac{E_B}{E_C} = \frac{\text{GGE}(q)}{\text{GGE}(H_{\max})} \cdot \frac{p^{1-q/H_{\max}} - 1}{1 - q/H_{\max}} \cdot \frac{1}{\ln p}$$

Inserting the gross growth efficiency underlying the allometric model,

$$\text{GGE}(H(N_0)) = \gamma H(N_0)/(k + H(N_0))$$

brings the ratios of initial numbers and recruitment for the critical points to the form,

$$\frac{E_B}{E_C} = \frac{q}{q+k} \cdot \frac{H_{\max} + k}{H_{\max} - q} \cdot \frac{p^{1-q/H_{\max}} - 1}{\ln p} ; \quad \frac{N_B}{N_C} = \frac{E_B}{E_C} \cdot p^{q/H_{\max} - 1}$$

Note that this recruitment ratio is independent of the amount of food (F_p), the assimilation efficiency (γ), the exponent m as well as the initial weight (w_0).

Suppose $q = 0.15$ and $k = 0.05$ as in the example in Section 10.1. All units are in $(\mu\text{g dry wt})^{0.25} \text{ d}^{-1}$ because $m = 0.25$. Putting $H_{\max} = 0.40$ gives a maximum growth rate of 18% d^{-1} for Atlantic cod and 12% for Atlantic herring at the onset of feeding. After gaining a factor of p in weight, the specific growth rate is reduced by a factor of $p^{-0.25}$. At the beginning of the juvenile stage, the maximum specific growth rate is only ca. 4% d^{-1} for cod ($p = 269$) and ca. 3% d^{-1} for herring ($p = 181$). Food-specific recruitment to the juvenile cod stage is reduced by a factor of 0.23 (i.e. $N_B/N_C = 0.23$) when the number of first feeding larvae increases by a factor of 7.7 (i.e. $E_B/E_C = 7.7$). In terms of biomass,

$$B_1 = B_0 p^{1-q/H(N_0)},$$

point C represents an increase of a factor of $269^{0.625} = 33$ and point B the *status quo* situation. For herring ($p = 181$) the critical recruitment ratio is slightly higher ($N_B/N_C = 0.25$) but the critical ratio of initial number somewhat lower ($E_B/E_C = 6.4$) compared to cod ($p = 269$). For a treatment of the predator-prey size ratio (cf. Fig. 10.1), suppose $p = 100$. The critical recruitment ratio is then 0.28 corresponding to a factor 4.9 increase in initial numbers. The critical recruitment ratio is, thus, rather insensitive to changes in p but, E_B/E_C , the relative domain of variation in initial numbers increases from about 5 in case of $p = 100$ to almost 15 for $p = 1000$.

In order to obtain an expression for the recruitment curve we first insert the relationship for GGE in the F_p -equation and obtain

$$N_0 = \frac{\gamma F_p}{w_0} \cdot \frac{H(N_0) - q}{H(N_0) + k} \cdot \frac{1}{p^{1-q/H(N_0)} - 1}$$

Inserting $p^{-q/H} = N_1/N_0 = l_1$ or $H = -q \ln p / \ln l_1$ gives the transcendental equation for the food and size-specific recruitment curve,

$$N_0 = \frac{\gamma F_p}{w_0} \cdot \frac{\ln(pl_1)}{(pl_1 - 1) \ln(pl_1^{-k/q})}$$

The formula permit us to calculate N_0 , the initial number for a specific value of the survivorship l_1 , and then obtain recruitment by $N_1 = l_1 N_0$.

Fig. 10.2 shows the curve for food-specific recruitment to gain a factor of 100 in weight when the situation in the example of Section 10.1 (e.g. $H = 0.25$ and $q = 0.15$ $(\mu\text{g dry wt})^{0.25} \text{ d}^{-1}$) is considered to be valid at an initial number of 10^{13} first feeding cod larvae. The maximum rate of growth is, again, put to $0.40w^{-0.25} \text{ d}^{-1}$. Recruitment is $N_1 = 6.3 \cdot 10^{11}$ because the instantaneous rate ratio of mortality to growth is $q/H = 0.6$ and the survivorship of the $N_0 = 10^{13}$ larvae becomes $100^{-0.6}$ or 6.3%. Hence, the initial biomass of $24.5 \cdot 10^{13} \mu\text{g dry wt}$ or 245 tons dry wt increases by a factor of 6.3 to 1546 tons dry wt at recruitment after $\tau_1 = 77$ days. The amount of food eaten is

$$F_{100} = \frac{245}{0.7} (1 + 1/5) \frac{100^{0.4} - 1}{0.4} = 5575 \text{ tons dry wt}$$

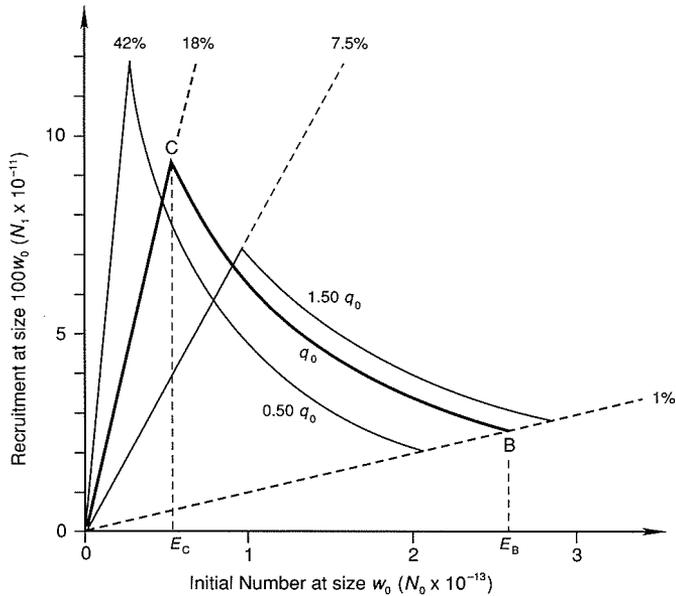


Fig. 10.2. The food-and-size-specific recruitment curve for $F_{100} = 5575$ tons dry wt and $q_0 = 0.15 (\mu\text{g dry wt})^{0.25} \text{ d}^{-1}$ in the allometric model. The assimilation efficiency is 70% and the specific rate of fasting metabolism is $0.05w^{-0.25} \text{ d}^{-1}$. N_0 denotes the number of first feeding larvae with body weight $24.5 \mu\text{g dry wt}$ (such as for Atlantic cod). N_i denotes the number of recruits of size 2.45 mg dry wt ($p = 100$). The maximum specific growth rate is $0.40w^{-0.25} \text{ d}^{-1}$ or 2.67 times the rate of mortality. The maximum survival at point C (reached after 48 days) is, therefore, $0.01^{1/2.67}$ or 17.8% giving rise to a 17.8-fold increase in the biomass of the year-class. When the rate of growth is reduced by a factor of 2.67 the time required to reach the size of recruitment increases by the same factor, i.e. point B of 1% survival is reached after 128 days (during which the biomass remains constant). The recruitment curves for 50% reduction ($q = 0.075$) and 50% increase ($q = 0.225$) in the rate of mortality are also shown.

This requirement for a consistent amount of food consumption has been used to obtain the recruitment curve connecting points C and B in Fig. 10.2. Curves for 50% change in the rate of mortality (but with unchanged F_{100}) are also shown. Point B moves up along the 1% survival line when the coefficient of size-specific mortality (q) increases. Point C of maximum growth follows a descending curve (i.e. recruitment N_C decreases but E_C increases with higher levels of mortality). Point C thus approaches point B and they coincide when $q = H_{\max}$ at an initial number of

$$E_C = E_B = \frac{\gamma F_p H_{\max}}{w_0 (k + H_{\max}) \ln p} ; \quad q = H_{\max}$$

or, at $N_0 = 3.07 \cdot 10^{13}$ in the present case. The equivalent situation in the case of density-dependent growth in the elaborated S&C model is shown in Fig. 9.1.

10.3. Recruitment to meet a constant average rate of food consumption

The average rate of food consumption by the year-class, C_p , is obtained by dividing the total amount of food eaten with the time required to gain a factor of p in weight. That is

$$C_p = F_p / \tau_1 = \gamma^{-1} N_0 w_0^{1-m} (k + H(N_0)) \cdot \frac{m}{p^m - 1} \cdot \frac{p^{1-q/H(N_0)} - 1}{1 - q/H(N_0)}$$

For example, in the case of $N_0 = 10^{13}$ considered in Fig. 10.2, 5575 tons dry wt is consumed in the course of 77 days which gives an average rate of food consumption of 72.4 tons dry wt per day. The actual rate of food consumption increases from ca. 47 tons on the day of first feeding to ca. 94 tons on day 77. This follows from a computation of $C(w)$, i.e.

$$C(w) = N(w)i(w) = \gamma^{-1} N_0 (k + H(N_0)) w_0^{q/H(N_0)} w^{1-m-q/H(N_0)}$$

which implies that the rate of food consumption is constant if $H(N_0) = q/(1-m)$ or 0.20 ($\mu\text{g dry wt}$) $^{0.25}$ d^{-1} in the present case of $q = 0.15$ ($\mu\text{g dry wt}$) $^{0.25}$ d^{-1} and $m = 0.25$. The rate of food consumption by the year-class bears a decreasing relationship to weight if $0.15 \leq H < 0.20$ and an increasing relationship if $0.20 < H \leq 0.40$. The general situation is as follows

$$\begin{aligned} 1 - m < q/H(N_0) \leq 1 \quad \text{or} \quad q \leq H(N_0) < q/(1 - m) & : C(w) \text{ decreases} \\ q/H_{\max} \leq q/H(N_0) < 1 - m \quad \text{or} \quad q/(1 - m) < H(N_0) \leq H & : C(w) \text{ increases} \end{aligned}$$

Replacing the F_p -requirement with the C_p -requirement, we obtain a new recruitment equation from the C_p -condition above,

$$N_0 = \frac{\gamma C_p}{m w_0^{1-m}} \cdot \frac{1 - q/H(N_0)}{k + H(N_0)} \cdot \frac{p^m - 1}{p^{1-q/H(N_0)} - 1}$$

Recruitment is, then, calculated by the procedure described in Section 10.2, i.e. inserting $l_1 = p^{-q/H}$. Alternatively, one may obtain N_0 and l_1 for a specific value of H and then $N_1 = N_0 l_1$.

Fig. 10.3 shows the C_{100} -specific recruitment curves under the same conditions as the F_{100} -specific curves in Fig. 10.2. Point C is the reference point, i.e. $C_{100} = 5575/48.1 = 115.9$ tons dry wt d^{-1} . The time required to reach the critical point of maximum growth is 48.1 days irregardless of the rate of mortality. Point C, therefore, follows exactly the same descending curve as in the case of F_p -recruitment when the coefficient of size-specific mortality (q) increases. However, since τ_1 is inversely proportional to $H(N_0)$, point B of *status quo* biomass will be raised by a factor of H_{\max}/q compared to the F_p -recruitment situation. The equation for E_B reads,

$$E_B = \frac{\gamma C_p}{m w_0^{1-m}} \cdot \frac{p^m - 1}{k + q} \cdot \frac{1}{\ln p} \quad \left(= E_B \text{ in } F_p\text{-case} \times \frac{H_{\max}}{q}; \quad H_{\max} = H_{\text{ref}} \right)$$

At the low mortality level, $q = 0.075$, point B is, thus, raised by a factor of 5.33 in Fig. 10.3 compared to Fig. 10.2. The raising factor is 2.67 in the case of $q = 0.15$ and only 1.78 for the high level of mortality considered ($q = 0.225$). This is why

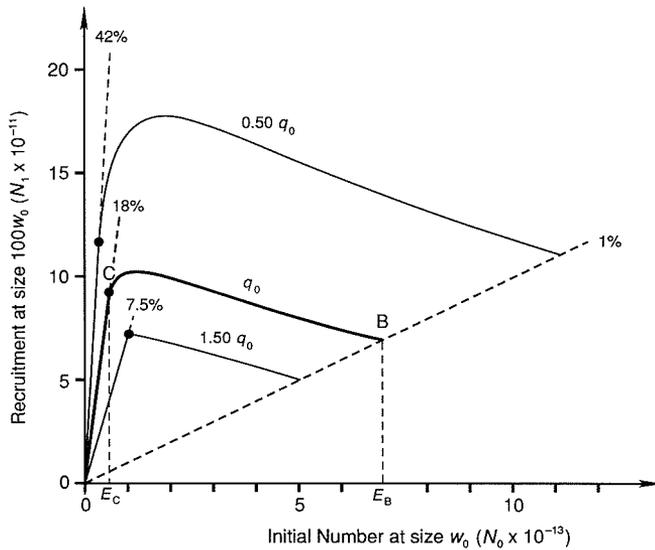


Fig. 10.3. Size-specific recruitment in the case of an average rate of food consumption of $C_{100} = 116$ tons dry wt per day in the allometric model. The specification of the model is otherwise identical to the situation in Fig. 10.2. Point C of maximum growth has been chosen as the common reference for the two situations. That is the amount of food eaten when point C is reached after 48 days equals the $F_{100} = 5575$ tons criterion used in Fig. 10.2. The recruitment curves for $\pm 50\%$ changes in the rate of mortality (but with unchanged C_{100} -criterion) are also shown.

the curves in Fig. 10.3 shows the opposite q -trend to the equivalent curves in Fig. 10.2. When q increases, point B moves down the 1%-survival line, recruitment at point C decreases at about the same rate and the recruitment window narrows down (because, $l_{\max} = p^{-q/H_{\max}}$, the slope of the initial C-recruitment line decreases). Points C and B coincide (see $E_C = E_B$ formula in Section 10.2) when $q = H_{\max}$ at $N_0 = 3.07 \cdot 10^{13}$ in the present case.

The ratio of initial numbers, E_B/E_C , and hence, the ratio of recruitment, N_B/N_C , are consequently also raised by a factor of H_{\max}/q compared to the F_p -case in Section 10.2. This raising (by a factor of 2.67 in case of $q = 0.15$) creates a higher degree of recruitment stability against variations in initial numbers in the present C_p -case compared to F_p -recruitment. The E -ratio or the relative span in critical initial numbers increases from 4.9 in Fig. 10.2 (q_0 -curve) to more than 13 in Fig. 10.3 and the recruitment ratio is raised from 0.28 to 0.74. The deviation in recruitment measured at the critical points is actually less than a factor of 2 when q varies between zero and H_{\max} although the E -ratio represents a large domain of variations in initial numbers (increasing from 13 for $q = 0.15$ to $2p = 200$ for $q = 0$). However, at low levels of mortality, the recruitment curve has a pronounced maximum (see top curve for $q = 0.075$ in Fig. 10.3) and the ratio of critical recruitment does not reflect the true variability in recruitment.

10.4. Discussion and conclusions

One aim of this example was to consider a simple extension to the models presented in Ex. 7 in order to obtain a sensible description of larval growth and mortality. In this respect, the allometric model is attractive since it is specified by only three constants (q , H and m) and cannot be rejected immediately based on our limited knowledge on growth and mortality of larval fish (e.g. Houde, 1987). With $m \approx 0.25$, the model has the desired properties. The specific growth rate is, then, inversely proportional to the body weight to the power of 0.25. The rapid reduction in the specific growth rate in case of the B&H exponent of $1/3$ is considerably moderated with this weight exponent of $1/4$ (ca. 50% for $p = 100$). A value of 0.25 is also in agreement with general knowledge on the weight exponent of specific metabolism (Hemmingsen, 1960, Fenchel, 1974). Furthermore, empirical evidence seems to support a value of 0.25 for the weight exponent of the general trend in decreasing mortality rate with increasing body size throughout the pelagic ecosystem (Peterson & Wroblewski, 1984). Based on data on larval haddock, plaice and mackerel as well as theoretical reasoning, Ware (1975) also concluded that the mortality rate is inversely proportional to particle size whether it is an egg or a larva. The consideration in Fig. 10.1 of mass balance in the predation-food-consumption process gives a direct answer as to why we may expect proportionality between the mortality rate and the specific rate of food consumption. Peterson & Wroblewski (1984) reach a similar conclusion but their approach is based on more complicated psd theory (Silvert & Platt, 1980) and the important points become less transparent.

Based on these brief comments, it can be concluded that the allometric model is good enough to go on with as a general but simple stage-specific description of the vital rates during larval and juvenile life. The model can be applied to consecutive stages of the development of the year-class. For example, if the total size range from the egg stages to the size of first maturity is divided into r stages each of which is governed by a constant set of (q , H) values, the total survivorship is obtained by the multiplicative rule,

$$l = p_1^{-q_1/H_1} \cdot p_2^{-q_2/H_2} \cdot \dots \cdot p_r^{-q_r/H_r}$$

where H_j may depend on N_{j-1} , the initial number of fish entering the j th stage. It is important that biological significance can be attached to the p s, the weight gaining factors. In the present example, we have only considered one stage and two alternative definitions of p are of particular interest for early life studies. The first relates to physiological reasonably well-defined sizes of beginning and ending the stage such as the considerations of the survival from the onset of feeding through metamorphosis. Based on Atlantic cod and herring (Houde, 1987), the value of p in this definition seems to be in the order of 200. The second relates to the size ratio between larvae and their prey. We have, here, reason to believe that p takes values in the order of 100. For example, a cod prefers prey of about $1/100$ of its own weight (Ursin, 1973). A $p = 100$ fits well with the fact that a ($24.5 \mu\text{g}$ dry wt) cod larva at the onset of feeding is able to eat *Calanus* eggs and small copepod nau-

plii of about 0.2 μg dry wt. When the cod larva has increased in weight by a factor of 100 and reached a size (2.45 mg dry wt) of about one-third of the weight at metamorphosis, then it is able to consume the adult stages of the small copepods (which typically show a factor of 100 in weight from egg to adult). It is actually also able to eat first feeding larvae. Thus, the 2.45 mg dry wt larva is much less dependent on the production of eggs and nauplii since it is also able to utilize the standing crop of various copepods (Jones, 1973). It is for this reason that it is of particular interest for recruitment studies to describe the death process as a size and density-dependent function of the available food supply and predation rate (see also Ware, 1975).

The concept of an allometric growth model was probably first considered in depth by Parker & Larkin (1959). Apart from more recent applications of psd-theory, very few investigations of the combined allometric model for growth and mortality seem to be available. However, Ware (1975) introduced a model similar to the allometric basis presented in this example. In his important considerations of egg size, Ware used an instantaneous rate ratio of mortality to growth of ca. 0.7 which is close to our example of $q/H = 0.15/0.25 = 0.6$. Ware's work in combination with Beverton & Holt's (1957) considerations of the Ricker & Foerster (1948) suggestion (see Ex. 7) actually creates an important basis for the extensions considered here in terms of incorporating a simple treatment of food supply and consumption rates.

The major difference between the present treatment and Ex. 7 lies in the expression for the growth coefficient, $H(N_0)$, as a function of the initial number, N_0 . The beginning point in Ex. 7 is the direct (empirical or qualified guess based) formulation of the function $H(N_0)$ from which we, then, derived the size-specific recruitment curve taking mortality into account as a separate process. The beginning point in the present example is the formulation of a food supply criterion from which the dependency of H on N_0 and on the specification of mortality etc. is derived. The resulting curve, therefore, represents size-specific as well as food-specific recruitment according to the particular criterion that has been applied. It is important to note that there is no need to replace $H(N_0)$ with, say, the equivalent start-density dependent version of the S&C model, $G_{\max}/(1 + N_0/A(N_0))$. The recruitment curve will be the same because the food criterion alone determines the growth coefficient as a function of N_0 .

Figs 10.2 and 10.3 illustrate that the shape of the recruitment curve indeed depends on the selection of the food criterion. Note that the C-line dynamics are determined by the density-independent rules (because $H(N_0) = H_{\max}$). The equations for point C are, therefore, the same in the two cases considered and also identical to the C-equations in Ex. 9.2 for the S&C model. Hence, the position of the C-line is very sensitive to changes in the mortality rate as discussed in Ex. 9.4.

As expected from the discussion in Ex. 9, the F_p -criterion in Fig. 10.2 does not stabilize recruitment against variations in N_0 to the same degree as with density-dependent growth (see Fig. 9.2). However, in the second case, considering F , the amount of food eaten as a variable that is proportional to the time required to gain a factor of p in weight (where C_p denotes the constant of proportionality), we ob-

tain a higher degree of stability (Fig. 10.3). This is to be expected because more food, $F = C_p \tau_1$, is available when growth is slow.

The food-criteria stabilizes recruitment at medium to high initial numbers against fluctuations in the mortality rate. For example, the survivorship at $N_0 = 10^{13}$ with the F_{100} -criterion in Fig. 10.2 is $l_1 = 0.063$ or 6.3%. Changing the mortality rate with $\pm 50\%$ causes the survival and, hence, recruitment to vary by a factor of $l_1^{-1} = 16$ if mortality had no effect on growth (i.e. the multiplicative rule is valid with no food criterion). In Fig. 10.2, recruitment varies with a factor of only ca. 1.5! The mortality-to-growth effect of the F_p -criterion is actually so strong that it creates the opposite trend than common believed. Recruitment increases when the rate of mortality increases! At the high level of mortality, the growth coefficient, $H(10^{13}) = 0.39$, almost attains the maximum value of $H_{\max} = 0.40$ whereas at the low mortality level, $q = 0.075$, the growth coefficient, $H(10^{13}) = 0.11$, almost reaches the minimum value of q . This reversed q -recruitment-trend is, in other words, achieved by an unrealistically high variation in the rate of growth (a factor of ca. 3.5). With the C_p -criterion, we obtain the expected trend (Fig. 10.3). Recruitment increases when the mortality rate decreases and *vice versa*. The growth rate varies by a factor of 2 when the mortality rate is changed by $\pm 50\%$ and recruitment varies by a factor of ca. 3.

It is not possible to obtain recruitment as an explicit function of initial numbers. One can, however, obtain a reasonable fit to the F_p -recruitment curves in Fig. 10.2 by a power function,

$$H(N_0) = \begin{cases} H_{\max} & , N_0 \leq E_C \\ H_{\max} (N_0/E_C)^{-\delta} & , N_0 \geq E_C \end{cases}$$

For the q_0 -case in Fig. 10.2, $\delta \approx 0.6$ but the exponent decreases with increasing p and/or increasing mortality rate (q). We conclude that the recruitment curve shows a resemblance to the δ -power-Ricker curve (Ex. 7.5). It also gives us an idea about the shape of the age-specific recruitment curve,

$$R = N_0 [p_{\tau_r}(H(N_0))]^{-q/H(N_0)}$$

where $p_{\tau_r}(H(N_0))$ is the weight gaining factor after time τ_r . That is, using the τ -equation in Section 10.1,

$$p_{\tau_r}(H(N_0)) = w(t_r)/w_0 = [1 + m H(N_0) w_0^{-m} \tau_r]^{1/m}; \quad \tau_r = t_r - t_0$$

Inserting the approximative relationship for $H(N_0)$, brings age-specific recruitment on the form,

$$R = N_0 [1 + C_0/x]^{-x}; \quad x = \frac{q}{mH_{\max}} \left(\frac{N_0}{E_C}\right)^{\delta}; \quad C_0 = \mu_0 \tau_r, \quad \mu_0 = q w_0^{-m}; \quad N_0 \geq E_C$$

This represents the max-min type of recruitment curve considered in Ex. 7 (see Fig. 7.4). The saddle-point situation occurs for $\delta C_0 = 4.625$ or, at recruitment after 114 days for $\delta = 0.6$ and $\mu_0 = 0.067 \text{ d}^{-1}$ (q_0 -case in Fig. 10.2). The initial part of the age-specific recruitment curve, the C-line, is obtained with $\delta = 0$ in the R-equation above. This age-specific situation is somewhat artificial because we first obtain a

function, $H(N_0)$, from the F_p -criterion (which in Fig. 10.2 implies that the time required to grow to size-specific recruitment increases from 48 days at point C to 128 days at point B). Second, using this $H(N_0)$, we derive recruitment to a specific age. However, the procedure provides the link to the considerations of start-density dependent growth in Ex. 7 and illustrates that age-specific recruitment takes a completely different form than size-specific recruitment.

We shall, briefly, consider a third food criterion. Assume that a constant amount of food, F_{τ_r} , is eaten during a specific period of time (τ_r). That is

$$F_{\tau_r} = \gamma^{-1} B_0 \frac{H(N_0) + k}{H(N_0) - q} \left\{ [p_{\tau_r}(H(N_0))]^{1 - q/H(N_0)} - 1 \right\}$$

where $p_{\tau_r}(H(N_0))$ is given by the above expression. The critical points are also described by the expressions for the F_p -situation in Section 10.2 but p is replaced with $p_{\tau_r}(H(N_0))$. Hence, the ratios of initial numbers and recruitment for the critical points are

$$\frac{E_B}{E_C} = \frac{q}{q + k} \cdot \frac{H_{\max} + k}{H_{\max} - q} \cdot \frac{[p_{\tau_r}(H_{\max})]^{1 - q/H_{\max}} - 1}{\ln p_{\tau_r}(q)}$$

$$\frac{R_B}{R_C} = \frac{E_B}{E_C} \cdot \frac{[p_{\tau_r}(H_{\max})]^{q/H_{\max}}}{p_{\tau_r}(q)}$$

Using $p(0.25) = 100$ as the reference to F_{100} -size-specific recruitment in Fig. 10.2, we obtain $\tau_r = 77$ days for cod ($w_0 = 24.5 \mu\text{g}$ dry wt). The entire dynamics of F_{77} -age-specific recruitment relative to Fig. 10.2 may be understood from the p values alone. We consider recruitment after 77 days (but omit the $\tau_r = 77$ (days) p -index for short notation). The p -value at point C for age-specific recruitment, $p(0.40) = 396$, decreases towards the p -value at point B, $p(0.15) = 28$, as the initial number increases from E_C to $E_B = 17 E_C$. Recruitment, hereby, increases by a factor of 5.6. This follows directly from the above formulas. What actually happens compared to the situation in Fig. 10.2 is that the recruitment window narrows down. The slope of the C-line decreases from 18% to $p(0.40)^{-0.15/0.40}$ or 11% and the slope of the B-line increases from 1% to $1/p(0.15)$ or 3.6%. Point C also moves down and point B up its line which results in the opposite recruitment course compared to Fig. 10.2. If we, instead, consider herring ($w_0 = 135 \mu\text{g}$ dry wt), then the reference point of $p = 100$ for $H = 0.25$ is obtained after $\tau_r = 118$ days. This means that recruitment after 118 days for herring also increases by a factor of 5.6 as the initial number increases by a factor of 17 (because the weight gaining factors, the $p(H)s$, and, hence, the critical ratios are independent of the initial weight (i.e., $\tau_r w_0^{-m}$ is constant in the two cases)).