10

Stock Recruitment Relationships

10.1 Recruitment and Fisheries

10.1.1 introduction

Ignoring immigration, recruitment and individual growth are the major contributors to the production of biomass within a stock. Akin to the study of growth, some people have dedicated huge efforts toward investigating fisheries recruitment, especially the relationship between mature or spawning stock size and subsequent recruitment (Cushing, 1988; Myers and Barrowman, 1996; Myers, 2001). Recruitment to fish populations naturally tends to be highly variable, and the main problem for fisheries scientists is whether recruitment is determined by the spawning stock size or environmental variation or some combination of both. To conduct stock assessments that include a risk assessment involves projecting the population forward in time, and this would require some notion of expected recruitment. To be able to do this, a minimum requirement is to have information about a stock's productivity. Either estimates of a time series of recruitment levels or a stock recruitment relationship can be used for these purposes.

In this chapter, we will consider the mathematical description of stock recruitment relationships, but as with growth, we will mostly ignore the biology behind the relationships. The biology will only be considered where it has a direct bearing on how the stock recruitment relationships are described. We will review the most commonly used mathematical models of stock recruitment and will discuss their use in stock assessment models of varying complexity.

10.1.2 r ecruitment Overfishing

Two types of overfishing are commonly discussed in the fisheries literature. The first is termed *growth overfishing*, and is where a stock is fished so hard that most individuals are caught at a relatively small size. This is the classic yield-per-recruit problem of balancing the stock losses due to total mortality against the stock gains from individual growth (see Chapter 2). The aim of

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such analyses is to determine the optimum size and age at which to begin harvesting the species. Growth overfishing is where the fish are being caught before they have time to reach this optimal size.

The second type of overfishing, the form particularly relevant to this chapter, is *recruitment overfishing*. This occurs when a stock is fished so hard that the stock size is reduced below the level at which it, as a population, can produce enough new recruits to replace those dying (either naturally or otherwise). Obviously, such a set of circumstances could not continue for long, and sadly, recruitment overfishing is usually a precursor to fishery collapse.

Growth overfishing is not difficult to detect. The data requirements for detection are a growth curve and an estimate of the age structure of the fishery. With this information, one could conduct a yield-per-recruit analysis and determine how close the fishery is to the theoretical optimum. There can be complicating factors, such as whether the fishery really is at an equilibrium and which criterion to choose when selecting the optimum mean size at capture (i.e., which target fishing mortality to use; $F_{0.1}$ remains common). However, the methods are well established and in common use. Sadly, the same cannot be said about the detection of recruitment overfishing, which could require a determination of the relation between mature or spawning stock size and recruitment levels. This has proven to be a difficult task for very many fisheries.

10.1.3 The existence of a Stock r ecruitment r elationship

There is a commonly held but mistaken belief that the number of recruits to a fishery is usually independent of the adult stock size over most of the observed range of stock sizes. This can be a dangerous mistake (Gulland, 1983). It suggests that scientists and managers can ignore stock recruitment relationships unless there is clear evidence that recruitment is not independent of stock size. The notion of no stock recruitment relationship existing derives from data on such relationships appearing to be very scattered, with no obvious pattern (Figure 10.1).

The fallacy of no relationship existing between stock size and subsequent recruitment originated because people made the invalid conclusion that because they could not observe a significant stock recruitment relationship, one did not exist. If, in fact, such relationships did not exist, then fishery collapses would be less common. Hilborn and Walters (1992, p. 241) were explicit: "While recruitment may be largely independent of stock size as a fishery develops, experience has shown that most fisheries will reach a point where recruitment begins to drop due to over-fishing." This implies a relationship between stock size and subsequent recruitment.

In a recent controversy there are strong arguments given for a relationship between recruitment and spawning stock biomass (Myers, 1996, 1997; Myers and Barrowman, 1996; Francis, 1997; Gilbert, 1997; Hilborn, 1997).

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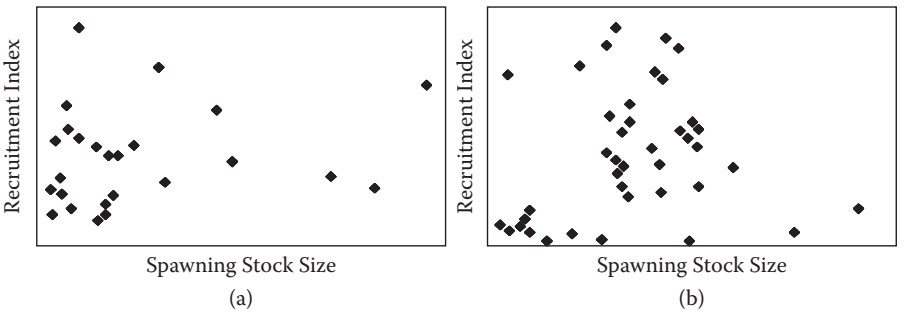

Fig ur e 10.1
Stock recruitment relationships with recruitment plotted against spawning adult stock size. The scales on the two plots differ. (a) For plaice. (After Beverton, 1962) (b) For Georges Bank haddock. (After Overholtz, 1986.) In both cases, a flat line provides an excellent fit.

10.2 Stock Recruitment Biology

10.2.1 Properties of "g ood" Stock r ecruitment r elationships

A good introduction to the biological processes behind the stock recruitment relationships that we are going to consider is given by Cushing (1988), who provides an overview of the sources of egg and larval mortality along with good examples and a bibliography on the subject. There is an enormous literature on the biology of stock recruitment relations and their modifiers. A great variety of influences, both biological and physical, have been recorded as affecting the outcome of recruitment. We will not be considering the biological details of any real species except to point out that the relation between stock size and resulting recruitment is not deterministic, and there can be a number of forms of feedback affecting the outcome. We will primarily be considering how best to model stock recruitment relationships from fisheries data. Various mathematical descriptions of stock recruitment relationships have been suggested, but we will only consider those by Beverton and Holt, Ricker, and Deriso-Schnute.

Ricker (1975) listed four properties of average stock recruitment relationships that he considered desirable:

1. A stock recruitment curve should pass through the origin; that is, when stock size is zero, there should be no recruitment. This assumes the observations being considered relate to the total stock, and that there is no "recruitment" made up of immigrants.
2. Recruitment should not fall to zero at high stock densities. This is not a necessary condition, but while declines in recruitment levels with increases in stock densities have been observed, declines to zero

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have not. Even if a population was at equilibrium at maximum stock biomass, recruitment should still match natural mortality levels.

3. The rate of recruitment (recruits-per-spawner) should decrease continuously with increases in parental stock. This is only reasonable when positive density-dependent mechanisms (compensatory) are operating (for example, an increase in stock leads to an increase in larval mortality). But if negative density-dependent mechanisms (depensatory) are operating (for example, predator saturation and Allee effects; Begon and Mortimer, 1986), then this may not always hold.
4. Recruitment must exceed parental stock over some part of the range of possible parental stocks. Strictly, this is only true for species spawning once before dying (e.g., salmon). For longer-lived, multi-spawning species, this should be interpreted as recruitment must be high enough over existing stock sizes to more than replace losses due to annual natural mortality.

Hilborn and Walters (1992) suggested two other general properties that they considered associated with good stock recruitment relationships:

5. The average spawning stock recruitment curve should be continuous, with no sharp changes over small changes of stock size. They are referring to continuity, such that average recruitment should vary smoothly with stock size, related to condition 3 above.
6. The average stock recruitment relationship is constant over time. This is stationarity, where the relationship does not change significantly through time. This assumption seems likely to fail in systems where the ecosystem, of which the exploited population is a part, changes markedly.

10.2.2 Data r equirements—Spawning Stock

There is potential for confusion over terms when we refer to the spawning stock biomass in discussions of stock recruitment relationships. What is being considered is not necessarily a biomass but a measure of the reproductive productivity of the mature population. The optimal measurement of spawning stock is the number of eggs spawned (Rothschild and Fogarty, 1989). This measure of reproductive capability may be estimated from the average fecundity by age and the proportion of each age. Alternatively, one could estimate the number of mature females and multiply by the average fecundity, or use total biomass of mature individuals, or even an index of abundance for the population in the year of spawning. It is important to note that all of these methods would have a degree of uncertainty about the estimated values. Of the four methods listed, ignoring measurement errors, the methods were described in descending order of reliability (thus, an index

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of abundance would be the least reliable). By using measures other than egg production, some of the assumptions of the recruitment–stock relationship may be broken (Rothschild and Fogarty, 1989). The uncertainty associated with each indicator of spawning stock implies that the accuracy of the x axis spawning stock size values is suspect even before attempting to estimate recruitment. This calls into question analyses where the independent variable is supposed to be measured without error.

10.2.3 Data r equirements—r ecruitment

Generally, in a fisheries sense, recruitment often refers to the life stage that first becomes vulnerable to fishing gear. But for purposes of stock recruitment relationships, recruitment may be defined as the population still alive at any given time after the egg stage. These two uses can lead to confusion; one relates to recruitment to the fishery, and the other to recruitment to the biological population. In some fortunate fisheries (large fish in freshwater) the number of recruits can be counted directly as they pass through artificial weirs, but in almost all fisheries only indices of relative abundance are possible (possibly from traps or trawl surveys for juveniles).

Once again, there will be errors in estimation as well as natural variation in recruitment levels from year to year. These levels of variation and error in the estimates are very important for the assessment of reliability of the final stock recruitment relationship derived. If the estimates are not especially reliable, then even if a deterministic stock recruitment relationship exists between the spawning stock size and subsequent recruitment, it may be difficult to identify or recognize. Such variation may be confused with environmentally induced recruitment variability, and it would be difficult to distinguish the two (see later).

Before we investigate the possible effects of uncertainty, we will first consider a number of equations that have become part of the tool kit of fisheries modellers for describing stock recruitment relationships.

10.3 Beverton–Holt Recruitment Model

10.3.1 The equations

The Beverton–Holt model of the spawning stock recruitment relationship was devised to incorporate density-dependent survival rates reflecting intracohort competition for critical resources (Figure 10.2, Appendix 10.1):

$$R = \frac{S}{\alpha + \beta S} e^{\varepsilon} \tag{10.1}$$

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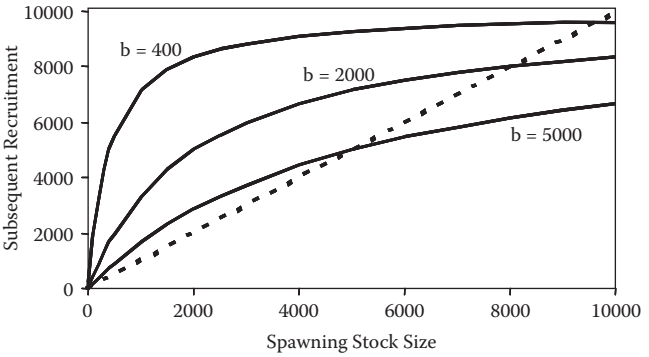

Fig ur e 10.2
A comparison of Beverton–Holt curves relating recruitment against spawning stock size using Equation 10.2 with different values of *a* and *b*. In all cases the value of *a* is 10,000, which is thus the maximum recruitment possible. Note that the steepness at the origin alters considerably as *b* alters (because a recruitment of 5,000 = *a*/2 occurs at a spawning stock size of *b*). The straight, dotted line on the diagram is the line of replacement, so curves to the left of this represent growing populations, while curves to the right represent shrinking populations. In practice, only species that have multiple years of spawning could be to the right of the dotted line (Example Box 10.1).

where R is the recruitment, S is the measure of spawning stock size, and α and β are parameters of the Beverton–Holt relationship. The e^{ε} indicates that the residual errors between the relationship and observed data are expected to be lognormal. The β value determines the asymptotic limit ($= 1/\beta$), while the differing values of α are inversely related to the rapidity with which each curve attains the asymptote, thus determining the relative steepness near the origin (the smaller the value of α, the quicker the recruitment reaches a maximum). As with all stock recruitment equations, this is an average relationship and the scatter about the curve is as important as the curve itself.

There are a number of different formulations used for the Beverton–Holt stock recruitment relationship. Perhaps the most commonly seen is

$$R = \frac{aS}{b+S} e^{\varepsilon} \tag{10.2}$$

which is a restructuring of Equation 10.1 so that R is recruitment, S is the spawning stock, a is the maximum number of recruits produced (the asymptote = $1/\beta$), and b is the spawning stock ($= \alpha/\beta$) needed to produce, on average, recruitment equal to half maximum ($a/2$). It is clear that the initial steepness of the Beverton–Holt curve (Figure 10.2), along with the asymptotic value, captures the important aspects of the behaviour of the equation. The asymptote is given by the value of the parameter a, while the initial steepness is approximated by the value of ($a/b = 1/\alpha$), which happens when S is very small (see Equation 10.2, Example Box 10.1).

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EXAMPLE BOX 10.1

The Beverton–Holt stock recruitment equation. The rows of the *a* and *b* parameters extend from column B to column D. Extend column A, the spawning stock size, down to a value of 10,000 in steps of 500 (to row 30). Copy B5 across to D5, and then copy B5:D5 down to row 30. Plot columns B to D against A, as solid lines to mimic Figure 10.2. Add the dotted line if you wish. Modify the *b* values to observe how this modifies the shape of the curve. Clearly, with an extremely steep curve (*b* very small), the relationship resembles a straight line from very low to very high biomass values. Change the equation in B5:B30 to become =((B$1*$A5)/(B$2+$A5))*loginv(rand(),0,B$3), to see the effect of random error on recruitment. Alter the line for column B to a scatter of points with no connecting line. Give C1:C2 the same values as in B1:B2. Change the value of the errors in B3 to 0.5 and press F9 a few times. What impact does that have on the apparent shape of the Beverton–Holt stock recruitment curve?

	A	B	C	D
1	*a*	10000	10000	10000
2	*b*	5000	2000	400
3	**Error**	0.000001		
4	**Spawn**	**Recruit 1**	**Rec 2**	**Rec 3**
5	1	=(B$1*$A5)/(B$2+$A5)	=(C$1*$A5)/(C$2+$A5)	24.9
6	10	=(B$1*$A6)/(B$2+$A6)	=(C$1*$A6)/(C$2+$A6)	243.9
7	100	=(B$1*$A7)/(B$2+$A7)	=(C$1*$A7)/(C$2+$A7)	2000.0
8	200	Copy down to row 30	Copy down to row 30	3333.3
9	300	566.0	1304.3	4285.7
10	400	740.7	1666.7	5000.0
11	500	909.1	2000.0	5555.6
12	1000	1666.7	3333.3	7142.9
13	1500	2307.7	4285.7	7894.7
14	2000	2857.1	5000.0	8333.3

10.3.2 Biological Assumptions/implications

The Beverton–Holt model of stock recruitment derives from the balance between density-independent and density-dependent juvenile mortality (see Appendix 10.1). This linear relationship implies that the larger the spawning stock, the faster the juveniles will die. There is an inverse relationship between the average number of recruits-per-spawner and the spawning stock size.

The idea of attempting to interpret the parameters of Equation 10.2 draws attention to the differences between an equation as a theory and an equation

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as a summary description of a natural process. Essentially, Equations 10.1 and 10.2 attempt to describe the continuous reduction through mortality in the numbers of recruits from their initial egg production numbers as spawning stock size increases (see Appendix 10.1).

Each of the parameters can be interpreted in terms of the observable world. However, despite the possibility of giving a real interpretation to the parameters, this description of recruitment is too simple to have great explanatory power and generally should be considered simply as a convenient mathematical description of the stock recruitment relationship. All this means is that just because it may be possible to fit the equation to real data, this does not imply that the population concerned really has a stable, asymptotic limit to the number of recruits its population can produce.

Historically, Beverton and Holt (1957) introduced their curve because it had a simplistic interpretation, which meant it could be derived from first principles. But it was also mathematically tractable, which was important to them with the requirement at the time to use analytical methods. In fact, its continued use appears to stem a great deal from inertia and tradition. You should note that if we are to treat the Beverton–Holt curve simply as a mathematical description, then effectively any curve, with the good properties listed earlier, could be used.

10.4 Ricker Model

10.4.1 The equation

As with the Beverton–Holt model, there are a number of different formulations of the Ricker equation, but one that is commonly used is

$$R = aSe^{-bS}e^{\varepsilon} \tag{10.3}$$

where R is the recruitment from S, the spawning stock, a is the recruits-per-spawner at low stock levels, and b relates to the rate of decrease of recruits-per-spawner as S increases. The e^{ε} indicates that the residual errors between the relationship and observed data are expected to be lognormal. Note that parameters a and b are very different from those in the Beverton–Holt equation. This equation does not attain an asymptote but instead exhibits a decline in recruitment levels at higher stock levels (Figure 10.3, Appendix 10.1, Example Box 10.2). It has been criticized for this detail (Hall, 1988) as being a theoretical input with no empirical support. But there has been argument on both sides, and our coming discussion on uncertainty due to measurement errors may also illuminate the matter.

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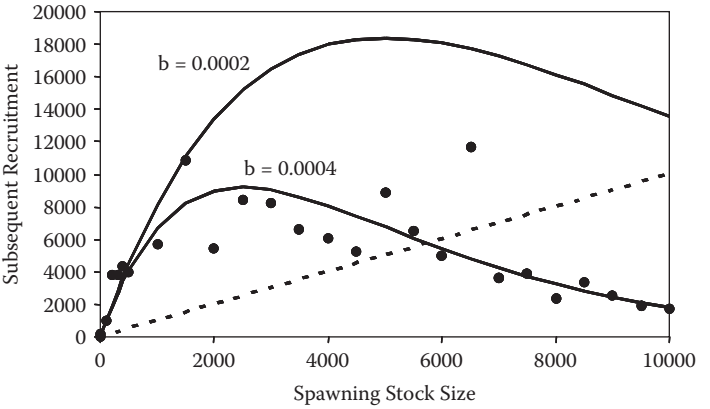

Fig ur e 10.3
Two Ricker stock recruitment curves based on Equation 10.3. Each of the data series has an *a* of 10, with the *b* values indicated. The separate points are the same as the *b* = 0.0004 curve, except they have lognormal error with a standard deviation of 0.5 associated with it. Note that the *b* value mainly influences the degree of recruitment decline with increasing stock and has little effect on initial steepness (Example Box 10.2).

EXAMPLE BOX 10.2

The Ricker stock recruitment relationship. Extend column A, the spawning stock size, down to a value of 10,000 in steps of 500 (to row 30). Copy B5 across to D5, and then copy B5:D5 down to row 30. To mimic Figure 10.3, plot columns C and D against A, as solid lines, and add column B as a scatter of points. Modify the *a* and *b* values in D1 and D2, to observe how this modifies the shape of the curve (leave B1:B2 alone). Change the error standard deviation value in B3 and press F9 a few times. Note how the scatter of points does not always mimic the deterministic curve.

	A	B	C	D
1	**a**	=C1	10	10
2	**b**	=C2	0.0004	0.0002
3	**error**	0.0001	0.0001	0.0001
4	**Spawn**	**Recruit**	**Rec 2**	**Rec 3**
5	1	=(b$1*$a5*exp(–b$2*$a5))*loginv(rand(),0, b$3)	10.0	10.0
6	10	=(b$1*$a6*exp(–b$2*$a6))*loginv(rand(),0, b$3)	99.6	99.8
7	100	Copy Down to Row 30	960.8	980.2
8	200	3566.3	1846.2	1921.6
9	300	2419.6	2660.8	2825.3
10	400	5203.6	3408.6	3692.5
11	500	3240.6	4093.7	4524.2

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The Ricker model of stock recruitment differs from that by Beverton–Holt in that the density-dependent mortality term for eggs and juvenile stages relates to the total stock size rather than only to the cohort size.

10.4.2 Biological Assumptions/implications

Various mechanisms have been suggested for generating this form of density dependence (dependent upon total stock size and not just the cohort size). These include the cannibalism of the juveniles by the adults (hence stock density is more important than cohort density), density-dependent transmission of disease, damage by spawning adults of each other's spawning sites (occurs primarily in rivers with fish like salmon), and finally, density-dependent growth combined with size-dependent predation. Each of these mechanisms can lead to different interpretations of the parameters of the Ricker curve.

Once again, the distinction between whether the equation should be interpreted as a theoretical or explanatory statement about the observable world instead of just a convenient empirical description of the average recruitment becomes important. In addition, while the parameters can certainly be given a real-world interpretation, the equations still tend to be overly simplistic and are best regarded as an empirical description rather than an explanation of events.

10.5 Deriso's Generalized Model

10.5.1 The equations

The Beverton–Holt and Ricker stock recruitment curves are special cases of a more general model proposed by Deriso (1980). Schnute (1985) restructured Deriso's equation to produce an even more flexible version with even greater flexibility:

$$R = \alpha S\left(1-\beta\gamma\ S\right)^{1/\gamma} \tag{10.4}$$

where, as before, R is recruitment and S is the spawning stock, and there are three parameters, α, β, and γ. By modifying the value of γ, different special cases can be produced (Schnute, 1985):

$$\begin{aligned}
\gamma = -\infty \quad &: \quad R = \alpha S \\
\gamma = -1 \quad &: \quad R = \alpha S / \left(1+\beta S\right) \\
\gamma \to 0 \quad &: \quad R = \alpha S e^{-\beta\ S} \\
\gamma = 1 \quad &: \quad R = \alpha S\left(1-\beta S\right)
\end{aligned} \tag{10.5}$$

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The first form in Equation 10.5 is a simple constant productivity model where α recruits are produced for each unit of stock; this is density-independent recruitment. The same result follows from setting $\beta = 0$ in Equation 10.4. The next three cases correspond to the standard stock recruitment relationships of Beverton–Holt (1957), Ricker (1954, 1958), and Schaefer (1954), respectively. The Beverton–Holt equation is yet another version of that model, but it has the same properties (asymptotic) as Equation 10.2. The arrow in the Ricker-equivalent merely means "approaches"; thus, as γ approaches zero, the equation becomes equivalent to the Ricker model. Finally, the Schaefer equivalent is really a form of the logistic equation, which is equivalent to the number of recruits-per-spawner declining linearly with increasing spawning stock. Mathematically, the Schaefer equation could lead to negative recruitment if spawning stock managed to rise above the level that could generate the theoretical maximum recruitment. Parameters α and β should always be positive, although γ can have either sign. The curve always passes through the origin, but its shape will depend upon the balance between the three parameters (Figure 10.4, Example Box 10.3).

There are some mathematically unstable properties to the Deriso–Schnute model; consider the implication of $\gamma = 0$, which would lead to a mathematical singularity (divide by zero). The parameter limits should rather be $\gamma \to 0$, from either the negative or the positive direction.

10.6 Residual Error Structure

The stock recruitment curves we have considered are all average expected curves. Observations concerning the stock recruitment relationship would have values that stray above and below the expected average curve (the residual errors from the curve). Consideration of the form these residuals take in wild populations has led to the conclusion that observed variations should be distributed lognormally and reflects the possibility of spawning stocks giving rise to occasional very large recruitment levels.

Hilborn and Walters (1992) recommend that a lognormal distribution of residuals about the average stock recruitment relationship be used unless there is evidence to the contrary. This will generally mean the data or the parameters for each model will have to be log-transformed before being fitted to data (Figure 10.5, Example Box 10.4).

There is also a theoretical justification for using the lognormal distribution to describe the residual errors around stock recruitment relationships. The stock recruitment process can be considered to be the outcome of a whole series of successful survivorships, from the egg stage to recruit. The overall survivorship is simply the product of all of these separate events:

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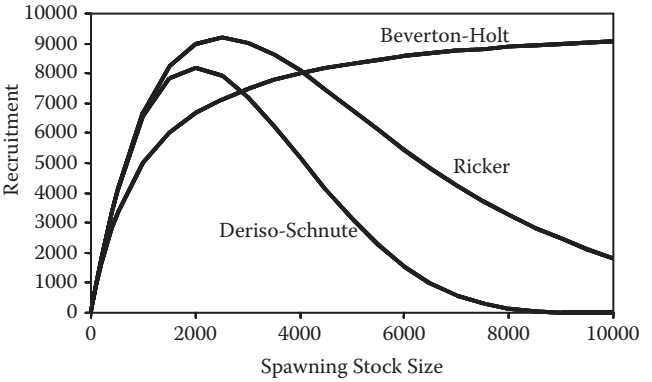

Fig ur e 10.4
An array of stock recruitment curves using the Deriso–Schnute equation (Equation 10.4), the Ricker equation (Equation 10.5), and a version of the Beverton–Holt equation (Equation 10.5). In all cases $\alpha = 10$. For the Deriso–Schnute and Ricker curves, $\beta = 0.0004$, but for the Beverton–Holt equivalent, $\beta = 0.001$. For the particular Deriso–Schnute curve illustrated, $\gamma = 0.25$. If the γ is set = 0.000001 (approaches zero), the curve becomes very similar to the Ricker curve illustrated. If the β is set to 0.001 and the γ is set to –1, the Deriso–Schnute curve will sit on the Beverton–Holt curve (Example Box 10.3).

EXAMPLE BOX 10.3

The Deriso–Schnute generalized stock recruitment model. In B5 put =B$1*A5*(1–B$2*B$3*A5)^(1/B$3), in C5 put as shown below, and in D5 put =($D$1*A5)/(1+$D$2*A5). Extend column A down to 10,000 in steps of 500. Copy B5:E5 down to row 30. To mimic Figure 10.4, plot columns B to D against A. Slowly change B3 toward zero and inspect the graph and the differences in column E. Set B2 = D2, set B3 = –1, and E5 =D5–B5 (and copy down). How close to the Beverton–Holt in column D is the result?

	A	B	C	D	E
1	**alpha**	10	10	10	
2	**beta**	0.0004	0.0004	0.001	
3	**gamma**	0.25			
4	**Spawn**	**Deriso-Schnute**	**Ricker**	**Bev–Holt**	**Diff**
5	1	10.00	=C$1*A5*exp(–C$2*A5)	9.99	=C5–B5
6	10	99.60	=C$1*A6*exp(–C$2*A6)	99.01	=C6–B6
7	100	960.60	=C$1*A7*exp(–C$2*A7)	909.09	=C7–B7
8	200	1844.74	Copy down to row 30	1666.67	1.496
9	300	2655.88	2660.76	2307.69	4.883

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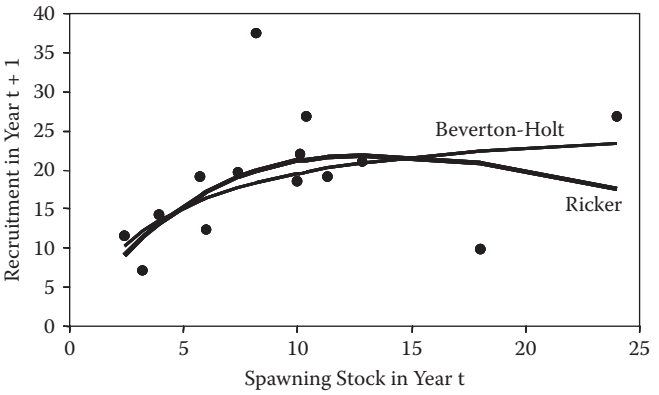

Fig ur e 10.5
Two different stock recruitment models fitted to data from Penn and Caputi (1986) concerning tiger prawns (*Penaeus esculentus*) from Exmouth Gulf, Western Australia. The data points refer to the thirteen years between 1970–1971 and 1983–1984 (Table 10.1, Example Box 10.4).

$$S = S_1 S_2 S_3 \ldots\ldots\ldots\ldots S_n \tag{10.6}$$

where S is the total survivorship over n life stages, and the S_i are the survivorships (probabilities) through life history stage i. To convert the product into a summation, we can take logs on both sides:

$$Ln(S) = \sum Ln(S_i) \tag{10.7}$$

The central limit theorem states that the sum of a long series of independent, identically distributed random variables ($Ln[S_i]$ in this example) will have a distribution that approaches the normal distribution as n increases. Thus, if each S_i is an independent random variable, and there are no particular stages that dominate the sum, the overall survivorship should be lognormally distributed, represented as

$$R_i = \bar{R} e^{N\left(0,\sigma_i^2\right)} \tag{10.8}$$

where the $N(0,\sigma^2_i)$ is a normally distributed random variate with a mean of zero and a standard deviation of σ_i. The lognormal distribution has two properties of interest in this context. It occasionally gives rise to very high recruitment values (skewed tail out toward high values), and the amount of variation will be proportional to the average recruitment. We would thus expect to see higher variation at high levels of recruitment, although this may also be related to the geographical distribution of the species Myers (1991).

In order to fit a stock recruitment model with lognormal residual errors to raw data, it is best to log-transform the equations to normalize the error

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EXAMPLE BOX 10.4

Fitting the Ricker and Beverton–Holt stock recruitment models to Exmouth Gulf tiger prawn data (after Penn and Caputi, 1986). Rather than log-transform the data we will log-transform the parameters as in Equations 10.9 and 10.10. Thus, copy the data from Table 10.1 into columns B and C (down to row 18). In D5 put =Ln($D$1)–($D$2*B5), in E5 put =(Ln(C5/B5)–D5)^2, and in F5 put =$D$1*B5*exp(–$D$2*B5); copy D5:F5 down to row 18. Then in G5 put =Ln($G$1)–Ln($G$2+B5), in H5 put =(Ln(C5/B5)–G5)^2, and in I5 put =$G$1*B5/($G$2+B5), and copy G5:I5 down to row 18. The sum of squared residuals for the Ricker fit is in E3; put =sum(E5:E18). That for the Beverton–Holt fit is in H3; put =sum(H5:H18). Mimic Figure 10.5 by plotting column C against B, as a scatter of points. Add columns F and I as solid lines. Fit the two curves by minimizing E3 through changing D1:D2, and minimizing H3 through changing G1:G2. Which curve provides the smallest sum of squared residuals? While this is the best fitting curve, does it really differ from the alternative by very much? Which curve would be least conservative?

	A	B	C	D	E	F	G	H	I
1			**a**	4.0		**a**	25.0		
2			**b**	0.1		**b**	3.0		
3	**Year**	**Spawn**	**Recruit**	**Ssq_R**	3.6336		Ssq_BH	1.7552	
4	**Date**	**Si**	**Ri**	**Ricker**	**(O–E)²**	**E(R)**	**BevHolt**	**(O–E)²**	**E(B–H)**
5	82–83	2.4	11.6	1.146	0.184	7.552	1.532	0.0019	11.111
6	81–82	3.2	7.1	1.066	0.073	9.295	1.394	0.3569	12.903
7	83–84	3.9	14.3	0.996	0.092	10.562	1.287	0.0001	14.13

structure. Then one can use ordinary least squares or normally distributed likelihoods. Thus, with the Ricker equation (Equation 10.3), we divide through by S and transform using natural logarithms:

$$\mathrm{Ln}\left(\frac{R}{S}\right) = \mathrm{Ln}(a) - bS + \varepsilon \tag{10.9}$$

where the right-hand side provides the expected value of Ln(R/S). This can be compared with the observed value to provide a residual that can be used in a least squares determination of the optimal values of the parameters a and b (see Example Box 10.4). Equation 10.9 has the form of a linear relation, and the parameters could be determined using a linear regression rather than a nonlinear technique.

Similarly with the Beverton–Holt model of stock recruitment (Equation 10.2), we divide through by S and then transform using natural logarithms:

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TABLe 10.1

Stock Recruitment Data for Exmouth Gulf Tiger Prawns (*Penaeus esculentus*), Including Relative Rainfall as an Index of Cyclonic Activity (Figure 10.5, Example Box 10.4)

Year	Spawning Stock Index	Recruitment Index	Cyclone Index	
			January	February
82–83	2.4	11.6	0	0
81–82	3.2	7.1	85	28
83–84	3.9	14.3	0	54
71–72	5.7	19.1	0	1
80–81	6	12.4	18	19
79–80	7.4	19.7	14	41
74–75	8.2	37.5	0	213
73–74	10	18.5	102	22
76–77	10.1	22.1	2	1
77–78	10.4	26.9	4	10
78–79	11.3	19.2	0	0
72–73	12.8	21	1	5
70–71	18	9.9	353	19
75–76	24	26.8	23	38

Source: After Penn and Caputi, 1986.
Note: Sorted on index of spawning.

$$\mathrm{Ln}\left(\frac{R}{S}\right) = \mathrm{Ln}(a) - \mathrm{Ln}(b+S) + \varepsilon \tag{10.10}$$

where, once again, the right-hand side provides the expected value of Ln(R/S), which can be used in a least squares determination of the optimal values of the parameters a and b (see Example Box 10.4). Equation 10.10 does not have a linear form, and so the use of a nonlinear solving method is required.

10.7 The Impact of Measurement Errors

10.7.1 Appearance over r eality

In Section 10.1, we briefly discussed the fallacy that because stock recruitment relationships are poorly defined, they can reasonably be ignored. This idea originated with inadequate data being used to describe the stock recruitment relationship. Such problems were especially significant when indices of catch-per-unit-effort of juveniles were compared with spawning biomass

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estimates. The resulting scatterplots gave the appearance of a random or flat distribution of recruitment relative to stock size. This is what suggested (although it was sometimes taken to be an implication) that there was no relation between spawning stock size and subsequent recruitment. Using catch-per-unit-effort as an index of spawning stock size can be considered as estimating stock size with large errors. We can summarize the problem to be where large estimation errors make recruitment appear to be independent of spawning stocks.

This whole problem is another instance of the "errors in variables" problem where the independent variable in a relationship (the x axis) cannot be measured or estimated without a large component of error. Therefore, because this violates all the assumptions of such analyses, it should not be used as an independent variable in correlation and regression analyses.

10.7.2 Observation errors Obscuring r elationships

Walters and Ludwig (1981) and Ludwig and Walters (1981) carried out some simulations in which they modelled the impact of observation or measurement errors on estimating the spawning stock size. They assumed that the spawning stock size was measured with some error ε, lognormally distributed with mean zero, and standard deviation σ_ε. Taking into account bias in the estimates of spawning stock size, the estimated spawning stock size is given by

$$\hat{S} = Se^{\varepsilon} \tag{10.11}$$

Similarly, for observing recruitment levels,

$$\hat{R} = Re^{\varepsilon} \tag{10.12}$$

Using these equations, even small levels of error can transform an underlying linear stock recruitment relationship into one showing little relation between spawning stock and recruitment (Figure 10.6, Example Box 10.5).

The inference to draw from this simple demonstration is that the uncertainty surrounding estimates of spawning stock size and subsequent recruitment can badly obscure the detection of any underlying stock recruitment relationship. In part, how one then proceeds will depend upon the use to which the stock recruitment relationship is to be put. In simulation models, one can define the desired model structure, but when fitting a stock assessment model, the form of the stock recruitment relationship may be important. Typically, however, annual recruitment levels are estimated directly from the model (either directly as recruitment levels or as residual errors around some mean annual recruitment or some deterministic stock recruitment equation). Thus, the precise form of the relationship may not be critical.

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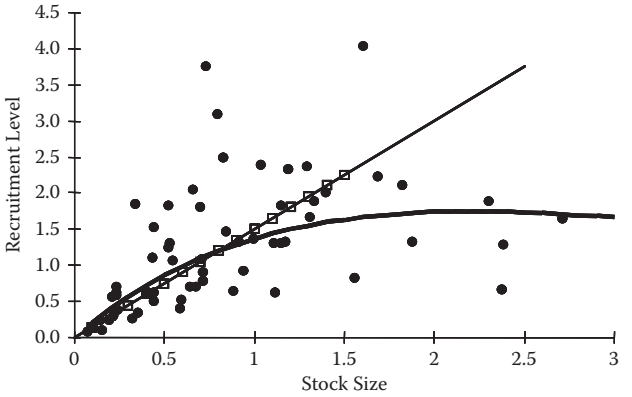

Fig ur e 10.6
Comparison of a hypothetical linear stock recruitment relationship (squares and fine straight line) with the observed relationship (filled circles and curve) with Equations 10.11 and 10.12, plus σ_ε of 0.5 in both cases. The solid curve is the best fitting Ricker curve fitted to the resulting error-ridden data (Example Box 10.5).

Clearly, observation errors may be introducing a great deal of uncertainty into any assessment we make. What can be done about this problem is less clear. Ludwig and Walters (1981) and Walters and Ludwig (1981) both suggest bias corrections for use when attempting to estimate the underlying model. It is debateable whether there would be sufficient information in such data to be able to distinguish between the Beverton–Holt and the Ricker curve.

10.8 Environmental Influences

It is often stated that the effects of the physical environment may influence recruitment success, and this is certainly the case. However, clear examples of taking account of environmental effects in stock recruitment relationships are not common. Penn and Caputi (1986) provide an excellent example where environmental effects are explicitly recognized and included in a Ricker stock recruitment relationship (Figure 10.7).

Penn and Caputi (1986) obtained a series of indices of spawning stock (derived from a detailed study of catch effort data and research cruises) plus the recruitment in the following year. This was described by the log-transformed Ricker equation:

$$Ln(R_{t+1}) = Ln(a) + Ln(S_t) - (bS_t) + \varepsilon \tag{10.13}$$

When this is fitted to the available data, the parameters $a = 4.339$ and $b = 0.0761$ lead to the smooth curve in Figure 10.7. In order to account for the monthly

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EXAMPLE BOX 10.5

Influence of measurement error on detection of any underlying stock recruitment relationship. As in Figure 10.6, the underlying relationship is linear (R = 1.5 × S), as depicted in columns A and B. Column A contains values ranging from 0.1 to 1.5 in steps of 0.1, with four replicates of each value (i.e., down to row 64). To include lognormal measurement error to both sets of observations, in C5 put =A5*loginv(rand(),0,$B$1), and put =B5*loginv(rand(),0,$B$2) into D5. E5 is as shown. This column of transformed data is to facilitate the calculation of the Ricker curve relating to the data in columns C and D. Copy C5:E5 down to row 64. Plot column B against A, as empty squares, and add the line defined by F1:G2 (copy the selection, select the graph, paste special/tick New Series and Categories (X values) in first column) to mimic Figure 10.6. Add column D against C on the same graph in the same way as above, as a set of points. To obtain the Ricker curve using a linear regression on the transformed data, select D1:E1 and put =linest(E5:E64,C5:C64,true,true), using <Ctrl><Shift><Enter> to enter the array function (check the help for this function). Sexp and Rexp provide the back-transformed data for drawing the Ricker curve onto the graph. Fill column F with values from 0.1 down to 3, then put =F5*exp($E$1+$D$1*F5) into G5 and copy down. Add column G against F as a curve to the graph (to fully mimic Figure 10.6). Press F9 to obtain new random numbers and new dispersions of the "observed" values along with their respective Ricker curve. Alter the degree of variability and observe the impact (see Walters and Ludwig, 1981). Think of a way to compare a Ricker curve fitted to this data with a Beverton–Holt recruitment model. It will require copying columns C and D and pasting their values somewhere before analysis. Instead of a linear relationship, install a Beverton–Holt relationship. How does the initial steepness affect the outcomes? See Example Box 10.1.

	A	B	C	D	E	F	G
1	**Sigma1**	0.5		–0.4821	0.88987	0	0
2	**Sigma2**	0.5		Gradient	Intercept	2.5	=F2*1.5
3	**Actual Values**		**Observed with Error**				
4	**Sp**	**Rec**	**ObsSp**	**ObsRec**	**Ln(R/S)**	**Sexp**	**Rexp**
5	0.1	=A5*1.5	0.056	0.587	=ln(D5/C5)	0.100	0.232
6	0.1	=A6*1.5	0.271	0.117	=ln(D6/D6)	0.200	0.442
7	0.1	=A7*1.5	0.079	0.177	=ln(D7/C7)	0.300	0.632
8	0.1	0.15	0.087	0.095	0.086	0.400	0.803
9	0.2	0.3	0.200	0.473	0.863	0.500	0.957
10	0.2	0.3	0.136	0.110	–0.209	0.600	1.094
11	0.2	0.3	0.159	0.307	0.656	0.700	1.216
12	0.2	0.3	0.155	0.244	0.451	0.800	1.324
13	0.3	0.45	0.430	0.330	–0.262	0.900	1.420

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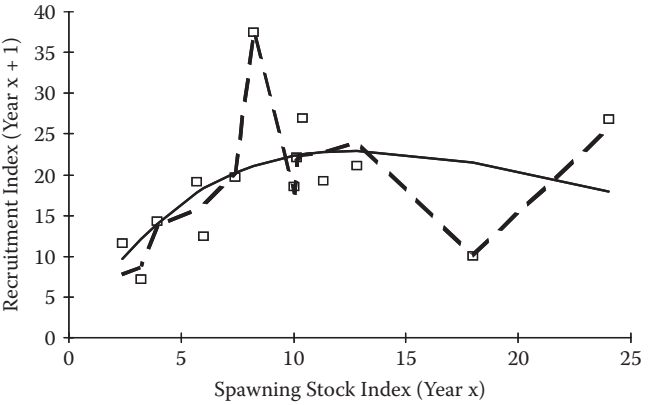

Fig ur e 10.7
The Ricker stock recruitment relationship for tiger prawns in the Exmouth Gulf as described by Penn and Caputi (1986). The open squares are the data points, the smooth curve is the best fitting standard Ricker curve, and the dashed line is the same curve but with the effects of rainfall in January and February included (Equation 10.14, Table 10.1, Example Box 10.6).

rainfall (a cyclone index), Penn and Caputi (1986) added further terms to the Ricker model (Table 10.1, Example Box 10.6)

$$R_{t+1} = aS_t e^{-bS} e^{cJ_t} e^{dF_t} e^{\varepsilon} \tag{10.14}$$

where c and d are the new parameters relating, respectively, to the January cyclone index J_t in year t, and the February cyclone index F_t (see Table 10.1). On log transformation this gives

$$Ln(R_{t+1}) = Ln(a) + Ln(S_t) - (bS_t) + (cJ_t) + (dF_t) + \varepsilon \tag{10.15}$$

which can be solved for the optimal parameters using multiple regression or some minimizer. When this is done, $a = 3.769$, $b = 0.0575$, $c = -0.00029$, and $d = 0.0027$, which gives rise to the dashed line in Figure 10.7. Clearly, the fit of the line accounting for the cyclone index is a much better fit than without. The rainfall during the two months induces different effects on recruitment (one increasing recruitment, the other decreasing success); this is indicated by the parameters c and d being of opposite sign. In January, the recruits are still in shallow water and are vulnerable to storm actions; in February, the recruits are in deeper water and the increased turbidity is thought to increase survivorship. By adding this change, Equation 10.14 is clearly no longer a general equation but is certainly more informative about the Exmouth Gulf fishery. Ideally, the relationships between the cyclone indices and the stock recruitment relationship should be tested experimentally, but the dramatic improvement in fit certainly suggests the hypothesis of cyclones affecting survivorship would be worth testing. This relates back to how one might design a model.

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EXAMPLE BOX 10.6

The influence of environmental factors on recruitment in tiger prawns in Exmouth Gulf, Australia (after Penn and Caputi, 1986). Copy the four columns of data from Table 9.1 into columns A to D. In E8 put the modified Ricker =Ln($B$1)+Ln(A8)–($B$2*A8)+($B$3*C8)+($B$4*D8). The squared residuals are shown as in F8. The predicted value for the Ricker curve is as shown in G8; note the back transformation. The initial transformation is required to normalize the residual errors. Plot columns B against A as a scatterplot. Add column G as a solid line to mimic Figure 10.6. To fit the Ricker curve only, as shown, put zero into the January and February cells, B3:B4, and use the solver to minimize B5 by altering B1:B2. To completely mimic Figure 10.6, save the values from column G into H and add those to the plot as a line. Then, use the solver again to minimize B5, but this time by altering B1:B4. Note the relative values attributed to January and February. Which is likely to increase recruitment and which to decrease it? Compare the two lines on the graph. Is the improvement worth the alteration? Using the AIC to compare the two models, which one is to be preferred? (AIC = $n\text{Ln}(\sigma^2) + 2K$, where n is the number of observation =14, K is the number of parameters =2 or 4, and σ^2 is the sum of squared residuals (B5) divided by n, $=\Sigma\varepsilon^2/n$.)

	A	B	C	D	E	F	G
1	**a**	4.50974					
2	**b**	0.075674					
3	**Jan – c**	0.0					
4	**Feb – d**	0.0					
5	**SSQ**	=sum(F8:F21)					
6	**Spawn**	**Recruit**	**Cyclone Index**				
7	**Si**	**Ri**	**Jan**	**Feb**	**Ricker**	**(O–E)2**	**Model**
8	2.4	11.6	0	0	2.2001	=(Ln(B8)–E8)^2	=exp(E8)
9	3.2	7.1	85	28	2.4272	=(Ln(B8)–E9)^2	=exp(E9)
10	3.9	14.3	0	54	2.5721	0.0078	13.093
11	5.7	19.1	0	1	2.8154	0.018	16.699
12	6	12.4	18	19	2.844	0.1064	17.184
13	7.4	19.7	14	41	2.9477	0.0011	19.063
14	8.2	37.5	0	213	2.9899	0.4026	19.883

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A second look at the data and model makes it clear that we have added two extra parameters to account for three data points that have very large residuals. Using four parameters to describe fourteen data points, it is not surprising that a reasonable quality of fit was obtained. Clearly, more data in the time series would be needed, and independent tests of the assumptions behind the two parameters relating to the cyclonic indices would be required before one could conclude that the modified model would lead to better predictions in the future than the average or general model (Example Box 10.6).

10.9 Recruitment in Age-Structured Models

10.9.1 Strategies for including Stock r ecruitment r elationships

A standard problem in fisheries stock assessment is to model an age-structured population through time. Data in the form of a time series of the relative catch-at-age need to be available along with some index of total relative abundance (e.g., catch rates or biomass estimates).

The two main age-structured stock assessment approaches (Megrey, 1989) use either some version of virtual population analysis (VPA) or some form of statistical catch-at-age analysis (CAGEAN). Both of these approaches attempt to determine the historical recruitment levels that would be consistent with the proportional age structure as observed by current sampling. Thus, a large number of five-year-old fish present in one year implies that recruitment was relatively successful five years previously. Similarly, relatively low numbers of three-year-olds (taking selectivity of gear into account) would indicate a relatively poor recruitment three years previously. The statistical catch-at-age methodology (see later) would entail varying the hypothesized recruitment values during the search for a maximum likelihood or minimum least squares.

Recruitment can be implemented either deterministically or stochastically in such a CAGEAN model. If one used a deterministic relationship, one of the stock recruitment equations would be included in the model. Most models, however, would tend to use a stochastic representation of recruitment. For this, one could either estimate the (assumed) annual recruitment level directly or, alternatively, assume an underlying deterministic stock recruitment relationship and estimate a set of residual errors around that. The two approaches produce the same result in terms of the predicted/expected values of recruitment in each year. A major advantage of including a deterministic stock recruitment relationship and working with residuals around that is that in years where there are no ageing data for predicting the level of recruitment, the deterministic recruitment level could be used to fill in the gap in knowledge.

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10.9.2 Steepness

In the discussion of the Beverton–Holt and Ricker stock recruitment equations, reference was made to the importance of the initial steepness of the curves as representing important aspects of the behaviour of each curve. With the Beverton–Holt model, if the steepness were very high, the asymptote would be reached at relatively small spawning stock sizes. With the addition of measurement error, any relationship might be difficult to distinguish from a scattered straight line. Under such circumstances, it might be said that environmental variation was more important than spawning biomass in the determination of recruitment levels. Alternatively, if the steepness were relatively low, a stock recruitment relationship might be more apparent. If, in Example Box 10.5, you replaced the original underlying linear relationship with a Beverton–Holt equation, the impact of steepness could have been determined easily. With a shallow, less steep curve, environmental variation still has effects, but at low spawning stock sizes there could not be high levels of recruitment. Obscuring the relationship would be more difficult and spawning stock size cannot be ignored (see also Example Box 10.1).

The steepness of any underlying stock recruitment relationship can either be included or investigated by including a stock recruitment equation in one's model. Apart from determining the annual recruitment levels, one could also be capturing other ideas/beliefs concerning the species involved in relation to whether recruitment year class strength is dependent upon either environmental factors or spawning biomass. The common option is to include the deterministic stock recruitment relationship but to search for the residual errors around this to obtain the optimum fit. Of course, this would only be possible for those years where there were sufficient data available for estimating the recruitment residuals. If the model in which the recruitment relationship was included was attempting to describe events in years where there was no information concerning recruitment, then the stock recruitment relationship would provide estimates of mean expected levels that could fill the gap.

10.9.3 Beverton–Holt r edefined

By assuming that the unfished or virgin population had attained a stable age distribution, Francis (1992) was able to provide a biologically meaningful reparameterization of the Beverton–Holt stock recruitment model in terms of the steepness of the stock recruitment curve, h, the initial recruitment, R_0, and the given virgin biomass, B_0. The steepness parameter h is defined by a consideration of the deterministic number of recruits arising when the mature biomass is reduced to 20% of its virgin level; thus,

$$R_0 = \frac{A_0}{\alpha + \beta A_0} \tag{10.16}$$

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and, by definition,

$$hR_0 = \frac{0.2A_0}{\alpha + \beta 0.2A_0} \tag{10.17}$$

where α and β are the Beverton–Holt parameters. A_0 is the total mature biomass per recruit from the stable age distribution found in a virgin population. The per-recruit part is important because this permits us to determine a relationship between R_0 and B_0 independently of Equation 10.1 (see Appendix 10.3). The 0.2 is present because hR_0 is defined as the constant number of recruits that occur at 20% of the virgin mature biomass. The stable age distribution derives from a constant recruitment level, R_0, exposed to a constant level of natural mortality, leading to a standard exponential decline on numbers at age. If natural mortality is low, then a plus group may be needed (Example Box 10.7, Equation 10.18):

$$n_{0,i} = \begin{cases} R_0 e^{-Mi} & i < t_{\max} \\ R_0 e^{-Mt_{\max}} / \left(1 - e^{-M}\right) & i = t_{\max} \end{cases} \tag{10.18}$$

where $n_{0,i}$ is the virgin number of fish per recruit of age i and $t_{\max}$ is the maximum age being modelled. The $t_{\max}$ class acts as a plus group, and hence the necessity for the division by $1 - e^{-M}$ (to provide the sum of an exponential series, see Chapter 12). The biomass A_0 corresponds to the stock biomass that would give rise to a constant recruitment level of one. Thus, at a biomass of A_0, distributed across a stable age distribution, the resulting recruitment level would be $R_0 = 1$. A_0 acts like a scaling factor in the recruitment equations by providing the link between R_0 and B_0 (Example Box 10.7):

$$A_0 = \left(\sum_m n_{0,i} w_i \right) e^{-0.5M} \tag{10.19}$$

where m is the age at maturity (assumed to equal age of recruitment to the fishery), $n_{0,i}$ is the virgin number of animals per recruit of age i, and w_i is the weight of an animal of age i. The $e^{-0.5M}$ is half the natural mortality imposed upon the population. This imposition implies that half the mortality for the year will have occurred before reproduction occurs (i.e., A_0 is the mid-year per-recruit mature biomass). This suggests spawning must occur at least halfway through the year. Without this optional term, spawning could occur at either the beginning or end of each year, depending on whether natural mortality occurs before or after spawning.

A_0 acts as a scaling factor, because a stable age distribution will arise in the unfished population given any constant recruitment level. The magnitude of A_0 will be scaled by the estimated virgin biomass, but its value, relative

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EXAMPLE BOX 10.7

The calculation of the deterministic Beverton–Holt stock recruitment relationship, given the growth properties and natural mortality of a species. Ages in column A extend from 0 to 20 down to row 29. The value in B9 is the constant recruitment value, and the rest of column B generates the stable age distribution. In B10 put =B9*exp(–$B$4). Column C is the von Bertalanffy equation; put =$B$1*(1–exp(–$B$2*(A9–$B$3))) into C9. The **a** and **b** values for males and females (B6:C7) define the weight-at-length relationship. In D9 put =B$6*$C9^B$7 and copy across to E9. Fill F9 as shown. Select B10:F10 and copy down to row 29. In B29, put =B28*exp(–$B$4)/(1–exp(–$B$4)), to act as the plus group (see Equation 10.18 and Chapter 12 on age-structured models). Put the equations shown into F2:F7. Note that Ro is determined by a rearrangement of Equation 10.22. Notice that, by definition, Ao should relate to mature biomass per recruit. However, unlike F7, the Ao value in F6 is not divided by the number of recruits. If the constant recruitment level in B9 is altered from 1, Ao in F6 also alters. However, the actual mature biomass per recruit in F7 always remains the same. Alter the value in B9 and see what happens to F6 and F7. See the effect of altering the growth parameters and the natural mortality. See Example Box 10.8 for how to link these calculations into a workable model.

	A	B	C	D	E	F
1	**Linf**	152.5			**h**	0.75
2	**K**	0.15			**Alpha**	=F5*(1–F1)/(4*F1*F4)
3	**t0**	0			**Beta**	=(5*F1–1)/(4*F1*F4)
4	**M**	0.15			**Ro**	=F5/F6
5		**Females**	**Males**		**Bo**	=F6
6	**a**	0.000271	0.000285		**Ao**	=sum(F12:F29)*exp(–0.5*B4)
7	**b**	3.135	3.114		**Ao/Rec**	=F6/B9
8	**Age**	**Nage**	**Length**	**Wt Fem**	**Wt Mal**	**Biomass**
9	0	1.00	0.0	0.0	0.0	=(B9/2)*(D9+E9)/1000
10	1	0.86	21.2	3.9	3.9	=(B10/2)*(D10+E10)/1000
11	2	0.74	39.5	27.5	26.8	=(B11/2)*(D11+E11)/1000
12	3	0.64	55.3	78.6	76.0	0.0493
13	4	0.55	68.8	156.3	150.4	0.0842
14	5	0.47	80.5	255.3	244.8	0.1181

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to the constant recruitment needed to maintain the stable age distribution, will remain the same (Example Box 10.7, Equation 10.22). Given the mature biomass per recruit, A_0, Francis (1992) was able to provide definitions of α and β as used in Equation 10.1:

$$\alpha = \frac{B_0(1-h)}{4hR_0} \quad \text{and} \quad \beta = \frac{5h-1}{4hR_0} \tag{10.20}$$

Alternatively, if we want to use Equation 10.2, we could use (Appendix 10.3)

$$a = \frac{4hR_0}{5h-1} \quad \text{and} \quad b = \frac{B_0(1-h)}{5h-1} \tag{10.21}$$

At the virgin biomass per recruit, $B_0 = A_0$, the R_0, virgin recruitment parameter, is directly related to the virgin mature, or recruited, biomass, B_0:

$$B_0 = R_0\left(\sum_m n_{0,j}w_j\right) = R_0A_0 \tag{10.22}$$

By determining A_0, from a constant recruitment level of one, the recruitment levels from realistic B_0 levels can be obtained by applying Equation 10.22. When these equations are being used in a stock assessment model, it does not matter whether the model is fitted by varying R_0 or B_0. Given A_0, which is derivable from growth and mortality characteristics (Equation 10.19), the other two parameters can be obtained from each other. In order to include this relationship into a model, one needs to provide parameters describing growth, natural mortality, and h. From these it is first necessary to estimate A_0. This provides us with the link between B_0 and R_0, so that if we provide an estimate of B_0, during a model fitting or simulation process, each of the stock recruitment parameters can be determined and the relationship is defined (Example Box 10.8).

When fitting an age-structured model, the algorithm is often to select a B_0 value, generate the expected mature biomass, calculate the deterministic recruitment level, and finally, estimate the additional residual error needed to fit each of the recruitments.

10.10 Concluding Remarks

The review given here is extremely brief relative to the amount of work extant on stock recruitment relationships in fished populations. Nevertheless, sufficient material is given to capture the requirements for including a stock recruitment relationship into a model. Keep in mind that there is usually a great deal of uncertainty over the form of the stock recruitment relationship,

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EXAMPLE BOX 10.8

The extension of Example Box 10.7 to permit the plotting of the Beverton–Holt stock recruitment curves derived from the growth parameters, natural mortality, and steepness, *h*. Extend Example Box 10.7 by copying F1:F6 across into G1:G6. Replace G6 with =F7 to keep the correct virgin biomass per recruit. Give a particular value to Bo, such as the 2,478 shown, and see the impact on the two parameters alpha and beta. In G9 and below set out a series of stock biomass levels (steps of 200 below row 12 will lead to 3,800 in row 29). In H9 put =G9/($G$2+$G$3*G9), which is the Beverton–Holt Equation 10.1. In I9 put =$I$2*G9/($I$3+G9), which is Equation 10.2. Select H9:I9 and copy down to the extent of column G. Note that they generate identical numbers. Plot column H against column G as a solid line. Note how this changes when the Bo value is altered. Clearly, given a Bo value, the expected recruitment for any calculated stock biomass could then be calculated.

	E	F	G	H	I
1	**h**	0.75	0.75		
2	**Alpha**	0.225162	=G5*(1–G1)/(4*G1*G4)	a	=1/G3
3	**Beta**	0.916667	=(5*G1–1)/(4*G1*G4)	b	=G2/G3
4	**Ro**	1	=G5/G6		
5	**Bo**	2.7019	2478		
6	**Ao**	2.7019	=F7		
7	**Ao/Rec**	2.70194			
8	**Wt Mal**	**Biomass**	**Spawning Biomass**	**Recruit**	**Recruit**
9	0.0	0.000	10	42.5	42.5
10	3.9	0.003	100	307.6	307.6
11	26.8	0.020	200	470.5	470.5
12	76.0	0.049	400	640.0	640.0

so there is little benefit to strictly adhering to one equation over another. Reducing uncertainty over recruitment levels will almost always make modelling a population more convincing. However, empirical estimates of recruitment are very difficult to obtain, so they remain the Achilles' heel as well as the Holy Grail in fisheries.

Appendix 10.1: Derivation of Beverton–Holt Equations

Beverton and Holt (1957, pp. 48–49) considered intraspecific competition to be the main cause of the density-dependent effects. Their model of stock size

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and subsequent recruitment was devised to incorporate density-dependent survival rates (μ) thought to reflect intracohort competition for critical resources. As stated by Beverton and Holt (1957, p. 48): "The simplest assumption we can make, and that which is in best agreement with data from many population studies … is that the mortality coefficient is itself linearly related to the population density." If there are density-independent (μ_1—intercept) and density-dependent (μ_2—gradient) mortality terms, then, in a manner exactly analogous to that described for simple population models in Chapter 2, the simple exponential model becomes linear:

$$\frac{dN}{dt} = -\left(\mu_{r,1} + \mu_{r,2}N\right)N \tag{A10.1}$$

where the *r* subscript denotes a particular stage/period during the prerecruit phase. Beverton and Holt go on to point out that mortality rates during the various early stages of a fish's life can vary greatly with age, so the parameters μ_1 and μ_2 would not be expected to remain constant during the prerecruit stages in the life cycle (the different *r* periods). They continue by demonstrating that the expected recruitment from an initial number of eggs is the product of the effect of each of these separate *r* periods. By implication, any particular stage in the spawning cycle can be substituted for the number of eggs (e.g., spawning biomass can be converted to eggs simply through multiplying by average fecundity). It is strongly recommended that readers consult Beverton and Holt's (1957, pp. 48–49) original proof to see their demonstration of this relationship. As a general rule, such classic texts in fisheries science are well worth the effort it might take to read them. Thus, Beverton and Holt concluded with

$$R = \frac{1}{\left[\alpha + \left(\beta/E\right)\right]} \tag{A10.2}$$

which is one version of the Beverton–Holt recruitment model, where *R* is recruitment, *E* is the number of eggs produced by the spawning biomass, and α and β are the recruitment parameters. It would be more common to relate recruitment levels directly to spawning stock biomass (Quinn and Deriso, 1999), and this can be achieved by including an inverse average fecundity term into the β and substituting *S* for *E* (some additional algebra gives rise to a more commonly seen version):

$$R = \frac{1}{\left[\alpha + \left(\beta/S\right)\right]} = \frac{S}{\alpha S + \beta S/S} = \frac{S}{\beta + \alpha S} \tag{A10.3}$$

It is common practice, though possibly confusing, to alter the parameter usage and replace the β with an α, and the α with a β, as in Equation 10.1.

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Appendix 10.2: Derivation of the Ricker Equations

The Ricker model of stock recruitment differs from that by Beverton–Holt in that the density-dependent mortality term for eggs and juvenile stages relates to the stock size and not only to the cohort size. We would thus have (Hilborn and Walters, 1992)

$$\frac{dN}{dt} = -(q + pS)N \tag{A10.4}$$

which is equivalent to Equation A10.1, except inside the brackets on the left-hand side we have S (spawning stock size) instead of N, the cohort size. In it q is the instantaneous, density-independent mortality rate, and pS is the density-dependent, instantaneous mortality rate for the cohort N. Solving this for any time t,

$$N_t = N_0 e^{-pSt} e^{-qt} \tag{A10.5}$$

where N_0 is the initial cohort size (= fS, where f is the average number of eggs per spawner) and N_t is the number of recruits at time t; thus

$$R = fSe^{-ptS} e^{-qt} \tag{A10.6}$$

Now, e^{-qt} is the density-independent mortality rate; if this is multiplied by the fecundity and relabelled a, and if we combine p and t into a new parameter b, then Equation A10.6 becomes the familiar

$$R = aSe^{-bS} \tag{A10.7}$$

Appendix 10.3: Deriving the Beverton–Holt Parameters

Francis (1992) provides definitions of the Beverton–Holt parameters in terms of the more biologically meaningful terms relating to steepness (h), virgin mature biomass (B_0), and virgin recruitment (R_0). He does this for the recruitment equation

$$R_i = \frac{S_{i-1}}{\alpha + \beta S_{i-1}} \tag{A10.8}$$

where R_i is the recruitment in year i, S_{i-1} is the spawning stock size in the year prior to i, and α and β are the usual Beverton–Holt parameters

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(see Equation 10.1). In fact, it is easier to derive the definitions from the common alternative form of the Beverton–Holt equation ($R = aS/[b + S]$), which is what we will do here. If we assume that recruitment in the virgin stock derives from the virgin biomass we have

$$R_0 = \frac{aB_0}{b + B_0} \tag{A10.9}$$

Steepness is defined as the recruitment obtained at 20% of virgin biomass:

$$hR_0 = \frac{0.2aB_0}{b + 0.2B_0} \tag{A10.10}$$

Substituting Equation A10.9 into Equation A10.10 leads to

$$h = \frac{(0.2aB_0)(b + B_0)}{(b + 0.2B_0)(aB_0)} = \frac{0.2(b + B_0)}{(b + 0.2B_0)} \tag{A10.11}$$

Multiplying through and exchanging terms leads to

$$hb - 0.2b = 0.2B_0 - 0.2hB_0 \tag{A10.12}$$

Multiplying both sides by 5 and simplifying leads to

$$b(5h - 1) = B_0(1 - h) \tag{A10.13}$$

and therefore

$$b = \frac{B_0(1 - h)}{5h - 1} \tag{A10.14}$$

Reverting to Equation A10.9 we can see that

$$R_0 = \frac{aB_0}{\frac{B_0(1 - h)}{5h - 1} + B_0} \tag{A10.15}$$

which multiplies through to become

$$\frac{R_0B_0(1 - h)}{5h - 1} + R_0B_0 = aB_0 \tag{A10.16}$$

Dividing through by B_0 and multiplying the second R_0 by $5h - 1$ allows the simplification

$$a = \frac{R_0 - hR_0 + 5hR_0 - R_0}{5h - 1} = \frac{4hR_0}{5h - 1} \tag{A10.17}$$

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Remembering that $\alpha = b/a$ and $\beta = 1/a$, we finish with

$$\alpha = \frac{B_0(1-h)}{4hR_0} \quad \text{and} \quad \beta = \frac{5h-1}{4hR_0} \tag{A10.18}$$

as in Francis (1992). This has redefined the parameters in terms of h, B_0, and R_0. However, this means we cannot use Equation A10.9 to define the relationship between B_0 and R_0, because they are used in the generation of the α and β values used in the equation. The solution is to assume that the virgin population had a stable age distribution. The mature biomass generated per recruit from the stable age distribution (A_0) therefore defines the relationship required between B_0 and R_0.

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