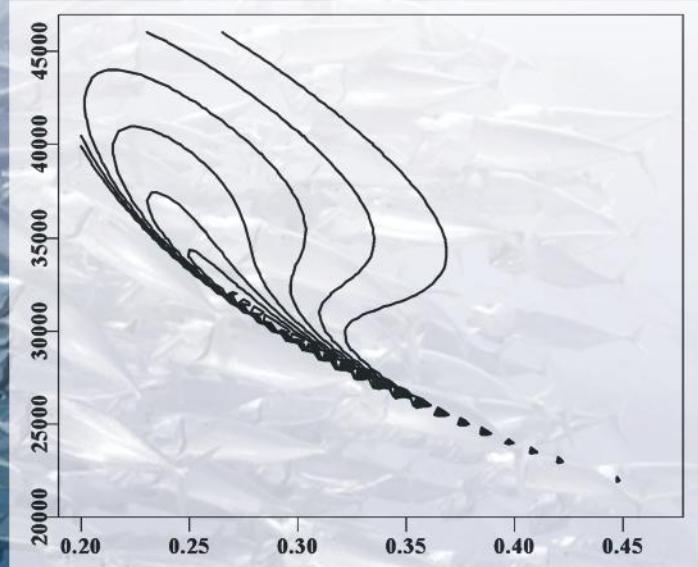


Modelling and Quantitative Methods in Fisheries

Second Edition

Malcolm Haddon



CRC Press
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A CHAPMAN & HALL BOOK

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Preface to the Second Edition

This book is intended as an introduction to some of the analytical methods used by fisheries scientists and ecologists. However, keeping it an introductory text that is accessible to the majority is something of a challenge when covering some of the more important though intrinsically complex methods. In this second edition, I have tried to keep the book an introductory text, and so much of the material remains close to the original. While I have revised and tidied all chapters, improving a number of the examples used, the main additions to this new edition are the two chapters on characterizing uncertainty (Chapter 8) and on size-based models (Chapter 13). Keeping such material introductory was certainly a challenge; however, I have not shied away from discussing relatively complex ideas. Hopefully, I have done so in a manner that assists people to reach an understanding of the material. Both new chapters made me question whether I should continue to use Excel for the example boxes. For example, in Chapter 8, on characterizing uncertainty, a generalized Gibbs sampler is developed for conducting Markov chain Monte Carlo (MCMC) analyses. I would never seriously suggest using Excel to conduct an MCMC, but it continues to be a useful teaching tool, and my hope is that by following the examples and seeing the nuts and bolts of how they work, the underlying principles will become clear; Excel remains excellent for such a task.

I have been pleased to receive communications from people in many countries about various sections within the book. I thank everyone who has written to me, asking questions, pointing out problems, and making suggestions; I have appreciated all such comments and interactions. It serves as a nice reminder of the community of endeavour among science workers. It was especially useful to me to see what aspects of the example boxes caused problems for people. This has led me, I hope, to clarify some of the details in some of the more complex example boxes.

I thank Dr. Jessica André of the University of Tasmania for the trouble she took in going through the example boxes in Chapters 2 to 8; her help has been greatly appreciated. Any remaining errors, of course, are all mine.

The example boxes are provided in a zip file that can be found by searching for the book title or author at <http://www.crcpress.com> and going to the “downloads” tab.

Malcolm Haddon
CSIRO, Hobart
May 2010

Preface to the First Edition

This book aims to introduce some of the methods used by quantitative ecologists and modellers. The emphasis throughout the book is focused upon fisheries and models used in fisheries, but the ideas relate to many other fields of endeavour. The first few chapters, on simple population models, on parameter estimation (principally using maximum likelihood methods), and on computer intensive methods, should be of interest to all population ecologists. Those chapters on growth, recruitment, and explicit fisheries models are obviously focused on the needs of fisheries scientists.

From 1995 to 1997, I was fortunate enough to be in a position to develop and present short and intensive courses on modelling and quantitative methods to a large number of fisheries scientists and others at fisheries laboratories and universities around Australia. I am grateful to the Australian Fisheries Research and Development Corporation (FRDC) for funding this project and giving me the opportunity to meet so many of Australia's fisheries community. Unfortunately, there was no single text that covered the details of what I felt was necessary for an adequate grounding in the skills required for the quantitative study of marine populations. The course notes I prepared were a first attempt to fill that gap but were designed to complement the presentations given in the short courses rather than as a stand-alone product. For this book, the material has been completely rewritten and expanded with the inclusion of many active examples. While this rewrite greatly slowed the production of the final book, a reader should now be able to pursue a course of independent study of the material and others could use this book as the foundation for a formal course in quantitative fisheries science.

The main objective of this book is to provide a working resource that guides the reader towards an understanding of some of the analytical methods currently being used in quantitative biology and fisheries science. While a theoretical treatment has been provided, a major aim was to focus on understanding the details of how to perform the analyses described. An integral part of this description was to include Microsoft Excel workbooks relating to each example and problem discussed. Excel was chosen because of its flexibility, general availability, and relative ease of use. The appendix on the use of Excel in fisheries should provide sufficient details for those who are not versed in using this program. For maximum benefit the example boxes scattered through the text should be constructed and perhaps modified as the reader becomes more confident. Doing something leads to a much better understanding than just reading about it. These workbooks, and other examples, can be found on the download pages of the following web addresses: www.utas.edu.au/docs/tafi/TAFI_Homepage.html and www.crcpress.com/us/ElectronicProducts/downandup.asp. The files should be downloaded but

try to construct them before considering the finished versions. The reader should try to use them only as a check on what was produced or if he or she becomes deeply stuck. I have tried to use real examples wherever possible in the belief that these are more acceptable.

When I was at school, one of my mathematics teachers used to write an equation on the board and then exclaim, "... as we all know ..." while writing a derived equation underneath. He clearly believed that the algebraic transition from one equation to the other should have been very clear to his pupils. Unfortunately, it was often the case that only a few people understood. Although it is true that omitting the details of the steps between the algebraic changes leads to brevity, it certainly does not improve clarity or ease of understanding. In this book, whenever the details of a set of equations or model are given, an attempt has usually been made to avoid omitting any of the steps needed to understand their derivation equations.

For most of the time it took, I enjoyed writing this book. I hope it helps people move forward in their work.

Malcolm Haddon
Hobart, January 2001

1

Fisheries and Modelling

1.1 Fish Population Dynamics

Natural fish populations undergo many changes in response to harvesting. These include changes to numbers-at-age, numbers-at-size, total numbers, total biomass, and spatial distributions. While attempting to understand the dynamics of exploited populations fisheries science has naturally developed into using mathematical and statistical descriptions. The underlying assumption is that if it is understood how populations respond to different perturbations, then it should be possible to manage those fisheries toward particular objectives.

Unhappily, the astonishing local abundance of some fish species in the wild can lead individuals to adopt the unfortunate intuition that fishing can only have minor impacts on stocks. Thomas Huxley was a famous nineteenth-century scientist and he wrote about schools of North Sea herring:

In these shoals the fish are closely packed, like a flock of sheep straying slowly along a pasture, and it is probably quite safe to assume that there is at least one fish for every cubic foot of water occupied by the shoal. If this be so, every square mile of such a shoal, supposing it to be three fathoms deep, must contain more than 500,000,000 herrings. (Huxley, 1881, p. 609) [1 fathom = 1.83 m]

Huxley was explicit about his belief that human fishing could not have a significant impact upon marine fish stocks. In a speech made in 1883, he claimed that most fish populations were so numerous and fecund that they could not be affected by the limited activities of human fishing.

I believe then that the cod fishery, the herring fishery, pilchard fishery, the mackerel fishery, and probably all the great sea fisheries are inexhaustible: that is to say that nothing we do seriously affects the numbers of fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case to be useless. (Huxley, 1884, p. 22)

Such arguments from astonishment are still met with today and have been referred to as the inexhaustibility paradigm (Mace, 1997). That some people still fail to grasp that unrestrained fishing can impact on fished populations is remarkable given the weight of evidence to the contrary. The sad pseudo-experiment of stopping commercial fishing in the North Sea during the years of the First World War demonstrated conclusively that catch levels were at that time already too high around Europe. The respite from fishing during the war years allowed stocks to recover so that catch rates of large fish after the war were much higher than before. Unfortunately, this improvement did not last long once unrestrained fishing resumed. Sadly, this ghastly pseudo-experiment was repeated during the Second World War with similar results (Smith, 1988). Despite a great deal of evidence, the debate on why assessment and management of commercial fish stocks were required continued for many decades (Hardy, 1959; Smith, 1994).

Many developments in fisheries science assisted the change in perceptions, but it was at least three decades into the twentieth century before mathematical treatments of aspects other than simple summaries of catch-per-unit-effort (CPUE) were considered. Russell (1931) clarified the “overfishing problem” with a simple, almost qualitative, algebraic expression.

It is my aim here to formulate in a simplified and general way, and without mathematical treatment, the broad facts of the case, to state in simple language those elementary principles that are at the back of everyone's mind who deals with the problem of the rational exploitation of the fisheries. (Russell, 1931, p. 3)

Russell started by recognizing that a stock could be divided into animals of a size liable to capture (already recruited to the fishery) and those smaller than this limit. He also considered only entire stocks so that emigration and immigration were not relevant. Russell focused on what would induce an increase in the population and what would lead to a decrease. He summarized stock biomass dynamics as

$$S_{i+1} = S_i + (A + G) - (C + M) \quad (1.1)$$

where S_i is the stock biomass in year i , A is the total weight of all individuals recruiting to the stock each year, G is the total growth in biomass of individuals already recruited to the stock, C is the total weight of all fish caught, and M is the total weight of all fish that die of natural causes during the year. Nowadays we might use different notation (perhaps $B_{i+1} = B_i + (R + G) - (C + M)$) than that used by Russell, but that is a trivial difference (Krebs, 1985). Be careful not to confuse the M used here with the symbol used for the instantaneous natural mortality rate (see Chapter 2). The essential aspect of fish stock dynamics, described by Russell, was that the stock biomass had

gains (recruitment and individual growth) and losses (natural and fishing mortality). Russell said of his simple formulation:

This is self-evident, and the sole value of the exact formulation given above is that it distinguishes the separate factors making up gain and loss respectively, and is therefore an aid to clear thinking. (Russell, 1931, p. 4)

Russell's work had a great deal of influence (Hardy, 1959; Krebs, 1985). Beverton and Holt (1957) pointed to other workers who had identified the basic principles of the dynamics of exploited fish populations before Russell (Petersen, 1903; Baranov, 1918). However, Russell appears to have had a more immediate influence, with the others being of more historical interest. Baranov's work, especially, was very advanced for his day but was published in Russian, and its value was only recognized much later (Ricker, 1944, 1975). Russell was almost dismissive of his own statements, but characterizing the factors he identified (lately within age- or size- or spatially structured models) has been the main focus of single species fisheries scientists ever since. Methods of modelling the details of these processes have varied greatly, but the underlying factors conveyed in Equation 1.1 are standard.

The obvious factors missing from Russell's formulation are the effects of other species (competitors, predators, etc.), the physical environment in which the species lives, which can include everything from *el niño* effects to pollution stress (Pitcher and Hart, 1982), and any spatial structuring of the fished stock (Haddon et al., 2003; Punt, 2003). It is still the case in most fish stock assessments that the effects of other species and the physical environment are largely ignored. However, there are movements toward encouraging ecosystem and multispecies management that are challenging that view (Pitcher and Pauly, 1998; Pauly et al., 2001; Pitcher, 2001; Walters and Martell, 2004). "Ecosystem-based fishery management" is becoming a more popular phrase in resource management, and the requirement for assessing the impacts of fishing on habitats and food webs is becoming a political reality before the technical ability is developed to understand ecosystem dynamics in any way directly useful to management. As Fulton et al. (2005, p. 540) politely put it: "Unfortunately, the legislation requiring such evaluation has developed ahead of the science needed to provide appropriate assessments." If resource management is to be guided by science rather than public opinion, then ecosystem management may still prove a great challenge.

The intuitions behind much of quantitative fisheries science are mostly the same now as in the twentieth century. The rising interest in multispecies and ecosystem management, with the need for a precautionary approach (Garcia, 1996) and explicit spatial management, can be seen as a move to adopt a new set of intuitions about fished stocks and our interactions with them. These multispecies approaches are still under development (Garcia and Grainger, 1997; Walters and Bonfil, 1999; Walters and Martell, 2004; Fulton et al., 2005).

An alternative direction is being followed by users of simulation models such as EcoPath or EcoSim (introductions to EcoPath can be found on the World Wide Web; for EcoSim see Walters et al., 1997). Despite all of this, in this present work we will concentrate on single species systems, although the effects of environmental variability on recruitment and growth will be included.

1.2 The Objectives of Stock Assessment

1.2.1 Characterizing Stock Dynamics

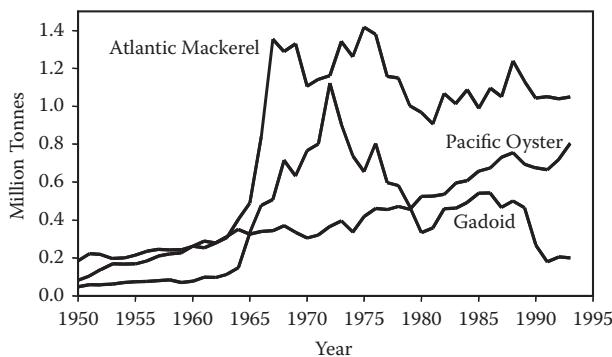
Understanding the variations exhibited in the catches of different fisheries (Figure 1.1) is a major objective for fisheries scientists. By referring to the yield from a fishery as its production there is a potential for confusion. Take care not to mix up a stock's production or yield with its productivity. The two would only tend to be the same if a fishery were being harvested in a sustainable manner.

Fishing industries have the potential to fish stocks too hard and bring about a reduction in the potential sustainable harvest or even a fishery collapse (fishing becomes inefficient and uneconomic). Variations in the yield from a fishery arise through the combined effects of variations in effort, in recruitment, and in natural mortality and growth. Understanding which aspects of production are driving a fishery is an important aspect of stock assessment. The fisheries illustrated in Figure 1.1. are, in some cases, combinations of species, which could confuse the situation, but similar patterns of increasing harvest levels followed by declines or relative stability can also be seen in particular species (Figure 1.2).

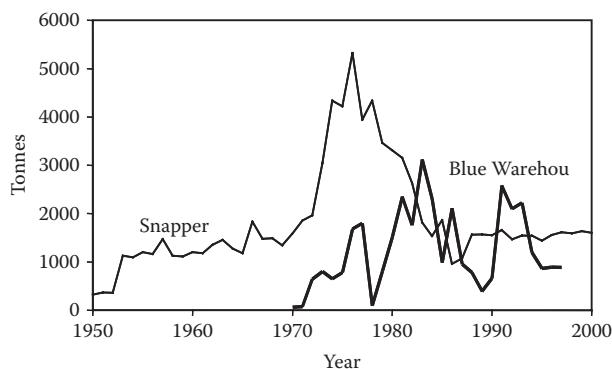
The question for the fisheries scientist is to decide whether a particular effort or catch level is sustainable for a given future time. This can be made especially difficult to answer if the major sources of productivity vary through time. It is certainly the case that in many exploited species, recruitment is a highly variable element of production (Sissenwine et al., 1988). Cushing stated:

From year to year, recruitment varies between a factor of about three to more than two orders of magnitude. The response of recruitment to changes in spawning stock is obscure.... But this natural variation provides the mechanism by which the stock remains adapted to its environment. (Cushing, 1988, p. 105)

Time series of data suggest that different species can have very different patterns of recruitment (Figure 1.3). The biotic and abiotic factors affecting recruitment variation will thus strongly influence the resilience of those

**Figure 1.1**

The yield of three different fisheries from 1950 to 1993 (data from FAO, 1995). Pacific oyster refers to all oysters reported from the Pacific region and illustrates an increasing trend; Atlantic mackerel might include snoeks and cutlassfishes and exhibits a rise to a relatively stable fishery. Finally, Gadoids includes cods, hakes, and haddocks from the Arctic Atlantic, illustrating a fishery rising to a peak and then declining to a much lower level.

**Figure 1.2**

The yield from two New Zealand fisheries. The snapper (*Pagrus auratus*) is from the west of North Island. It shows a fishery developing, the impact of pair trawlers in the 1970s, and a subsequent serious decline to stability forced through a total allowable catch. The blue warehou (*Seriola brama*) is from the east and south of South Island and shows a naturally variable fishery in which availability varies between years. (Data from Annala et al., 2001.)

populations to perturbations (especially disturbances due to harvesting). Generally, any influence the biotic environment has will be upon the natural mortality rates (including those of prerecruits, thereby affecting recruitment success). These effects could include predation, disease, parasitism, and availability of food and intra- and interspecific competition. High recruitment success can lead to reduced growth rates for the cohorts concerned, presumably due to competition, while low recruitment may have the opposite effect (Punt et al., 2001; Ziegler et al., 2007).

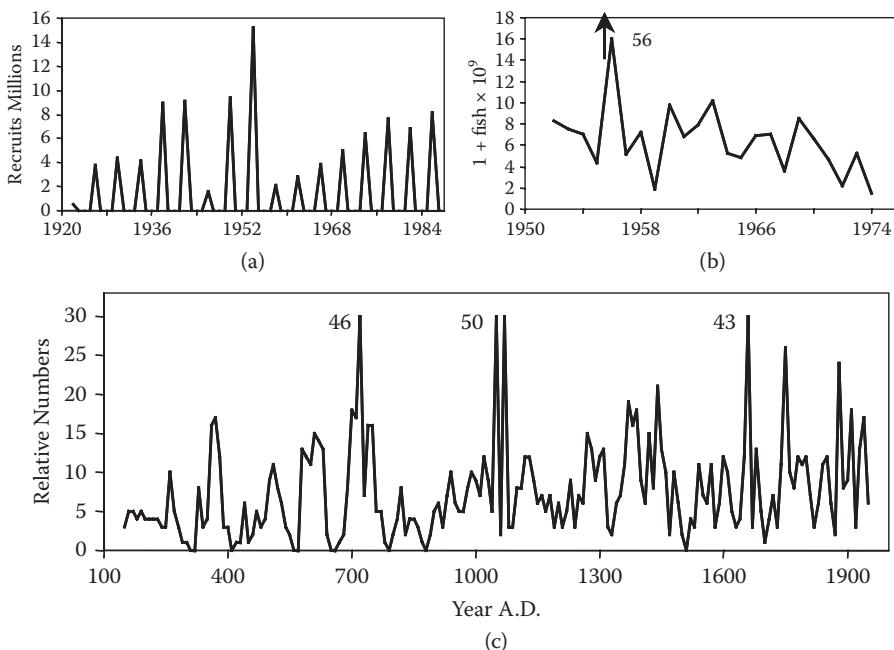


Figure 1.3

Recruitment variability in three species of fish across different timescales. (a) Relates to the dominant cohort of Fraser River sockeye salmon. (Data from Ricker, 1997.) (b) Relates to North Sea herring; the arrow refers to an exceptional recruitment in 1956. (Data from Cushing, 1988.) (c) Relates to 1+ and older Pacific hake; note the exceptionally long timeline extending back nearly two thousand years. (Data from Soutar and Isaacs, 1969.) 1+ refers to fish that are between one and two years old. Numbers by spikes refer to high recruitments.

If the natural mortality term (M) relates to a species' interactions with its ecological context, we should remember to question the commonly used assumption of a constant level of natural mortality through time.

Unfortunately, even into the 1980s, many mathematical treatments of fish population dynamics were limited to determining the expected behaviour of fish stocks that had attained equilibrium in relation to the fishing pressure being experienced. “Equilibrium” just meant that the population is assumed to have reached a stable balance between numbers surviving and those dying. Emphasis on equilibrium conditions was unfortunate because even if a stock appears to have reached equilibrium, it will undoubtedly be, at best, a dynamic equilibrium. One reason why this assumption is dangerous is if CPUE is declining through time, then, because equilibrium analyses assume that all catch levels are sustainable, such analyses are invariably less conservative than dynamic nonequilibrium analyses.

Different exploited fish populations may express a wide range of dynamic behaviours (Figures 1.1 and 1.2). One of the key goals of stock assessment is

to understand both the natural variation found in exploited populations and how harvesting affects their dynamics. This requires an understanding of the productive stock (stock structure) as well as the individual components of productivity (recruitment processes, individual growth, and mortality processes). We will thus consider each of the components of productivity.

We will not explicitly consider stock structure, but it is consistent with Russell's formulation that we can regard two populations as being from different stocks if their growth and natural mortality characteristics are significantly different. These two aspects of stock dynamics have a large influence on productivity, and so the dynamics of the two populations will be different, and ideally they should be managed separately for maximum efficiency and stock sustainability (Haddon and Willis, 1995). Stock discrimination is one reason that studies of the biology of exploited species, instead of just their population dynamics, can have great value to fisheries management decisions.

Classical fisheries science and management has a very poor track record peppered with numerous fishery collapses (Pitcher, 2001; Hilborn et al., 2004). This cannot be denied, but we must remember the politico-economic system under which fisheries research is undertaken and used. "If fisheries scientists have failed, it is in not educating those who make decisions in fisheries management to work within the limits of what is biologically possible instead of within the bounds set by what is economically required" (Haddon, 1980, p. 48). Awareness of the uncertainty inherent in all fisheries assessments is growing, but this is still not always reflected in management decisions. Whichever future path is taken by natural resource managers, knowledge of the strengths and weaknesses of the kinds of mathematical models used will assist in using them more effectively.

1.2.2 Characterizing uncertainty

Stock assessments attempt to model the population dynamics of strongly perturbed aquatic systems, often extending over a large geographical scale. Formal mathematical models are often used to represent the dynamics of fished stocks, and these models can range from the relatively simple to the very complex. Exactly which model is used is important because generally it is still standard practice to use only one model to produce an assessment. Early stock assessments (1960s to 1980s) were often used to generate simple management advice, sometimes as simple as a single number defining the maximum sustainable level of catch. Unfortunately, this approach was often overly optimistic. However, since the beginning of the 1990s there has been a growing recognition of the importance for stock assessments of characterizing the uncertainty included in any analysis (Francis, 1992; Punt and Hilborn, 1997; Sainsbury et al., 2000). Uncertainty is added to an assessment from almost every input to the analysis. Input data (be they age structures, length frequencies, catch rates, etc.) are often noisy and may not necessarily

be as representative of the stock as desired. But beyond the data there is also uncertainty in the selection of which model is used to represent the dynamics (a different model may represent the dynamics better). In fact, there are many sources of potential uncertainty, and this means that it becomes invalid to attempt to generate a simple predicted outcome. In reality, instead of a single number, one would do better to generate a probability distribution of possible outcomes. Thus, it should be possible to generate decision tables (Hilborn and Walters, 1992) in which the relative likelihood of different outcomes (e.g., likelihood of the stock being depleted below a given reference point) under different management options (e.g., different allowable catch levels) can be predicted. Fisheries management is often a trade-off between the objectives of optimizing profits while maintaining sustainability. Decision tables can assist managers in weighing the relative risks against the benefits.

1.2.3 Management Objectives

The classical fisheries management target of maximum sustainable yield is now recognized as being a risk-prone harvest strategy. Instead, it is becoming more common (Australia, New Zealand, Europe) to define desirable states for a fishery in terms of target reference points (TRPs). In addition, there are limit reference points (LRPs) that define a state that it is deemed the stock should be managed away from (Smith, 1997). LRP s and TRPs relate to fishery or stock performance measures such as harvest rates, the spawning stock biomass, or any measure that can characterize the status of the fishery. Ideally, these reference points should be explicitly linked to a series of decision rules that determine appropriate management action, depending on the estimates of the performance measures and how they relate to the reference points. If ever a LRP is approached, then some robust management action may be required that will have the effect of moving the stock back toward the TRP. The reference points are often framed in terms of probabilities, e.g., the likelihood that the spawning stock biomass in the year 2012 will be greater than or equal to 40% unfished biomass will be at least 75%. There are many alternatives, depending on the performance measure being estimated, but all such decision rules should be couched in probabilistic terms.

The development of such reference points combined with decision rules is a recent innovation (Smith, 1997; Collie and Gislason, 2001; Haddon, 2007) and is of most use for those species that have a formal stock assessment. Formal models can usually provide estimates of performance measures, such as harvest rates and spawning stock biomass, with their associated uncertainty, which directly indicate the status of the stock. Alternatively, performance measures can be as simple as catch rates, but generating acceptable objective reference points for such measures is more difficult. Generally, empirical levels are set, such as a target catch rate that is greater than the average across some given period. In addition, generating defensible decision rules for such indirect performance measures is also difficult. Nevertheless,

an aim of developing such management frameworks is to provide a stronger element of predictability about management responses to stock changes so that the fishing industry can plan appropriately (Smith et al., 2008).

1.3 Characteristics of Mathematical Models

1.3.1 General Properties

We have considered just a few of the properties of wild aquatic populations that affect what we can know and what we should attempt to discover when trying to manage such stocks adequately. Fisheries assessments are generally based upon mathematical models of the production processes and the populations being fished. Before considering any particular model in detail, it would be helpful to consider models in general.

Mathematical models are a subset of the class of all models. Models may take many forms, ranging from a physical representation of whatever is being modelled (e.g., a ball-and-stick model of DNA, as produced by Watson and Crick, 1953), diagrammatic models (such as a geographical map), and the more abstract mathematical representations being discussed here. Despite this diversity, all models share certain attributes. All models constitute an abstraction or simulation by the modeller of the process or phenomenon being modelled.

1.3.2 Limitations Due to the Modeller

Models are never perfect copies of the modelled subject, so there must be some degree of abstraction or selection of what the modeller considers to be essential properties of the system being modelled. A fundamental idea behind modelling is therefore to select the properties to be included in order that the behaviour of the model may be expected to exhibit a close approximation to the observable behaviour of the modelled system. This selection of what are considered to be the important properties of a system permits the modeller to emphasize particular aspects of the system being modelled. A road map shows roads greatly magnified in true geographical scale because that is the point of the map. The selection of what aspects of a system to include in a model is what determines whether a model will be generally applicable to a class of systems, or is so specialized that it is attempting to simulate the detailed behaviour of a particular system (for *system* one might read *stock* or *population*). By selecting particular parts of a natural system the model is being limited in what it can describe. The assumption is that it will provide an adequate description of the process of interest and that those

aspects not included will not unexpectedly distort the representation of the whole (Haddon, 1980).

1.3.3 Limitations Due to Model Type

A model can be physical, verbal, graphical, or mathematical; however, the particular form chosen for a model imposes limits on what can be described. For example, if one produces a verbal description of a dynamic population process, one is invariably limited in how well one can capture or express the properties of the populations being described. This limitation is not necessarily due to any lack of expository skills of the narrator. Instead, it is because spoken languages do not seem well designed for describing dynamic processes, especially where more than one variable is changing through time or relative to other variables. Fortunately, mathematics provides an excellent alternative for describing dynamic systems.

1.3.4 The Structure of Mathematical Models

There are many types of mathematical models. They can be characterized as descriptive, explanatory, realistic, idealistic, general, or particular; they can also be deterministic, stochastic, continuous, and discrete. Sometimes they can be combinations of some or all of these things. With all these possibilities, there is a great potential for confusion over exactly what role mathematical models can play in scientific investigations. To gain a better understanding of the potential limitations of particular models, we will attempt to explain the meaning of some of these terms.

Mathematical population models are termed *dynamic* because they represent the present state of a population/fishery in terms of its past state or states with the potential to describe future states. For example, the Schaefer model (Schaefer, 1957) of stock biomass dynamics (of which we will be hearing more) can be partly represented as

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t \quad (1.2)$$

Here the variables are C_t , the catch during time t , and B_t , the stock biomass at the start of time t (B_t is also an output of the model). The model parameters are r , representing the population growth rate of biomass (production), and K , the maximum biomass that the system can attain (these parameters come from the logistic model from early mathematical ecology; see Chapter 2). By examining this relatively simple model one can see that expected biomass levels at one time ($t + 1$) are directly related to catches and the earlier biomass (time = t ; they are serially correlated). The influence of the earlier biomass on population growth is controlled by the combination of the two parameters r and K . By accounting for the serial correlations between variables

from time period to time period, such dynamic state models differ markedly from traditional statistical analyses of population dynamics. Serial correlation removes the assumption of sample independence required by more classical statistical analyses.

1.3.5 Parameters and Variables

At the most primitive level, models are made up of variables and parameters. Parameters are the things that dictate quantitatively how the variables interact. They differ from a model's variables because the parameters are the things estimated when a model is fitted to observed data. A model's variables must represent something definable or measurable in nature (at least in principle). Parameters modify the impact or contribution of a variable to the model's outputs, or are concerned with the relationships between the variables within the model.

In any model, such as Equation 1.2, we must either estimate or provide values for the parameters. With the variables, either one provides observed values for them (e.g., a time series of catches, C_t) or they are an output from the model. Thus, in Equation 1.2, given a time series of observed catches plus estimates of parameter values for r and K , a time series of biomass values, B_t , is implied by the model as an output. As long as one is aware of the possibilities for confusion that can arise over the terms *observe*, *estimate*, *variable*, *parameter*, and *model output*, one can be more clear about exactly what one is doing while modelling a particular phenomenon. The relation between theory and model structure is not necessarily simple. Background knowledge and theory may be the drive behind the selection of a model's structure. The relationships proposed between a set of variables may constitute a novel hypothesis or theory about the organization of nature.

1.4 Types of Model Structure

1.4.1 Deterministic/Stochastic

We can define a model parameter as *a quantitative property (of the system being modelled) that is assumed either to remain constant over the period for which data are available, or to be modulated by environmental variation*. Roughly speaking, models in which the parameters remain constant on the timescale of the model's application are referred to as *deterministic*. With a given set of inputs, because of its constant parameters, a deterministic model will always give the same outputs. Because the relationships between the model variables are fixed (constant parameters), the output from a given input is "determined" by the structure of the model. One should not be confused by situations

where parameters in a deterministic model are altered sequentially by taking one of an indexed set of predetermined values (e.g., a recruitment index or catchability index may alter and be changed on a yearly basis). In such a case, although the parameters are varying, they are doing so in a repeatable, deterministic fashion (constant over a longer timescale), and the major property that a given input will always give the same output still holds.

Deterministic models contrast with *stochastic* models in which at least one of the parameters varies in a random or unpredictable fashion over the time period covered by the model. Thus, given a set of input values, the associated output values will be uncertain. The parameters that vary will take on a random value from a predetermined probability distribution (either from one of the classical probability density functions (pdfs) or from a custom distribution). Thus, for example, in a model of a stock, each year the recruitment level may attain a mean value plus or minus a random amount determined by the nature of a random variate:

$$R_y = \bar{R} e^{N(0, \sigma_R^2) - \sigma_R^2/2} \quad (1.3)$$

where R_y is the recruitment in year y , \bar{R} is the average recruitment across years, $N(0, \sigma^2)$ is the notation used for a random variable whose values are described in this example by a normal distribution with mean zero (i.e., has both positive and negative values) and variance σ^2 , and $-\sigma_R^2/2$ is a bias correction term for lognormal errors within recruitment time series (Haltuch et al., 2008).

Given a set of input data, a deterministic model expresses all of its possible responses. However, stochastic models form the basis of so-called Monte Carlo simulations where the model is run repeatedly with the same input data, but for each run new random values are produced for the stochastic parameters (e.g., as per Equation 1.3). For each run a different output is produced, and these are tabulated or graphed to see what range of outcomes could be expected from such a system. Even if the variation intrinsic to a model is normally distributed, it does not imply that a particular output can be expected to be normally distributed about some mean value. If there are nonlinear aspects in the model, skew and other changes may arise. We will be looking more closely at this phenomenon when discussing stock recruitment relationships and considering Monte Carlo models.

Future population projections, risk assessment, and determining the impact of uncertainty in one's data all require the use of Monte Carlo modelling. Simulation testing of model structures is a very powerful tool. One of the objectives of this book is to enable readers to attain a level of experience such that they may create and run Monte Carlo simulations.

1.4.2 Continuous versus Discrete Models

Early fishery modellers used continuous differential equations to design their models, so the time steps in the models were all infinitesimal. At that time computers were still very much in their infancy and analytical solutions were the culture of the day. Early fishery models were thus formed using differential calculus (Jeffrey, 1969), and parts of their structures were determined more by what could be solved analytically than because they reflected nature in a particular accurate manner. At the same time, the application of these models reflected or assumed equilibrium conditions. Fortunately, we can now simulate a population using easily available computers and software, and we can use more realistic, or more detailed, formulations. While it may not be possible to solve such models analytically (i.e., if the model formulation has that structure its solution must be this), they can usually be solved numerically (informed and improving trial and error). Although both approaches are still used, one big change in fisheries science has been a move away from continuous differential equations toward difference equations, which attempt to model a system as it changes through discrete intervals (ranging from infinitesimal to yearly time steps). Despite the increases in complexity, all of these models retain, in essence, the structure of Russell's (1931) formulation.

There are other aspects of model building that can limit what behaviours can be captured or described by a model. The actual structure or form of a model imposes limits. For example, if a mathematical modeller uses difference equations to describe a system, the resolution of events cannot be finer than the time intervals with which the model is structured. This obvious effect occurs in many places. For example, in models that include a seasonal component the resolution is quite clearly limited depending on whether the available data are for weeks, months, or some other interval.

1.4.3 Descriptive/explanatory

Whether a model is discrete or continuous, and deterministic or stochastic, is a matter of model structure and clearly influences what can be modelled. The purpose for which a model is to be used is also important. For a model to be descriptive it only needs to mimic the empirical behaviour of the observed data. A fine fit to individual growth data, for example, may usually be obtained by using polynomial equations:

$$y = a + bx + cx^2 + dx^3 \dots + mx^n \quad (1.4)$$

in which no attempt is made to interpret the various parameters used (usually one would never use a polynomial greater than order six, with order two or three being more common). Such descriptive models can be regarded as black boxes, which provide a deterministic output for a given

input. It is not necessary to know the workings of such models; one could even use a simple lookup table that produced a particular output value from a given input value by literally looking up the output from a cross-tabulation of values. Such black box models would be descriptive and nothing else. No notice need be taken of any assumptions used in their construction. Such purely descriptive models need not have elements of realism about them except for the variables being described.

Explanatory models also provide a description of the empirical observations of interest, but in addition they attempt to provide some justification or explanation for why the particular observations noted occurred instead of a different set. With explanatory models it is necessary to take into account the assumptions and parameters, as well as the variables that make up the model. By attempting to make the parameters and variables, and how the variables interact, reflect nature, explanatory models attempt to simulate real events in nature. A model is explanatory if it contains theoretical constructs (assumptions, variables, or parameters), which purport to relate to the processes of nature and not only to how nature behaves.

1.4.4 Testing explanatory Models

Explanatory models are, at least partly, hypotheses or theories about the structure of nature and how it operates. They should thus be testable against observations from nature. But how do we test explanatory models? Does fitting a model to data constitute a test of the model? If the expected values for the observed data, predicted by a model, account for a large proportion of the variability within the observed data, then our confidence that the model adequately describes the observations can be great. But the initial model fitting does not constitute a direct test of the structure of the model. A good fit to a model does not test whether the model *explains* observed data; it only tests how well the model *describes* the data (Haddon, 1980). The distinction between explanation and description is very important and requires emphasis (which is why this sentence is here). A purely descriptive or empirical model could provide just as good a fit to the data, which hopefully makes it clear that we need further, independent observations against which to really test the model's structure. What requires testing is not only whether a model can fit a set of observed data (i.e., not only the quality of fit), but also whether the model assumptions are valid and whether the interactions between model variables, as encoded in one's model, closely reflect nature.

Comparing the now fitted model with new observations does constitute a test of sorts. Ideally, given particular inputs, the model would provide a predicted observation along with confidence intervals around the expected result. An observation would be said to be inconsistent with the model if the model predicted that its value was highly unlikely given the inputs. But with this test, if there is a refutation, there is no indication of what aspect of the model was at fault. This is because it is not a test of the model's structure

but merely a test of whether the particular parameter values are adequate (given the model structure) to predict future outcomes! Was the fitting procedure limited because the data available for the fitting did not express the full potential for variation inherent in the population under study? Was it the assumptions or the particular manner in which the modeller has made the variables interact that was at fault? Was the model too simple, meaning were important interactions or variables left out of the structure? We cannot tell without independent tests of the assumptions or of the importance of particular variables.

If novel observations are in accord with the model, then one has gained little. In practice, it is likely that the new data would then be included with the original and the parameters reestimated. But the same could be said about a purely empirical model. What are needed are independent tests that the structure chosen does not leave out important sources of variation; to test this requires more than a simple comparison of expected outputs with real observations.

While we can be content with the quality of fit between our observed data and those predicted from a model, we can never be sure that the model we settle on is the best possible. It is certainly the case that some models can appear less acceptable because alternative models may fit the data more effectively. The process of fitting a model can have the appearance of using the quality of fit as a test between different models. We can illustrate that this is not necessarily the case by considering that we could always produce a purely descriptive model with many parameters that provides an extremely good fit, but this would not be considered a better model than a more realistic one (Figure 1.4).

Discussion over which curve or model best represents a set of data depends not only upon the quality of fit, but also upon other information concerning the form of the relationship between the variables (Figure 1.4). Clearly, in such cases, criteria other than just quality of numerical fit must be used to determine which model should be preferred. In Chapter 3, we consider methods for assessing whether increasing the number of parameters in a model is statistically justifiable. Any explanatory model must be biologically plausible. It might be possible to ascribe meaning even to the parameters of a completely arbitrary model structure. However, such interpretations would be *ad hoc* and only superficially plausible. There would be no expectation that the model would do more than describe a particular set of data. An explanatory model should be applicable to a new data set, although perhaps with a new set of particular parameters to suit the new circumstances.

Precision may not be possible even in a realistic model because of intrinsic uncertainty either in our estimates of the fitted variables (observation error) or in the system's responses, perhaps to environmental variation (process error in the model's parameters). In other words, it may not be possible to go beyond certain limits with the precision of our predicted system outcomes (the quality of fit may have intrinsic limits).

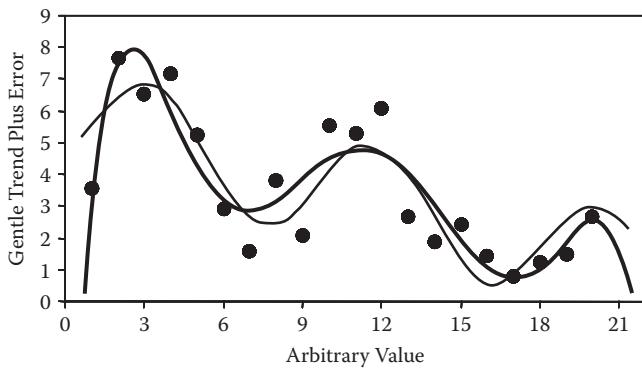


Figure 1.4

Artificial data generated from a straight line ($Y = 6 - 0.25X$) plus normal random error [$N(0,2)$]. A fitted straight line gives $Y = 6.1583 - 0.2429x$, describing 44.1% of the variation in the data. The thick curved line is a sixth-order polynomial equation with four more parameters than the straight line ($Y = -0.000045x^6 + 0.0031x^5 - 0.08357x^4 + 1.0714x^3 - 6.7133x^2 + 18.0600x - 8.9261$). It describes 88.25% of the variation in the data and is clearly a better fit, at least when not extrapolated. The fine curved line is a straight line with an intrinsic cycle [$Y = a + bx + C \sin((2\pi(x - s))/D)$], which has three more parameters than the straight line. In this case we know the straight line is the model that best represents the underlying process; the appearance of cycles is a chance event.

1.4.5 Realism/generality

Related to the problem of whether or not we should work with explanatory models is the problem of realism within models. Purely descriptive models need have nothing realistic about them. But it is an assumption that if one is developing an explanatory model, then at least parts of it have to be realistic. For example, in populations where ages or sizes can be distinguished, age- or size-structured models would be considered more realistic than a model that lumped all age or size categories into one. But a model can be a combination of real and empirical.

For a model to be general, it would have a very broad domain of applicability; it could be applied validly in many circumstances. There have been many instances in the development of fisheries science where a number of models describing a particular process (e.g., individual growth) have been subsumed into a more general mathematical model of which they are special cases (see Chapter 8). Usually this involves increasing the number of parameters involved, but nevertheless, these new models are clearly more mathematically general. It is difficult to draw conclusions over whether such more general equations/models are less realistic. That would be a matter of whether the extra parameters can be realistically interpreted or whether they are simply *ad hoc* solutions to combining disparate equations into one that is more mathematically general. With more complex phenomena, such as age-structured models, general models do not normally give as accurate predictions as more

specialized models tuned to a particular situation. It is because of this that modellers often consider mathematically general models to be less realistic when dealing with particular circumstances (Maynard-Smith, 1974).

1.4.6 When is a Model a Theory?

All models may be considered to have theoretical components, even supposedly empirical models. It becomes a matter of perception more than model structure. With simple models, for example, the underlying assumptions can begin to take on the weight of hypothetical assertions. Thus, if one were using the logistic equation to describe the growth of a population, it imports the assumption that density-dependent compensation of the population growth rate is linearly related to population density. In other words, the negative impact on population growth of increases in population size is linearly related to population size (see Chapter 2). This can be regarded either as a domain assumption (that is, the model can only apply validly to situations where density-dependent effects are linearly related to population density) or as a theory (nonlinear density-dependent effects are unimportant in the system being modelled). It is clearly a matter of perception as to which of these two possibilities obtains. This is a good reason one should be explicit concerning the interpretation of one's model's assumptions.

If one were to restrict oneself purely to empirical relationships, the only way in which one's models could improve would be to increase the amount of variance in the observations accounted for by the model. There would be no valid expectation that an empirical model would provide insights into the future behaviour of a system. An advantage of explanatory/theoretical models is that it should be possible to test the assumptions, the relationships between variables, and the error structures, independently from the quality of fit to observed outcomes.

It should, therefore, be possible to present evidence in support of a model, which goes beyond the quality of fit. Those models where the proposed structure is not supported in this way may as well be empirical.

2

Simple Population Models

2.1 Introduction

2.1.1 Biological Population Dynamics

A biological population is a collection of individuals that has identifiable emergent properties not possessed by individual organisms. These properties include the population's size, its growth rate, its immigration and emigration rates, its age and size structure, and its spatial distribution. The dynamic behaviour of a population relates to changes in these properties through time. One objective of population modelling is to describe and possibly explain how a population's properties change through time.

Mathematical equations used to model biological populations provide an abstract representation of their dynamics. This requires emphasis because the equations in many population models can exhibit dynamic behaviours that biological populations either do not or could not exhibit; models are, after all, only models. For example, a mathematical model might predict that under some circumstances the modelled population was made up of a negative number of organisms or produced a negative number of recruits. Such obvious discrepancies between the behaviour of the mathematical equations and possible biological behaviours are of little consequence because usually they are easily discovered and avoided. Unfortunately, purely mathematical behaviours can also arise that are less obvious in their effects. It is thus sensible to understand the dynamic behaviour of any equations used in a modelling exercise to avoid ascribing nonsensible behaviours to innocent populations.

2.1.2 The Dynamics of Mathematical Models

The purpose of this chapter is to give a brief introduction to the properties of models and how their dynamic behaviours are dependent upon both their particular mathematical form and the particular values given to their parameters. To do this we will consider some of the mathematical models that are commonly used in both ecology and fisheries to describe population dynamics. We will also be distinguishing between models that do not include age structure and those that do. This is a natural progression,

as certain whole-population models can be combined in particular ways to produce an age-structured model.

First, we will consider exponential population growth and its relationship to both the logistic model of population growth, commonly used in basic fisheries models, and age-structured models, such as those used in the analysis of yield-per-recruit. This will lead us to a more detailed study of the logistic population growth model. As we shall see, the discrete logistic model can exhibit a wide range of dynamic behaviours, ranging from monotonically damped equilibria (a smooth rise to a stable equilibrium population size) to chaotic behaviour (unpredictable sequential behaviour). The simple age-structured models we will consider will demonstrate that if the right information is available, we can investigate how the productivity of any population is distributed between new recruits to the population and the growth of individuals already in the population.

2.2 Assumptions—Explicit and Implicit

2.2.1 All Assumptions Should Be explicit

A model can be viewed as a purely abstract mathematical system, or we can make the step of relating its variables and parameters to the real world. An explicit listing of a model's assumptions about its relation to reality, along with their implications, should be standard practice but is not as common as it ought to be. The most important assumptions of simple exponential population growth are (Slobodkin, 1961; Pianka, 1974):

1. **All animals in the population have identical ecological properties.** This means that morphology, genetics, and behaviour have no effect on population dynamics. Age-structured models are one way to alter this assumption. In addition, we are dealing with a single population or stock; that is, either there is no immigration ($I = 0$) or emigration ($E = 0$), or alternatively, ($E = I$) immigration equals emigration; we are ignoring biogeography.
2. **There are no significant time delays in population processes.** The whole population responds immediately to any changes in population size irrespective of season, geographical scale, or distance. Age-structured models also affect this assumption, at least by introducing time lags between reproduction and growth.
3. **The parameters of the model are constants.** This ignores random variations as well as seasonal and environmentally induced natural variations in such things as maximum population size and maximum

population growth rate. It also ignores long-term changes in parameter values—it assumes stationarity.

These assumptions, about the relation between the model and reality, are either unlikely or unrealistic, but for the moment, they are necessary if we are to keep the model simple (Slobodkin, 1961). Wherever we have used the term *population* in the aforementioned three assumptions, we could have used the term *stock*. The idea is that the model is concerned with a self-sustaining population that does not depend upon immigration to maintain its size. By making our assumptions explicit, we are helping to determine how to interpret the terms of our mathematical model. The assumptions also determine the domain of applicability (meaning the range of situations to which the model is expected to relate; Lakatos, 1970). It is excellent practice to inspect statements about the assumptions of models in the literature to see if one can add to the list given.

2.3 Density-Independent Growth

2.3.1 exponential growth

Population growth at its abstract simplest can be imagined as a population growing in an unlimited environment. An example, which might approximate this theoretical possibility of unrestricted growth, could arise where resources may not yet be limiting for a colonizing species when it first arrives in a new and empty location. Large parts of the world's human population are still growing as if this were the case, but sadly they will soon discover that resources are, in fact, limited. Further examples might be the populations of organisms that first colonized the new volcanic island of Surtsey, which started to form in November 1963 off Iceland, or on the remains of the volcanic island of Krakatoa, which blew up in August 1883 (Krebs, 1985). The initial, accelerating growth exhibited by such populations is described as exponential growth.

If birth and death rates are constant at all population sizes, it implies a constant proportional increase in population size each time period. The rate at which a population's size changes can be described by

$$\frac{dN}{dt} = (b - d)N \equiv rN \quad (2.1)$$

In this differential equation (Lotka, 1925, p. 101), dN/dt translates as the rate of change of the population size N relative to time t , b is the birth rate, d is the death rate, and the symbol \equiv denotes "is equivalent to." In ecology textbooks, where $r = (b - d)$, r is often termed the intrinsic rate of increase,

the “instantaneous rate of population growth,” or even the “per-capita rate of population growth” (Krebs, 1985, p. 212). The point to note is that the per capita growth rate ($b - d$), or r , is a constant and is assumed independent of population size N . Not surprisingly, this type of growth is termed density independent. Good summaries of population growth can be found in many ecological texts (e.g., Begon and Mortimer, 1986; Caughley, 1977; Caughley and Sinclair, 1994; Christiansen and Fenchel, 1977; Krebs, 1985; Pianka, 1974).

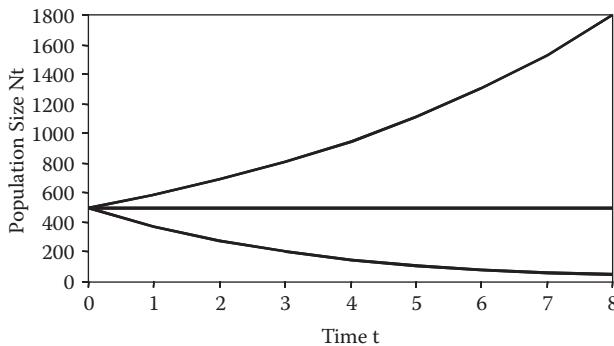
There is a possible source of confusion over the term *rate*. A constant birth rate at all population sizes does not mean that the same absolute number of offspring will be produced at all population sizes, but rather that the population increases by the same proportion at all sizes. Thus, a growth rate of 0.1 implies a population of 100 will increase by 10, while a population of 1,000 will increase by 100. As population size increases, the absolute number by which the population grows in each time interval will also increase, but the proportional increase will stay constant.

Equation 2.1 is a differential equation relating the rate of change of population size to time. This can be integrated to produce an equation describing the expected numbers in the population at any time after some given starting population size and time. The integral of Equation 2.1 is

$$N_t = N_0 e^{(b-d)t} \equiv N_0 e^{rt} \equiv N_{t-1} e^r \quad (2.2)$$

where N_t is the expected population size at time t and N_0 is the population size at time zero (the starting population size). Because the irrational constant e is used (Jeffrey, 1969), this model is termed exponential growth, and that phrase often brings to mind a continuously increasing population. However, depending upon the balance between births and deaths, exponential growth can describe a population going to extinction, staying stable, or growing rapidly (Figure 2.1; Berryman, 1981; Krebs, 1985). In simple whole-population models, Equation 2.2 is of limited use. Knowledge of its properties is worthwhile, however, as it is used in age-structured models that follow individual cohorts whose numbers only decline after birth.

Note that exponential increase produces an accelerating curve in which the proportional increase in population size is constant each time period (Equation 2.2, Figure 2.1, Example Box 2.1), but where the absolute numbers of individuals entering the population each time period increases more quickly with time. In the case of exponential decrease this is a decelerating curve where the proportional decrease is constant throughout but the actual number dying each time period reduces so the population approaches zero ever more slowly with time. This distinction between constant proportional rates of change and increasing or decreasing absolute numbers of individuals is an important one to grasp when considering the exponential model of population changes. The intuitions concerning this phenomenon may come more easily if one recognizes that this process is analogous to compound interest

**Figure 2.1**

Population growth curves from Equation 2.2 under different net balances of birth and death rates (Berryman, 1981). When the net reproductive rate is positive, the exponential increase produces an accelerating curve, leading to ever-increasing population sizes. When there are more deaths than births, an exponential decrease produces a decelerating curve that approaches zero ever more slowly (Example Box 2.1). Obviously, when births balance deaths, an equilibrium ensues.

in financial terms. Positive interest rates lead to exponential growth, and this is a common property for anything that is increased or decreased by a constant proportion through a series of time periods.

2.3.2 Standard Transformations

The mathematical form of exponential population growth has a number of properties that can simplify our representation of population growth processes. The most important property for the practice of population dynamics is that a natural logarithm transformation linearizes the pattern of growth (natural logs, denoted \ln , are logs to base e). Thus,

$$\ln(N_0 e^{rt}) = \ln(N_0) + \ln(e^{rt}) = \ln(N_0) + rt \quad (2.3)$$

In a population growing exponentially, a plot of the natural log of numbers against time should produce a straight line, and the gradient would be an estimate of the growth rate r and the intercept an estimate of $\ln(N_0)$ (Equation 2.3).

2.3.3 Why Consider equilibrium Conditions?

Exploited populations rarely appear to be in equilibrium. Nevertheless, to understand a mathematical model's properties it is usual to consider under what conditions equilibrium could be attained. At equilibrium, by definition, the rate of change of population size with respect to time will be zero ($dN/dt = 0$), and with Equation 2.2 that could occur under two conditions.

EXAMPLE BOX 2.1

Three exponential curves in Excel. Each population starts with five hundred individuals, and how it grows depends on whether the birth rate (row 1) is greater than the death rate (row 2). The equation in column B must be copied into columns C and D, and down to whatever time is required. By calculating down to a time of eight (row 21) and plotting the numbers for the three populations (columns B to D) against time (column A), one should be able to generate curves similar to Figure 2.1. The growth model is Equation 2.2. Investigate the properties of this growth model by varying any of the parameters in B1:D3. Try setting the vertical axis of the plot of exponential growth to a logarithmic scale or plot the natural log of numbers against time (put =Ln(B5) into column E, etc.). See Appendix A for guidance with the use of Excel in fisheries.

	A	B	C	D
1	b: births	0.1	0.1	0.1
2	d: deaths	0.04	0.1	0.125
3	N_0	500	500	500
4	Time	Pop 1	Pop 2	Pop 3
5	0.0	=B\$3*EXP((B\$1-B\$2)*\$A5)	500	500
6	0.5	=B\$3*EXP((B\$1-B\$2)*\$A6)	500	493.8
7	1.0	=B\$3*EXP((B\$1-B\$2)*\$A7)	500	487.7
8	1.5	'	500	481.6
9	2.0	'	500	475.6
10	Cont. down	Copy down	Copy down	Copy down

The trivial case is when $N = 0$, i.e., the population is extinct (because with no immigration, at all subsequent times N will equal 0). The more interesting case biologically is when the birth rate exactly equals the death rate and both are positive. With Equation 2.2 this is what is termed an astable equilibrium, in which any perturbation to the birth or death rates will disrupt the equilibrium and lead to either an exponential increase or a decrease toward extinction.

If the birth and death rates stay constant but there is a perturbation to the population size (possibly immigration or emigration), a new equilibrium population size will result. The key point being that the population does not return to its previous equilibrium. At equilibrium, $N_{t+1} = N_t$, so there can be no change in numbers from time t to time $t + 1$. Hopefully, it is clear that there can be an astable equilibrium at any population size as long as births equal deaths. When not in equilibrium the populations will either increase to infinity or contract to extinction at a rate dependent upon how dissimilar births are from deaths.

2.4 Density-Dependent Models

2.4.1 An upper Limit and Persistence

Few general characteristics can be ascribed to all biological populations. However, as Linnaeus implied (Stauffer, 1960), Malthus pointed out (Malthus, 1830), and the world's human population will soon discover, no population can grow indefinitely because all populations live in limited environments. Thus, positive exponential growth can only be a relatively short-term phenomenon. Another general property of populations is that most are believed to persist despite random environmental perturbations (although long-term persistence is not guaranteed as the continuing spate of extinctions around the world testifies). Unfortunately, our first model, Equation 2.2, allows for very little other than indefinite growth or extinction. While it is true that some "weedy" species exhibit a boom and bust lifestyle (Andrewartha and Birch, 1954), if there is to be population self-regulation, then an obvious option is to alter the simple exponential model to account for the general properties of a maximum population size and persistence.

2.4.2 The Logistic Model of growth

One of the simplest models to be derivable from exponential growth is the logistic model. It is worth noting that in the past a number of fisheries were managed using equilibrium analyses of continuous models based upon the logistic (details will be given when we consider surplus production models in Chapter 11). It has also been suggested that at least part of the sad history of failures in fishery advice and management stems from this combination (Larkin, 1977); this suggestion is often followed by implied abuse at the logistic and its implications, as well as the people who use it. However, invective against the logistic is misplaced. The logistic is simply a convenient model of linear density-dependent effects (similar fisheries advice would have come from any equilibrium analysis using a linear model of population regulation). Beverton and Holt (1957) pointed out the weaknesses inherent in using the logistic population growth curve, but they recognized that in the absence of detailed information this approach might still have value if used carefully. They stated:

It is when such detailed information does not exist that the sigmoid curve theory, by making the simplest reasonable assumption about the dynamics of a population, is valuable as a means of obtaining a rough appreciation from the minimum of data. (Beverton and Holt, 1957, p. 330)

The exponential population growth model was density independent in its dynamics; that is, the birth and death rates were unaffected by the population

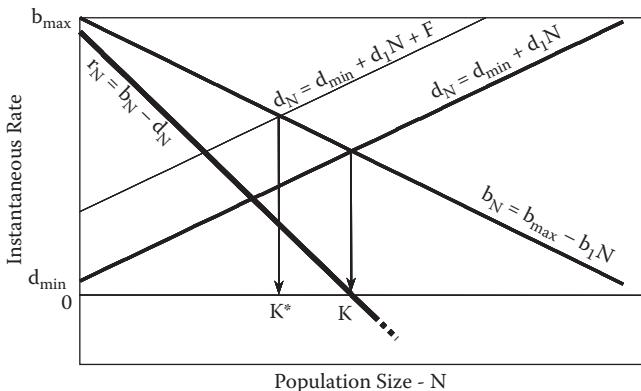


Figure 2.2

Comparison of the influence of population size on the instantaneous rate of increase in a density-dependent model (after Pianka, 1974, p. 86; this is fundamental population biology and Pianka's discussion of these relationships is highly recommended). The death (d_N) and birth (b_N) rates are both described by linear equations (see Equation 2.4), hence the term *linear density dependence*. The junction of the two is where births balance deaths, leading to the equilibrium population size K , and with an imposed fishing mortality F , a new, lower equilibrium, K^* , is produced.

size. If population growth was regulated such that the difference between births and deaths was not a constant but became smaller as population size increased and greater as the population decreased, then the likelihood of runaway population growth or rapid extinction could be greatly reduced. Such a modification of the dynamic response with respect to density is what makes such models density dependent. In a density-dependent model, the population rate of increase (as a balance between births and deaths) alters in response to population size changes (Figure 2.2).

A decline in the rate of increase in a density-dependent model can be brought about by a decline in the birth rate with population size, or an increase in the death rate, or a combination of the two. We will consider the general case where both rates are affected by population size, but the same outcomes would derive from just one being affected.

The simplest model to include density dependence would be where the birth and death rates are linearly related to population size (Figure 2.2; Pianka, 1974). For this to be the case instead of the rates being a simple constant, we would have to include population size and some modifying parameter in a linear equation (Equation 2.4).

If fishing were able to take a constant proportion from the stock, this would be equivalent to an added density-independent increment to the death rate (the fine line in Figure 2.2, $d_N = d_{\min} + d_1N + F$), leading to a new equilibrium at K^* (these terms are explained later; see Example Boxes 2.2 and 2.3 and Figure 2.5). The modification this would make to the reproductive rate r_N is not shown (the new r_N line would pass through K^*). Linearly relating birth

and death rates to population size would be represented by a change in the gradient terms:

$$\begin{aligned} b_N &= b_{\max} - b_1 N \\ d_N &= d_{\min} + d_1 N \end{aligned} \quad (2.4)$$

where b_{\max} and d_{\min} are the birth and death rates when population size, N , is very small, and b_1 and d_1 are parameters that scale the rates at which the birth and death rates change with population size. Equation 2.4 implies that births decrease linearly as N increases and the death rate increases linearly as population increases (Figure 2.2). These changes introduce the possibility of population regulation. If the terms in Equation 2.4 are substituted for b and d in Equation 2.1, our original model becomes

$$\frac{dN}{dt} = [(b_{\max} - b_1 N) - (d_{\min} + d_1 N)]N \quad (2.5)$$

which can be rearranged:

$$\frac{dN}{dt} = [(b_{\max} - d_{\min}) - (b_1 + d_1)N]N = (b_{\max} - d_{\min})N - (b_1 + d_1)N^2 \quad (2.6)$$

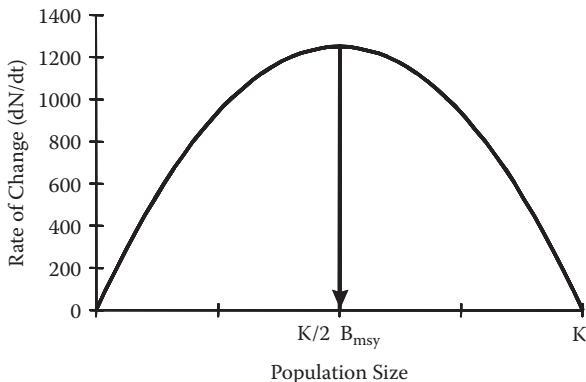
This has the effect of putting the intercepts ($b_{\max} - d_{\min}$), which is the rate of population increase when population density is very low, together in one term. The properties of the model can be explored by determining the conditions required for equilibria to exist (where $dN/dt = 0$); thus,

$$(b_{\max} - d_{\min})N = (b_1 + d_1)N^2 = (b_{\max} - d_{\min}) = (b_1 + d_1)N^* \quad (2.7)$$

and therefore (Pianka, 1974),

$$N^* = K = \frac{(b_{\max} - d_{\min})}{(b_1 + d_1)} = \frac{r}{(b_1 + d_1)} \quad (2.8)$$

where N^* or K is the equilibrium population size, often called the carrying capacity in the logistic equation, referring to the hypothetical maximum number or biomass that the environment can maintain if no changes occur. Pearl and Reed (1922) were the first to use the term K to represent the population upper limit. By including these density-dependent effects, this population model is using a form of negative feedback. Thus, as population size increases, the birth rate decreases (possible mechanisms could include increased competition or reduced growth, which would affect fecundity or reduce energy allocated to reproduction) or the death rate increases (possibly due to starvation, cannibalism, or predator aggregation).

**Figure 2.3**

Plot of the equilibrium rate of change of population size vs. population size (production vs. stock size curve; Schaefer, 1954). Maximum productivity occurs at half K (in terms of biomass, this is B_{msy}); equilibria occur at zero and K . The symmetry of the production curve about $K/2$ is unrealistic. Permitting asymmetry of the production curve will be considered in Chapter 11.

If we simplify the model (reparameterize by amalgamating constants) by letting $r = (b_{\max} - d_{\min})$, then from Equation 2.6 the rate of population change becomes

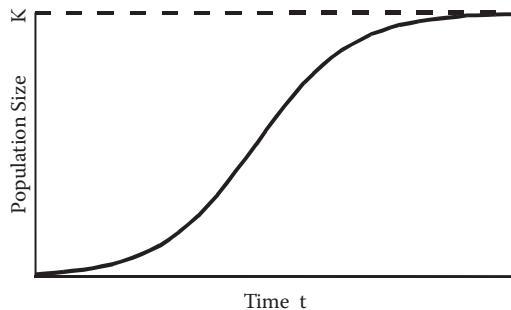
$$\frac{dN}{dt} = rN - (b_1 + d_1)N^2 = rN \left(1 - \frac{(b_1 + d_1)N}{r} \right) \quad (2.9)$$

and making the further substitution of $K = r/(b_1 + d_1)$, i.e., $1/K = (b_1 + d_1)/r$, leads to

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (2.10)$$

which is the more common form of the well-known logistic equation (Krebs, 1985). The derivation of K reveals why the two parameters, r and K , are always strongly correlated. Equation 2.10 tells us about the rate of change of population size (related to stock production). By searching for where this is maximum we find that the maximum rate of population change occurs when $N = K/2$ (Figure 2.3).

Thus, a population growing according to the logistic equation will grow at its fastest rate when it is at half the theoretical equilibrium population size. In addition, the population growth rate (dN/dt) will be zero when the population is extinct and when it is at its maximum equilibrium size, the carrying capacity. Integrating Equation 2.10 produces the continuous solution to the logistic equation (Equation 2.11), giving the expected population size N_t at time t after some starting time and initial population size N_0 . By setting

**Figure 2.4**

Population trajectory when growing according to the logistic curve (Equation 2.11). The top dashed line represents the asymptotic carrying capacity K . Maximum growth rate is at $K/2$, where the inflection exists in the curve. Note the classic *sigmoid* shape described by Beverton and Holt (1957).

$(K - N_0)/N_0 = \gamma$, where K refers to the equilibrium population size, t is time, and r is the maximum rate of population change, then

$$N_t = \frac{K}{1 + \frac{(K - N_0)}{N_0} \frac{1}{e^{rt}}} = \frac{K}{1 + \gamma e^{-rt}} \quad (2.11)$$

Following the population trajectory through time for this logistic model generates the familiar S-shaped curve (Figure 2.4; Pearl and Reed, 1922). First, there is accelerating growth with a rapid increase in population size before the compensation of density-dependent regulation has much effect (when $(1 - N/K) \sim 1.0$). The acceleration slows until a maximum rate of increase is reached at half the maximum population size. After that, there is a deceleration of growth rates in a way symmetric to the manner in which it accelerated (due to the symmetry of the production curve; Figure 2.3), and the asymptotic population size is eventually reached when $(1 - N/K) \sim 0.0$.

One aspect of the continuous logistic curve that should be noted is the smoothness of the population growth trajectory. There are no oscillations or population overshoots beyond the asymptotic value. This is due to the differential equations dealing with infinitesimals and the instantaneous response to any change in population size that this implies.

2.4.3 Discrete Logistic Model

Differential equations implicitly introduce the assumption of no significant time delays. The assumption that the population can respond immediately to changed population size appears unrealistic. It might be approximated in a large homogeneous population where births and deaths occurred continuously through time and generations overlapped completely. It is also

possible to add explicit time delays to differential equations (Nicholson, 1958). However, for populations in seasonal environments, especially with nonoverlapping generations or discrete cohorts, a discrete time model may be more appropriate. Such models can be referred to as difference equations because they are literally formed to illustrate the difference between time intervals. A logistic model setup as a difference equation could be

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K} \right) \quad (2.12)$$

which is Equation 2.10 converted to discrete time intervals instead of infinitesimals. If there were an extra source of mortality, such as fishing mortality, this could be included by adding an extra term (C_t is the catch at time t):

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K} \right) - C_t \quad (2.13)$$

2.4.4 Stability Properties

The exponential model of population growth was astable (any perturbation led either to extinction or runaway growth). The discrete logistic model, however, has more interesting properties. Density-dependent growth means it is more capable of compensating for increases in mortality brought on by such things as fishing. Again, an equilibrium exists where $N_{t+1} = N_t$, which can be represented by a diagonal line on a phase diagram (Figure 2.5, Examples Boxes 2.2 and 2.3) in which time is implicit. The logistic model has

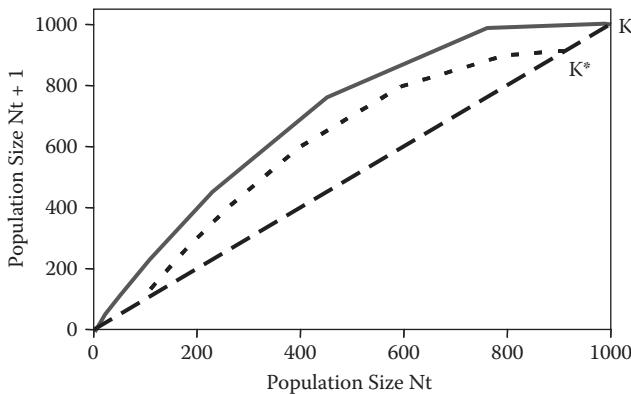


Figure 2.5

Phase diagram of the discrete logistic growth. The diagonal line of equilibrium is $N_{t+1} = N_t$. The upper curved line is the productivity beyond replacement (i.e., beyond the equilibrium line) at each possible population size. The equilibrium carrying capacity is at K . With an extra constant source of mortality (e.g., $C_t > 0$; see Figure 2.2), a lower equilibrium carrying capacity K^* is obtained at the end of the dotted lower curved line. Strictly, this applies only to nonoscillatory situations (see Example Boxes 2.2 and 2.3).

EXAMPLE BOX 2.2

The discrete logistic population growth model (Equation 2.13). By plotting population size (column B) against time (column A), and varying the r , K , and N_0 parameters, one should be able to generate the equivalent to Figure 2.4. Time is implicit in column B because each cell after B5 refers to the cell immediately above. That is, the cell for N_{t+1} refers to the cell for N_t , immediately above, and hence the time steps are implicit. Investigate the influence of a constant catch level, C_t , by varying the value in D1; be sure to increase the starting population size in B3 to be greater than the constant catch level or else the population would instantly go negative. Negative numbers are avoided by using =Max(Eq 2.13,0). For convenience, the final population size is copied to D3 to aid with the interpretation of the graph. Column C, which duplicates N_{t+1} , should only be copied to one row less than N_t .

	A	B	C	D
1	r: growth	0.5	C _t	0
2	K: popmax	1000		
3	N ₀	50	N ₂₀	=B25
4	Time	N _t	N _{t+1}	
5	0		=B3	=B6
6	1	=max(B5+\$B\$1*B5*(1-B5/\$B\$2)-\$D\$1,0)		=B7
7	2	=max(B6+\$B\$1*B6*(1-B6/\$B\$2)-\$D\$1,0)		=B8
8	3	=max(B7+\$B\$1*B7*(1-B7/\$B\$2)-\$D\$1,0)		=B9
9	4	Copy Down to at least Row 25	Copy down	
10	Continue down to row 25		to row 24	

a nonlinear relationship between successive generations (the curved line on the phase diagram, Figure 2.5). The population must take a value somewhere on the curved trajectory, the actual shape of which will be determined by the particular parameter values adopted in the model.

The productivity, above that required to replace the breeding population at any time, is that which, if the predictions of this simplistic model held in practice, could be cropped without damaging the population. That is, the difference between the curve of the production line and the dashed equilibrium line is the hypothetical quantity that could be harvested from the population in a sustainable fashion. The maximum difference, which occurs at $K/2$, is known as the maximum sustainable yield (MSY), and this is the origin of the idea (Schaefer, 1954, 1957).

The stock biomass needed to generate this level of productivity is the B_{msy} (pronounced B.M.S.Y.). This simplistic/historical view underlies the intuitions that many people have about population productivity in fisheries.

EXAMPLE BOX 2.3

The phase diagram for the discrete logistic equation. From the spreadsheet in Example Box 2.2, plot N_{t+1} (column C) against N_t (column B) as a solid line with no dots and vary the parameters r , K , and N_0 until the graph approximates Figure 2.5. To include the equilibrium line, type in, select, and copy H23:I24, as below, then “paste special” these data onto the graph ticking the “New Series” and “Categories (X values) in First Column” boxes, formatting the series to represent a dashed line. At any population size, the distance between the curved line and the equilibrium line is an estimate of the surplus production. You should adjust the value of the constant catch, C_t , in D1, and observe how this affects the final equilibrium, i.e., where the curved line crosses the straight line of equilibrium. To retain multiple curved lines one can copy columns B and C, as values, into columns further to the right and, as before, copy and paste special them into the graph. In this way, one can duplicate Figure 2.5.

	G	H	I	J
23		0	0	
24		1000	1000	

When we discuss stock production models in Chapter 11, we will see why this notion is too simplistic and too risky a view of what is possible.

2.4.5 Dynamic Behaviour

Equation 2.12 (Equation 2.13 with C_t set to zero) has a wide variety of different behaviours depending upon the value given to its r parameter. The fact that very complex dynamic behaviour can be obtained from a simple deterministic difference equation was highlighted by May (1973). This was surprising at the time because the model is a completely deterministic equation and the belief had been that the behaviour of deterministic equations should be capable of being completely understood in an analytical fashion. There are four characteristic forms of dynamic behaviour expressed by the model (Table 2.1, Figure 2.6, Example Box 2.4).

Clearly there are a number of complex behaviours that Equation 2.13 can exhibit, and most of these relate to imbalances in the density-dependent compensation for changes in population size. This is a remarkable field of research, and the visual patterns that can be produced once one starts investigating chaos are undoubtedly fascinating. The detailed dynamics of a model in chaos are unpredictable. Given the state of the model at a given time, it is impossible to predict with certainty what will happen at a later

TABLe 2.1

Dynamic Behaviour of Equation 2.12 Given a K Parameter Set at 1,000 and the Following Different r Parameter Values

r Values	Description of Behaviour
$0 < r \leq 1$	Monotonically damped equilibrium. No oscillations, leading smoothly to a stable equilibrium.
$1 < r < 2.03$	Damped oscillatory equilibrium. Oscillates but, given enough time, will return to a single equilibrium point following a perturbation.
$2.03 < r < 2.43$	Stable limit cycles, 2. The model system oscillates in a cyclic fashion with two alternative population levels.
$2.43 < r < 2.54$	Stable limit cycles, 4. The model system oscillates in a cyclic fashion with four alternative population levels.
$2.54 < r < 2.57$	Stable limit cycles, ≥ 4. These cycles continue but reach higher orders, first 8, then 16, but then it becomes difficult to distinguish events from chaotic behaviour.
$\sim 2.575 < r$	Chaos. Unpredictable behaviour that changes depending on starting conditions.

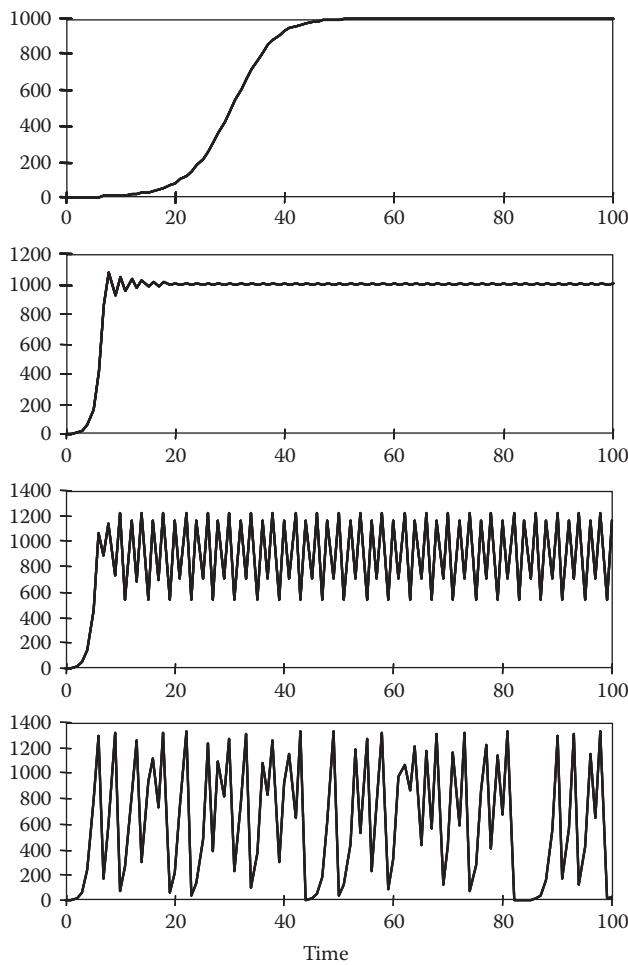
Note: See Figure 2.6 for representations of the types of behaviour described. The values of r listed are only approximate, but the behaviour itself may be investigated in Example Box 2.4.

point in time. However, the phase plot for the discrete logistic model illustrates the notion of a strange attractor, and indicates that beneath the chaotic behaviour there are constraints operating on the behaviour of the model. In this case the chaotic behaviour of the various population sizes possible is constrained to lie on a parabola (Figure 2.7; cf. Figure 2.3).

Monotonically damped equilibria occur when changes in the population size are sufficiently slow that the density-dependent mechanisms are able to compensate perfectly, leading to smooth and orderly population growth. This can only occur if the growth rate does not rise through the limits indicated in Table 2.1. If the rate of population increase is too high, then the linear density-dependent compensation built into the model is inadequate to counteract the rapid changes in population size that can occur. At this stage, we would say that nonlinear density-dependent effects are being expressed.

With damped oscillatory equilibria the under- and overcompensation are limited in their lack of balance so that a relatively stable equilibrium eventually arises. With stable limit cycles, the under- and overcompensation for population size changes interact in such a way as to oscillate in a stable manner between multiple quasi-stable states (Figure 2.6). Finally, when the growth rate passes the chaos threshold, the degree of under- and overcompensation is so great that unpredictable behaviour arises (though constrained within the bounds of the strange attractor).

Fascinating though an examination of chaos theory can be (Gleick, 1988; Lauwerier, 1991), a question remains about exactly how useful knowing about such matters is going to be in the modelling of natural populations.

**Figure 2.6**

Examples of the dynamic behaviour exhibited by the discrete logistic when K was set at 1,000, N_0 set to 1, $C_t = 0$, and each panel is the product of a different r value. Four different r values are illustrated: an r of 0.25 (top; monotonically damped equilibrium), r of 1.85 (second; damped oscillatory equilibrium), r of 2.5 (third; four-way stable limit cycle), and an r of 3 (bottom; chaos). In chaos, if the starting population size N_0 is altered, even only slightly, a completely different and unpredictable outcome is produced (Example Box 2.4).

There are few publications concerning the population dynamics of marine species that use chaos theory in their explanations. Some publications are even explicit in denying that observations of apparently random behaviour are brought about by the nonlinearity introduced by overcompensation in a density-dependent model. Instead, it is claimed that the randomness in observations is brought about by population responses to stochastic environmental effects (Higgins et al., 1997).

EXAMPLE BOX 2.4

Investigation of a model's dynamic behaviour. Alter the model described in Example Boxes 2.2 and 2.3 by extending time down to 100, N_t (column B) by copying down to row 105 and N_{t+1} (column C) down to row 104. Plot, as points, columns B and C in a new graph in two series (B5:C55 and B56:C104). Colour the first series blue and the second series red. In this way, if the population eventually reaches equilibrium, its form should be more discernible in the phase diagram as a red point. By comparing the phase diagram with a plot of N_t against time (column B against A; cf. Figure 2.6), the manner in which the dynamics alters with changes to r , K , and N_0 can be followed. Using Table 2.1 as a guide, investigate the boundaries of the different dynamic behaviours.

Investigate the impact of a constant fishing mortality rate by setting C_t to >0 . Is the impact the same on all the dynamical behaviours? See Section 2.5 for a discussion.

For an alternative model equation in column B, replace $B5+r*B5*(1-B5/K)$ with $r*B5*exp(-K*B5)$ and copy down. With the alternative equation the meaning of the parameters has changed, so start with r set to 2.0, K set to 0.0005, and N_0 set to 50. Find the boundaries between the different dynamical behaviours in this model. Is it more or less robust than the logistic?

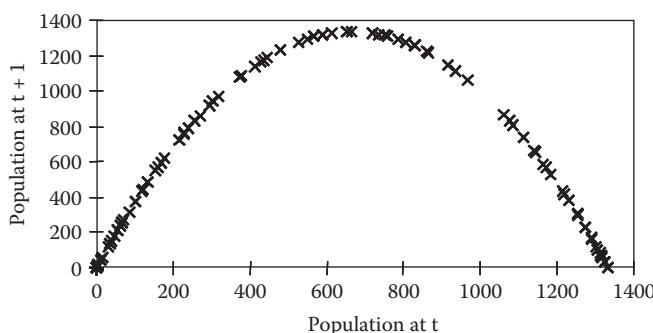


Figure 2.7

The time phase diagram for the discrete logistic equation exhibiting chaos (see Figure 2.6). The points plotted are the first one hundred population sizes when the population started at a size of 1, has a K of 1,000, and an r of 3. The order of appearance on the parabola appears to be random, but the population sizes are obviously constrained to lie on a definite line. The pattern arising from this constraint is known as a strange attractor. Note the upper limit to stock size is no longer K .

An inspection of the time phase diagram (Figure 2.7; in which the dynamic behaviour of a model system is illustrated) provides one with an indication of the bounds within which biological behaviour can occur as compared to mathematical behaviour. Such inspections permit one to determine which combinations of parameter values will lead to what would be pathological or impossible biological behaviour. In this way, such behaviours could be excluded by constraining the parameter values possible. It should be noted that complex dynamic behaviour in a model should therefore be considered with suspicion unless there are good biological reasons to think that such behaviour could be expected.

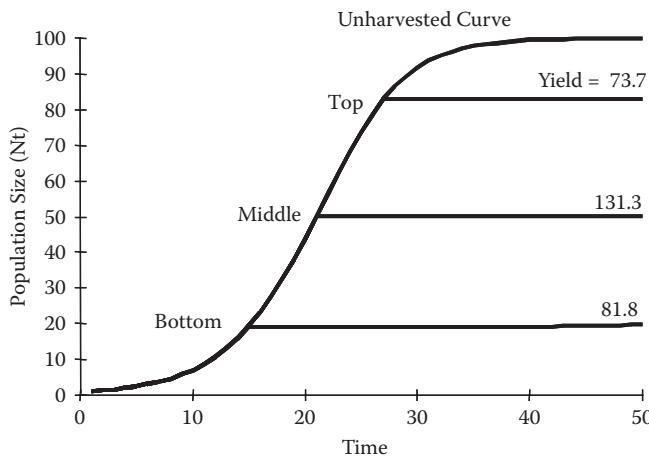
2.5 Responses to Fishing Pressure

Density-dependent effects compensate for population changes by altering the population growth rate. However, they may under- or overcompensate and so lead to oscillations (see the logistic model in Example Box 2.4). Overcompensation occurs when a population's growth rate is reduced too much, and undercompensation is where the growth rate is not reduced enough. Undercompensation can lead to a population rising to levels beyond its theoretical asymptotic equilibrium. The imposition of extra density-independent mortality onto a model population can often stabilize a relatively unstable situation.

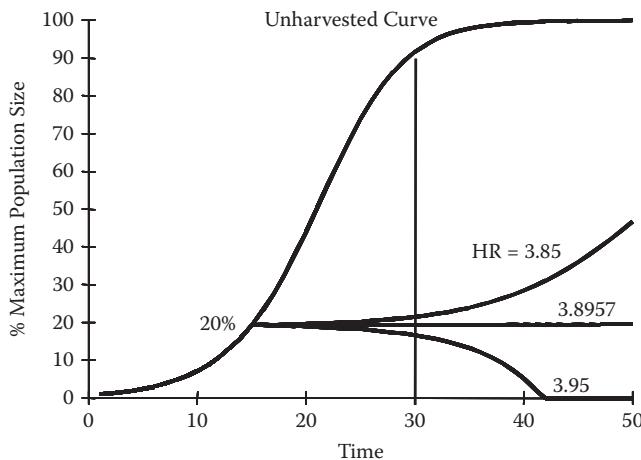
If a constant catch mortality is imposed, this can reduce the variation in a model population's behaviour through effectively offsetting any undercompensation. Of course, if there is no undercompensation, then additional mortality through fishing will simply increase the mortality rate at a given population size (overcompensation). In addition, if the increased mortality is too great, it can lead to a population collapse (see Example Box 2.4).

Maximum productivity occurs at half the maximum population size with lower productivity at either side (Figures 2.3 and 2.4). Thus, we would expect to be able to harvest a population safely more intensively when the biomass was only at half its equilibrium level than we could at other levels (Figure 2.8). This theory is overly simple, but nevertheless one can determine theoretical sustainable harvest rates for population levels below, at, and above the theoretical optimum population size (Figure 2.8), which means these amounts can be harvested each time period without altering the population size.

In each case the harvest rate would equal the surplus production at the given population size. Populations that are harvested when they are near their maximum population size have more resilience to perturbations (such as fishing pressure) than populations harvested when at lower population sizes. The sensitivity to perturbations becomes extreme toward the lower population sizes (Figure 2.9). In practice, with the model, this means more

**Figure 2.8**

A population growing according to a discrete logistic population model with a regular harvest being taken at three different levels of standing crop ($K = 100$, $r = 0.25$, and $N_0 = 1$). The upper and lower levels' total sustainable yield is slightly less than half that from the middle level (Pitcher and Hart, 1982). In this model, 3.51 units are harvested each time period from the top population, while 6.25 and 3.8957 units can be taken from the middle and bottom populations, respectively. The fourth decimal place is necessary with the bottom curve because it is very sensitive to changes in harvest rate (see Figure 2.9 and Example Box 2.4).

**Figure 2.9**

Sensitivity to changes in harvest rate of a population growing according to a discrete logistic population model with a regular and constant harvest being taken at a population size approximately 20% of the maximum. Taking 3.8957 population units per time period leads to a constant population size. A slight deviation in this harvest rate (HR) leads to either rapid population growth or a rapid decline to extinction. See Example Box 2.4.

significant digits are required when defining catch levels with the population at 20% of its maximum; otherwise, the population can grow rapidly or shrink to extinction (Figure 2.9). A rapid decline occurs when the harvest rate is greater than the sustainable yield at population size well below the optimum. If such a decline occurs, then the situation can only become worse as each harvest event lowers the standing crop so that the productivity becomes even less and the decline accelerates. Accelerating population growth occurs if the harvest rate is less than the surplus production. In this case, each harvest event leaves the standing crop slightly larger than the previous period, and hence more productive and so likely to increase even more the next time step (Figure 2.9).

2.6 The Logistic Model in Fisheries

The models we have dealt with so far may not be thought to have much relevance to fisheries. However, if we extend the logistic model to include catch we obtain

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t \quad (2.14)$$

where B_t is stock biomass at time t , r is the intrinsic rate of growth, K is the unfishered or virgin biomass equivalent to the carrying capacity, and C_t is the catch taken over time t . It is common practice to assume that catch is proportional to fishing effort and stock size (though this is only the case if the catchability coefficient, q , does not vary through time or with stock size). If we implement these further changes, then Equation 2.14 becomes a dynamic version of the surplus production model proposed by Schaefer (1954, 1957):

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - qE_t B_t \quad (2.15)$$

where E is the fishing effort and q is a parameter describing fishing gear efficiency (the catchability coefficient is the proportion of the stock biomass B taken by one unit of effort, i.e., $C_t = qE_t B_t$). This was the general form of model used in our simple fishery simulation (Figure 2.9), and we will see more of this and other slightly more complex models when we discuss surplus production models.

Some key changes that have occurred recently in fisheries stock assessment methods have been a shift away from equilibrium analyses, and a move away from the traditional interpretation of maximum sustainable yield

(MSY) toward investigating alternative harvesting strategies. Also, models are no longer constrained to express only linear or symmetrical responses to changes in population density. There is no point in criticizing the logistic equation when the actual problem was that it was inappropriate to use a linear relation between density-dependent effects and population size. The changes in methods mentioned earlier should lead to the production of better fisheries management advice. Unfortunately, it is also more capable of leading to the conclusion that one's data are inadequate for the production of useful advice. Using the old equilibrium methods and inappropriate models, definite management advice could usually be produced. However, the equilibrium methods often produced completely inappropriate conclusions. It is far better to know that one's data are uninformative than to provide bad advice.

2.7 Age-Structured Models

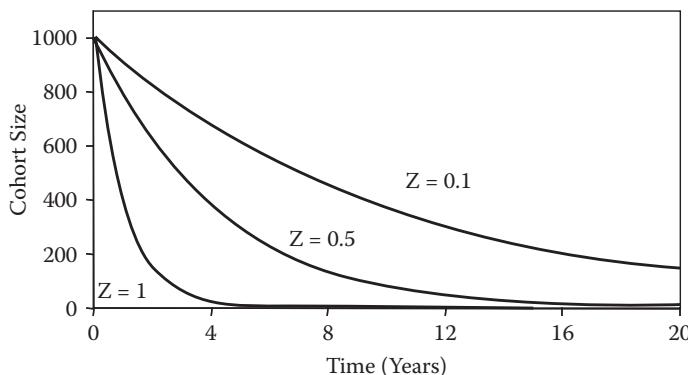
2.7.1 Age-Structured and exponential growth Models

An age-structured model attempts to capture the composite behaviour of the cohorts making up a population, which entails following the development and changes in each cohort separately. This is an improvement over a simple whole-population model for the obvious reason that different aged animals tend to have different growth rates and be different sizes (weights). A larger individual will clearly contribute more biomass to a catch than a smaller one, and generally will contribute a higher egg production. If the necessary information is available, then an age-structured model has the potential to reflect natural population processes and the impacts of harvesting better than simpler models.

If the model concerns a good biological population or stock, then immigration and emigration will be, or is assumed to be, minimal. If this is the case, then once a cohort has recruited, the numbers in that cohort or age class can only decline. How this decline is modelled determines the design of the model. In the introduction to this chapter, it was pointed out that at least some age-structured models have a relationship with the exponential model of population growth. The explanation is quite simple when we remember that the exponential model of population growth can be used to model a declining population. An equation denoting the changing numbers within a cohort can be represented as

$$N_{t+1} = N_t e^{-Z} \quad (2.16)$$

where N_t is the number in the cohort at time t , Z is the total rate of instantaneous mortality (fishing + natural mortality), and e^{-Z} is the

**Figure 2.10**

Cohort declines with different levels of total mortality (see Equation 2.16). Because e^{-Z} has a negative exponent, it can never be greater than 1 and equates to the proportion of each cohort that survives over each time interval.

proportional survivorship. The relationship with the exponential growth model (Equation 2.2) is clear, but note that the Z value is given as negative, indicating that there can only be an exponential decline in cohort size through time (Figure 2.10).

2.7.2 Annual versus instantaneous Mortality rates

The use of the exponential term in Equation 2.16 is fundamental to population modelling. At the start of this chapter (after Equation 2.1) it was pointed out there was a possibility of confusion over rates of change referring to either proportional changes or absolute changes in population size. One place where this is often a problem and which leads us into an important foundation of fisheries science is the confusion over annual and instantaneous rates of change.

An important aspect of the relationship between fish stocks and fishing is captured by the notion of the mortality imposed by fishing. As in Section 2.5, in a model, fishing constitutes an extra source of mortality that can greatly influence the dynamics of both the natural population and the model. Before we can determine if a level of fishing is sustainable, we would, ideally, obtain an estimate of the level of mortality introduced by the fishing activities. An important distinction is the one between annual mortality (easily understood) and instantaneous mortality rate (less easy to grasp intuitively).

Fishing mortality is invariably referred to by the capital letter F , which refers to the instantaneous rate of fishing mortality. If this is mistaken for the proportion of the fish stock caught annually (the annual mortality, often H for the harvest rate or A for annual), then confusion can arise, especially if F is greater than or equal to 1 (Figure 2.10).

TABLe 2.2

Outcome of Applying a Constant Mortality Rate Apportioned among Shorter and Shorter Time Periods That Add to One Year

Time Period	Fraction of a Year (Number of Times the Rate Applied)	Mortality Rate Applied Each Time Period	Number Remaining after One Year
6 months	0.5	(2)	0.34657
3 months	0.25	(4)	0.17329
1 month	0.08333	(12)	0.05776
1 week	0.019231	(52)	0.01333
1 day	0.00274	(365)	0.00189
½ day	0.00137	(730)	0.00095
3 hours	0.000342	(2920)	0.00024
Infinitesimal	~0.0	(∞)	~0.0
			500.00

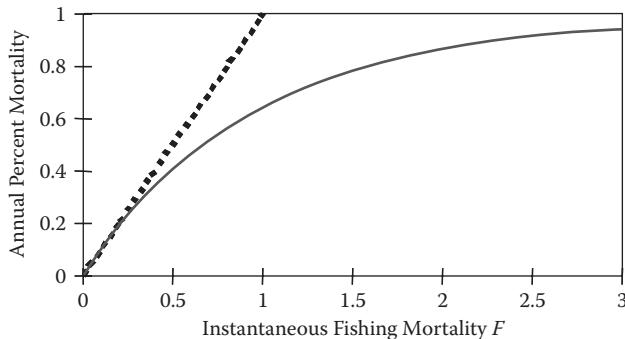
Note: The instantaneous mortality rate was 0.693147, which when translated using Equation 2.17 produces an annual mortality rate of 0.5 (i.e., 50% of the remaining cohort dies each year).

$(1 - e^{-0.693147}) = (1 - 0.5) = 0.5$, the annual mortality rate derived from the instantaneous rate. To apply this rate twice in a year, we divide 0.693147 by 2; to apply it each week we divide by 52. Note how as the time interval becomes shorter, the number remaining approaches the expected five hundred.

Most people are aware of the exponential growth properties of compound interest, which arise through increasing a starting amount by a constant proportion each time interval. Population or cohort mortality is similar to compound interest: only the starting amount (the cohort size) is decreased by a constant proportion each period. In a biological population, this leads to an exponential decline in numbers.

It is also common knowledge that if interest is compounded at intervals shorter than a year, then the overall effect is greater over a year than if it were merely compounded once. Hence, we would expect that, given a particular proportional decrease, the effect, if compounded daily, would be greater than if compounded weekly, which would be greater than if compounded monthly (Table 2.2). Equally obviously, it is also a more gradual process. If this procedure of shortening the time over which the interest is compounded is taken to extremes and very tiny periods of time are used, this would approximate the infinitesimals for which the exponential format of the equations operate (Table 2.2).

The exponential function acts to produce proportional changes out of events (such as a mortality) acting over very small time intervals on the same population. This is the same as compounding a negative interest rate many times. The repeated application of a constant proportional decline (divided into however many time intervals are being considered) is what leads to the changes being able to be represented by the exponential equation. The

**Figure 2.11**

The relationship between instantaneous and annual fishing mortality. Note that at low levels of F the two are approximately equal (the curve approximates the straight dotted line, which is a 1:1 reference line), but with F values greater than about 0.2 the equivalence disappears and much larger values of F are required to increase the annual proportion killed by fishing. The relationship is asymptotic with extremely high levels of instantaneous fishing mortality required to catch 100% of the population in a single year.

instantaneous rate of fishing mortality is denoted F , and this is related or translated to the annual mortality due to fishing (the harvest rate, H) using

$$\text{Proportional Annual Mortality} = H = 1 - e^{-F}$$

$$F = -\ln(1 - H) \quad (2.17)$$

A general symbol for annual mortality would be useful, but we cannot use lowercase f , as this is one of the generally accepted symbols for fishing effort (and sometimes fecundity). We cannot use M , as this is generally used to designate instantaneous natural mortality. Some people use E to represent the exploitation rate, but that can also be confused with effort and also commonly refers only to recruited or legal-sized fish. In this book, we will use the letter H to indicate annual fishing mortality, the harvest rate.

The important distinction to understand is the one between the F that everyone tends to talk about, the instantaneous rate, and H , the proportion of the stock taken as catch each year (Figure 2.11).

2.7.3 Selection of a Target Fishing Mortality

An important question to answer is what level of fishing mortality to impose on a stock and the manner in which the catch should be harvested. In fisheries management several standard reference or target levels of fishing mortality exist, and a number of these derive from the analysis of yield-per-recruit. A yield-per-recruit analysis is the simplest form of age-structured population model. A discussion of these methods will thus provide a gentle introduction to age-structured modelling and suggest some fishing targets.

2.8 Simple Yield-per-Recruit

2.8.1 Is There an Optimum Fishing Mortality Rate?

Most exploited aquatic populations are made up of a number of discrete cohorts of different ages. In polar, temperate, and subtropical regions, most commercial species produce one cohort each year. Even in the tropics, despite breeding seasons sometimes being extended throughout much of the year, similar cohort-based population structure can be discerned (even if it is just size based, a form of ecological-cohort). Russell's (1931) equation of stock dynamics can be applied to each cohort separately in an age-structured population. The effects of age structure on stock dynamics become especially important when individual growth and the time delays of ageing are taken into account.

A common intuition is that total yield from a fishery will always increase with increases in total effort. However, this idea was shown to be incorrect before the 1930s. When trying to formalize this idea, the first problem was to find a clear demonstration of what was, at the time, a counterintuitive notion. Also, there is the implication that if maximizing effort does not necessarily maximize catch, is there such a thing as an optimal fishing rate that would lead to a maximum yield? Russell (1942) provided a nice empirical demonstration that the optimal harvest was not necessarily taken by fishing as hard as possible (i.e., that an intermediate fishing mortality could give a bigger yield in an age-structured population).

Russell's (1942) example fished a hypothetical fish species at two different levels (Table 2.3). The major implication of having a high harvest rate of 80% mortality per annum (an $F = 1.609$) relative to a lower rate of 50% per annum (an $F = 0.693$) is that in this particular example, despite basically the same number of fish being taken, the total catch weight was over 60% greater with the lower F . This result stems simply from the lower catch rate leaving more fish in the sea for longer so that they grow to a heavier weight before being caught. At the lower harvest rate there is a greater biomass caught and the number of fish remaining in the sea after fishing is also greater. Hence, the lower fishing mortality yields a larger catch and yet is more risk averse (Table 2.3, Example Box 2.5). Even if the population were not in equilibrium the same principle holds. The benefit in yield remains clear, but obviously the potential stable population size cannot be determined or compared.

By carrying out these analyses for a wider range of different fishing mortality rates one can search for the fishing mortality rate that would be expected to produce the maximum yield from the fishery. This is commonly termed F_{\max} (pronounced F max) and was a common fisheries target mortality rate in the past (Figure 2.12).

The yield drops off at very low levels of F (Figure 2.12) because very few fish are caught. This type of analysis suggests that an obvious refinement to fishing would be to use selective fishing gear that only catches the larger individuals

TABLe 2.3

Comparison of the Effects of Two Fishing Mortality Rates on a Hypothetical Fishery in Which Natural Mortality Is Ignored

Age	Mean Wt kg	Annual Mortality of 80% $F = 1.61$ $H = 0.8$			Annual Mortality of 50% $F = 0.69$ $H = 0.5$		
		Stock Size #	Catch #	Catch Wt kg	Stock Size #	Catch #	Catch Wt kg
1	—	1,000.0	—	—	1,000.0	—	—
2	0.082	200.0	800.0	65.6	500.0	500.0	41.0
3	0.175	40.0	160.0	28.0	250.0	250.0	43.8
4	0.283	8.0	32.0	9.1	125.0	125.0	35.4
5	0.400	1.6	6.4	2.6	62.5	62.5	25.0
6	0.523	0.3	1.3	0.7	31.3	31.3	16.3
7	0.700	0.1	0.3	0.2	15.6	15.6	10.9
8	0.850	0	0.1	0	7.8	7.8	6.6
9	0.925	0	0	0	3.9	3.9	3.6
10	0.990	0	0	0	2.0	2.0	1.9
11	1.000	0	0	0	1.0	1.0	1.0
Yield	—	1,250.0	1,000.0	106.1	1,999.0	999.0	185.6

Note: The total number of fish caught in each case is effectively the same, but the total yield is much greater with the lower fishing mortality, more stock numbers remain, and presumably that stock has a greater resilience. # refers to numbers of fish. (Data from Russell, 1942.)

Each cohort assumes one thousand recruits each year, with mortality held constant so the system is in equilibrium. The population with the lower fishing mortality ends with a higher standing stock and the greatest yield. As an exercise, construct an Excel worksheet to duplicate this table (see Example Box 2.5).

in which the gains through individual growth would be maximal. The tabular approach is too simple (Table 2.3), however, because it ignores natural mortality and differing vulnerability to fishing gear of different sized/aged animals. If these factors are included, the problem would then be one of estimating the optimal size (or equivalent age class) at first capture for a given F .

One aspect of standard yield-per-recruit analysis that must be emphasized is that this analysis only takes into account growth and mortality; generally recruitment variation is not included. Because recruitment is not modelled explicitly but is assumed to be constant (hence yield-per-recruit), the standard yield-per-recruit analysis does not attend to the issue of whether the fishing rate predicted to produce the maximum yield is likely to be sustainable.

2.8.2 What is the Optimum Age or Size at First Capture?

If fishing gear can be made to be age (meaning average size) selective, this opens the possibility of attempting to catch some cohorts while avoiding others

EXAMPLE BOX 2.5

Simplified yield-per-recruit. This Excel sheet calculates the yield from two different schedules of natural (annual M) and fishing (annual H) mortality: (C1:C2) and (F1:F2). The annual harvest rate (in C3 and F3 for the two populations) is used to calculate the animals captured (in columns D and G). The total mortality in C3 and F3 determines the survivorship =C6-(C6*C\$3) in C7 and copied down; with =F6-(F6*F\$3) in F7 and copied down). By summing the respective columns (using =sum(C6:C16) in C17, etc.), the standing stock (N total) and yield (catch Kg total) from each fishery can be determined. By saving as values (edit/paste special/values) in columns to the right, along with their respective mortality rates, build up the information required to duplicate Figure 2.12. By setting the natural mortality to zero, the contents of Table 2.3 can be duplicated. The age at first capture (tc) is used later in Example Box 2.6.

	A	B	C	D	E	F	G	H
1	Annual H		0.8			0.5		
2	Annual M		0.1			0.1		
3	Total A	=C1+C2			=F1+F2			
4	tc	1				1		
5	Weight Kg	Age	N	Catch N	Catch Kg	N	Catch N	Catch Kg
6	0.042	0	1000.0			1000.0		
7	0.082	1	100.0	=C6*C\$1	=A7*D7	400.0	=F6*F\$1	=A7*G7
8	0.175	2	10.0	=C7*C\$1	=A8*D8	160.0	200.0	35.0
9	0.283	3	1.0	8.0	2.3	64.0	80.0	22.6
10	0.400	4	0.1	0.8	0.3	25.6	32.0	12.8
11	0.523	5	0.01	0.08	0	10.2	12.8	6.7
12	0.700	6	0	0.01	0	4.1	5.1	3.6
13	0.850	7	0	0	0	1.6	2.0	1.7
14	0.925	8	0	0	0	0.7	0.8	0.8
15	0.990	9	0	0	0	0.3	0.3	0.3
16	1.000	10	0	0	0	0.1	0.1	0.1
17	Totals		1111.1	888.9	82.2	1666.6	833.2	124.7

(i.e., treating the cohorts differently). If individual growth is an important component of productivity, then we would wish to catch cohorts selectively and would also want to include the effects of natural mortality in the analysis.

In Australia, a fine example of the value of fishing for the right-sized animals is seen in the banana prawns (*Penaeus merguiensis*) of the northern prawn fishery (Pownall, 1994). This species is found in large breeding aggregations (fishers refer to these as boils); they are relatively short-lived and start

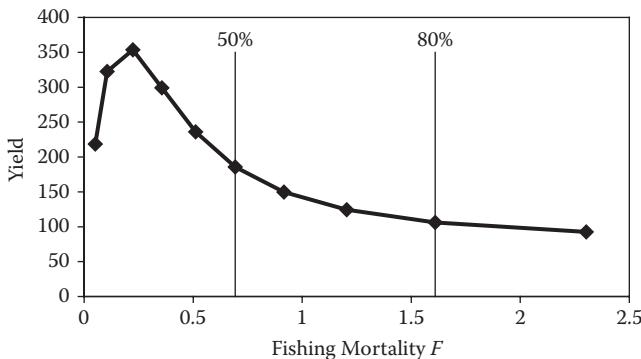


Figure 2.12

The equilibrium yield-per-recruit obtained from Russell's (1942) example with different annual harvest rates (5, 10, 20, and 30%, up to 90%). Given zero natural mortality and assuming fish are all equally vulnerable to fishing from age class 1, then the optimal fishing mortality, the F_{\max} in terms of maximum yield, is $F = 0.223$, or 20% annual harvest rate (Table 2.3 and Example Box 2.5).

life as very small animals. The best prices for prawns are obtained for the larger individuals, so it would be bad economics to begin the harvest of the banana prawns too early.

The fishing season is very short, with catch rates becoming unprofitable after only a few weeks (nowadays often just three to four weeks). Year-to-year variations in catch are considered to be the result of variation in recruitment and not in fishing effort, so the assumption has been made that despite the high fishing mortality there will always be sufficient prawns to provide adequate recruitment in subsequent years. The opening date for the banana prawn season was set by an economic analysis and model of the fishery that was developed early on.

The northern prawn fishery is open from April until the end of November with a midseason closure in June and July. By opening the fishery in April new season banana prawns have had a chance to grow to a larger, more valuable size. Catchability of banana prawns is also higher in April as they congregate for spawning. Owing to these factors, effort is focused mainly on banana prawns following the opening of the fishery. (Dann and Pascoe, 1994, p.11)

The Australian management of banana prawns is based on a yield-per-recruit argument (optimum size of individual animal), and an effort has been made to ensure that the animals at least approach this size before they are fished. Where the management is risky is in the assumption that unrestrained fishing effort will not affect subsequent recruitment. Short-lived fast-growing species like tropical prawns can certainly be recruitment overfished (see next section; Garcia et al., 1989). However, in species with highly variable recruitment it is hard to detect recruitment failure until after it has happened.

2.8.3 From empirical Table to Mathematical Model

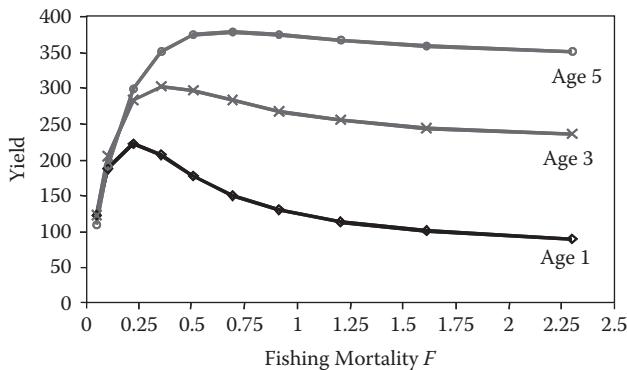
Given the objective of maximizing yield (total catch), analytical methods were developed in the 1950s for calculating the optimum age or size at which to first begin capture for a particular fishing mortality. However, standard yield-per-recruit analyses do not attend to whether such catches would be sustainable (i.e., they ignore absolute recruitment). If a species grew to a large size before it was mature and suffered a significant natural mortality, the equilibrium yield-per-recruit analysis could lead to recommending that heavy fishing be imposed upon immature individuals. The development of the alternative technique of egg-per-recruit analyses, which takes yield-per-recruit one step further, is an attempt to avoid the risk of recruitment overfishing.

The example of prawns given earlier is exceptional because the gains through individual growth so outweigh the possible losses through natural mortality (e.g., predation, disease) that the benefits of waiting for the animals to grow are obvious. Russell (1942) demonstrated the value of searching for the optimum fishing mortality (Table 2.3). The benefits of avoiding the capture of fish in younger age classes by using selective gear can be demonstrated in a similar manner. Using the same hypothetical model, we can arrange that no fishing mortality occurs until either the third or fifth year. If we also add a level of natural mortality to all years, so as to increase reality, we can derive a range of optimum yield curves (cf. Figure 2.12) each for a different age at first vulnerability to fishing (Figure 2.13).

2.8.4 The Model Structure and Assumptions

A yield-per-recruit analysis is carried out by constructing a model of the development of a cohort through time, taking into account the growth and mortality of individuals. For these simple calculations to be valid, a major assumption is made that the age structure of a fish population has attained equilibrium with respect to the mortality imposed upon it. This would imply that recruitment is constant and what happens to one cohort as it ages is representative of what happens to all cohorts, and so represents a cross section of the entire population at any one time (Pitcher and Hart, 1982).

The assumption of equilibrium is quite unrealistic because in many fisheries recruitment variation leads to the age structure of the population changing markedly with time. However, this assumption simplifies the model considerably and is useful for introducing the ideas involved. It is a major weakness of the method, however, and implies that any results should be assumed to be uncertain and potentially risky. This is one reason F_{\max} is no longer considered a safe management target. In our cohort model we assume that R individuals of age t_r are recruited (become vulnerable to possible capture) to the fishery each year. Hence, by definition, t_r is the minimum age at which fish could be targeted by the fishery. Note that there is a distinction between being vulnerable and being targeted. To add a little

**Figure 2.13**

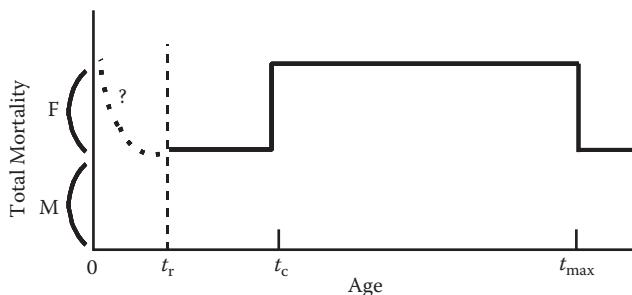
Yield-per-recruit from Russell's (1942) example with $M = 0.1054$ (annual = 10%) included. Calculations are repeated assuming fish are vulnerable to fishing from three different age classes onwards. The yield curves suggest that the optimal yield would be obtained with a fishing mortality of $F = 0.693$ or $H = 50\%$, with fish capture starting at age 5 (see Example Box 2.6). The global optimum is different again with $t_c = 8$ and $F = \infty$.

EXAMPLE BOX 2.6

To take account of the age of first capture, replace the contents of C7 in Example Box 2.5 with `=if(B7>=C$4,C6-(C6*C$3),C6-(C6*C$2))`. Copy this down to C16. This is now equivalent to Equation 2.19. In D7 put `=if(B7>=C$4,C6*C$1,0)` and copy down. Do the equivalent changes in columns F and G. Now, by changing the ages of first capture in C4 and F4 it should be possible to develop the information needed to duplicate Figure 2.13.

There are many ways to implement the same model. The mortality rates could be put in columns as *if* statements, turning on if the age were greater or equal to the age at first capture. One could use the formal Equations 2.20 to 2.23. As an exercise, put together an alternative worksheet that implements these formal equations.

more realism, we will also impose natural mortality to underlay the fishing mortality. To keep things simple to start with, we will assume that once fish are recruited (at age t_r), they are subject to a constant rate of instantaneous natural mortality, M . Fishing mortality effects are then added to the model, and this can be done in a number of ways. In our simplest of models we will arrange things so that we can set the age at first capture (t_c) to be greater than the age at recruitment. With this arrangement, because of targeting, fish are not vulnerable to harvesting before the age t_c , but thereafter they are subject to a constant rate of fishing mortality, F (again, measured as an instantaneous rate). To allow for those fisheries where older, larger fish are no longer

**Figure 2.14**

A diagram of the assumptions made in simple yield-per-recruit analysis. Here t_r is the age at recruitment, t_c is the age at first possible capture, and t_{\max} is the age at which fish cease to be vulnerable to fishing. The model does not consider the dynamics of individuals younger than t_r years of age but simply assumes that there are R recruits of this age entering the stock each breeding period. M and F are the constant instantaneous rates of natural and fishing mortality, respectively. Knife-edge selection is shown by the vertical rise in mortality at t_c .

selected, the model structure is completed by assuming that fish older than t_{\max} years of age are no longer vulnerable to fishing so that only natural mortality remains. Note that the model assumes both knife-edge recruitment at age t_r and knife-edge selection at t_c ; i.e., either none or all fish in an age class are either recruited or not or are vulnerable to harvesting or not, and once vulnerable, all age classes are equally vulnerable (Figure 2.14).

2.8.5 The Model equations

To generate yield-per-recruit information in a comparative manner for various ages at first capture (Figure 2.13) we need to translate Russell's (1942) example into our first version of an age-structured model. In the empirical depiction of the imposition of fishing mortality and growth (Table 2.3), all ages or cohorts experienced the same level of fishing mortality.

Obviously, as a year concludes, the members of one age class progress to become the members of the next age class. We require an equation with which we can follow the progression of a particular cohort of individuals as they proceed through the possible age classes. The cohort begins at age t_r with a particular level of recruitment R and then, through time, the numbers will decline as natural and fishing mortality have their respective impacts. A representation of the numbers N at t_r , N_0 is $N_{t_r} = N_0 = R$.

We need to find a way to model natural mortality acting throughout the life of the animals in a cohort, while fishing mortality only acts between ages t_c and t_{\max} . As per the equation for exponential decline (Equation 2.14), the numbers at any age $t + 1$ will be

$$N_{t+1} = N_t e^{-(M+F)} \quad (2.18)$$

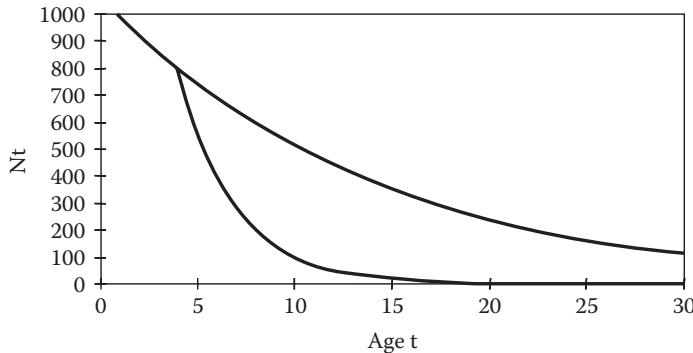


Figure 2.15

The age structure of a cohort starting with an R of 1,000 at age 1 ($t_r = 1$), an age of first capture ($t_c = 5$), no t_{\max} , an M of 0.075, and an F of 0.25. The upper line is what would happen if fishing mortality was zero for all ages. This exhibits a standard exponential decline of numbers through time. The lower curve is identical to the upper until age 5, when fishing mortality is added, whereupon the numbers drop far more precipitously. Without F there is still 0.1% of the initial cohort left by the age of 60, while with an F of 0.25 the same population level is reached by the age of 17. Fishing can obviously affect the age structure of a stock.

This is simply an exponential decline where the growth rate is negative and equal to M plus F (the exponential term represents survivorship and is equivalent to $1 - H$). Note there are two sets of subscripts, those for time or age (t) and those for ages vulnerable to selective fishing (i). The value of F is only greater than zero for ages where $i \geq t_c$, the age of first capture t_c , and $\leq t_{\max}$. The exponential decline brought about by natural mortality is made more severe by the onset of fishing mortality (Figure 2.15).

If this model is run, and the population is assumed to be in age-structured equilibrium, the curves in Figure 2.15 also represent the age structure of the population. Clearly, fishing mortality can have a major impact on the age structure, effectively removing all older animals. This occurs even without size selectivity because it is an expression of the repeated application of a constant mortality rate. The older a fish is, the greater the number of years the cohort will have been exposed to mortality.

This analysis only describes how the population changes in terms of numbers, whereas we need to know how much yield would be obtained under different regimes of age at first capture and different levels of F . The number dying at any time N_Z is simply the difference between the numbers at time $t + 1$ and time t :

$$N_Z = N_t - N_{t+1} \quad (2.19)$$

Remember that N_{t+1} will always be less than N_t . By substituting Equation 2.18 into Equation 2.19, replacing the N_{t+1} , we obtain

$$N_Z = N_t - N_t e^{-(M+F_i)} = N_t \left(1 - e^{-(M+F_i)}\right) \quad (2.20)$$

where the term in large brackets is the proportion that dies from all causes (cf. Equation 2.17). This is simply the complement of the survivorship ($e^{-(M+F)}$). Equation 2.20 determines the number of individuals of age t that die as the cohort proceeds to time $t + 1$. The numbers that die due to fishing mortality (i.e., the number caught, N_{ct}) is simply the fraction (F/Z) of the numbers that die, where Z is the total instantaneous mortality rate:

$$N_{ct} = \left(\frac{F_i}{F_i + M} \right) N_t \left(1 - e^{-(M+F_i)}\right) \quad (2.21)$$

This is now known as the Baranov catch equation, though the equation's properties were also examined by others (Beverton and Holt, 1957). Remember that F_i is the instantaneous fishing mortality at age i , which is zero before age t_c and constant afterwards. The total numbers caught under any particular regime of age at first capture and constant fishing mortality are simply the sum of all the N_{ct} . To convert this to a yield, Y , the numbers caught at each age are multiplied by the average weight w_t for each age:

$$Y = \sum_{t=t_c}^{t_{\max}} w_t N_{ct} \quad (2.22)$$

Finally, the yield in Equation 2.22 is that expected for a recruitment of R or N_0 . To generate the strict yield-per-recruit calculations, we need to divide the estimated yield, Y , by the initial recruitment to scale the calculations to units of yield-per-recruit (Equation 2.23). A common alternative would be to carry out the calculations with an initial recruitment of one:

$$\frac{Y}{R} = \sum_{t=t_c}^{t_{\max}} w_t N_{ct} \quad (2.23)$$

Using Equation 2.23, the data required to generate Figure 2.13 can be produced. This can then be used to compare different harvesting strategies for different species, which perhaps have different levels of natural mortality operating (Figure 2.16).

As natural mortality becomes very large, an analysis of yield-per-recruit on a timescale of years becomes less useful because it simply predicts that fishing mortality should become extremely large for the youngest age class in the fishery (Figure 2.16). In such circumstances (e.g., with prawns), data would be required from shorter time intervals such as months, whereupon useful answers could again be determined.

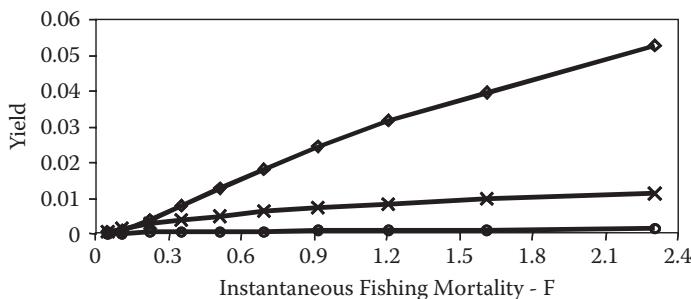


Figure 2.16

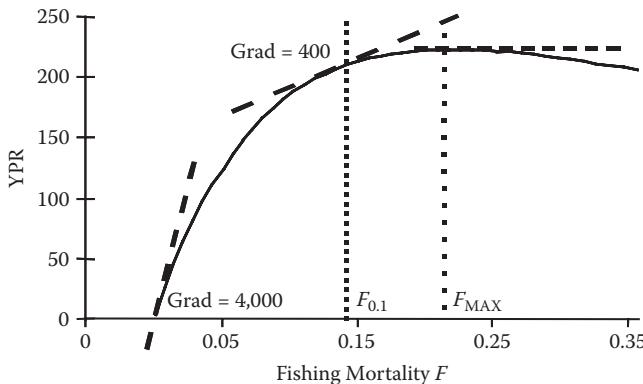
Annual natural mortality of 0.75 ($M = 1.386$) with a range of F fishing mortality rates measured over a year and three different ages at first capture. The order of the three age at first capture lines is reversed relative to Figure 2.13. Here the upper curve is the yield for a harvesting from year 1, the middle line is for year 3, and the lower line (almost coincident with the x axis) is for harvesting at year 5. The reversal of the lines arises because with high levels of M , most fish die before growing to a large size, so it is optimal for yield to catch them earlier. It may not be optimal in terms of allowing animals to reach maturity and breed, but that is a different objective for the fishery. Note the greatly reduced yield that has occurred because the weight at age data was not changed.

2.8.6 Yield-per-recruit Management Targets

The expected outcomes from a yield-per-recruit analysis are a target fishing mortality (the mortality rate to aim for) and a target age at first capture. Age at first capture would be used to set regulations regarding gear type (e.g., mesh sizes, hook sizes, escapement holes, minimum sizes) or season start date, while the target fishing mortality (related to the amount of fishing effort) could be used to set a constant fishing rate harvesting strategy (one of the options possible when managing a fish stock). This all assumes the overall objective is to maximize yield from the fishery.

Remember that yield-per-recruit (YPR) analyses by themselves do not attend to the sustainability of the predicted optimal F values. The actual target mortality chosen should reflect this fact. An obvious target fishing mortality to choose might be taken to be the fishing mortality, F_{\max} , which gives rise to the maximum yield (in Figure 2.13, this would be approximately $F_{\max} = 0.69$, starting on age class 5; in Figure 2.16, $F_{\max} = 2.4$ or greater, starting on age class 1). Empirical evidence indicates that, in part, because of uncertainties inherent in equilibrium YPR analyses, F_{\max} tends to be too high and leads to stock declines. Instead of F_{\max} , many fisheries around the world are now being managed using an $F_{0.1}$ (pronounced F zero point one) strategy (Hilborn and Walters, 1992). The value of $F_{0.1}$ is determined numerically by finding the fishing mortality rate at which the slope of the YPR curve is 10% of the slope at the origin (Figure 2.17).

Hilborn and Walters (1992) considered the introduction of the $F_{0.1}$ strategy to be remarkable:

**Figure 2.17**

The concepts of the reference fishing mortalities $F_{0.1}$, which is the mortality where the gradient of the yield-per-recruit (YPR) curve is 10% that at the origin, and F_{\max} , which is the mortality that predicts the highest YPR (gradient = zero). In this case $F_{0.1} = 0.139$ (12.98% per annum) with a yield of 213 units, while $F_{\max} = 0.196$ (17.8% per annum) with a yield of 222 units. Therefore, for a 33% decrease in annual mortality there is a loss of only 4% from the yield.

$F_{0.1}$ policies may be one of the most significant changes in fisheries harvesting practice since the earlier widespread acceptance of MSY. They are significant not because of any theoretical breakthrough, or any intrinsic elegance, but simply because they provide a replacement for F_{\max} and MSY and appear to often be robust. (Hilborn and Walters, 1992, p. 461)

Note that the $F_{0.1}$ strategy is *ad hoc* and has no theoretical justification except that empirically it appears more conservative or risk averse to departures from the assumptions of yield-per-recruit analyses. For a small loss in yield, one often gains a great deal in stock resilience to years of poor recruitment and other sources of uncertainty. It is possible that even the $F_{0.1}$ strategy is insufficiently conservative, and this can only be determined by further experience with more fisheries. By being less than the F_{\max} strategy, however, it is possible that the resulting strategy would be somewhat less economically optimum, although this would depend upon the relationship between effort and fishing mortality. It should also be noted that F_{\max} is not necessarily the same fishing mortality as would give rise to the MSY (F_{MSY}); they are different fishing target reference points.

2.8.7 Management Targets and Limits

As stock assessments have improved, the objectives of fishery management have also become more sophisticated (Haddon, 2007). The classical MSY target is now seen to be a risk-prone strategy. Instead, it is becoming more common to adopt both target reference points (TRPs), which define a desirable state for a fishery and fish stock, and limit reference points (LRPs), which define a state

below which the stock should not go (Smith, 1997). Meaningful management action is required if ever a LRP is approached by the stock. Both TRPs and LRPs refer to fishery or stock performance measures that can relate to a range of things, including (ideally) spawning stock biomass, or fishing mortality rates, or any measure that characterizes the state of the stocks. These reference points should be linked with preagreed decision rules that govern management action. Thus, if a LRP is passed, then some remedial action should be defined that will drive the stock back toward the TRP.

By definition, overfishing is said to occur when a stock is being fished at a higher rate than the prescribed limit fishing mortality for the given fishery. Similarly, a stock is said to be overfished if its biomass is below the prescribed limit reference point. If a stock is large but is being fished too hard, it is possible for overfishing to occur while a stock is not yet overfished. Similarly, a depleted stock may be rebuilding and only being fished lightly, and so be overfished without overfishing occurring.

2.8.8 Uncertainties in Yield-per-recruit Analyses

Unfortunately, there are a number of limitations to the yield-per-recruit analyses that go toward adding appreciable uncertainty to the estimates of optimum age/size at first capture and optimum fishing mortality (estimates of all parameters can only be made with limited statistical precision). Using $F_{0.1}$ instead of F_{\max} is an attempt to mitigate for these uncertainties.

Yield-per-recruit (YPR) analyses assume that the fishery concerned has reached an equilibrium with the given fishing mortality. This is a very severe limitation for some, especially intrinsically unstable, fisheries (especially those with high recruitment variability). It also assumes that natural mortality and the growth characteristics of the population are constant with stock size. There is also the problem that management measures that can be taken to implement the recommended age limits can only be implemented using size-selective gear. Age classes are rarely uniform in size, so the outcome will never be as optimistic as that predicted. With annual species, YPR recommendations can be enforced through using closed seasons.

Finally, setting or estimating F is a very difficult process requiring an accurate estimate of the population size and good records of total commercial catch. One always ends with an estimate of F ; there is no real way of eliminating the inherent uncertainty in any fisheries assessment parameter. One method of trying to avoid recruitment overfishing is to conduct egg-per-recruit analyses as well as the more traditional yield-per-recruit.

2.8.9 Types of Overfishing

While implementation of the predictions of the yield-per-recruit approach may be difficult, if the primary objective of management is to maximize yield of biomass from a fishery, then this sort of analysis is fundamental. If one is

dealing with a fishery in which most fish are being caught before they reach their optimum for yield, then growth overfishing is said to occur. If a stock is being fished so hard there are appreciable impacts upon subsequent recruitment, then there is said to be recruitment overfishing.

There are sometimes good (or at least economic) reasons for catching a species at less than its optimum size/age for yield—perhaps, if the optimal price is obtained for individuals smaller than that optimum for yield. In such cases it might be better to perform a dollar-per-recruit analysis, although with the volatility of fish prices this would probably not be practical. On the other hand, fishing a stock so hard that recruitment overfishing is the result can lead to a vicious cycle of stock reduction until it collapses (i.e., recruitment overfishing is risk prone and not risk averse).

3

Model Parameter Estimation

3.1 Models and Data

3.1.1 Fitting Data to a Model

A mathematical model of a biological population is always a simulation of nature. When a model is descriptive or explanatory of a situation in nature, it is necessary to estimate values for at least some of its parameters by optimizing the fit between the expectations from the model and data observed from nature. Parameter estimation is fundamental to the science of modelling populations, and this chapter focuses on the different ways that data can be fitted to a model.

The design of a model, such that it adequately represents the structure of the modelled system, primarily relates to determining which variables are to be included (i.e., whether the model will include age structure, relate to numbers or biomass, etc.) and the relationships between them (linear, nonlinear, etc.). Model specification is clearly a vital step in modelling any system, and one tends to proceed by development from a simple model to a more complex representation. Development of model complexity tends to stop due to a lack of data rather than a desire to keep a model simple.

Once the model has been designed, if it is not just a simulation model, then it remains to be fitted, or have its parameters “tuned” to the observable world, using whatever data are available from the system. Fitting a model to data implies estimating values for the model’s parameters to optimize the agreement between the model’s predictions and the data to be fitted from nature.

When fitting a model to observed data, three things are required:

1. A formal mathematical model of the system, which is capable of generating predictions about the observable world
2. Data from the system to be used when estimating the parameter values
3. A criterion (sometimes called a merit or objective function) to judge the quality of fit between the model’s predictions and the observed data

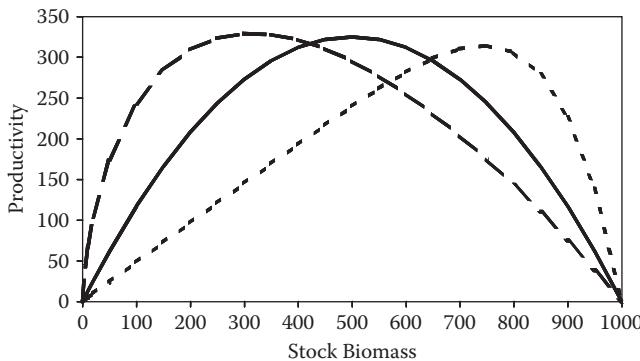
An example could be a fishery stock assessment model that predicts changes in catch rates and age structure through time. Fitting the mathematical model to nature entails varying trial values of the model parameters until an optimum agreement is found, according to the criterion selected, between the model predictions of how catch rates and catch-at-age will change through time and the observed time series of real information. However, as described in Chapter 1, there is more to the process of modelling than the three formal requirements listed earlier. If this were not the case, then one would invariably finish with a multiparameter empirical model providing the best statistical fit, but not being interpretable in a realistic way. If an explanatory model is wanted, then we need a rather obvious but non-quantifiable extension to the third requirement of the quality of fit criterion. As well as optimizing some best fit criterion, the optimum model should also give rise to biologically sensible predictions. It can happen that a model fit that generates an optimal mathematical solution still predicts biological nonsense (e.g., predictions of an enormous initial population size and almost no productivity, with the history of fishing being one of the gradual erosion of the accumulated biomass). Not all such deviations from biological reality are so obvious, so we need to guard against a lack of realism in the outcomes of fitting a model. In short, we generally want our models to be simple but realistic. It comes down to how one selects which model to use and what is meant by quality of fit.

3.1.2 Which Comes First, the Data or the Model?

We should always be asking the question: Given a particular model, with particular parameter values, how well does it predict (how likely are) the observed data?

The process of model fitting has two parts. First, a set of one or more models is selected or designed, and second, values for the model's parameters are found that optimize the quality of fit according to the formal criterion selected by the modeller. Except for at least some of the variables used, model selection is independent of the data (the variables we observed, against which the model is to be compared, must obviously be included in the model). Thus, we always determine how well the selected model(s) can emulate the available data. Once a particular model has been selected, the optimum parameter values for that model are determined by the fixed set of observed data. In fact, what tends to happen is that one starts with a relatively simple representation of whatever is being modelled, and that is fitted to available data, extending and articulating the model in steps.

The process of positing a model plus parameter values and comparing its implications against nature reflects the hypothetico-deductive approach to scientific practice (Popper, 1963; Lakatos, 1970). However, remember, from Chapter 1, that fitting a model to data only tests how successfully it can describe the data, not how well it explains the data.

**Figure 3.1**

Three different biomass production curves (cf. Chapter 2). The equation used was productivity $= (r/p)*B(1 - (B/K)^p)$, where r is a growth rate, K is the equilibrium biomass, B is the stock biomass, and p is the coefficient of asymmetry. When $p = 1$ (solid line), the equation simplifies to the standard logistic Schaeffer production curve, symmetric about $K/2$. When p is less than 1, the production curve has a mode lower than $K/2$ ($p = -0.25$, dashed line), and when p is greater than 1, the mode is to the right of $K/2$ ($p = 7$, dotted line). Whenever $p < 1$ or > 1 , the curve is asymmetric and needs to be rescaled to have an absolute maximum productivity similar to that of the Schaeffer curve.

3.1.3 Quality of Fit versus Parsimony versus Reality

With a set of structurally different models, there are criteria other than just quality of numerical fit that should be used to determine the preferred model. For example, consider the difference between two models of stock production; the first assumes a symmetric production curve against stock size (linear density dependence) while the second has no such restriction (Figure 3.1). The asymmetric production curve is an improvement over the symmetric in terms of both biological reality and mathematical generality (because it is less restricted in its biological interpretation and because it contains the symmetric model as a special case when $p = 1$).

Using the asymmetric model enhances the potential for realism and probably the quality of fit, but there has also been an increase in model complexity. If the quality of fit between two models were equivalent (i.e., $p \sim 1.0$), one would tend to use the most realistic or the simplest. The general question to be answered is: Do the benefits derived from adding extra parameters to a model outweigh the losses and thereby justify their addition? There is no simple answer to this question because the realism of a model is not quantifiable.

Adding parameters to a realistic model may convert it into a multiparameter empirical model (cf. Figure 1.6). Extra parameters are likely to improve the quality of fit of most models because they permit greater flexibility in the model outcomes. In the extreme, one could have the same number of parameters as one had data points and could obtain a perfect fit of the model to the data. Such a model would be both *ad hoc* and useless, but it would certainly

fit the data points well. Clearly, the quality of fit between a model and data is not everything.

Selecting an optimum explanatory model requires a trade-off between improving the quality of fit between the model and the data, keeping the model as simple as possible, and having the model reflect reality as closely as possible. Increasing the number of parameters will generally improve the quality of fit but will increase the complexity and may decrease the reality. The latter quality is the hardest to assess.

Ignoring the problem of whether a model is realistic, quantitative measures have been developed that assess the balance between the relative quality of fit (the variation in the data accounted for) and the number of parameters fitted. Following our intuitions, these measures suggest that parameter addition be rejected if the improvement in quality of fit is only minor. Such measures include likelihood ratio tests and Akaike's information criterion (AIC; see Burnham and Anderson, 1998); these will be introduced after we have considered maximum likelihood methods.

A further problem with selecting an optimum fit relates to data quality. If the available data are limited in quantity or quality (sadly this is common when modelling fisheries), the number of parameters that can be estimated adequately is also limited. The data might be said to be uninformative about those extra parameters. Adding extra parameters to a model that can already be fitted to data reasonably well may make the fitting procedure unstable. A more complex model that provides a significantly better fit may be possible, but the solution may be less precise or more biased. Punt (1990) appeared to have this problem with data on Cape hake (Haddon, 1998).

3.1.4 Uncertainty

Irrespective of how closely one can fit a model to a set of data, there is no logical or automatic implication that the model chosen is necessarily the best representation of the system being modelled. In addition, there is no guarantee that the model will accurately predict how the system will behave in the future, or even that the parameter estimates are the optimum values for the system. Very often, it is possible to obtain essentially equally good fits to one's data with sometimes widely different sets of parameters (roughly, the more parameters being estimated, the more likely this is to occur). This is especially the case when there are strong correlations between parameters. The correlations act to offset the effects of changing one parameter, as altering the values of others means that different sets of parameter values describe the available data almost equally well. The different sets may even produce similar predictions. Model selection is especially difficult under such circumstances. When the results of a model fitting exercise are this uncertain, it suggests that the data are insufficiently informative to distinguish between the alternative possibilities. Uncertainty is an unpleasant

commonplace in stock assessment, and how best to approach it is a vital part of fisheries modelling (Francis, 1992; Punt and Hilborn, 1997; see Chapter 8).

It is undoubtedly valuable knowing how to estimate model parameters, but the value of this is greatly increased if we also have some way of determining the confidence with which we can use the estimated parameter values and other model outputs. We need to be able to characterize the uncertainty inherent in our analyses. The uncertainty in any analysis stems both from the data, which will contain random variation from observation errors and variation due to random factors, and from model uncertainty, where the model fails to capture the processes and stochasticity in nature. How to characterize this uncertainty will be addressed in Chapter 8.

3.1.5 Alternative Criteria of goodness of Fit

Three criteria of model fit are commonly used today. Most biologists new to modelling will only be familiar with the least squared residual error approach. We will consider methodologies that use least squares, maximum likelihood, and Bayesian statistics as their criterion of model fit. The choice of the criterion of fit remains a controversial field (Dennis, 1996; and associated papers). Some researchers stoutly defend a maximum likelihood approach, but others imply that if an assessment is not conducted using a Bayesian approach, it must be next to useless. It is hoped that this chapter will illustrate that much of this controversy is misplaced, and that the choice of criterion of fit should depend upon the objectives of the modelling process. The assessment strategy to use should be whichever is most convenient and can do the job required without distorting the results.

3.2 Least Squared Residuals

3.2.1 introduction

The most commonly used criterion of fit is still the one known as *least squares*. It is so called because it involves a search for parameter values that minimize the sum of the squared differences between the observed data (e.g., time series of catch rates or catch-at-age) and the predictions from the combination of model and particular parameter values. Typical fisheries data would never exactly fit a proposed model, even if that model were correct. The differences between the models' predictions and data observations are known as residual errors (sometimes called noise on the signal). A statement made about a model's error structure is making a claim about the expected statistical distribution of the residual error around each of the predicted observations. It is important to understand that when using the least squared

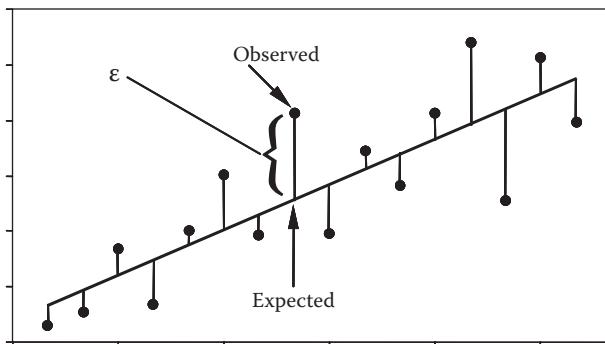


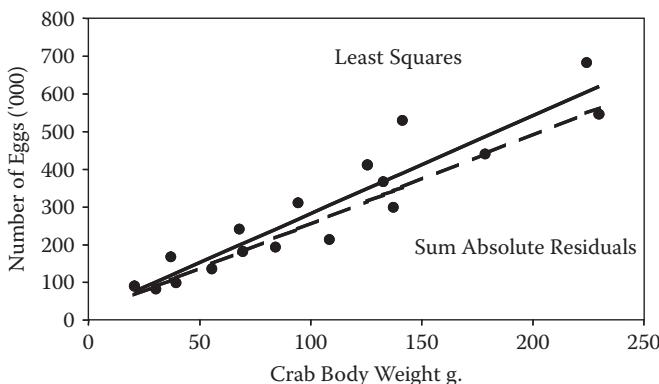
Figure 3.2

View of the residual errors for a linear relation between two variables. The error terms represented are those for the regression of Y on X , where the observed and expected values are on the Y axis ($Y = a + bX + \epsilon$) for given values of the X variable. The residuals for a regression of X on Y would be horizontal. The residual errors (the ϵ s) are the differences between the expected values of the Y variable, given by the regression line, and the observed values. Clearly, for a well-fitted line they will be both positive and negative in value.

residual criterion of model fit, the residual errors are always assumed to be normally distributed. The term $N(\mu, \sigma^2)$ is the standard nomenclature for such normal, random residual errors, and should be read as implying a normal distribution with a mean of μ and a variance of σ^2 . In general terms, observed value = predicted value + ϵ , or observed – predicted = ϵ , where ϵ (epsilon) is the residual or random error. Strictly, the phrase used should always be “residual error,” but it is very common to use just one or the other term (*residual* or *error*) interchangeably. Note that the residual error term is added and not multiplied to the predicted (fitted or expected) value (Figure 3.2). It is common to use the two terms (*residual* and *error*) to describe one concept and three terms (*predicted*, *fitted*, and *expected*) to describe another single concept. By pointing out the equivalence within these sets of terms, it is hoped that possible confusion might be avoided.

Normal residuals can be either positive or negative (Figure 3.2). Thus, it would not suit our purpose just to search for parameter values that would minimize the sum of the residuals, as the negative values would cancel some of the positive in an *ad hoc* manner. However, it would be a real option to minimize the sum of the absolute values of the residuals, although this is not particularly convenient mathematically (Birkes and Dodge, 1993; see Example Box 3.1).

Squaring each residual error removes the problem of negative residuals and is mathematically very convenient. With absolute residuals each value would have equal weight, whereas squaring each residual gives extra weight to larger residuals and less weight to residuals less than one. For this reason, absolute residuals are sometimes used to implement model fitting methods that are robust to outliers (Sokal and Rohlf, 1995). Such differences in

**Figure 3.3**

Number of eggs vs. body mass for the New Zealand swimming crab *Ovalipes catharus*. (Data from Haddon, 1994.) The upper line is the best fitting least squares linear regression ($\text{eggs} = 25.51 + 2.599 \times \text{Wt}$), while the lower dashed line is the best fitting least sum of absolute residuals ($\text{eggs} = 17.08 + 2.37 \times \text{Wt}$). The lines differ because the error structures used to fit the lines are different and the lines cannot be directly compared statistically. Both are optimal fits according to their respective criteria (see Example Box 3.1). Most people tend to prefer the line that keeps the data around it in a symmetrical fashion.

emphasis are why one obtains a different “optimal” fit, depending on which criterion is used (Figure 3.3, Example Box 3.1).

The objective when using the least squares criterion is to minimize the sum of the residual errors squared. From this we gain:

$$SSQ = \sum (Observed - Expected)^2 \quad (3.1)$$

where SSQ is the sum of the squared residuals, e.g., for a linear regression, $SSQ = \sum [Y - (a + bX)]^2$. It should be remembered that there is an analytical solution for the simple least squares linear regression, which can be found in any statistical text (e.g., Snedecor and Cochran, 1989; Sokal and Rohlf, 1995). It is invariably more efficient to use an analytical solution to a problem, and one should do so wherever it is possible.

A major assumption of least squares methodology is that the residual error terms exhibit a normal distribution about the predicted variable with equal variance for all values of the observed variable; that is, the σ^2 in the $N(0, \sigma^2)$ is a constant. If data are transformed in any way, the transformation effects on the residuals may violate this assumption. Conversely, a transformation may standardize the residual variances if they vary in a systematic way. As always, a consideration or visualization of the form of the residuals is good practice.

The sum of absolute residuals (SAR) is intuitively attractive in that it gives all data points equal weight. However, at least in the linear model, it is a fact

EXAMPLE BOX 3.1

Fitting a straight line using the sum of absolute residuals (SAR) and the sum of squared residuals (SSQ). Size relates to drained body weight in grams and eggs is the fecundity in thousands for the crab *Ovalipes catharus* (data selected from Haddon, 1994). PredSSQ and PredSAR are the predicted values of eggs using the parameters defined for the two different criteria of fit, respectively. Totals represents the respective sums of both types of residual errors. The intercepts and gradients are clearly different (Figure 3.3). The solutions are found in each case using the solver, minimizing E3 and F3 in turn. The solution for the SAR criterion is highly unstable; try different starting points and compare the apparently optimal solution found. Compare this with the relative stability of the least squares criterion. The SSQ solution must pass through the mean of each variable. The SAR solution must pass through two of the points. Plot columns A to D as in Figure 3.3. Which line fit looks best to your eyes? Body size and fecundity for rows 11 to 21 are (69.46, 181.713), (84.12, 193.161), (94.31, 310.425), (108.47, 213.247), (125.54, 411.056), (132.7, 366.567), (137.31, 298.439), (141.34, 529.351), (178.60, 440.394), (224.31, 683.008), and (229.89, 545.681).

	A	B	C	D	E	F
2	Intercept		21.50974	17.07990	Totals	
3	Gradient		2.59998	2.37019	62764.18	=sum(F5:F21)
4	Size	Eggs	PredSSQ	PredSAR	SSQ	SAR
5	20.71	89.35	=C\$2+A5*C\$3	=D\$2+A5*D\$3	=(B5-C5)^2	=abs(B5-D5)
6	30.35	82.399	=C\$2+A6*C\$3	=D\$2+A6*D\$3	=(B6-C6)^2	=abs(B6-D6)
7	37.04	166.97	=C\$2+A7*C\$3	=D\$2+A7*D\$3	=(B7-C7)^2	=abs(B7-D7)
8	39.50	98.324	Copy	down	to	Row 21
9	55.60	135.427		166.07	148.86	938.92
10	67.90	240.713		198.05	178.02	1820.25
						62.70

that the best fitting line must always pass literally through two of the points (Birkes and Dodge, 1993; also see Figure 3.3). This has the disadvantage of sometimes forcing the residuals to be asymmetric.

It should be noted that the standard least squares linear regression is a regression of Y on X. This means that the X values are assumed to be measurable with no errors and to be independent of the Y values, while the Y values are assumed to be dependent upon the given X values. In the fitting process, this implies the residuals would be vertical (Figure 3.2). Of course, in most biological processes it would not be possible to measure the so-called independent variable without error. In an ideal world, it would perhaps be best to have residual errors that were perpendicular to the expected line

(i.e., neither Y on X or X on Y), as in functional regression or principal components analysis. Ricker (1973) and McArdle (1990) discuss this problem at length. Generally, the bias that using Y on X might introduce is likely to be small, although it would become greater as the variability about the predicted curve becomes greater.

3.2.2 Selection of residual error Structure

A common alternative criterion of quality of fit is *maximum likelihood*. Parameters are selected that maximize the probability density or likelihood that the observed values (the data) would have occurred given the particular model and the set of parameters selected.

One great advantage of the maximum likelihood approach is that it forces one to be explicit about the statistical form of the expected residual errors, that is, whether they are normal and additive, as with the regression examples we have seen ($Y = a + bX + \epsilon$), or lognormal and multiplicative (as in $Y = aX^b e^\epsilon$), or follow some other distribution (more on this later). Whichever error structure is selected, with least squares it is necessary to devise a linearizing transformation to convert the selected error structure into normally distributed residuals. Thus, with lognormal errors, a log transformation will permit linear, least square methods (e.g., $y = ax^b e^\epsilon$ becomes $\ln(y) = \ln(a) + b\ln(x) + \epsilon$). If no normalizing transformation is possible, or if it fails to linearize the modelled relation, then it becomes necessary to use nonlinear methods to fit the models to data. In such cases, if one still used normal residuals, this would greatly influence the optimum fit. If the residuals required are not normal and there is no normalizing transformation, then the least squares approach is not an option, but one could use maximum likelihood methods. Generally, it must be remembered that with least squares, the selection of the residual error structure is implicit, and at worst, it is *ad hoc*.

We will consider maximum likelihood methods in detail after we have introduced nonlinear parameter estimation methods and expanded on the method of least squares.

3.3 Nonlinear Estimation

3.3.1 Parameter estimation Techniques

Our examples have so far been limited to the estimation of parameters for simple linear models. Using least squares, it would be simpler to use the analytical solution for linear regression rather than invoking the solver facility built into Excel. Of course, most fisheries models are far more

complex, involving many more parameters and nonlinear relationships between the variables. There are usually no simple analytical solutions or linearizing transformations available for these more difficult to fit models. Numerical methods are needed when fitting these multiparameter, nonlinear models to data. In order to understand the strengths and weaknesses of such numerical methods, it is necessary to have some understanding of the algorithms or strategies used in the more commonly available methods used for fitting complex models. When no analytical solution exists for fitting a model to data, we need to search for the optimum parameter values. We can define three types of search: graphical searches, directed searches, and heuristic searches. To understand nonlinear parameter estimation, we will first consider the graphical approach to searching for optimal parameter values.

3.3.2 Graphical Searches for Optimal Parameter Values

Consider the simple problem of fitting a curve to the relationship between carapace width and eggs carried per batch in the crab *Ovalipes catharus* (Figure 3.4; Haddon, 1994). The values exhibited by the data points suggest the exponential relationship

$$\text{Eggs} = a \cdot e^{b \cdot \text{CWidth}} e^{\epsilon} \quad (3.2)$$

where Eggs refers to fecundity, CWidth refers to the carapace width, and a and b are the parameters to be estimated. Because the residual errors in Equation 3.2 are lognormal, it can be linearized by natural logarithmic transformation:

$$\ln(\text{Eggs}) = \ln(a) + b \cdot \text{CWidth} + \epsilon \quad (3.3)$$

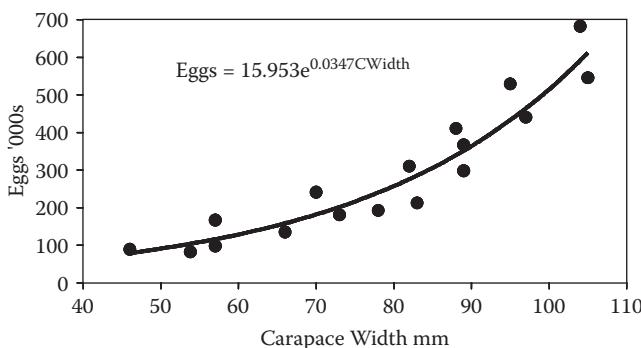


Figure 3.4

The exponential relationship between number of eggs in an egg mass and carapace width (CWidth) for the New Zealand crab *Ovalipes catharus*. (Data are a subset from Haddon, 1994.) The exponential relationship describes over 90% of the variation in the data. The solid line illustrates the given optimal solution (see Example Box 3.2).

EXAMPLE BOX 3.2

Fitting an exponential curve to eggs at carapace width data. Width is in mm and eggs is fecundity in thousands for *Ovalipes catharus* (cf. Figure 3.4; data are from Haddon, 1994). The Predicted column is the expected number of eggs. SSQ represents the sum of squared residuals (in C1). The solution is found using the solver, minimizing C1 by changing C2 and C3; an exact solution can be found using the array function Linest, but that would require a separate column of transformed egg numbers (try this; don't forget to use <Ctrl><Shift><Enter> to enter the array function). Note the log transformation of the predicted number of eggs in column D (see Equation 3.3). By plotting column B against A as separate points, and then exp(column C) against column A as a connected line, you should be able to mimic Figure 3.4. Use this sheet to investigate the relative precision of different solutions. The values in columns E and F represent different trial values of $\ln(a)$ and b with their respective sum of squared residuals. Paste the values of your trial values and SSQ into spare cells in columns E and F; i.e., copy B1:C3 to keep a record of your trials. Do different parameters that give a similar SSQ alter the graph visually? How precise should one try to be when using biological data of limited original accuracy? For rows 10 to 21 the data for width and fecundity are (70, 240.713), (73, 181.713), (78, 193.161), (82, 310.425), (83, 213.247), (88, 411.056), (89, 366.567), (89, 298.439), (95, 529.351), (97, 440.394), (104, 683.008), and (105, 545.681).

	A	B	C	D	E	F
1		SSQ	=sum(D5:D21)			
2		Ln(a)	2.7696		1) SSQ	0.630620
3		b	0.034734		1) Ln(a)	2.7696
4	Width	Eggs	Predicted	ResidSQ	1) b	0.034734
5	46	89.35	=C\$2+A5*C\$3	=(Ln(B5)-C5)^2		
6	53.8	82.399	=C\$2+A6*C\$3	=(Ln(B6)-C6)^2	2) SSQ	0.630620
7	57	166.97	=C\$2+A7*C\$3	=(Ln(B7)-C7)^2	2) Ln(a)	2.77
8	57	98.324	Copy down	To row 21	2) b	0.03473
9	66	135.427	5.062	0.024		

Equation 3.3 has the form of a linear regression, which can be solved analytically, leading to $\ln(a) = 2.7696$ and $b = 0.0347$. By back-transforming the $\ln(a)$, i.e., $\text{Exp}(2.7696)$, we obtain $a = 15.953$, which produces a satisfactory fitted line (Figure 3.4; see Example Box 3.2).

An alternative approach would be to carry out a grid search across plausible parameter values and plotting the resulting sum of squared residuals as a contour plot (Figure 3.5). This defines a valley or pit in the sum of squares

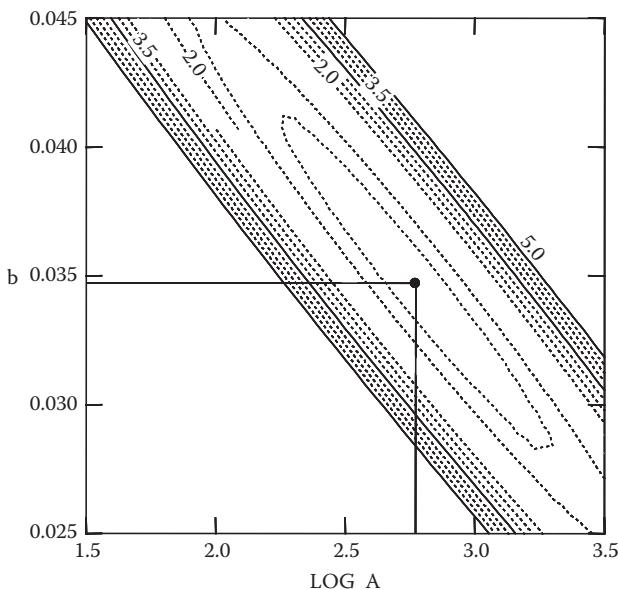


Figure 3.5

Graphical search for the optimal parameter values for Equation 3.5 given the data in Example Box 3.2. Different combinations of the two parameters produce different values of the sum of squared residuals. Plotting these as contours makes it possible to home in on the optimum values. The optimal solution is indicated (at 0.0347 and 2.769).

surface of possible values and the optimal parameter values relate to the bottom of the pit. Obviously, the graphical search grid must bracket the minimum sum of squares.

The contour plot makes it possible to constrain the parameter values being used in the search for the minimum least squares. This is a downhill search for the bottom or minimum of the surface. Each of the contours represents combinations of parameter values that give rise to the same value of sum of squared residuals, meaning they provide fits of equal quality.

Instead of a simple trial-and-error search for the minimum, it is possible to use this analogy of a downhill search and, using information gained from previous trials, conduct an informed trial-and-error search. The contour map indicates visually how to improve the parameter estimation. This entails moving the trial parameters to form combinations that are most likely to lead to a maximal reduction in the sum of squares (the bottom of the pit). This informed trial and error is continued until there is no detectible improvement to the sum of squares.

As we have seen from the contours in Figure 3.5, the same sum of squares can be obtained from different combinations of parameters. If we contemplate the sixth significant digit in the parameter estimates, then the optimum

fit would be graphed as a point on a very small contour circle. If there is no analytical solution and the model has to be fitted using some numerical method, then the optimal fit is a compromise between the time taken to find the solution and the accuracy of the fit. In Example Box 3.2, the impact of different trial values of the two parameters on the predicted values and graph (Figure 3.4) can be determined.

The graphical search is informative in a number of ways. The shape of the contour plot provides information about relationships between the parameters of the model. If the parameters were completely independent of one another (the ideal but rare case), then the contours would form either perfect circles or vertical ovals. If the contours were ovals, but at some angle, then parameter correlation is indicated (e.g., Figure 3.5).

3.3.3 Parameter Correlation and Confounding effects

The resolution of the contours shown in Figure 3.5 is sufficient to indicate approximately where the “best” fit solution would lie. The fact that the sum of squared residual values forms a diagonal trough (left to right) indicates that there is a negative correlation between the two parameters. This means we cannot readily distinguish between different combinations of the two parameters. What it implies is that if we were to force a particular value of a on the model, we could still recover a reasonable fit because the value of b could be altered accordingly to produce a similar curve. The plot provides us with a visual indication of the quality of fit and the confidence we can have that our best fit provides a good indication of the actual situation.

Very strong parameter correlation is a problem that occurs with many fisheries statistics. For example, the total mortality for a fish population is a combination of natural and fishing mortalities, and there is always difficulty in separating these different phenomena. Parameter correlations imply that the so-called independent variables (X axis variables) cannot be independently determined and, in fact, are often strongly correlated. When supposedly independent variables are correlated, it becomes impossible to determine which “independent” variable is most closely related to changes in the so-called dependent variable; their effects are said to be confounded.

Sadly, the graphical search strategy is of limited use for models with more than three parameters. In the example of the fecundity vs. carapace width there were only two parameters, and the sum of squared residuals can be visualized as a third axis described by the a and b parameters to form a third dimension to generate a surface. With a three-parameter model the criterion of fit values would be described as a four-dimensional volume or three surfaces. With n parameters the criterion of fit would be described by an $n + 1$ dimensional hypervolume. Even with a hypervolume the analogy of moving downhill or over the surface of the criterion of fit is still a useful intuition to hold in mind.

The basic idea and strategy of the downhill search lies behind many of the numerical methods for fitting nonlinear models to observed data, even with n parameters. With the least squares criterion, the mathematical problem is one of minimization of the sum of the squared residuals. To move beyond the graphical search, some other, more efficient numerical method is required. The graphical approach is essentially a grid search that could be pursued with more and more precision once the minimum values had been bracketed. Automatic minimization routines do something similar without the need for the grid or human intervention. There are numerous algorithms, but here we will only describe the directed and heuristic searches.

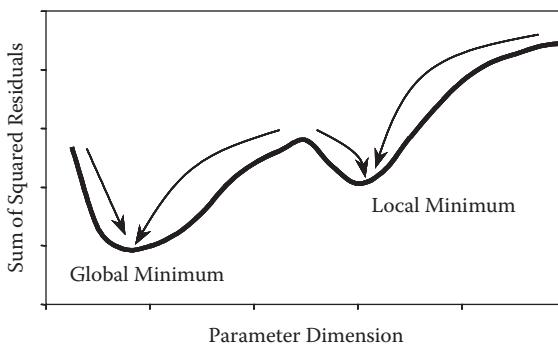
3.3.4 Automated Directed Searches

A common approach, known as the Levenberg-Marquardt algorithm, uses the downhill analogy directly (Press et al., 1989). It requires a single set of starting parameter values to begin the search. These guessed parameters specify a particular point on the sum of squared residuals (SSQ) surface (which has the same number of dimensions as there are parameters, and so may be a hypervolume).

Despite the number of dimensions, the analogy remains of a surface having a steepest path downwards to a minimum. By automatically making tiny increments to each of the parameter values in turn, the algorithm can estimate the gradient of the surface along each of the parameter dimensions (a form of numerical partial differentiation). The algorithm then alters the parameters in the direction that should lead to the steepest decline down the SSQ surface. Given this new point on the surface, the relative gradients are considered once again from the new viewpoint and the parameters incremented again in whichever direction will lead to the greatest decline in the SSQ. This is continued until a minimum is reached or further benefits are minimal (Press et al., 1989). The algorithm automatically directs the new trial values along a path that should maximize the decline in the criterion of fit.

An obvious problem with this search strategy is the possibility of local minima on the SSQ surface that could be confused for the global minima by a non-linear-fitting algorithm (Figure 3.6). An equally obvious test of the generality of any solution is to start the search with initial parameter guesses that widely bracket the final estimated values. They should all converge on the same answer if it is to be considered an adequate estimate. Another potential problem, which is becoming less important, is that a large model with many parameters may take a very long time to converge on a possible solution for all parameters (Schnute et al., 1998). More likely is that the non-linear solver will fail through instability of some form.

The solver in later versions of Excel is surprisingly robust and is useful for many smaller problems. For larger problems, it may be necessary to resort to custom computer programs or to use a meta-programming language

**Figure 3.6**

Schematic representation of a single-parameter dimension with a local minimum that could confuse an automatic minimization routine. Once in the vicinity of the local minimum, every change in the parameter value makes the SSQ value get larger, and many routines would understandably stop and claim to have found a minimum.

such as AD-Model Builder (Schnute et al., 1998; see www.admb-project.org; AD-Model Builder is now open source).

3.3.5 Automated Heuristic Searches

A robust alternative to the Levenberg-Marquardt algorithm is the Simplex algorithm. This is an $n + 1$ dimensional bracketing search method (Nelder and Mead, 1965) where there are n parameters to be estimated. This method requires $n + 1$ sets of initial trial values that attempt to bracket the optimal solution or at least define the direction in which to move the set of trial values over the surface of the criterion of fit. By comparing the relative fit of the $n + 1$ different sets of trial parameter values, the direction that should lead to maximum improvement in fit can be determined approximately. $n + 1$ sets of trial values are required so it becomes possible for the overall set to bracket the optimum combination. The $n + 1$ set of trial values move over/through the n -dimensional hypervolume, always in the approximate direction that should improve the value of the criterion of fit. Some speak of the $n + 1$ dimensional search object “crawling” over the fitting criterion surface toward the minimum. The analogy with an amoeba flowing through n -dimensional space has been used (Press et al., 1989). This continues until the only way the set of trial values can improve the fit is for the $n + 1$ parameter combinations to contract toward each other (i.e., they really bracket the optimum solution and contract toward it). The simplex algorithm is very robust but can be slow, depending on the complexity of the model and how close the starting values are to the optimum.

Whichever approach is used, one should get to know the limitations of any particular nonlinear solver that might be used, and always attempt to find the same solution from a number of different sets of initial parameter guesses.

3.4 Likelihood

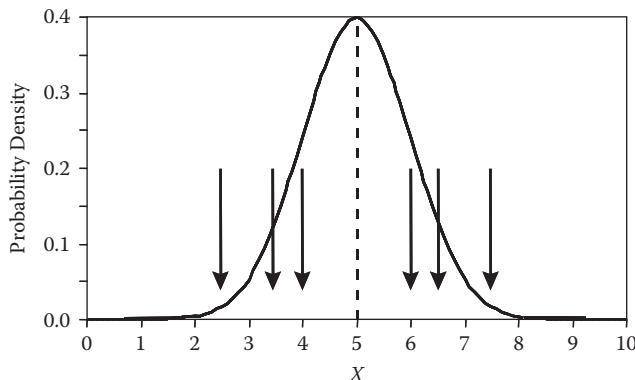
3.4.1 Maximum Likelihood Criterion of Fit

Maximum likelihood, used as the criterion of quality of fit, is usually characterized as the determination or search for the set of model parameters that maximize the probability that the observed values (the data) would have occurred given the particular model and the set of parameters selected (Press et al., 1989; Neter et al., 1996). Using maximum likelihood requires the model to be defined so that it specifies probabilities or likelihoods for each of the observations (the available data) as a function of the parameter values and other variables in the model. To obtain the likelihoods, one needs to define how the residual errors are distributed about the expected values derived from the model. To understand the idea of maximum likelihood parameter estimation we need first to formalize the idea of using probability distributions. Many different statistical probability distributions can be used to describe residual error structures. We will consider the normal, log-normal, binomial, Poisson, gamma, and multinomial distributions as well as some of their uses in fisheries modelling. There are many other distributions that could be used (Elliott, 1971; Hastings and Peacock, 1975).

3.4.2 The Normal Distribution

Most biological scientists would understand a claim that a set of observations is expected to exhibit a normal distribution about their expected value (the mean). What this implies is that the observed values of a variable X are expected to be distributed symmetrically about their mean, and that large deviations from the mean would occur less often than small deviations. The expected relative rates of occurrence of different-sized deviations from the mean are described by the probability density function (pdf) for the normal distribution (Equation 3.4, Figure 3.7). Relative frequency histograms count the occurrence of individuals in a population that are found in defined classes of the variable under study (e.g., body weight). A pdf for the normal distribution describes, in effect, the expected relative frequency (probability density) curve generated for a continuous variate instead of for discrete classes of the variate. The pdf for the normal curve has two parameters, the mean or expectation of the distribution (μ) and its standard deviation (σ). Once they are set for a variable X , substituting different values of the variable into the equation generates the well-known normal curve (Figure 3.7, Equation 3.4, Example Box 3.3).

$$\text{Probability Density} = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(X-\mu)^2}{2\sigma^2}\right)} = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(-\frac{1}{2}\left(\frac{X-\mu}{\sigma}\right)^2\right)} \quad (3.4)$$

**Figure 3.7**

The arrows represent a set of six observations, 2.5, 3.5, 4.0, 6.0, 6.5, and 7.5, with a mean of 5.0 and standard deviation of approximately 1.95. The probability density function (pdf) of a normal distribution with a mean of 5.0 and standard deviation of 1.0 (Equation 3.4), from which they are hypothesized to have been sampled, is superimposed about them. Note the symmetry. From Equation 3.4, with a mean of 5.0 and standard deviation of 1.0, the pdf value of X at 2.5 and 7.5 is 0.018, at 3.5 and 6.5 is 0.130, and at 4 and 6 is 0.242. These values are the probability densities of the respective X values given the selected parameter values. See Example Box 3.3.

For any given value of the variable X , the value of this function (Equation 3.4) defines its probability density. To someone unfamiliar with it, this equation may look rather daunting, but it can be implemented easily in most spreadsheet programs (see Example Box 3.3) or on a hand calculator. The right-hand version of the pdf (Equation 3.4) demonstrates that each observation is being converted into a residual and is then standardized by dividing by the standard deviation ($[(X - \mu)/\sigma]$, i.e., observation X minus the mean, μ , divided by the standard deviation). In other words, with the normal distribution, we are determining the probability density of particular values considered in terms of how many standard deviations these values are from the mean (look ahead to Figure 3.9).

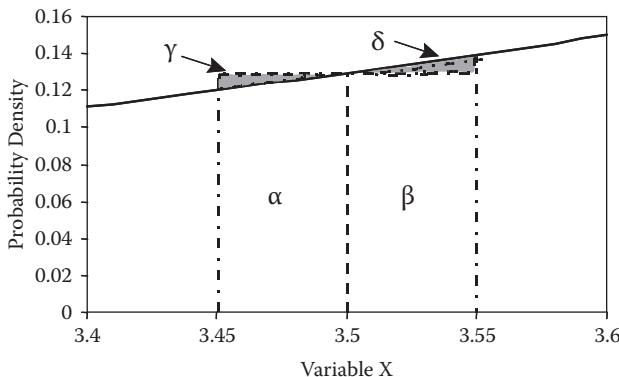
3.4.3 Probability Density

Note the use of the phrase “probability density” instead of probability. The sum of the probabilities of the full set of possible outcomes for a particular event must equal 1. Thus, when tossing an unbiased coin, the possible outcomes are a head or a tail, each with a probability of 0.5, and these add to 1 for any particular coin-tossing event (a discrete variable). With a continuous variable, an event would be the making of a single observation X . However, speaking mathematically, and ignoring such things as the limits of measurement, with a truly continuous variable there are an infinity of potential observed values of X within the range of what is possible. The sum of the probabilities of all possible events (i.e., X between $-\infty$ to $+\infty$) must equal 1, and

EXAMPLE BOX 3.3

Properties of the normal probability density function. In cell E1 put the equation $=1/(B2*sqrt(2*PI()))$; this is the constant. In cell B5 (and copy down to row 105, where $X = +5$ in column A), put Equation 3.4: $=\$E$1*exp(-((A5-\$B$1)^2)/(2*\$B$2^2))$. Alternatively, you could use the Excel function, `normdist(A5,B1,B2,false)`, which provides the same answer without having to bother with the constant in E1. Check the help for a description of this function. In C5 (and copy down), put the function `normdist(A5,B1,B2,true)`, to obtain the cumulative probability density. The last number in column C should be very close to 1. The sum in B3 should be close to 10, which reflects the increments of 0.1 that were used to step through from -5 to 5. If you reconstruct the worksheet to increment the values in column A by 0.05 instead of 0.1, don't forget to modify cell B3. What happens to the value in B3 when you make this change? Standardize the separate probability densities by dividing each one by their sum, as in column D. Cumulate column D in column E; it sums to 1. Column C doesn't quite reach 1 because there is a small but finite probability of values being greater than 5, given a mean of 0 and standard deviation of 1. Plot columns B and C against column A to see the standard normal curve and the cumulative normal curve (cf. Figure 3.9). Alter the values in B1 and B2 and see the impact on the curves. See the text for the difference between probability density (column B) and probability. Find the probability densities for the six X values in Figure 3.7.

	A	B	C	D	E
1	Mean	0		$1/\sigma \sqrt{2\pi}$	0.39894228
2	StDev	1			
3	Sum	=Sum(B5:B105)			
4	X	Prob. Density	Cumulative Prob. Density	Standardized	Cumulative
5	-5	1.4867E-06	2.871E-07	=B5/\$B\$3	=D5
6	-4.9	2.4390E-06	4.799E-07	=B6/\$B\$3	=D6+E5
7	-4.8	3.9613E-06	7.944E-07	3.9613E-07	7.887E-07
8	-4.7	6.3698E-06	1.302E-06	6.3698E-07	1.426E-06
9	.	<i>Copy down</i>	<i>Copy down</i>	<i>Copy down</i>	<i>Copy down</i>
105	5.0	1.4867E-06	0.9999997	1.4867E-07	1

**Figure 3.8**

Probability densities for a normally distributed variate X having a mean of 5.0 and a standard deviation of 1.0 (as in Figure 3.7). The pdf value at $X = 3.5$ is 0.129518. The true area under the curve between 3.45 and 3.55 is $\alpha + \beta + \delta$; an approximation to this is $\alpha + \beta + \gamma$ (see Example Box 3.4).

so, with an infinity of possibilities, the probability of any particular value (e.g., exactly 2.5) would be infinitesimally small. Instead, to obtain literal probabilities for continuous variates, we need to quantify an area under the pdf. Thus, we can have a probability for a range of a continuous variate X but not for a particular value.

Clearly there is a difference between probability density and probability because, given a known mean and standard deviation (Figure 3.7), the probability of observing an X value of exactly 3.5 is infinitesimal, but using the given parameter values, the probability density of exactly 3.5 is 0.130. To grasp the ideas behind using likelihoods, it is necessary to understand this difference between probability density and probability (Example Boxes 3.3 and 3.4).

The graph of the pdf values (Figure 3.7) is analogous to a histogram of expected relative proportions for a continuous variate. This reflects our intuitions with regard to the relative chance of obtaining different values of the continuous variable X . Thus, with our example (Figure 3.7) and the given parameter values, the pdf value for an observation of 4 (pdf = 0.242) is thirteen times greater than (more likely than) the pdf value for an observation of 2.5 (pdf = 0.018). We can use this characterization to determine whether the observed data are consistent with the hypothesized normal pdf curve from which they are assumed to be sampled.

The term *density* is used as an analogy to express the weight or mass of probability above particular values of the variable X . Of course, when the range over which each density operates is infinitesimal, the overall probability would also be infinitesimal. However, consider what would be the case if,

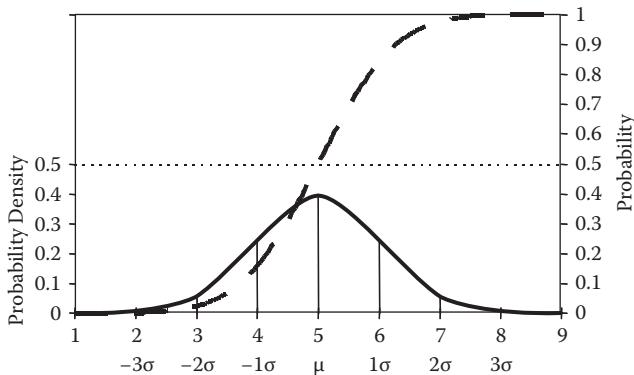
EXAMPLE BOX 3.4

Estimating probabilities under the normal distribution. The calculations involved reflect those seen in Figure 3.8. $P(3.45–3.55)$ refers to the probability of the variable lying between 3.45 and 3.55 and equals $\alpha + \beta + \delta$. The terms α and $(\beta + \gamma)$ are derived from the normdist function. The approximate probability can be derived from the single-value probability density for 3.5 multiplied by the area concerned, and the difference between the strict probability and the approximate (i.e., cells B6 and D6) can be seen. Note we need to use six decimal places to detect the difference. The use of the probability density in the approximation only becomes valid once we multiply it by the range over which it is intended to apply and thereby generate an area under the normal curve.

	A	B	C	D
1	3.45	=normdist(A1,5,1,true)		
2	3.5	=normdist(A2,5,1,true)	=normdist(A2,5,1,false)	
3	3.55	=normdist(A3,5,1,true)		$\alpha + \gamma = \beta$
4	α	=B2-B1		
5	$\beta + \delta$	=B3-B2		
6	$P(3.45–3.55)$	=B4+B5	Approx. $P(3.45–3.55)$	=2*D3
7	δ	=B5-D3	$\alpha + \beta + \delta = P(3.45–3.55)$	=B4+D3+B7
8	γ	=D3-B4		

as an approximation, one were to assume the same probability density operated over a small range of the variable of interest (Figure 3.8). Using the approximation that the probability density at $X = 3.5$ represents the probability density at values of X close to 3.5, the probability (as contrasted with probability density) of observing a value between 3.45 and 3.55 is the area $\alpha + \beta + \gamma = 0.129518 \times 0.1 = 0.0129518$. This is only an approximation to the real area under the pdf curve between those ranges (which is $\alpha + \beta + \delta = 0.0129585$). The difference, or error, is $\delta - \gamma$, and this would become smaller and smaller as the range over which the approximation was applied became smaller. The limit would be where the range was infinitesimal, whereupon the solution would be exact but also infinitesimal (Example Box 3.4).

Instead of summing under the curve in a series of discrete, small steps (which provides only an approximation, as in Figure 3.8 and Example Box 3.4), it is better to sum the area under the pdf curve in an infinitesimal way using integration. The assertion that the sum of the probabilities of the set of all possible outcomes for any given observation cumulates to 1 can be expressed by integrating Equation 3.4 between the maximum and minimum possible values for the variable X (Equation 3.5):

**Figure 3.9**

The relationship between the probability density function (solid line) and its integral (or the cumulative distribution function) for the normal distribution (in this instance with a mean of 5.0 and a standard deviation of 1.0). Integration is equivalent to summing the area under the pdf so we see that it sums to 1 across all possibilities. We can also see that the symmetry of the normal pdf leads to an observation being the mean or less than the mean, having a probability of 0.5.

$$\text{cdf} = 1 = \int_{x=-\infty}^{+\infty} \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(x-\mu)^2}{2\sigma^2}\right)} \quad (3.5)$$

where cdf refers to the cumulative distribution function. This provides an exact solution to the area under the pdf and translates the probability densities into true probabilities (Figure 3.9).

Integration of the pdf can be performed across more ranges of the variate to produce the probability of observing values within a given range (Example Box 3.4). For example, if we integrated the pdf between X values of 5 and 4, we would be calculating the probability of making an observation with a value between 4 and 5 (Figure 3.10). To do this does not require an exercise in calculus each time, as there are published tables of the cumulative normal frequency distribution (e.g., Table A3 in Snedecor and Cochran, 1967). Using such tables or the equivalent functions in Excel, one can determine the cdf value for 5.0 and subtract from it the cdf value for 4.0 to produce the area under the pdf between the limits of 4 and 5 (Figure 3.10).

The values we obtain by substituting real values into Equation 3.4 are known as probability densities, and these are infinitesimally summed or integrated between given limits to produce probabilities, as in Equation 3.5. Thus, in terms of true probability, with respect to continuous variates, pdf values can only be interpreted directly when referred to in the context of a range of the possible values (e.g., Figure 3.10). Later, when we consider discrete variates (e.g., the binomial distribution—heads or tails, tagged or

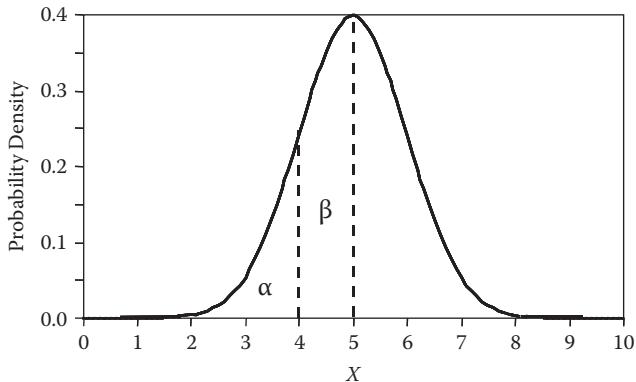


Figure 3.10

A normal distribution pdf with a mean of 5 and standard deviation of 1. The total area under this curve from $-\infty$ to $+\infty$ sums to 1. As the curve is symmetrical, we can conclude that the probability of observing a value of less than or equal to 5 would be 0.5. Therefore, the area $\alpha + \beta = 0.5$. To obtain the probability of a value falling between 4 and 5, we need the probability of obtaining a value of 4 or less (i.e., $=normdist(4,5,1,TRUE)$; $\alpha = 0.158655$), and this must be subtracted from the cdf for the value of 5 or less to leave the probability in which we are interested, i.e., $\beta (= 0.341345)$.

untagged), the pdfs generate discrete probabilities. With discrete variate pdfs, probability density and probability are the same because the number of possible outcomes to any particular event is limited by definition.

3.4.4 Likelihood Definition

With continuous variates the true probability of individual observations is infinitesimal. However, we have also repeated a statement found in many statistical texts about likelihood being the probability of the observed data given a set of parameters. This apparent anomaly requires clarification. With any model of a process there will be parameter sets for which the model predictions are obviously inconsistent with the available data and are thus unlikely. Conversely, there will be other parameter sets that produce predictions closely consistent with the data, and these we feel are far more likely. Maximum likelihood methods are attempting to find the parameter set that is most likely in this sense of the word *likely*. Press et al. (1989) present a clear statement of the problem of applying likelihood methods to parameter estimation.

It is not meaningful to ask the question, 'What is the probability that a particular set of fitted parameters $a_1 \dots a_M$ is correct?' The reason is that there is no statistical universe of models from which the parameters are drawn. There is just one model, the correct one, and a statistical universe of data sets that are drawn from it! (Press et al., 1989, p. 549)

What they are claiming is that a set of observations only constitutes a sample of what is possible. If we were able to take another sample, we would expect to obtain similar, but not exactly the same, values. This is because our sampling is based upon the assumption that there is some underlying explanatory model for the behaviour of the system, and this constrains the measurable variate's behaviour to follow the predicted model output plus the residual terms defined by the pdf of the errors. If this is the case, then, as stated, there is only one correct model and only one set of correct parameters. This means that each different set of parameter values is a separate hypothesis and not a sample from some statistical distribution of parameter values. Press et al. go further and state:

We identify the probability of the data given the parameters ... as the *likelihood* of the parameters given the data. This identification is entirely based upon intuition. It has no formal mathematical basis in and of itself.
 (Press et al., 1989, p. 550)

This appears to be a very weak foundation upon which to base the serious business of model parameter estimation. However, one will often see either a definition or an implied definition of likelihood that is very exact:

$$L(\theta) = \prod_{i=1}^n pdf(X_i|\theta) \quad (3.6)$$

which is read the likelihood the parameter(s) θ (theta) is the product of the pdf values for each of the n observations X_i given the parameter(s) θ . It is common knowledge that when events are independent, it is necessary to multiply their separate probabilities to obtain the overall probability (e.g., the probability of three heads in a row is $0.5 \times 0.5 \times 0.5 = 0.125$). With continuous variates, the same process is involved, so we use the product (capital Pi, Π) of the separate probability densities and not the sum. The product of all the separate pdf values when the parameters are set equal to the hypothesized values is called the likelihood value and is usually designated $L(\theta)$ (Neter et al., 1996). Thus, in our earlier example (Figure 3.7), we could assume a standard deviation of 1 and then search for the value of the mean that would lead to the maximum likelihood. We have observations at 2.5, 3.5, 4.0, 6.0, 6.5, and 7.5. If we were to assume a range of different values for the mean, we would find that the respective pdf values for each observation would alter so that their product, the likelihood for the particular guessed value of the mean, would also vary. Clearly, to search for the most likely value of the mean, we need to try different values and search for that value which maximizes the product of the pdf values (Example Box 3.5, Figure 3.11).

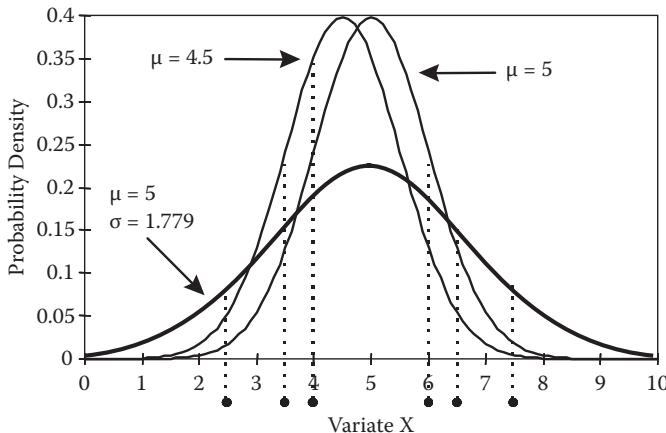
EXAMPLE BOX 3.5

Maximum likelihood (ML) search for an estimate of the mean value of a set of observations. Columns B to D are example trials (Figure 3.11). Row 9 contains the product of each set of likelihoods. Using the solver, maximize the value in E9 by changing cells E1:E2. The StDev of the data, =StDev(A3:A8) = 1.94936, is larger than the estimate in E2. The ML estimate of the standard deviation is =sqrt($\sum(x-\mu)^2/n$), the divisor is n and not n-1. In a separate cell calculate the usual StDev and beside it put =sqrt((E2*E2*6)/5). Are they the same? This difference between the usual population estimate of the standard deviation and the ML estimation of the same statistic becomes important when we want to use ML to fit data to a model and need to estimate the unbiased variance.

	A	B	C	D	E
1	Mean	4.5	5	5.25	5
2	Obs\StDev	1	1	1	1.7795
3	2.5	0.05399	0.01753	0.00909	=normdist(\$A3,E\$1,E\$2,false)
4	3.5	0.24191	0.12952	0.08628	=normdist(\$A4,E\$1,E\$2,false)
5	4	0.35207	0.24197	0.18265	=normdist(\$A5,E\$1,E\$2,false)
6	6	0.12952	0.24197	0.30114	Copy down to Row 8
7	6.5	0.05399	0.12952	0.18265	0.15715
8	7.5	0.00443	0.01753	0.03174	0.08357
9	Π(Likelihood)	0.1425 × 10 ⁻⁶	0.3108 × 10 ⁻⁶	0.2502 × 10 ⁻⁶	=product(E3:E8)

Probability densities only relate to probabilities in the context of a range of values, so it appears that the definition of likelihood we have been using is too strong. As we noted earlier, if the observed variate is a continuous variable, then the probability of each particular value would simply be infinitesimal. The common argument is that what we are really talking about is the product of the probability densities for our particular data values, but over a tiny range around this value (Edwards, 1972; Press et al., 1989). In practice, we just calculate the probability density for precise values and not a range of values. Edwards (1972) suggests we are effectively using a constant range of 1 about each data value, but this is hardly what would be called a tiny range.

There is no such conceptual problem with probability density functions for discrete statistical distributions (e.g., binomial) because the probability densities are exact probabilities. It is only with continuous pdfs that a problem of interpretation arises. While this may seem pedantic and only related to definitions, the source of likelihoods for continuous variates has concerned mathematical statisticians for decades, and a variety of solutions have been proposed (Edwards, 1972).

**Figure 3.11**

Different hypothesized normal distributions superimposed upon the example's six data points. Shifting the mean away from 5.0 leads to a decrease in the overall likelihood. However, increasing the standard deviation from 1.0 to 1.779 increased the likelihood to its maximum. This implies the best fitting normal distribution is one with a mean of 5.0 and standard deviation of 1.779. Note that increasing the standard deviation widens the spread of the distribution, hence increasing the probability densities of the observations at 2.5, 7.5, 3.5, and 6.5, while decreasing the pdf values of the central observations, 4.0 and 6.0.

3.4.5 Maximum Likelihood Criterion

Earlier we estimated parameters using the minimal sum of the squared residual errors as a criterion of fit. Using maximum likelihood instead, parameter estimation is a matter of finding the set of parameters for which the observed data are most likely. In order to apply the maximum likelihood method to parameter estimation we need two things:

1. A list of hypotheses to be considered with the particular model (i.e., what combinations of parameters we are going to try)
2. A function required to calculate the probability density/likelihood of the observed data if the hypotheses were true

It is usual to search over ranges of parameter values, focusing with more detail on combinations with the largest likelihoods, just as with the non-linear parameter searches already described and the likelihood search in Example Box 3.5.

3.4.6 Likelihoods with the Normal Probability Distribution

As already shown, probability densities for the normal distribution are calculated from the familiar

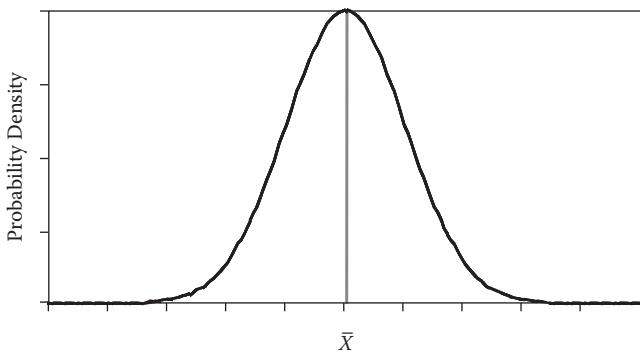


Figure 3.12

Likelihood distribution for the standard normal function (mean = 0 and variance = 1). Note the symmetrical distribution of values around the mean. The tick marks on the X axis are in units of standard deviations above and below the mean. The height on the likelihood curve indicates the relative likelihood of randomly obtaining a particular X value. A value of X approximately two standard deviations from the mean is approximately one-twentieth as likely to occur as the mean value. Likelihoods have meaning only relative to one another.

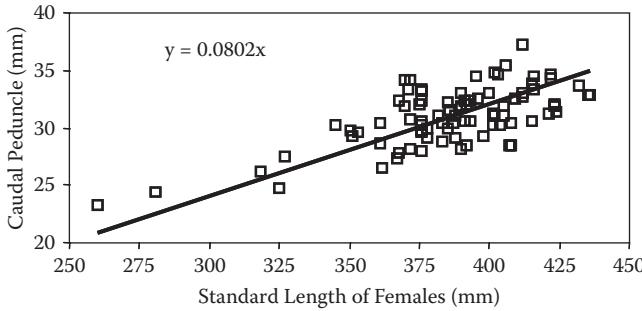
$$L\{X|\mu, \sigma\} = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(X-\mu)^2}{2\sigma^2}\right)} \quad (3.7)$$

where $L\{X|\mu, \sigma\}$ is the likelihood of any individual observation X , given, μ the population mean, and σ , the population standard deviation (that is, the likelihood of the data X , given the hypothesis about μ and σ ; Figure 3.12). Using this equation with a wide range of X values produces the bell-shaped curve everyone associates with the normal distribution (Figure 3.12); the value of the likelihood is determined by the various possible combinations of mean and standard deviation values. The y axis represents the relative likelihood of observing each specific X value if one is sampling a given population. This probability distribution can be used to estimate likelihoods wherever the residual errors in a model are normally distributed.

As an example, we can consider the relationship between the caudal peduncle width and standard length of female orange roughy from the Lord Howe Rise. This linear relationship (Figure 3.13) can be described by a very simple model, a one-parameter linear regression (where C is the caudal peduncle width and S is the standard length):

$$C_i = bS_i + \varepsilon_i = bS_i + N(0, \sigma^2) \quad (3.8)$$

The residuals (ε) are assumed to be normally distributed with a mean of zero and variance σ^2 , so if we use maximum likelihood methods, there are two parameters to estimate: b and σ . The probability density of any particular

**Figur e 3.13**

Relation between caudal peduncle and standard length for female orange roughy from the Lord Howe Rise. The regression line has an $r^2 = 0.3855$, $F = 52.1$, $P < 0.0001$, $df = 83$. (Data described in Haddon, 1995.)

observation C_i , given values for b , σ , and the data S_i , is $L\{C_i|b, \sigma, S_i\}$ and can be obtained:

$$L\{C_i|b, \sigma, S_i\} = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(C_i - bS_i)^2}{2\sigma^2}\right)} \quad (3.9)$$

The total probability density of all n observations given a particular pair of values for the parameters b and σ is just the product of the probability density for each of the n separate observations. Probability densities are calculated for independent events and, as such, have to be multiplied together and not added; hence, we do not use Σ (the sum) but instead \prod (capital Pi) the product:

$$L\{C|b, \sigma, S\} = \prod_{i=1}^n \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(C_i - bS_i)^2}{2\sigma^2}\right)} \quad (3.10)$$

As probability densities are commonly rather small numbers, the risk of rounding errors becomes great if many of them are multiplied together. So, given a function $f(X)$, we should remember that

$$\prod_{i=1}^n f(X_i) = e^{\sum \ln(f(X_i))} \quad (3.11)$$

which simply says that the \prod , or product, of a series of values is the same as the antilog of the sum of the logs of those same values. If we omit the antilog we would be dealing with log-likelihoods. Using this latter approach, tiny numbers and the potential for rounding errors may be avoided. Equation 3.10 would take the form

$$LL\{C|b, \sigma, S\} = \sum_{i=1}^n \ln \left[\frac{1}{\hat{\sigma}\sqrt{2\pi}} e^{\left(\frac{-(C_i - bS_i)^2}{2\hat{\sigma}^2} \right)} \right] \quad (3.12)$$

Equation 3.12 can be simplified by expanding the logarithm and removing the terms that stay constant from the summation term as the parameters change.

$$LL = n \ln \left(\frac{1}{\hat{\sigma}\sqrt{2\pi}} \right) + \frac{1}{2\hat{\sigma}^2} \sum_{i=1}^n \left[-(C_i - bS_i)^2 \right] \quad (3.13)$$

where $\hat{\sigma}$ hat squared

$$\hat{\sigma}^2 = \frac{\sum_{i=1}^n (C_i - bS_i)^2}{n} \quad (3.14)$$

is the variance estimated from the data (hence the hat). It is the maximum likelihood estimate so we divide by n and not $n - 1$. By expanding Equation 3.13, using Equation 3.14, we can produce a simplification that makes for easier calculation. The summation term in Equation 3.13 is cancelled by the inverse of $\hat{\sigma}^2$ from Equation 3.14, leaving $-n/2$. Further simplification is possible:

$$LL = n \ln \left(\left(\hat{\sigma}\sqrt{2\pi} \right)^{-1} \right) - \frac{n}{2} \quad (3.15)$$

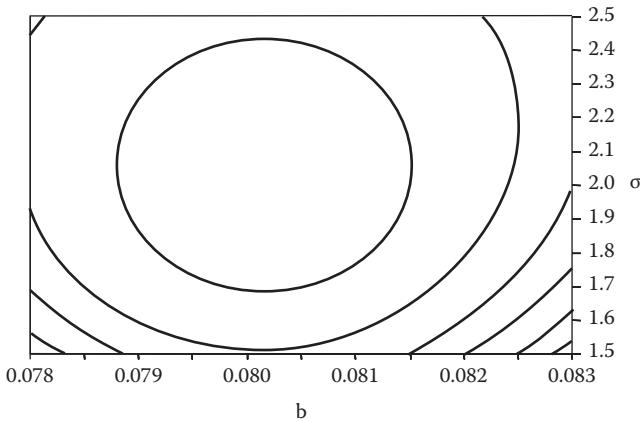
giving

$$LL = -n \left(\ln \left(2\pi^{\frac{1}{2}} \right) + \ln(\hat{\sigma}) \right) - \frac{n}{2} \quad (3.16)$$

and finally

$$LL = -\frac{n}{2} \left[\ln(2\pi) + 2\ln(\hat{\sigma}) + 1 \right] \quad (3.17)$$

The objective when fitting data to a model is to maximize the log-likelihood, and any of Equations 3.12, 3.15, 3.16, or 3.17 could be used. Among people working with nonlinear models, it appears to be a tradition to minimize instead of maximizing a criterion of fit. In practice, all this means is that one minimizes the negative log-likelihood (i.e., for normal errors remove the leading negative symbol from Equations 3.16 and 3.17).

**Figure 3.14**

Circular maximum likelihood contours for the female orange roughy from the Lord Howe Rise morphometric data (caudal peduncle vs. standard length) given different values of the single-parameter regression parameter b and the standard deviation of the residuals about the regression σ . Optimum fit at $b = 0.08016$ and $\sigma = 1.990$.

The log-likelihood, $LL\{C|b, \sigma, S\}$, can be back-transformed to the likelihood:

$$L\{C|b, \sigma, S\} = e^{LL\{C|b, \sigma, S\}} \quad (3.18)$$

The optimum combination of b and σ can then be found by searching for the maximum of either the likelihood $L\{C|b, \sigma, S\}$ or the log-likelihood (see Figure 3.14), or the minimum of the negative log-likelihood. In Excel, with this problem, the result obtained was the same irrespective of whether Equation 3.12 or Equation 3.17 was used. This occurred despite there being ninety-four pairs of data points. Generally, however, with large samples, Equation 3.17 would be the safest option for avoiding rounding errors and the machine limits to numbers (the likelihoods can become very small during the search).

There is no correlation between the parameter b and the standard deviation σ , as evidenced by the circular contours of the log-likelihood surface (Figure 3.14). The maximum likelihood produces the same estimate of b as the minimum sum of squared residual estimate ($b = 0.080155$).

3.4.7 equivalence with Least Squares

For linear and nonlinear models, having normally distributed residuals with constant variance, fitting the model by maximum likelihood is equivalent to ordinary least squares. This can be illustrated with a straight-line regression model:

$$y_i = \alpha + \beta x_i + \varepsilon_i \quad (3.19)$$

where the random deviations ε_i are independent values from a normal distribution with mean zero and variance σ^2 [$N(0, \sigma^2)$]. In other words, for a given value of the independent variable x_i , the response variable y_i follows a normal distribution with mean $\alpha + \beta x_i$ and variance σ^2 , independently of the other responses. The probability distribution for the set of observations y_1, y_2, \dots, y_n , is formed from the product of the corresponding normal pdf values (likelihoods), so that the likelihood of the parameters α and β is given by

$$L\{y|\alpha, \beta, \sigma\} = \prod \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(y_i - \alpha - \beta x_i)^2}{2\sigma^2}\right)} \quad (3.20)$$

To fit by maximum likelihood we need to find the parameter values (α , β , and σ) that maximize the total likelihood (Equation 3.20). Equivalently, we could maximize the sum of the logarithm of the likelihoods (or minimize the sum of the negative logarithms).

$$LL\{y|\alpha, \beta, \sigma\} = n \ln(\sigma\sqrt{2\pi})^{-1} + \frac{1}{2\sigma^2} \sum_{i=1}^n -(y_i - \alpha - \beta x_i)^2 \quad (3.21)$$

In Equation 3.21 the only part of the equation that is not constant as parameters alter and interact with the observed data is the summation term (the other terms being constant can validly be removed from the summation). The summation term is equivalent to the sum of squared residuals used in standard linear regression. Therefore, fitting by maximum likelihood will produce an equivalent result to fitting the line that minimizes the sum of the squared deviations of the observations about the fitted line, i.e., fitting by ordinary least squares. This is the case for all models as long as their residual errors are normal, additive, and with constant variance.

3.4.8 Fitting a Curve using Normal Likelihoods

The most commonly used equation to describe growth in fisheries modelling is still the von Bertalanffy (1938) growth curve:

$$\hat{L}_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) + \varepsilon \quad (3.22)$$

where L_t is the expected size at age t , L_∞ is the average maximum size, K is a growth rate parameter, t_0 is the hypothetical age at zero length, and ε is the normal error term (see Chapter 9). Kimura (1980) provided a set of data relating to the growth of male Pacific hake. To fit the von Bertalanffy curve using normal likelihoods, we compare the observed length at age with those predicted from Equation 3.22 (Example Box 3.6, Figure 3.15).

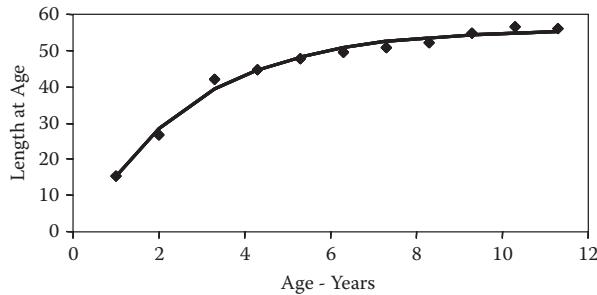
EXAMPLE BOX 3.6

Fitting a von Bertalanffy growth curve using normal likelihoods. Data on male Pacific hake from Kimura (1980). In column C put Equation 3.22 $=\$B$1*(1-exp(-\$B$2*(A6-\$B$3)))$ and copy down to row 16. Sum column D in E1. We use the equivalent of Equation 3.17 in E4. The values in E3 and E4 will differ unless you put =E2 in B4. Why is that the case? Plot columns B as points and C as a line, against A (Figure 3.15). Note that altering the value for σ has no effect on the location or shape of the curve; it only affects the relative likelihoods. Find the optimum fit by using the solver to minimize the negative log-likelihood in either E3 or E4 by changing L_∞ , K, and σ . Alternatively, solve by minimizing the sum of the squared residuals in E1. Do the results obtained with maximum likelihood differ from those obtained by least squares?

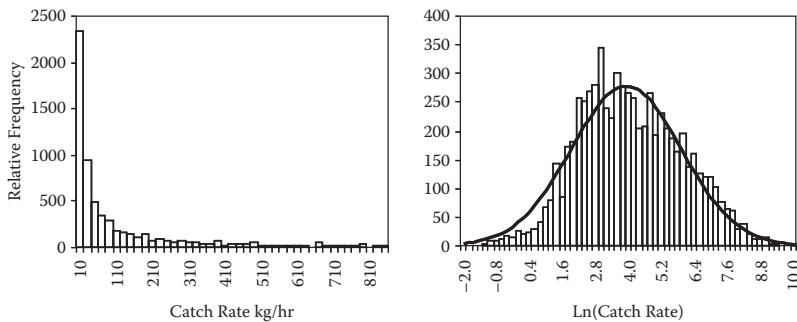
	A	B	C	D	E
1	L_∞	55.000		SSQ	=sum(D6:D16)
2	K	0.350		St Dev ML	=sqrt(E1/11)
3	t0	0.000		negLL	=-sum(E6:E16)
4	σ	1.000		negLL (eq 3.17)	$=(11/2)*(Ln(2^*PI())+2*Ln(E2)+1)$
5	Years	Length	Expect	Resid ²	Ln(Likelihood)
6	1	15.4	16.242	$=(B6-C6)^2$	$=Ln(normdist(B6,C6,\$B$4,false))$
7	2	26.93	27.688	$=(B7-C7)^2$	$=Ln(normdist(B7,C7,\$B$4,false))$
8	3.3	42.23	37.672	$=(B8-C8)^2$	-11.3074
9	4.3	44.59	42.789	3.243425	-2.5407
10	5.3	47.63	46.395	1.525007	-1.6814
11	6.3	49.67	48.936	0.538431	-1.1882
12	7.3	50.87	50.727	0.020470	-0.9292
13	8.3	52.3	51.989	0.096835	-0.9674
14	9.3	54.77	52.878	3.579456	-2.7087
15	10.3	56.43	53.505	8.557435	-5.1977
16	11.3	55.88	53.946	3.739299	-2.7886

3.4.9 Likelihoods from the Lognormal Distribution

In fisheries models, the probability density function that is perhaps most commonly used to describe untransformed residual errors is the lognormal distribution. The distributions of catches, and of efforts, across a fleet are often lognormally distributed, while catch rates can usually be described using lognormal multiplicative errors (Figure 3.16). Events that relate to each other in an additive manner tend to be described by the normal distribution, while those that relate in a multiplicative way tend to be described by the lognormal distribution.

**Figure 3.15**

Kimura's (1980) growth data for male Pacific hake. The solid line represents the expected values (Example Box 3.6) using additive, normal random residual errors.

**Figure 3.16**

The left-hand panel shows the raw data from south coast catches of Blue Warehou (*Seriola brama*) from the Australian Fisheries Management Authority's trawl database for the Australian South East Fishery. That this is lognormally distributed is illustrated in the right-hand panel, where the distribution is approximately normal with a mean (μ) of 3.93 and standard deviation (σ) of 2.0 after log transformation.

Natural logarithmic transformation of lognormally distributed data generates a normal distribution (multiplications are converted to additions). The probability density function for lognormal residual errors is (Hastings and Peacock, 1975)

$$L(x_i) = \frac{1}{x_i \sigma \sqrt{2\pi}} e^{\left[\frac{-(\ln(x_i) - \ln(m))^2}{2\sigma^2} \right]} \quad (3.23)$$

where $L(x_i)$ is the likelihood of the data point x_i in question, m is the median of the variable with $m = e^\mu$ (and $\mu = \ln(m)$), μ is estimated as the mean of $\ln(x_i)$, and σ is the standard deviation of $\ln(x_i)$. Equation 3.23 is equivalent to the pdf for normal distributions, with the data log-transformed and divided by each x_i value.

EXAMPLE BOX 3.7

Relationship between the normal pdf and the lognormal pdf. Column C is filled from C8:C1007, with numbers starting from 0.01 down to 10 in steps of 0.01. Column A is the natural log of column C, and column B is the normal likelihood (probability density) =normdist(A8,\$D\$4,\$D\$5,false). Column D is the lognormal likelihood (Equation 3.23), which is the normal likelihood in column B divided by the value of the observed data x in column C (i.e., =B8/C8 in D8). Column E uses the Excel function (e.g., =LogNormDist(C8, \$D\$4,\$D\$5) in E8), which provides the cumulative distribution by default. Notice that this function uses μ instead of the median m . Plot column B against A as one graph, and then column D against C, and column B against C as continuous lines. The first two should mimic Figure 3.17. Modify cells D3 and D5 and observe the effects on the shape and location of the different curves. Note the effect of division by x (column D). Note the value in D6. Why does it have this value (cf. Example Box 3.3)? Compare the value of D2 with the mode on the graph of column D; try putting 0.45 in D5. What is the impact on the sum in D6?

	A	B	C	D	E
1		Mean of the pdf	=D3*Exp((D5^2)/2)		
2		Mode of the pdf	=D3/(Exp(D5^2))		
3		Median m , of the pdf		1	
4		$\ln(m) = \mu = \text{Avg}(\ln(x))$		=Ln(D3)	
5		$\sigma = \text{StDev}(\ln(x))$		1	
6		Sum of Likelihoods	=sum(D8:D1007)		
7	Ln(x)	Normdist(μ, σ)	X	NormDist/x	Lognormdist
8	=Ln(C8)	=normdist(A8,\$D\$4,\$D\$5,false)	0.01	=B8/C8	2.06279E-06
9	=Ln(C9)	=normdist(A9,\$D\$4,\$D\$5,false)	0.02	=B9/C9	4.57817E-05
10	-3.50656	0.000853	0.03	0.0284287	0.00022702
11	-3.21888	0.002244	0.04	0.0560987	0.00064353
12	-2.99573	0.004489	0.05	0.0897783	0.00136900
13	Copy these columns down to row 1007	0.06		Copy down to row 1007	

To use the normal pdf to generate probability density values for the log-normal distribution, one would log-transform the observed and expected values of the variable x , find the normal likelihood value, and then, strictly, divide this by the untransformed observed x value. This last step, of dividing by the observed x value, has no effect on the optimization of model fitting and is often omitted. Strictly, however, if one wanted to plot up the pdf of a log-normal distribution, Equation 3.23 should be used in full (Example Box 3.7, Figure 3.17). When describing the parameters of the lognormal distribution

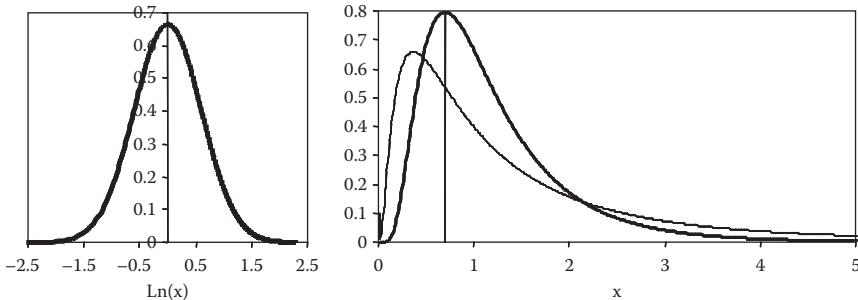


Figure 3.17

Probability density distributions for the same data expressed as a lognormal distribution in the right-hand panel and as a normal distribution in the left-hand panel after the x variate was log-transformed. The thick line in both panels relates to data having a median (m) of 1 (i.e., $\mu = 0$) and a σ of 0.6. The thin vertical line in the right-hand graph indicates the mode of $0.6977 = 1/e^{0.36}$. The thin curve in the right-hand graph relates to parameters $m = 1$ and $\sigma = 1$. The x axes in both graphs have been truncated to areas where the probability density or likelihood values were significantly greater than zero (see Example Box 3.7). As the variance increases for a given median, the mode moves toward zero and the curve skews further to the right.

there is a potential for confusion, so care must be taken. The location parameter (position along the x axis) is the median ($m > 0$) of the x variate and not the mean, but the shape parameter σ ($\sigma > 0$) is the standard deviation of the log of the x variate. Given a continuous variate x , the main parameters of the lognormal distribution are (Hastings and Peacock, 1975):

1. The median:

$$m = e^{\mu} \quad (3.24)$$

where μ is the mean of $\ln(x)$

2. The mode of the lognormal pdf:

$$m/e^{\sigma^2} = e^{(\mu-\sigma^2)} \quad (3.25)$$

where σ is the standard deviation of $\ln(x)$

3. The mean of the lognormal pdf:

$$me^{(\sigma^2/2)} = e^{(\mu+\sigma^2/2)} \quad (3.26)$$

The lognormal distribution is always skewed to the right (Figure 3.17). The most obvious difference between the lognormal and normal curves is that

the lognormal is always positive. In addition, as the mode is determined by both the median and the σ parameter (Equation 3.27), both can affect the location of the mode (Figure 3.17, Example Box 3.7).

The likelihood equation can be simplified as with the normal likelihoods. In fact, given the appropriate transformation, one can use the equivalent of Equation 3.17:

$$LL = -\frac{n}{2} \left[\ln(2\pi) + 2\ln(\hat{\sigma}) + 1 \right] - \sum_{i=1}^n \ln(x_i) \quad (3.27)$$

where

$$\hat{\sigma}^2 = \sum_{i=1}^n \frac{(\ln(x_i) - \ln(\hat{x}_i))^2}{n} \quad (3.28)$$

Note the maximum likelihood version of σ^2 using n instead of $n - 1$ (Example Box 3.5). The $\Sigma \ln(x)$ term is a constant and is usually omitted from calculations.

3.4.10 Fitting a Curve using Lognormal Likelihoods

Fitting a curve using lognormal residual errors is very similar to using normal random likelihoods. Recruitment in fisheries is notoriously variable, with occasional very large year classes occurring in some fisheries. Stock recruitment relationships are generally taken to exhibit lognormal residual errors. Numerous stock recruitment relationships have been described (see Chapter 10), but here we will restrict ourselves to the most commonly used equation, that by Beverton and Holt (1957). As an example, we will attempt to fit a stock recruitment curve to some real data. Hilborn and Walters (1992) indicate that there can be more than one form of the Beverton and Holt stock recruitment equation, but all would be expected to have lognormal residual errors. We will use the following version:

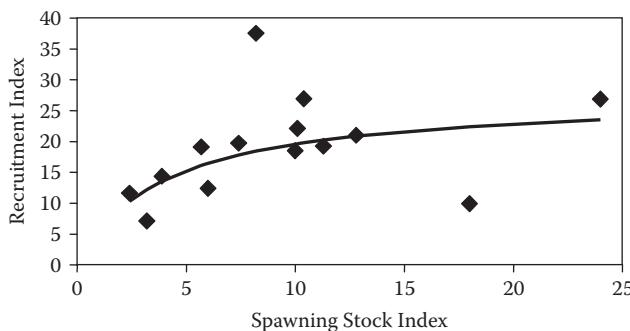
$$R_i = \frac{aS_i}{b + S_i} e^{N(0, \sigma^2)} \quad (3.29)$$

where R_i is the recruitment in year i , S_i is the spawning stock size that gave rise to R_i , a is the asymptotic maximum recruitment level, and b is the spawning stock size that gives rise to 50% of the maximum recruitment. The residual errors are lognormal with a μ of 0 and variance σ^2 (Example Box 3.8, Figure 3.18). Penn and Caputi (1986) provide data on the stock recruitment of Exmouth tiger prawns. They used a Ricker stock recruitment relationship, but we will use the Beverton and Holt relationship (Equation 3.29).

EXAMPLE BOX 3.8

Fitting a Beverton and Holt stock recruitment relationship using lognormal residual errors. The predicted recruitment values are in column C as $=($B$1*A6)/($B$2+A6)$ and copied down. In column D put the log-likelihood $=\text{Ln}(\text{normdist}(\text{Ln}(B6), \text{Ln}(C6), \$B\$3, \text{false}))$. The natural logarithmic transformations are important; without them one would be using normal random errors and not lognormal. In E4, put Equation 3.17 $=(C4/2)*(\text{Ln}(2*\pi())+2*\text{Ln}(E1)+1)$. Plot column B against A (as points) and C against A as a line (cf. Figure 3.18). Use the solver and minimize E3 by varying cells B1:B3 to find the optimum line. If E4 is minimized instead, only cells B1:B2 need be varied (σ is estimated directly). If you want E3 and E4 to be the same, then put =E1 into B3. To generate the strict lognormal likelihoods, the normal likelihoods need to be divided by each observed recruitment value, i.e., $=\text{Ln}(\text{normdist}(\text{Ln}(B6), \text{Ln}(C6), \$B\$3, \text{false})/B6)$. While this alters the likelihoods generated, compare the results obtained when using this version to those obtained using the simpler version. Try minimizing the sum of squared residuals in cell E2. Are the results different from those obtained using maximum likelihood?

	A	B	C	D	E
1	a	27.366		StDev ML	=sqrt(E2/C4)
2	b	4.0049		SSQ	=sum(E6:E19)
3	σ	0.3519		negLL	=-sum(D6:D19)
4		n	=count(E6:E19)	negLL (eq 1.17)	5.2425
5	Spawn	Recruit	Expect	LL	resid2
6	2.4	11.6	10.25	0.0642	$=(\text{Ln}(B6)-\text{Ln}(C6))^2$
7	3.2	7.1	12.15	-1.0416	$=(\text{Ln}(B7)-\text{Ln}(C7))^2$
8	3.9	14.3	13.50	0.1122	$=(\text{Ln}(B8)-\text{Ln}(C8))^2$
9	5.7	19.1	16.07	0.0053	0.0298
10	6	12.4	16.41	-0.1917	0.0786
11	7.4	19.7	17.76	0.082	0.0108
12	8.2	37.5	18.39	-1.9258	0.5080
13	10	18.5	19.54	0.1134	0.0030
14	10.1	22.1	19.60	0.0671	0.0145
15	10.4	26.9	19.76	-0.259	0.0952
16	11.3	19.2	20.21	0.115	0.0026
17	12.8	21	20.84	0.1253	0.0001
18	18	9.9	22.39	-2.5626	0.6657
19	24	26.8	23.45	0.0537	0.0178

**Figure 3.18**

A Beverton and Holt stock recruitment relationship (Equation 3.31) fitted to data from Penn and Caputi (1986) on Exmouth Gulf tiger prawns (*Penaeus semisulcatus*). The outliers to this relationship were thought to be brought about by extreme environmental conditions (see Chapter 10).

The estimated parameters obtained by using lognormal likelihoods are identical to those obtained through using either the minimum sum of squared residuals (on log-transformed data) or the normal likelihoods on log-transformed data (i.e., omitting the division by the observed recruitment, as with the x_i in Equation 3.23; see Example Box 3.8).

3.4.11 Likelihoods with the Binomial Distribution

Many texts introduce ideas relating to maximum likelihood estimation with a worked example using the binomial distribution. This seems to occur for two reasons. The first is that the binomial distribution can relate to very simple real examples, such as tagging-recapture experiments, where single parameters are to be estimated and only single likelihoods need be considered (i.e., no products of multiple likelihoods are required). The second is that the values calculated for this discrete distribution are true probabilities and not just probability densities. Thus, the complication of understanding likelihoods that are not true probabilities is avoided. Remember that this distinction is unnecessary with discrete probability distributions where the probability density function can only generate values (probabilities) for the possible discrete events. In fisheries stock assessment most analytical situations would need to use continuous probability density functions (pdfs), but there are situations where discrete pdfs, such as the binomial distribution, are necessary.

In situations where a study is determining whether an observation is true or false (a so-called Bernoulli trial; e.g., a captured fish either has or does not have a tag), and the probability of success is the parameter p , then it would generally be best to use the binomial distribution to describe observations. The binomial probability density function generates true probabilities and is characterized by two parameters, n , the number of trials, and p , the probability of success in a trial (an event proving to be true):

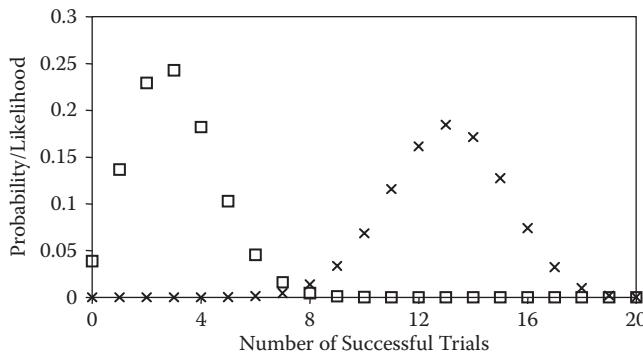
EXAMPLE BOX 3.9

Examining the properties of the binomial probability density function (Equation 3.30). The parameters of the binomial are n , the number of trials/observations, and p , the probability of a successful trial or observation. Set up a worksheet as below, where the column of m values (the number of observed successes) stretches from 0 to n down column A. Down column B insert and copy down =binomdist(A4, \$B\$1, \$B\$2, false) to obtain the likelihoods or probabilities directly (look up this function in the help). Down column C insert and copy down =fact(\$B\$1)/(fact(A4)*fact(\$B\$1-A4)) to obtain Equation 3.31. Put =(\$B\$2^A4)*(1-\$B\$2)^(\$B\$1-A4) into D4 and copy down, and then put =C4*D4 in E4 and copy down to obtain the likelihoods again. By plotting column B against column A as a simple scatterplot, you should be able to mimic Figure 3.19. Vary the value of p and observe how the distribution changes. Vary n (adjusting the length of the columns of numbers to match the n value) and see how above a value of 170 the binomdist() function operates beyond that of the fact() function. Look ahead to Equation 3.39 (the log-likelihood) and implement that on this worksheet to see how it handles the larger values of n .

	A	B	C	D	E
1	n	20			
2	p	0.25			
3	m	Binomdist	FactTerm	p(1-p)term	Likelihood
4	0	0.003171	1	0.003171	0.00317
5	1	0.021141	20	0.001057	0.02114
6	2	0.066948	190	0.000352	0.06695
7	3	0.133896	1140	0.000117	0.13390
8	4	0.189685	4845	3.92E-05	0.18969
	Extend down to equal n	Copy down to match column A			

$$P\{m|n,p\} = \left[\frac{n!}{m!(n-m)!} \right] p^m (1-p)^{(n-m)} \quad (3.30)$$

which is read as the probability of m events proving to be true out of n trials (a sample of n), where p is the probability of an event being true (see Example Box 3.9). The term $(1-p)$ is often written as q , that is, $(1-p) = q$. The “!” symbol denotes factorial. The term in the square brackets in Equation 3.30 is the number of combinations that can be formed from n items taken m at a time, and is sometimes written as

**Figure 3.19**

Two examples of the binomial distribution. The left-hand set of squares are for $n = 20$ and $p = 0.15$, while the right-hand set of crosses are for $n = 20$ and $p = 0.65$. Note that zero may have a discrete probability, and that large p values tend to generate discrete, approximately normal distributions.

$$\binom{n}{m} = \frac{n!}{m!(n-m)!} \quad (3.31)$$

It is always the case that $n \geq m$ because one cannot have more successes than trials. The binomial distribution can vary in shape from highly skewed to approximately normal (Figure 3.19, Example Box 3.9).

Tagging programs, designed to estimate the size of a population, provide a common example of where a binomial distribution would be used in fisheries. Thus, if one has tagged a known number of animals, n_1 , and later obtained a further sample of n animals from the population, it is possible to estimate the total population, assuming all of the assumptions of this form of tagging manipulation have been kept. The observation is of m , that is, how many in a sample of n are tagged (i.e., tagged = true, untagged = false).

A real example of such a study was made on the population of New Zealand fur seal pups (*Arctocephalus forsteri*) on the Open Bay Islands off the west coast of the South Island of New Zealand (York and Kozlof, 1987; Greaves, 1992). The New Zealand fur seal appears to be recovering after having been badly overexploited in the nineteenth century, with new haul-out sites starting to be found in the South and North Island. Exploitation officially ceased in 1894, with complete protection within the New Zealand Exclusive Economic Zone beginning in 1978 (Greaves, 1992). In cooperation with the New Zealand Department of Conservation, Greaves journeyed to and spent a week on one of these offshore islands. She marked 151 fur seal pups by clipping away a small patch of guard hairs on their heads, and then conducted a number of colony walk-throughs to resight tagged animals (Greaves, 1992). Each of these walk-throughs constituted a further sample of varying sizes, and differing numbers of animals

TABLE 3.1

Counts of New Zealand Fur Seal Pups Made by Greaves (1992) on Open Bay Island, West Coast, South Island, New Zealand

<i>m</i>	<i>n</i>	X	95%U	95%L	StErr
32	222	1,020	704	1,337	161.53
31	181	859	593	1,125	135.72
29	185	936	634	1,238	153.99

Note: She had tagged 151 animals (i.e., $n_1 = 151$). The column labelled *n* is the subsequent sample size, *m* is the number of tags resighted, X is the population size, and 95%L and 95%U are the lower and upper 95% confidence intervals, respectively, calculated as ± 1.96 times StErr, the standard error. Calculations are as per Equations 3.33 and 3.34. The first two rows are individual independent samples, while the last row is the average of six separate counts (data from Greaves, 1992). The average counts lead to population estimates that are intermediate in value.

were found tagged in each sample (Table 3.1). The question is: What is the size of the fur seal pup population (X) on the island?

All the usual assumptions for tagging experiments are assumed to apply; i.e., we are dealing with a closed population—no immigration or emigration, with no natural or tagging mortality over the period of the experiment, no tags are lost, and tagging does not affect the recapture probability of the animals. Greaves (1992) estimated all of these effects and accounted for them in her analysis. Having tagged and resighted tags in a new sample, a deterministic answer can be found with the Peterson estimator (Caughley, 1977; Seber, 1982):

$$\frac{n_1}{X} = \frac{m}{n} \quad \therefore \quad X = \frac{n_1 n}{m} \quad (3.32)$$

where n_1 is the number of tags in the population, *n* is the subsequent sample size, *m* is the number of tags recaptured, and X is the population size. An alternative estimate adjusts the counts on the second sample to allow for the fact that in such cases we are dealing with discrete events. This is Bailey's adjustment (Caughley, 1977):

$$X = \frac{n_1(n+1)}{m+1} \quad (3.33)$$

Like all good estimators, it is possible to estimate the standard error of this estimate and thereby generate 95% confidence intervals around the estimated population size:

$$\text{StErr} = \sqrt{\frac{n_1^2(n+1)(n-m)}{(m+1)^2(m+2)}} \quad (3.34)$$

Instead of using the deterministic equations, a good alternative would be to use maximum likelihood to estimate the population size X , using the binomial probability density function. We will continue to refer to these as likelihoods even though they are also true probabilities.

We are only estimating a single parameter, X , the population size, and this entails searching for the population size that is most likely given the data. With the binomial distribution, $P\{m|n,p\}$, Equation 3.30 provides the probability of observing m tagged individuals from a sample of n from a population with proportion p tagged (Snedecor and Cochran, 1967; Hastings and Peacock, 1975). If we implemented this exact equation in a spreadsheet, we would quickly meet the limitations of computer arithmetic. For example, in Excel, one can use the =fact() function to calculate the factorial of numbers up to 170, but beyond that leads to a numerical overflow, as the result is too large to be represented as a normal real number. Fortunately, Excel provides a =binomdist() function that can operate with much larger numbers. It seems likely that the binomial probabilities have been implemented as log-likelihoods for the calculation and then back-transformed. Given

$$P\{m|n,p\} = \left[\frac{n!}{m!(n-m)!} \right] p^m (1-p)^{(n-m)} \quad (3.35)$$

log-transforming the component terms

$$\ln\left(p^m (1-p)^{(n-m)}\right) = m\ln(p) + (n-m)\ln(1-p) \quad (3.36)$$

and

$$\ln\left[\frac{n!}{m!(n-m)!}\right] = \ln(n!) - (\ln(m!) + \ln((n-m)!)) \quad (3.37)$$

noting that

$$\ln(n!) = \sum_{i=1}^n \ln(i) \quad (3.38)$$

we obtain the log-likelihood

$$\text{LL}\{m|n,p\} = \sum_{i=1}^n \ln(i) - \left(\sum_{i=1}^m \ln(i) + \sum_{i=1}^{n-m} \ln(i) \right) + m\ln(p) + (n-m)\ln(1-p) \quad (3.39)$$

The proportion p of fur seal pups that are marked is, in this case, $p = 151/X$, and with the first example in Table 3.1, n_1 is 151, and with the Bailey correction, n is 222 + 1, and m is 32 + 1 (see Equation 3.33). The maximum likelihood

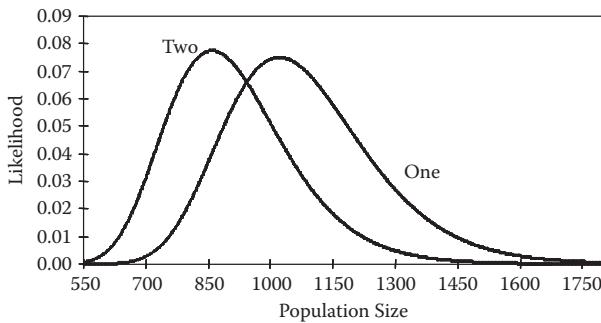


Figure 3.20

Likelihood distribution against possible population size X for two estimates of fur seal pup population size made through a tagging experiment. The right-hand curve is that from 151 pups tagged, with a subsequent sample of 222 pups found to contain 32 tagged animals (with a mode of 1,020). The left-hand curve is for the same 151 tagged pups, with a subsequent sample of 181 pups containing 31 tagged animals (with a mode of 859). The modes are the same as determined by Equation 3.33 (Example Box 3.10).

estimate of the actual population size X is determined by searching for the value of X for which $P\{m|n,p\}$ is maximized. Using the likelihood equation (Equation 3.30), we can write

$$L\{data|X\} = \left[\frac{(223)!}{33!(223-33)!} \right] \left(\frac{151}{X} \right)^{33} \left(1 - \frac{151}{X} \right)^{(223-33)} \quad (3.40)$$

Using Equation 3.35, and setting population size X to different values between 550 and 1,800, in steps of 1 (1,251 hypotheses), we gain a set of likelihoods to be plotted against their respective X values (outer curve in Figure 3.20). This can be repeated for the alternative set of observations from Table 3.1 (see Figure 3.20, Example Box 3.10).

3.4.12 Multiple Observations

When one has multiple surveys, observations, or samples, or different types of data, and these are independent of one another, it is possible to combine the estimates to improve the overall estimate. Just as with probabilities, the likelihood of a set of independent observations is the product of the likelihoods of the particular observations (Equation 3.41):

$$L\{O_1, O_2, \dots, O_n\} = L\{O_1\} \times L\{O_2\} \times \dots \times L\{O_n\} \quad (3.41)$$

This can be illustrated with the New Zealand fur seal pup tagging example (Example Box 3.10). The two independent resampling events, listed in Table 3.1, can be combined to improve the overall estimate. Instead of just taking the

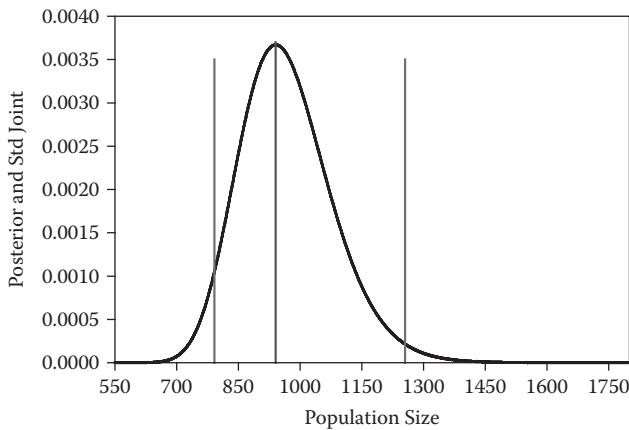
EXAMPLE BOX 3.10

Use the binomial distribution to estimate population size and confidence intervals. Column A must be extended in steps of 1 down to row 1261 so that the 1,251 hypothesized population sizes can have their relative likelihood calculated. Put =binomdist(B\$7+1,B\$6+1,B\$8/\$A11,false) in column B and copy across into column C (note the \$ symbols and their order). The +1s are the Bailey correction. The joint likelihoods are simply the separate values multiplied in column D, and these have been standardized to sum to 1 by dividing through by the sum of column D. Plot columns B and C against column A to obtain a graph akin to Figure 3.20. Vary the parameters in cells B6:C8 and consider how the likelihood profiles change. In the column next to the standardized likelihoods set out their cumulative distribution (i.e., in F11 put =E11, in F12 put =F11+E12, and copy down). Then search for the rows in which the values 0.025 and 0.975 occur. What do the population sizes at those cumulative likelihoods represent?

	A	B	C	D	E
1	Experiment	1	2		
2	Deterministic	1020.39	858.81		
3	Determ StErr	161.530	135.722		
4	Upper 95%	1336.99	=C2+1.96*C3		
5	Lower 95%	703.80	=C2-1.96*C3		
6	Sample n	222	181		
7	Tags found m	32	31		
8	Tagged p	151	151		
9	Σ Likelihoods	31.8084	=sum(C11:C1261)	1.1890	1
10	Pop. Size	1	2	Joint	Std Joint
11	550	2.906E-06	0.00058999	=B11*C11	=D11/\$D\$9
12	551	3.119E-06	0.00061706	=B12*C12	=D12/\$D\$9
13	552	3.345E-06	0.00064515	=B13*C13	=D13/\$D\$9
14	553	3.586E-06	0.00067430	Copy down	Copy down
15	Extend down	3.843E-06	0.00070453	2.707E-09	2.277E-09
16	To 1800 or to	4.116E-06	0.00073587	3.029E-09	2.548E-09
17	Row 1261	4.407E-06	0.00076835	3.386E-09	2.848E-09

average of the observations and putting those values through the deterministic equations (Table 3.1), the independent likelihood analyses can be combined using Equation 3.41. Thus, for each trial value of X , the separate likelihoods for each observation can be multiplied to give a joint likelihood (Figure 3.21, Example Box 3.10).

In this instance, where there were six separate sets of observations made, these could all, in theory, be combined to improve the overall estimate. In

**Figure 3.21**

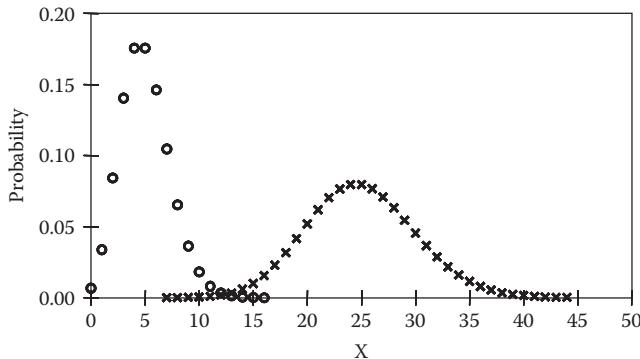
The combined likelihoods vs. possible population size for the two sets of observations made on the tagged population of New Zealand fur seal pups. The two sets of likelihood values from Figure 3.20 were multiplied together at each hypothesized instance of population size to produce this composite likelihood distribution. Note the changed scale of the likelihood axis. Also shown are the 95% confidence intervals derived from the empirical likelihood profile. Note how the upper and lower intervals are not equal, as would be the case if we used the usual standard error approach (Example Box 3.10).

practice, it might be argued that all six samples were not strictly independent and so should not really be combined. As with all analyses, as long as the procedures are defensible, then the analyses can proceed (i.e., in this case it could be argued that the samples were independent—taken sufficiently far apart so there was no learning the locations of tagged pups, etc.).

3.4.13 Likelihoods from the Poisson Distribution

The Poisson distribution is another discrete statistical distribution whose probability density function generates actual probabilities. As with the binomial distribution, however, we will continue to refer to these as likelihoods.

The Poisson distribution is often used in ecology to represent random events. Most commonly, it will be used to describe the spatial distribution of organisms (if the mean density is roughly the same as the variance of the density, this is taken to suggest a random distribution) (Seber, 1982). It reflects one of the properties of the Poisson distribution, which is that the expectation of the distribution (its mean) is the same as its variance (Hastings and Peacock, 1975). A variate X describes the number of events per sample, and this can only assume values from 0 and upwards. To be distributed in a Poisson fashion, the variable should have two properties: it should be rare, that is, its mean value should be small relative to the number of events possible; and each event must be independent of the other events, that is, each

**Figure 3.22**

Two examples of Poisson distributions. The left-hand distribution has a mean of 5, and the right-hand distribution a mean of 25. Note the top two values in each case (i.e., 4 and 5, and 24 and 25) have the same probabilities. The larger the value of μ , the closer the approximation is to a discrete normal distribution (Example Box 3.11).

event must be random with respect to each other. The Poisson probability density function has the following form:

$$P(X) = \frac{\mu^X}{e^\mu X!} \quad (3.42)$$

where X is the observed number of events and μ is the expected or mean number of events. As with the binomial distribution, the Poisson contains a factorial term, so the possibility of very small and very large numbers is a problem when computing the values of the distribution. The log transformation solves this problem (Figure 3.22, Example Box 3.11):

$$L\{X|\mu\} = \frac{\mu^X}{e^\mu X!} \quad (3.43)$$

Expanding the terms

$$LL\{X|\mu\} = \ln(\mu^X) - \ln(e^\mu X!) \quad (3.44)$$

and simplifying

$$LL\{X|\mu\} = X \cdot \ln(\mu) - \mu - \sum_{i=1}^X \ln(i) \quad (3.45)$$

Hilborn and Walters (1992) present a hypothetical example about the analysis of a tagging-multiple-recapture study, where the Poisson distribution could be used in a fisheries context. We will use a similar example to illustrate the

EXAMPLE BOX 3.11

The properties of the Poisson distribution. We can compare the Excel Poisson function with the result of the log-likelihood calculation. Name cell B1 as mu. In column A put potential values of X from 0 to 50 down to row 53. In column B put Equation 3.45 and copy down; back-transform it in column C to obtain the likelihood or probability of the X value. In column D use the Excel Poisson function for comparison. Plot column C against A as points to obtain a graph like Figure 3.22. Vary the value of μ and observe the effect on the distribution of values. How does the spread or variance of the distribution change as μ increases?

	A	B	C	D
1	μ	4		
2	X	Log-Likelihood	P(X)	P(X)
3	0	=A3*Ln(mu)-(mu+Ln(fact(A3)))	=exp(B3)	=poisson(A3,mu,false)
4	1	=A4*Ln(mu)-(mu+Ln(fact(A4)))	=exp(B4)	=poisson(A4,mu,false)
5	2	-1.9206	0.1465	0.1465
6	3	-1.6329	0.1954	0.1954
7	4	-1.6329	0.1954	0.1954
8	5	-1.8560	0.1563	0.1563
9	6	-2.2615	0.1042	0.1042
10	Extend and copy these columns down to row 53 (where X = 50)			

importance of selecting the correct probability density function to represent the residual errors for a modelled situation.

The objective of the tagging-multiple-recapture analysis here is to estimate the constant rate of total mortality consistent with the rate of tag returns. Such surveys are a form of simplified Schnable census (Seber, 1982). It is simplified because while it is based around a multiple-recapture-tagging study, there is only a single tagging event. By tagging a known number of animals and tracking the numbers being returned in a set of equally spaced time periods (could be weeks, months, or years), an estimate of the total mortality experienced by the animals concerned can be determined. We will assume 200 animals were tagged and 57, 40, 28, 20, 14, 10, and 6 fish were recaptured. In total, twenty-five tags were therefore not retaken. The instantaneous total rate of mortality (the parameter to be estimated) is assumed to apply at a constant rate through the sampling period. As time passes, the number of fish alive in a population will be a function of the starting number and the number dying. As we saw in Chapter 2, this relationship can be represented as

$$N_t = N_0 e^{-Zt} \quad \text{or} \quad N_{t+1} = N_t e^{-Z} \quad (3.46)$$

where N_t is the number of fish alive at time t , N_0 is the number of fish alive at the start of observations, and Z is the instantaneous rate of total mortality. This is a straightforward exponential decline in numbers with time, where the numbers at time t are being multiplied by the survivorship to give the numbers at time $t + 1$. If tagging has no effect upon catchability, this relationship (Equation 3.46) can be used to determine the expected rate of return of the tags.

The expected number of tags captured at time t (C_t), given N_t and Z , is simply the difference between the expected number of tagged fish alive at time t and at time $t + 1$:

$$C_t = N_t - N_{t+1} = N_t - N_t e^{-Z} = N_t (1 - e^{-Z}) = \mu \quad (3.47)$$

Thus, μ is simply the number of tags multiplied by the complement of the survivorship between periods. The Poisson distribution can give the probability of capturing X tags, given μ . For example, with two hundred tags in the population and a $(1 - e^{-Z})$ of 0.05, we have $\mu = 200 \times 0.05 = 20$, and we would expect to recapture twenty tags in the first time period. However, we can calculate the likelihood of only capturing eighteen tags:

$$L\{18|\mu = 20\} = \frac{20^{18}}{e^{20} 18!} = 0.08439 \quad (3.48)$$

By plotting likelihood/probability against hypothesized fishing mortality values in our example, a maximum can be seen to occur at approximately $Z = 0.35$ (Figure 3.23, Example Box 3.12). This plot also allows us to see that using a greater number of tags tends to increase the precision of the result (the spread of possible values becomes narrower).

It might seem to be a viable alternative to use a simple least squared residuals approach to match the number of tags observed against the predicted number of tags from Equation 3.47. Thus, we would be assuming normal random residual errors with a constant variance, and minimizing the sum of squared residuals should provide us with an optimum agreement between the observed number of tags and the expected:

$$SSQ = \sum \left(T_i - \left[N_t (1 - e^{-Z}) \right] \right)^2 \quad (3.49)$$

where T_i is the number of tags returned in period i . The difference between the two model fits relates to the different properties of the pdfs. With normal errors, the variance of the residuals is constant, but with Poisson errors, the variance increases with the expected number of tags. Strictly, with this model we should have used lognormal errors when using least squares; then the relationship with the classical catch curve of age against log numbers would become apparent and we would fit a regression to obtain

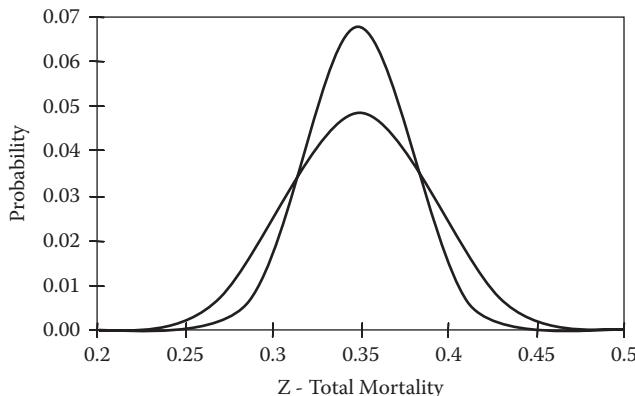


Figure 3.23

Hypothesized total mortality vs. the likelihood for the imaginary example of the results from a tagging experiment. The total mortality consistent with the tagging results using Poisson likelihoods was approximately 0.348 (Example Box 3.12). The two curves refer to different tag numbers but with equivalent relative numbers of returns; more tags give better precision expressed as a narrower distribution of possibilities.

an estimate of Z . If it seems more likely that the variance will increase with number of tags returned, then clearly the Poisson is to be preferred. This must be decided independently of the quality of fit, because both analyses provide optimum but different parameter estimations (Example Box 3.12).

3.4.14 Likelihoods from the gamma Distribution

The gamma distribution is less well known to most ecologists than the statistical distributions we have considered in previous sections. Nevertheless, the gamma distribution is becoming more commonly used in fisheries modelling, especially in the context of length-based population modelling (Sullivan et al., 1990; Sullivan, 1992). The probability density function for the gamma distribution has two parameters, a scale parameter, b ($b > 0$); an alternative sometimes used is λ , where $\lambda = 1/b$, and a shape parameter, c ($c > 0$). The distribution extends over the range of $0 \leq x \leq \infty$, where x is the variate of interest. The expectation or mean of the distribution, $E(x)$, relates the two parameters, b and c . Thus,

$$E(x) = bc \quad \text{or} \quad c = \frac{E(x)}{b} \quad (3.50)$$

The variance of the distribution is b^2c , and for values of $c > 1$, the mode is calculated as $b(c - 1)$, which is thus less than the expectation or mean (Figure 3.24).

A typical use of this distribution would be to describe the relative likelihood of each of a range of sizes to which a particular sized animal might

EXAMPLE BOX 3.12

A comparison of normal random residual errors and Poisson distributed residuals. Data from a hypothetical tagging program. The tags column records the number of tags returned over equal periods of time. Name cell C1 as Z, and cell F1 as N0. Fill columns D and E as shown. In C6 put the equivalent to Equation 3.45 = $(B6^*Ln(D6))-(D6+Ln(fact(B6)))$ and copy down. This contains the factorial function limited to a maximum X of 170. One could always use the Excel function =poisson(X, μ , false) to obtain the probabilities directly. Cell C3 is the negative sum of the log-likelihoods (=−sum(C6:C12)), and F3 the sum of the squared residuals (=sum(F6:F12)). Use the solver to minimize the negative log-likelihoods and the squared residuals in turn by changing Z (C1) and determine whether the results are the same. Plot column F against column D to observe the impact on the squared residuals of using the different residual structures. To observe the residuals proper, create a new column with =(B6-D6) in it and plot that against column D. With the least squares method the residuals are symmetrically and approximately equally arranged about the expected values. With the Poisson residuals there is an obvious trend with the expected value. Can you explain this in terms of the properties of the two statistical distributions? Put 400 in F1 and double each of the observed data values. Does the optimal solution change? What would be the advantage of tagging a larger sample at the start of the survey (cf. Figure 3.23)?

	A	B	C	D	E	F
1		Z	0.3479		N0	200
2						
3		ΣLL	17.103		SSQ	9.6696
4	t	Tags	P(Tags)	C _t = μ	Nt	(μ -Tags) ²
5	0				=N0*exp(−(Z*A5))	
6	1	57	−2.9686	=E5*(1-exp(−Z))	=N0*exp(−(Z*A6))	=(B6−D6) ²
7	2	40	−2.79279	=E6*(1-exp(−Z))	=N0*exp(−(Z*A7))	=(B7−D7) ²
8	3	28	−2.61751	29.30	70.4367	1.7026
9	4	20	−2.43277	20.69	49.7419	0.4828
10	5	14	−2.25752	14.61	35.1273	0.3777
11	6	10	−2.0836	10.32	24.8067	0.1028
12	7	6	−1.94994	7.29	17.5183	1.6599

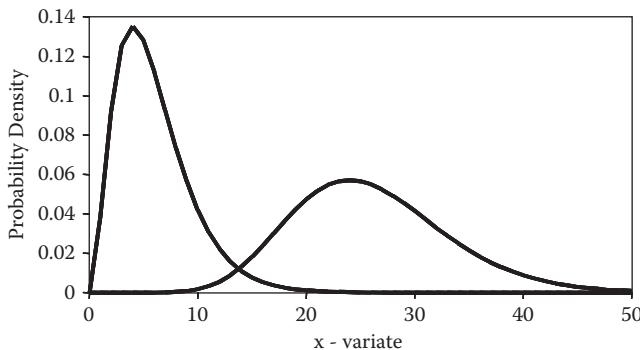


Figure 3.24

Two examples of the gamma distribution with different parameter combinations. Both curves have a scale parameter, $b = 2$. The left-hand curve has an expected value of 6 (giving a shape parameter $c = 3$), while the right-hand curve has an expectation of 26 ($c = 13$). Note the modes are at $b(c - 1)$ and not at the expectations of the distributions (Example Box 3.14).

grow. The probability density function for determining the likelihoods for the gamma distribution is (Hastings and Peacock, 1975)

$$L\{x|c,b\} = \frac{\left(\frac{x}{b}\right)^{(c-1)} e^{-\frac{x}{b}}}{b\Gamma(c)} \quad (3.51)$$

where x is the value of the variate, b is the scale parameter, c is the shape parameter, and $\Gamma(c)$ is the gamma function for the c parameter. Some books (and the Excel help file) give an alternative version:

$$L\{x|c,b\} = \frac{x^{(c-1)} e^{-x/b}}{b^c \Gamma(c)} \quad (3.52)$$

but these are equivalent algebraically. Where the shape parameter, c , takes on integer values the distribution is also known as the Erlang distribution (Hastings and Peacock, 1975):

$$L\{x|c,b\} = \frac{\left(\frac{x}{b}\right)^{(c-1)} e^{-\frac{x}{b}}}{b(c-1)!} \quad (3.53)$$

where the gamma function is replaced by factorial $(c - 1)$.

The gamma distribution is extremely flexible, ranging in shape from effectively an inverse curve, through a right-hand skewed curve, to approximately

EXAMPLE BOX 3.13

Likelihoods from the gamma and Erlang distributions. Continue the series of x values down to 50 (row 55), copying the respective column down. The Excel function in column B can give simple likelihoods or give the cumulative distribution function by using the “true” parameter instead of the “false” one. In this way, true probabilities can be derived. The Erlang distribution is identical to the gamma distribution when c is an integer; put $=((A5/\$B\$1)^{(\$B\$2-1)}*\exp(-A5/\$B\$1)) / (\$B\$1*fact(\$B\$2-1))$ into C5 and copy down. Plot column B against A to mimic Figure 3.24. Vary b and $E(x)$ and determine the affect upon the curve. When c is not an integer, the fact function in the Erlang distribution truncates c to give an integer.

	A	B	C	D
1	Shape b	2	Mode	$=B1*(B2-1)$
2	Scale c	4	Variance	$=(B1^2)*B2$
3	E(x)	8		
4	x	Gamma	Erlang	
5	0.1	$=gammadist(A5,\$B\$2,\$B\$1,false)$	9.91E-06	
6	1	$=gammadist(A6,\$B\$2,\$B\$1,false)$	0.006318	
7	2	0.030657	0.030657	
8	3	0.062755	0.062755	
9	4	0.090224	0.090224	
10		Extend or copy down to row 55 where x = 50		

normal in shape (Figure 3.24, Example Box 3.13). Its flexibility makes it a very useful function for simulations (see Chapter 7).

It is possible that one might fit the gamma function to tagging data in order to provide a probabilistic description of how growth proceeds in a species (but one would need a great deal of tagging data; Punt et al., 1997a). In these instances of fitting the gamma distribution, the presence of the gamma function in the equation implies that it will be liable to numerical overflow errors within the numerical limits of the computer used. It would always be risk averse to work with log-likelihoods instead of likelihoods:

$$LL\{x|c,b\} = \left((c-1) \ln\left(\frac{x}{b}\right) - \frac{x}{b} \right) - (Ln(b) + Ln(\Gamma(c))) \quad (3.54)$$

This may appear to be rather of little assistance, as we are still left with the trouble of calculating the natural log of the gamma function. Surprisingly, however, this is relatively simple to do. Press et al. (1989) provide an excellent

algorithm for those who wish to write their own procedure, and there is even a GammaLn function in Excel.

An example of using the gamma distribution in a real fisheries situation will be produced when we consider growth and its representation. It will be demonstrated when it is used to create the growth transition matrices used in length-based models.

3.4.15 Likelihoods from the Multinomial Distribution

We use the binomial distribution when we have situations where there can be two possible outcomes to an observation (true/false, tagged/untagged). However, there are many situations where there are going to be more than two possible discrete outcomes to any observation, and in these situations, we should use the multinomial distribution. In this multivariate sense, the multinomial distribution is an extension of the binomial distribution. The multinomial is another discrete distribution that provides distinct probabilities and not just likelihoods.

With the binomial distribution we used $P(m|n,p)$ to denote the likelihoods. With the multinomial, this needs to be extended so that instead of just two outcomes (one probability p), we have a probability for each of k possible outcomes (p_k) in our n trials. The probability density function for the multinomial distribution is (Hastings and Peacock, 1975)

$$P\{x_i|n, p_1, p_2, \dots, p_k\} = n! \prod_{i=1}^k \frac{\hat{p}_i^{x_i}}{x_i!} \quad (3.55)$$

where x_i is the number of times an event of type i occurs in n trials, n is the sample size or number of trials, and the p_i are the separate probabilities for each of the k types of events possible. The expectation of each type of event is $E(x_i) = np_i$, where n is the sample size and p_i the probability of event type i . Because of the presence of factorial terms that may lead to numerical overflow problems, a log-transformed version of Equation 3.55 tends to be used:

$$LL\{x_i|n, p_1, p_2, \dots, p_k\} = \sum_{j=1}^n Ln(j) + \sum_{i=1}^k \left[x_i Ln(\hat{p}_i) - \sum_{j=1}^x Ln(j) \right] \quad (3.56)$$

In real situations the factorial terms will be constant and are usually omitted from the calculations; thus,

$$LL\{x_i|n, p_1, p_2, \dots, p_k\} = \sum_{i=1}^k [x_i Ln(\hat{p}_i)] \quad (3.57)$$

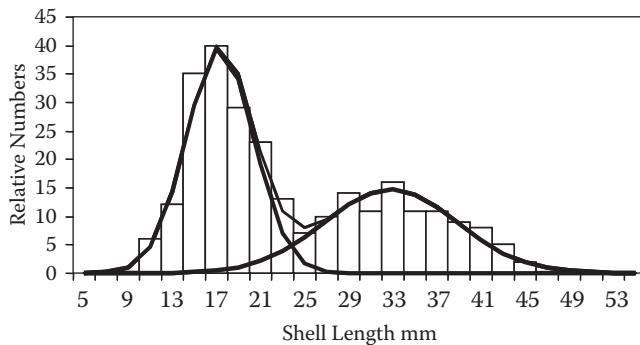


Figure 3.25

A subset of juvenile abalone data from Hope Island, Tasmania, taken in November 1992. Two modes are obvious and the solid line is the maximum likelihood best fit combination of two normal distributions (Example Box 3.14).

Examples may provide a better indication of the use of this distribution. Whenever we are considering situations where probabilities or proportions of different events or categories are being combined we should use the multinomial. This might happen in a catch-at-age stock assessment model that uses proportional catch-at-age. The model will predict the relative abundance of each age class, and these will be combined to produce sets of expected catch-at-age. The comparison of the observed with the expected proportions is often best done using the multinomial distribution. Another common use is in the decomposition of length frequency data into constituent modes (e.g., MacDonald and Pitcher, 1979; Fournier and Breen, 1983). We will consider the latter use and develop an example box to illustrate the ideas.

In November 1992, sampling began of juvenile abalone on Hope Island, near Hobart, Tasmania, with the aim of investigating juvenile abalone growth through the analysis of modal progression (Figure 3.25).

The main assumption behind the analysis of length frequency information is that observable modes in the data relate to distinct cohorts or settlements. Commonly a normal distribution is used to describe the expected relative frequency of each cohort (Figure 3.25), and these are combined to generate the expected relative frequency in each size class. The normal probability density function is commonly used to generate the expected relative proportions of each of the k observed size categories, for each of the n age classes. We subtract the cumulative probability for the bottom of each size class i from the cumulative probability of the top of each size class:

$$p_{S_k} = \int_{-\infty}^{TopS_i} \frac{1}{\sigma_n \sqrt{2\pi}} e^{\frac{-(S_i - \mu_n)^2}{2\sigma_n^2}} - \int_{-\infty}^{BotS_i} \frac{1}{\sigma_n \sqrt{2\pi}} e^{\frac{-(S_i - \mu_n)^2}{2\sigma_n^2}} \quad (3.58)$$

where μ_n and σ_n are the mean and standard deviation of the normal distributions describing each cohort n , and S_i is the observed frequency of size or length class i . Alternative cumulative statistical distributions, such as the lognormal or gamma, could be used in place of the normal. As we are dealing with expected relative proportions and not expected relative numbers, it is not necessary to be concerned with expected numbers in each size class. However, it is suggested that it is best to have a graphical output, similar to Figure 3.25, in order to have a visual appreciation of the quality of fit. To obtain expected frequencies, it is necessary to constrain the total expected numbers to approximately the same as the numbers observed. The log-likelihoods from the multinomial are

$$LL\{S|\mu_n, \sigma_n\} = -\sum_{i=1}^k S_i \ln(\hat{p}_i) = -\sum_{i=1}^k S_i \ln\left(\frac{\hat{S}_i}{\sum \hat{S}_i}\right) \quad (3.59)$$

where the μ_n and σ_n are the mean and standard deviations of the n cohorts being considered. There are k length classes and S_i is the observed frequency of size or length class i , while p_i hat is the expected proportion of length class i from the combined normal distributions. Being the negative log-likelihood, the objective would be to minimize Equation 3.59 to find the optimum combination of the n normal distributions (cohorts; Example Box 3.14).

3.5 Bayes' Theorem

3.5.1 introduction

There has been a recent expansion in the use of Bayesian statistics in fisheries science (McAllister et al., 1994; McAllister and Ianelli, 1997; Punt and Hilborn, 1997; Chen and Fournier, 1999; see Dennis, 1996, for an opposing view). An excellent book relating to the use of these methods was produced by Gelman et al. (2004). Here we are not going to attempt a review of the methodology as it is used in fisheries; a detailed introduction can be found in Punt and Hilborn (1997), and there are many more recent examples. Instead, we will concentrate upon the foundation of Bayesian methods as used in fisheries and draw some comparisons with maximum likelihood methods.

Bayes' theorem is based around a manipulation of conditional probabilities. Thus, if an event, labelled A follows a number of possible events B_i , then we can develop Bayes' theorem by considering the probability of observing a particular B_i given that A has occurred:

$$P(B_i|A) = \frac{P(A \& B_i)}{P(A)} \quad (3.60)$$

EXAMPLE BOX 3.14

Using the multinomial to fit multiple normal distributions to length-frequency data, extend the series in column A in steps of two down to 55 in row 32, and similarly in column B. Extend the observed frequencies such that, as shown, in row 15 with the bottom of the size class at 21 and the top at 23, obs = 23, then Bot of 23 has obs = 13, then extending column F downwards, 7, 10, 14, 11, 16, 11, 11, 9, 8, 5, 2, and then zero for Bot of 47 to 55. Put $=\text{normdist}(\$B7,C\$1,C\$2,\text{TRUE})-\text{normdist}(\$A7,C\$1,C\$2,\text{TRUE})^*\text{C}3$ into C7 (Equation 3.58 times N), and copy it into D7, and down to row 32. Row 5 contains the sum of each of the columns, as in C5, $=\text{sum}(C7:C32)$. Plot column F as a histogram against column A. Add column E to this plot as a line chart (cf. Figure 3.25). The values in C1:D3 are initial guesses, the quality of which can be assessed visually by a consideration of the plotted observed vs. expected. Cell G2 contains $(-\text{sum}(H7:H32))+(\text{F5}-\text{E5})^2$. The second term is a penalty term designed to force the sum of the expected frequencies to equal the observed total. This has no effect on the relative proportions of each cohort. Use the solver to minimize G2 by changing cells C1:D3. Try different starting points. Set up a new column that provides normal residuals, i.e., $=(\text{F7}-\text{E7})^2$, sum, and minimize them (use the same penalty term to limit the relative frequencies). Are the optimum answers different? Compare the graphical images. Which do you prefer, that from multinomial or that from normal random residuals?

	A	B	C	D	E	F	G	H
1		Mean	18.3318	33.7929				
2		Var	2.9819	5.9919			ML	706.2087
3		N	151.0604	110.9462				
4								
5		Sum	151.060	110.940	262	262		
6	Bot	Top	Cohort1	Cohort2	Expt	Obs	P _L	LL
7	5	7	0.01033	0.00035	=C7+D7	0	=E7/E\$5	=F7*Ln(G7)
8	7	9	0.12135	0.00152	=C8+D8	0	=E8/E\$5	=F8*Ln(G8)
9	9	11	0.92078	0.00595	0.92673	0	0.00354	0.00000
10	11	13	4.51878	0.02096	4.53973	6	0.01733	-24.33285
11	13	15	14.35710	0.06603	14.42313	12	0.05505	-34.79413
12	15	17	29.55476	0.18633	29.74109	35	0.11352	-76.15351
13	17	19	39.43916	0.47081	39.90997	40	0.15233	-75.26872
14	19	21	34.12401	1.06524	35.18926	29	0.13431	-58.22050
15	21	23	19.14159	2.15824	21.29983	23	0.08130	-57.72184
16	23	25	6.95823	3.91567	10.87390	13	0.04150	-41.36572

In an analogous fashion, we can consider the conditional probability of the event A given a particular B_i :

$$P(A|B_i) = \frac{P(A \& B_i)}{P(B_i)} \quad (3.61)$$

Rearranging Equation 3.61,

$$P(A|B_i)P(B_i) = P(A \& B_i) \quad (3.62)$$

Substituting Equation 3.62 into Equation 3.60, we obtain the basis of Bayes' theorem:

$$P(B_i|A) = \frac{P(A|B_i)P(B_i)}{P(A)} \quad (3.63)$$

If we translate the A as the data observed from nature and the B_i as the separate hypotheses (as models plus parameter values), we can derive the form of Bayes' theorem as it is used in fisheries. The $P(A|B_i)$ is just the likelihood of the data A given the hypothesis B_i . The $P(B_i)$ is the probability of the hypothesis before any analysis or consideration of the data. This is known as the prior probability of the hypothesis B_i . The $P(A)$ is simply the combined probability of all the combinations of data and hypotheses, which is why this works so well for closed systems such as card games and other constrained games of chance.

$$P(A) = \sum_{i=1}^n P(A|B_i)P(B_i) \quad (3.64)$$

3.5.2 Bayes' Theorem

As stated earlier, Bayes' theorem relates to conditional probabilities (Gelman et al., 2004), so that when we are attempting to determine which of a series of n discrete hypotheses is most probable, we use

$$P\{H_i|data\} = \frac{L\{data|H_i\}P\{H_i\}}{\sum_{i=1}^n [L\{data|H_i\}P\{H_i\}]} \quad (3.65)$$

where H_i refers to hypothesis i out of the n being considered (a hypothesis would be a particular model with a particular set of parameter values) and the data are just the data to which the model is being fitted. $P\{H_i|data\}$ is the *posterior* probability of the hypothesis (a strict probability between 0 and 1)

given the data (and any prior information). $P\{H_i\}$ is the *prior* probability of the hypothesis before the observed data are considered; once again, this is a strict probability where the sum of the priors for all hypotheses being considered must be 1. Finally, $L\{data|H_i\}$ is the likelihood of the data given hypothesis i , just as previously discussed in the maximum likelihood section (analogous, for example, to Equations 3.7 and 3.35). If the parameters are continuous variates (e.g., L_∞ and K from the von Bertalanffy curve), alternative hypotheses have to be described using a vector of continuous parameters instead of a list of discrete parameter sets, and the Bayesian conditional probability becomes continuous:

$$P\{H_i|data\} = \frac{L\{data|H_i\}P\{H_i\}}{\int L\{data|H_i\}P\{H_i\}dH_i} \quad (3.66)$$

In fisheries, to use Bayes' theorem to generate the required posterior distribution we need three things:

1. A list of hypotheses to be considered with the model under consideration (i.e., the combinations of parameters and models we are going to try)
2. A likelihood function required to calculate the probability density of the observed data given each hypothesis i , $L\{data|H_i\}$
3. A prior probability for each hypothesis, normalized so that the sum of all prior probabilities is equal to 1.0

Apart from the requirement for a set of prior probabilities, this is identical to the requirements for determining the maximum likelihood. The introduction of prior probabilities is, however, a big difference, and is something we will focus on in our discussion.

If there are many parameters being estimated in the model, the integration involved in determining the posterior probability in a particular problem can involve an enormous amount of computer time. There are a number of techniques used to determine the Bayesian posterior distribution, and Gelman et al. (2004) introduce the more commonly used approaches. We will introduce and discuss one flexible approach to estimating the Bayesian posterior probability in Chapter 8, dealing with the characterization of uncertainty. This is effectively a new method for model fitting, but for convenience will be included in the section on uncertainty. The explicit objective of a Bayesian analysis is not just to discover the mode of the posterior, which in maximum likelihood terms might be thought to represent the optimum model. Rather, the aim is to explicitly characterize the relative probability of the different possible outcomes from an analysis, that is, to characterize the uncertainty about each parameter and model output. There may be a most probable

result, but it is presented in the context of the distribution of probabilities for all other possibilities.

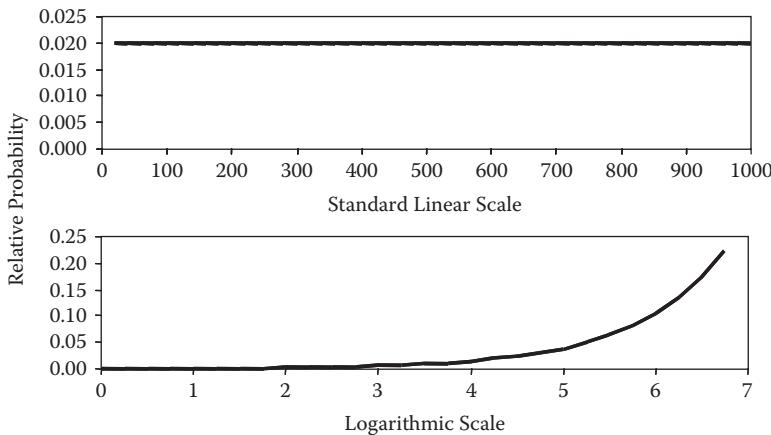
3.5.3 Prior Probabilities

There are no constraints placed on how prior probabilities are determined. One may already have good estimates of a model's parameters from previous work on the same or a different stock of the same species, or at least have useful constraints on parameters (such as negative growth not being possible or survivorship > 1 being impossible). If there is insufficient information to produce informative prior probabilities, then commonly a set of uniform or noninformative priors are adopted in which all hypotheses being considered are assigned equal prior probabilities. This has the effect of assigning each hypothesis an equal weight before analysis. Of course, if a particular hypothesis is not considered in the analysis, this is the same as assigning that hypothesis (model plus particular parameters) a weighting or prior probability of zero.

One reason why the idea of using prior probabilities is so attractive is that it is counterintuitive to think of all possible parameter values being equally likely. Any experience in fisheries and biology provides one with prior knowledge about the natural constraints on living organisms. Thus, for example, even before thorough sampling it should have been expected that a deep-water (>800 m depth) fish species, like orange roughy (*Hoplostethus atlanticus*), would likely be long-lived and slow growing. This characterization is a reflection of the implications of living in a low-temperature and low-productivity environment. One of the great advantages of the Bayesian approach is that it permits one to move away from the counterintuitive assumption of all possibilities being equally likely. One can attempt to capture the relative likelihood of different values for the various parameters in a model in a prior distribution. In this way, prior knowledge can be directly included in analyses.

Where this use of prior information can lead to controversy is when moves are made to include opinions. For example, the potential exists for canvassing a gathering of stakeholders in a fishery for their belief on the state of such parameters as current biomass (perhaps relative to five years previously). Such a committee-based prior probability distribution for a parameter could be included into a Bayesian analysis as easily as could the results of a previous assessment. There is often debate about whether priors from such disparate sources should be equally acceptable in a formal analysis. In a discussion on the problem of justifying the origin of priors, Punt and Hilborn (1997, p. 43) state:

We therefore strongly recommend that whenever a Bayesian assessment is conducted, considerable care should be taken to document fully the basis for the various prior distributions.... Care should be taken when selecting the functional form for a prior because poor choices can lead to incorrect inferences. We have also noticed a tendency to underestimate uncertainty, and hence to specify unrealistically informative priors—this tendency should be explicitly acknowledged and avoided.

**Figure 3.26**

The same data plotted on a linear scale (upper panel) and a natural logarithmic scale (lower panel). The uniform distribution on the linear scale is distorted when perceived in logarithmic space. Note the vertical scale in the log panel is an order of magnitude greater than on the linear scale.

The debate over the validity of using informative priors has been such that Walters and Ludwig (1994) recommended that noninformative priors be used as a default in Bayesian stock assessments. However, besides disagreeing with Walters and Ludwig, Punt and Hilborn (1997) highlighted a problem with our ability to generate noninformative priors (Box and Tiao, 1973). The problem with generating noninformative priors is that they are sensitive to the particular measurement system. Thus, a prior that is uniform on a linear scale will not appear linear on a log scale (Figure 3.26).

As fisheries models tend to be full of nonlinear relationships, the use of noninformative priors is controversial because a prior that is noninformative with respect to some parameters will most likely be informative toward others. While such influences may be unintentional, they cannot be ignored. The implication is that information may be included into a model in a completely unintentional manner, which is one source of controversy when discussing prior probabilities. If priors are to be used, then Punt and Hilborn's (1997) exhortation to fully document their origin and properties is extremely sensible advice.

3.5.4 An example of a useful informative Prior

We already have experience with a form of Bayesian analysis when we were considering binomial likelihoods (see Example Box 3.10). We took two likelihood profiles of a fur seal pup population estimate, each made from 1,251 separate likelihoods, multiplied the respective likelihoods for each of 1,251 hypothesized population sizes, and standardized the results to sum to 1 in order to obtain approximate percentile confidence intervals. This algorithm may be represented as

$$P\{H_i|data\} = \frac{L_1\{data|H_i\}L_2\{data|H_i\}}{\sum_{i=1}^{1251} [L_1\{data|H_i\}L_2\{data|H_i\}]} \quad (3.67)$$

where L_i refers to the likelihoods for the i th population estimation and the H_i refer to the 1,251 separate hypothesized population sizes. If we had standardized the first population estimate's likelihood profile to sum to 1, we could then have treated that as a prior on the population size. This could then have been used in Equation 3.65, along with the separate likelihoods for the second population estimate, and a formal posterior distribution for the overall population estimate been derived. Although these two algorithms sound rather different, they are, in fact, equivalent, as can be seen algebraically. Treating the first estimate as a prior entails standardizing each hypothesized population size's likelihood to sum to 1:

$$P\{H_i\} = \frac{L\{data|H_i\}}{\sum_{i=1}^n L\{data|H_i\}} \quad (3.68)$$

where n is the number of separate hypotheses being compared (1,251 in Example Box 3.10; see Example Box 3.15). The denominator in Equation 3.68 is, of course, a constant. Thus, expanding Equation 3.65 using Equation 3.68 we obtain

$$P\{H_i|data\} = \frac{L_2\{data|H_i\} \frac{L_1\{data|H_i\}}{\sum_{i=1}^n L_1\{data|H_i\}}}{\sum_{i=1}^n \left[L_2\{data|H_i\} \frac{L_1\{data|H_i\}}{\sum_{i=1}^n L_1\{data|H_i\}} \right]} \quad (3.69)$$

As the sum of separate likelihoods term is a constant, it can be moved out of the denominator's overall summation term and we can shift the numerator's inverse sum of likelihoods below the divisor. When the two are brought together, they can thus cancel out:

$$= \frac{L_2\{data|H_i\}L_1\{data|H_i\}}{\sum_{i=1}^n L_1\{data|H_i\} \sum_{i=1}^n [L_2\{data|H_i\}L_1\{data|H_i\}]} \quad (3.70)$$

EXAMPLE BOX 3.15

Bayesian posteriors are equal to standardized likelihoods when the prior probability is uniform. Recover Example Box 3.10 and extend it to include a column (perhaps in G or H) in which the likelihoods for experiment 1 are standardized. Thus, in G11 put =B11/\$B\$9, and copy down. Use this as a prior by generating another column of numbers, so in H11 put =G11*C11, and copy down. Sum that column into H9. Finally, in column I (cell I11) put =H11/\$H\$9, and copy down. Column I would then contain the posterior distribution according to Equation 3.65. Plot this against column A and compare the curve with that found in column E (the standardized joint distribution). How similar are to two curves?

which is identical to Equation 3.67. Thus, the combination of two likelihood profiles from two separate assessments can be considered as an acceptable form of Bayesian analysis; that is, the origin of the prior distribution is not problematical.

With discrete statistical distributions, there is no problem with combining the separate likelihoods because they are probabilities and not just likelihoods. With the continuous variables found in most fisheries models, numerical methods would be needed to conduct the integration required, and this means that the answers would only be approximate. Nevertheless, the approximation would be acceptable assuming the integral step was sufficiently fine.

3.5.5 Noninformative Priors

If there is no earlier assessment and noninformative prior probabilities are to be used, then an even simpler adjustment can be made to Bayes' theorem. In the case of truly noninformative priors, the prior probability for each hypothesis would be equal or constant for each hypothesis, and thus the prior probability term could be removed from the summation term in the denominator:

$$P\{H_i | \text{data}\} = \frac{P\{H_i\} P\{\text{data}|H_i\}}{P\{H_i\} \sum_{i=1}^n P\{\text{data}|H_i\}} \quad (3.71)$$

whereupon the prior terms can be cancelled and we are left simply with the standardized likelihoods (each separate likelihood divided by the sum of the likelihoods). Thus, using truly noninformative priors is the same as not using priors at all. The simplest approach then would be to omit them from the analysis altogether. Walters and Ludwig (1994) also point this out, but then proceed to discuss the problem of the difficulty of generating noninformative priors, and so do not take this further.

This all raises the importance of the problem of the apparent impossibility of generating priors that are noninformative over all parameters and model outputs. For a particular model, if generating a truly noninformative prior across all parameters and model outputs requires a great deal of work, or it even appears to be impossible, then trying to use noninformative priors would actually risk generating a biased analysis. If these interactions between prior distributions for different parameters and the effects of nonlinearity within the model act to distort the priors so that they are no longer truly noninformative, then we are left in a quandary. What this would imply is that even if we restrict ourselves to a straightforward maximum likelihood analysis as in Equation 3.70 (equivalent to using uniform priors in the linear scale), then we are really imputing informative priors in some parts of the model. This unwitting imputation of potential bias is startling and raises many questions about the optimum approach to any nonlinear analyses. It appears to imply that it is impossible to conduct a standardization of a full set of likelihoods without implying an unknown set of informative prior probabilities.

In opposition to this idea of the automatic imputation of informative priors, it appears that if priors are simply omitted from the analysis, then, from Equation 3.71, the omitted priors must have been, by definition, noninformative (on all scales) and somehow equal on all scales. This is a matter for more formal investigation, but its importance is crucial for the wide acceptance and further developments in the use of Bayesian analysis in fisheries modelling.

3.6 Concluding Remarks

Fisheries modellers can be an argumentative crowd, and each seems to have developed a set of methods that they favour. As seen above, there does not appear to be a criterion of quality of model fit that has no associated problems. Claims made that identify a particular strategy of analysis as being the optimum or best practice should therefore be contemplated with some doubt. One can use either maximum likelihood methods or Bayesian methods to generate assessments giving similar forms of output. At least some of the expressed enthusiasm for Bayesian methods appears to be excessive.

The optimum method to use in any situation depends largely on the objectives of the analysis. If all one wants to do is to find the optimum fit to a model, then it does not really matter whether one uses least squares, maximum likelihood, or Bayesian methods. Sometimes it can be easier to fit a model using least squares and then progress to using likelihoods or Bayesian methods to create confidence intervals and risk assessments.

Confidence intervals around model parameters and outputs can be generated using traditional asymptotic methods (guaranteed symmetric and, with strongly nonlinear models, only roughly approximate), using likelihood

profiles or by integrating Bayesian posteriors (the two are obviously strongly related), or one can use bootstrapping or Monte Carlo techniques.

It is not the case that the more detailed areas of risk assessment are only possible using Bayesian methods. Bootstrapping and Monte Carlo methods provide the necessary tools with which to conduct such work. The primary concern should be to define the objective of the analysis. It would be bad practice to fit a model and not give some idea of the uncertainty surrounding each parameter and the sensitivity of the model's dynamics of the various input parameters.

Because there is no clear winner among the methodological approaches, if one has the time, it is a reasonable idea to use more than one approach (especially a comparison of likelihood profiles, Bayesian posteriors, and bootstrapping). If significant differences are found, then it would be well to investigate the reasons behind them. If different procedures suggest significantly different answers, it could be that too much is being asked of the available data and different analyses would be warranted.

4

Computer-Intensive Methods

4.1 Introduction

“Computer-intensive methods” is a phrase used to refer to a number of methods that include randomization tests (= permutation tests), jackknife techniques, bootstrap techniques, and Monte Carlo simulations and tests. In this chapter we will briefly introduce all four methods along with some of their uses. Fuller descriptions and examples will be presented in the following chapters.

Computer-intensive can sound daunting, but only if it is confused with meaning intensive computer programming (though some facility with writing relatively simple macros or computer programs is necessary). The word *intensive* refers to the use of available computing power. Such statistics and methods are not new. Randomization tests were discussed by Fisher (1936), but have recently become much more widespread and popular as a direct result of the easy availability of powerful computers (Good, 1994; Manly, 1991, 1997).

The history of statistics is relatively short and has a number of phases. The first developments in statistics of importance to our work here relate to parametric statistics. These statistics are dependent upon known probability distributions (such as the normal or binomial distributions, as in Chapter 3), and when they are used they require that the populations being sampled adhere to assumptions peculiar to the distributions concerned. Parametric statistics form the core of “traditional” statistics (analysis of variance (ANOVA), regression, sample comparison, experimental design, etc.).

The second phase of particular interest to us was the production of nonparametric statistics. Ronald A. Fisher (1936) first mooted the idea of testing hypotheses concerning observed patterns between groups of individuals by using a randomization test. These tests compare an observed pattern among groups with those possible by randomly allocating the available data across the groups of interest. Of course, with any reasonable amount of data such an approach was simply not practical at a time (1930s) when all calculations had to be done by hand or on a mechanical hand calculator. Nevertheless, as a theoretical insight it eventually led to the development of a wide range of nonparametric test statistics. Almost all common nonparametric statistics

have their basis in replacing the observed test data with ranks and computing test statistics based upon permutation tests (Good, 1994). Using ranks removes the unique or idiosyncratic aspects of each situation so that the same probability distribution of possible arrangements can be applied to every hypothesis test. The term *nonparametric* implies that the parametric form of the underlying population distribution need not be specified exactly. In other words, the data do not have to match the assumptions behind any particular probability density function.

Most recently there has been a growth of interest in general randomization tests, plus the development of the newer methods of jackknife and bootstrap statistics. All of these require far more calculations than classical methods, but with increasing computing power, these approaches may supersede older methods that depend on parametric statistical distributions. They will certainly constitute an important part of the future of statistical analysis, especially of biological data, which often is nonnormal.

4.2 Resampling

The notion of resampling a population is fundamental to many statistics. If a set of data is normally distributed, then given its mean and standard deviation, we can estimate the standard error of the mean analytically:

$$\text{StErr} = \frac{\sigma}{\sqrt{n}} \quad (4.1)$$

where n is the number of observations and σ is the standard deviation.

An alternative to this standard analytical method would be to obtain a number of independent samples from the original population (i.e., resample the population a number of times). The standard deviation of the multiple sample means would also provide an estimate of the standard error. Thus, the notion of resampling should not be considered remarkable. This is fortunate because resampling in one form or another is the foundation of all the computer-intensive methods to be discussed. While resampling is not unusual, what is resampled, and how it is resampled, differs between the methods.

In the following sections and examples we will be considering a range of available computer-intensive methods. Before this, we need to introduce a distinction concerning the approach used when making observations (sampling) that will be important in what follows. Sampling without replacement means making an observation from a population by removing individuals. Further observations from a sample could obviously not contain those particular individuals again. This contrasts with sampling with replacement, where an observation is made nondestructively, i.e., without removing individuals.

Clearly, when sampling with replacement, subsequent observations could be repeats of observations already made.

4.3 Randomization Tests

Randomization tests are used to test the null hypothesis that an observed pattern is typical of a random event. The null hypothesis suggests that each group of observations merely represents a random sample from a single population. The observed pattern among groups must be characterized by a test statistic (e.g., a mean difference between two groups). To test whether the observed pattern is significantly different from a random pattern, the data from all groups are first combined. The observed test statistic is then compared with that obtained by randomly reallocating individuals from the combined data back to the groups to be compared (i.e., resampling without replacement). Of course, it is of no value to do this only once. The random resampling without replacement into the groups and recalculating the test statistic must be repeated many times (1,000+ being typical). The observed test statistic for the original arrangement is compared with the empirical distribution of that test statistic given the data available. If the pattern observed is not different from random, then the observed test statistic value will be typical of those generated by random groupings. A significant difference is indicated by the observed test statistic lying beyond or at the extremes of the empirical distribution obtained from randomizing the data among the groups.

Permutation tests are good for testing hypotheses, but standard errors cannot be calculated using this approach, and confidence intervals on parameter estimates can only be fitted very inefficiently (Curnow, 1984).

Fisher (1936) first provided a theoretical description of randomization tests (Pitman, 1937a, 1937b). Reviews of randomization techniques, with contrasting views on some methods, are given by Manly (1997) and Edgington (1995). There is a large and expanding volume of literature on randomization tests providing both examples and theoretical developments (Lindley and Novick, 1981). Some controversy has occurred, but this has not prevented continued development (Basu, 1980, plus associated comments; e.g., Hinkley, 1980; Kempthorne, 1980; Lane, 1980; Lindley, 1980). A detailed review and bibliography relating to randomization tests is given by Good (1994).

4.4 Jackknife Methods

The name is reported as coming from considering this statistical method as a flexible tool rather like a multifunction pocketknife. By considering known

subsets of the available data, one can produce estimates of standard errors as well as detect whether any parameter estimates are biased. Subsetting the data involves estimating the statistics of interest on all possible combinations of the available data minus one data point: in a data set of n values there will be n subsets of $(n - 1)$ data points, and these are used to calculate the jackknife replicates. Using the jackknife replicates, one can calculate what are known as pseudovalues for the statistic of interest. The difference between the original sample mean and the mean of the n pseudovalues provides the estimate of bias. The value of this methodology comes when one is not estimating the sample mean (which is an unbiased estimate) but some other parameter. The pseudovalues can also be used to calculate jackknife estimates of the parameter of interest and its standard error. Confidence intervals can be fitted using this standard error estimate, but there is a problem deciding how many degrees of freedom to use, so this approach is no longer recommended.

The jackknife methodology was first discussed by Quenouille (1956), who recommended the approach as a method for removing bias from parameter estimates. Tukey gave a paper to a conference of the American Institute of Statistics at Ames in Iowa. He introduced the notion of using the jackknife approach to produce parameter estimates with estimates of standard errors. Only the abstract of the conference talk was printed (Tukey, 1958), but that and his talk were enough to set off a number of developments (Hinkley, 1983). Jackknifing is discussed in Chapter 6.

4.5 Bootstrapping Methods

Data sampled from a population are treated as being (assumed to be) representative of that population and the underlying probability density distribution of expected sample values. Given an original sample of n observations, bootstrap samples would be random samples of n observations taken from the original sample with replacement. Bootstrap samples (i.e., random resampling from the sample data values with replacement) are assumed to approximate the distribution of values that would have arisen from repeatedly sampling the original sampled population. Each of these bootstrapped samples is treated as an independent random sample from the original population. This approach appears counterintuitive to some, but can be used to fit standard errors, confidence intervals, and to test hypotheses. The name *bootstrap* is reported to derive from the story *The Adventures of Baron Munchausen*, in which the baron escaped drowning by picking himself up by his own bootstraps and thereby escaping from a well (Efron and Tibshirani, 1993).

Efron (1979) first suggested bootstrapping as a practical procedure. He states (Efron and LePage, 1992; Lepage and Billard, 1992) that development of the bootstrap began as an attempt to better understand the jackknife but

quickly developed beyond the potential of the jackknife. The bootstrap could be applied to problems beyond those of estimating bias and standard errors; in particular, it was an approach that could provide better confidence intervals than those from the jackknife. Bickel and Freedman (1981) provided a demonstration of the asymptotic consistency of the bootstrap (convergent behaviour as the number of bootstrap samples increased). Given this demonstration, the bootstrap approach has been applied to numerous standard applications, such as multiple regression (Freedman, 1981; ter Braak, 1992) and stratified sampling (Bickel and Freedman, 1984, who found a limitation). Efron eventually converted the material he had been teaching to senior-level students at Stanford into a general summary of progress to date (Efron and Tibshirani, 1993).

4.6 Monte Carlo Methods

Monte Carlo simulations are carried out with a mathematical model of a situation plus a series of model parameters. Some of the parameters will not be known perfectly (i.e., there is uncertainty), so that instead of a particular value, one would have a probability density distribution from which the parameter values are derived (e.g., normal, lognormal, hypergeometric, etc.). Each run of a Monte Carlo simulation involves randomly selecting a value for the variable, parameter, or data values, from the known distribution(s), and then determining the model's output. This process can be repeated many times to test hypotheses or determine confidence intervals. Such resampling from a theoretical distribution of values is effectively sampling with replacement (one could, in theory, obtain the same value more than once). The probability density distribution can never be exhausted of values.

Monte Carlo testing is often about comparing what was actually observed in a system with what one obtains from a model of the system. It involves an assessment of the properties of the system. In a hypothesis testing situation, if any of the hypotheses included in the model are incorrect, then the model output would not be expected to be consistent with the available observations.

Monte Carlo simulations are also the basis of risk assessment methods in fisheries by projecting the expected path of a fishery when it is exposed to a particular harvest strategy (e.g., a constant fishing mortality rate or constant catch level). When more than one of a model's parameters are each free to vary over a range of values, then the model output also becomes variable. If the model is run enough times, one would expect to be able to generate a frequency distribution of possible outcomes (perhaps the biomass remaining in a stock after some years of exploitation at a given total allowable catch (TAC)). From this distribution one could derive the likelihood of various outcomes (e.g., stock collapse—defined in a particular way, or current biomass falling below defined levels). In New Zealand, for example, such a model

was used to determine the impact on orange roughy (*Haplostethus atlanticus*) stocks of different projected catch rates over the next twenty years (Francis, 1992). Thereby, the option of reducing the commercial catch slowly was demonstrated to be more risky for the stock than a rapid decline in catch levels.

4.7 Bayesian Methods

It is becoming common for many fisheries' stock assessments to be conducted using a Bayesian framework. This cannot be well characterized using only a few sentences and will be introduced more completely later. Having said that, Bayesian analyses can be thought of as attempting to describe the uncertainty around model estimates using a multidimensional likelihood profile. Bayesian methods attempt to combine maximum likelihood methods in a formal manner with prior information to produce the final posterior probability distributions that describe the relative probability of different outcomes. This involves combining the probability density function selected for the maximum likelihood analysis of the data used in the stock assessment with the probability density function used to describe the prior probability distribution of the various parameters being estimated. Some combinations of likelihood distributions and prior probabilities (so-called conjugate priors; Gelman et al., 2004) permit an analytical solution for the Bayesian analysis; however, most fisheries' assessments are sufficiently complex that no such simple solution is possible (Walters and Ludwig, 1994). In most fisheries' assessment situations there are so many parameters, each with a prior probability distribution that no simple solution exists. Under these more usual circumstances the analysis becomes a multidimensional integration problem and alternative computer-intensive approaches can be used. Sampling importance resampling (SIR) and Markov chain Monte Carlo (MCMC) are different Monte Carlo methods commonly used to combine the many probability distributions relating to each of the model parameters. They are not in themselves Bayesian methods; they are merely different algorithms used to conduct the multidimensional integration needed to find the posterior probability distributions produced by the Bayesian analysis. An example of how to run a MCMC is given in Chapter 8.

4.8 Relationships between Methods

All the computer-intensive methods we are going to consider may be viewed as different forms of random resampling where the observed sample data or

TABLe 4.1

Relationships between Computer-Intensive Methods and Their Strategies for Resampling from Probability Distributions

Method of Resampling	Computer-Intensive Method
Resampling a theoretical PDF (e.g., t distribution, χ^2 distribution) Implicitly this is sampling with replacement	Parametric statistics (analytically) Parametric Monte Carlo simulations Includes Bayesian methods
Resampling an empirical distribution (as represented by a sample) with replacement	Nonparametric bootstrap Nonparametric Monte Carlo Includes Bayesian methods
Resampling an empirical distribution (as represented by a sample) without replacement	Randomization tests Jackknife statistics

Note: PDF refers to probability density function. Parametric statistics are included for completeness but are not usually considered computer intensive. The nonparametric Monte Carlo and bootstrap methods are equivalent.

its properties are taken to represent the expected range of possible data from the sampled population. So, instead of sampling from a theoretical probability distribution, one can resample from the empirical distribution that is represented by the values in the sample (Table 4.1). Alternatively, one can sample from a parametric statistical distribution whose parameters are estimated from the original sample.

Randomization tests can be considered to be a special case of Monte Carlo testing where the original sample data are resampled without replacement so that each run uses all the available data. The only thing that changes is the assortment of data between groups.

Jackknife analysis is also a special case of Monte Carlo sampling where the available data forms the empirical distribution sampled. In this case it is systematically subsampled without replacement. It is the fact that values are omitted systematically that leads to there being a fixed number ($n - 1$) of jackknife replicates.

Nonparametric bootstrapping is another special case of the Monte Carlo process where the observed sample takes the place of a parametric probability distribution, or even the original population. In this case the situation is much more akin to parametric Monte Carlo sampling. The observed sample is sampled repeatedly, with replacement, just as if it were a continuous probability distribution.

Resampling from either theoretical probability density distributions or empirically derived distributions forms the basis behind the computer-intensive methods used to integrate the multidimensional problems that arise in Bayesian stock assessments.

4.9 Computer Programming

We will implement all of these computer-intensive methods in Excel workbooks using surprisingly little macro coding. Excel macros, however, can often be too slow for serious analyses when they are doing a great deal of work (the whole point of computer-intensive statistics). Ideally, in those cases, we might wish to write an executable program in some programming language such as Pascal, C++, or Fortran (even R, an interpreted language, is far more efficient for these purposes than Excel). Manly (1991) and Edgington (1987) provide program code for subroutines in Fortran for randomization tests, while Efron and Tibshirani (1993) provide the necessary code in the S statistical package for carrying out bootstrapping routines (also available in R). Many statistical packages now include bootstrapping as an option for many of their statistical routines. In addition, many statistical packages can now be macro-programmed into conducting computer-intensive statistics. For our purposes in this book, the Excel spreadsheet and its Visual Basic macro language will suffice.

5

Randomization Tests

5.1 Introduction

When used to test hypotheses, standard parametric statistics such as analysis of variance (ANOVA) require the samples and data involved to adhere to at least one restrictive assumption. If data fail to meet the conditions laid down in such assumptions, any conclusions drawn from the analyses can be suspect. Randomization methods can also be used to test hypotheses but require fewer assumptions. Given this extra flexibility, it is surprising that there is not a greater awareness of randomization tests. In this chapter we will examine randomization or permutation testing and its potential value to ecological and fisheries research.

5.2 Hypothesis Testing

5.2.1 introduction

Many hypothesis tests involve determining the likelihood that the situation one has observed could have arisen by chance events alone. What this means is that one is testing whether an observed pattern is unusual. But something can only be unusual relative to something else, usually one sample relative to one or more other samples, or relative to a hypothesis of how the sample ought to be. This is tested by determining whether there is a good chance that a perceived pattern between groups could have come about by random variations of whatever components make up the pattern of interest. For example, one could ask whether any differences observed in the size frequencies of a fish species found on the open coast and in coastal bays arose due to chance mixing or if the observed pattern is highly unlikely to be due to random movements between sites.

5.2.2 Standard Significance Testing

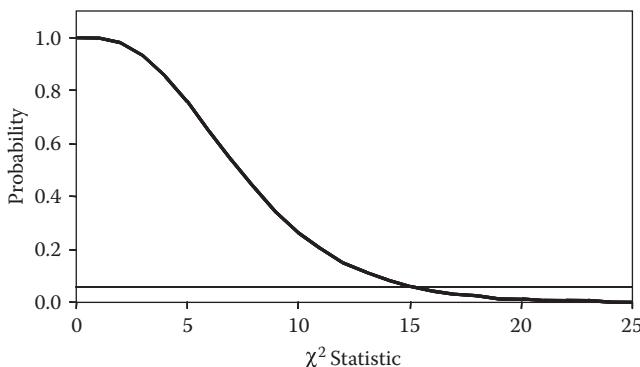
When attempting to test a hypothesis, at some stage one invariably calculates a test statistic. Given a value for a particular test statistic (e.g., a t statistic comparing the difference between two means), one then wishes to know if the value one has denotes a significant difference. This is such a common event that it is simple to forget what lies behind the steps leading to the test statistic and the meaning of its test of significance. Three things are needed when testing a hypothesis statistically:

1. A hypothesis ideally should be stated formally and is often translated into a null hypothesis that is the inverse or complement of the hypothesis we wish to test. This inversion is necessary because of the logical asymmetry between disproof of a general statement (possible) and its proof (not possible). Hypotheses are testable theoretical constructs, e.g., average fork lengths of fish from the open coast and coastal bays are the same (are not different).
2. A test statistic, any single-valued (smooth and continuous) function of the data. Commonly used test statistics include the F ratio, the t statistic, χ^2 , and r the correlation coefficient.
3. Some means of generating the probability distribution of the test statistic under the assumption that the null hypothesis is true is required to permit a determination of how likely the observed value of the test statistic is if the null hypothesis is true.

The first two requirements are straightforward and need little discussion. The third requirement may not be immediately familiar but is strongly related to the second requirement of using a particular test statistic. The many commonly used parametric statistics are used because their underlying assumptions are known, which means the expected probability density function (e.g., Figure 5.1) of a test statistic under the conditions of a particular situation can be calculated analytically. The value of the test statistic obtained from nature can be compared with the expected values given the circumstances of the particular test (degrees of freedom, etc.).

In this way, assuming the sampled population adheres to the assumptions of the test statistic, it is possible to determine how likely the observed value would be assuming the null hypothesis to be true. For common parametric test statistics the comparison of calculated values with the theoretical probability density function is made simple by its translation into tables relating degrees of freedom to likelihood or significance (Figure 5.1).

By convention, if the value of a test statistic is only expected to occur less than once in twenty replicated samples (i.e., <5% of the time), then usually a “significant” difference is claimed. This is taken to mean that unusual patterns (e.g., four heads in a row when tossing a coin) are not impossible; they are just unlikely chance events relative to the many other possible events

**Figure 5.1**

A one-tailed probability distribution curve (probability density function (pdf)) for the χ^2 statistic with 8 degrees of freedom. The fine horizontal line indicates a probability of 0.05. One could utilize this curve to determine the likelihood of obtaining a χ^2 value as large as the one observed between two populations, if one assumes they are from the same population. An observed χ^2 statistic greater than 15.507 would be expected to occur less than one time in twenty (i.e., <5% of the time). The shape of the curve varies with the degrees of freedom.

EXAMPLE BOX 5.1

Three different test statistics and their respective cumulative density functions indicating the probability that the value of the observed test statistic for the observed pattern being tested could have arisen through chance alone. Examine the Excel help files for descriptions of the functions used. Try varying the test statistic value and the degrees of freedom for each statistic and see the response. For the χ^2 statistic with 1 degree of freedom a value of approximately 3.84 should give a probability of 0.05. Compare the outputs from the Excel functions with published tables.

	A	B	C	D
1	Test statistic	χ^2	F	t
2	Test statistic value	2.9	2.9	1.98
3	Degrees of freedom 1	1	1	120
4	Degrees of freedom 2		25	
5	Probability	=chidist(B2,B3)	=fdist(C2,C3,C4)	=tdist(D2,D3,2)

that can occur. Because convention has established the levels of significance at 5%, 1% (1 chance in 100), and 0.1% (1 chance in 1,000), values of test statistics at these levels tend to be printed in statistical tables (Example Box 5.1). By comparing the observed value of the test statistic with these published values, one determines whether one has a significant difference and at what level.

5.2.3 Significance Testing by Randomization Test

Unfortunately, the theoretically derived tables of the various test statistics are only valid if the data adhere to the assumptions of the statistical test employed. The important problem is that if the assumptions are not met, then the analytically derived probability density function will not usually be applicable validly and erroneous conclusions can be made. The effect of such failure to match assumptions is an increased chance of rejecting a real difference between groups or of accepting a difference where none exists. This is one reason it behooves an ecologist to know about the effects of data transformations. For a *t* test, the assumptions would be that the two groups being compared are independently and normally distributed random variables with constant means and variances. The only part of this hypothesis that one really wishes to test is the “independently distributed” part (i.e., they come from independent populations), but all the rest is necessary, else the probability density distribution of the test statistic (the *t* distribution) cannot be used validly (though it is, in fact, relatively robust to departures from these assumptions).

We need to know the probability distribution of the selected test statistic to determine the likelihood of the value observed/calculated assuming the null hypothesis to be true. A problem with using a theoretically derived probability density function (pdf), as in the *t* test example above, is that if the observed test statistic value is not significant, we cannot tell without further analyses whether the test failed because the samples are not independently distributed (the thing being tested) or because the samples were not from normally distributed populations (the data or sampled populations failed to conform to the assumptions necessary for the test to be valid). This is where randomization tests exhibit their strength. They are independent of any analytically determined (parametric) probability density function because, during the test, the randomization procedure generates an empirical pdf for the test statistic from the available data (Manly, 1997).

If the hypothesis to be tested claims to explain a particular pattern in a set of data (e.g., inshore fish sizes are smaller on average than those offshore), then the null hypothesis would claim that the observed pattern found in the data is typical of any random allocation of the available data (fish sizes) among the inshore and offshore groups. The original pattern observed is represented in the test by a single value of a test statistic (perhaps a *t* statistic). Obviously, the test statistic should be chosen to be sensitive to the pattern of interest.

Given a null hypothesis, the expected probability density function for the test statistic chosen can be generated by repeatedly randomizing the data with respect to the sample group membership and recalculating the test statistic. In the inshore/offshore example, the membership of inshore and offshore groups is randomized. Fisher (1936) would have suggested that all the fish lengths should be written on separate cards, the cards shuffled, and

then the pack dealt out into the inshore/offshore groups in their original relative frequencies. When this process of randomization and calculation of test statistic is done many times (generally a minimum of one thousand randomizations are used), the frequency of occurrence of different values of the test statistic can be tabulated, and this may be compared with the value observed from the original unrandomized data. If the original value of the test statistic is found to be an unusual event relative to the values generated by the permutations of the data, then the null hypothesis may be rejected. The null hypothesis is, in effect, that the groups being compared are random samples from the same population. Speaking in terms of shuffling cards, Fisher (1936, p. 59) wrote: "Actually, the statistician does not carry out this very simple and very tedious process, but his conclusions have no justification beyond the fact that they agree with those which could have been arrived at by this elementary method."

A test of significance is thus really an attempt to answer whether the observed samples could have been drawn at random from the same population. The answer is a probability, and if it is large, then it is likely that the pattern could have arisen due to chance and one could answer that the samples might have derived from the same population (we could never claim they definitely were from the same population). However, if the probability of the pattern arising through randomly sampling the same population is small, we can be more definite and claim they were not likely to be from the same population. This asymmetry is why one uses a falsifiable null hypothesis.

5.2.4 Mechanics of randomization Tests

An example will illustrate the ideas that have been discussed and hopefully make the methods clearer (Figure 5.2, Example Box 5.2).

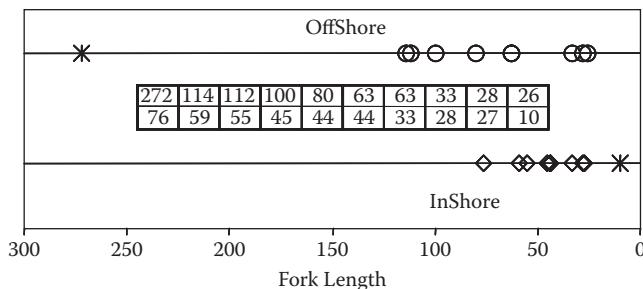


Figure 5.2

Two samples showing the data both numerically and graphically. Note the extreme values specially marked in both groups. Conventional t tests of the two groups, both including and excluding the extreme values (and assuming unequal variances), indicate that the groups are not significantly different despite the mean difference being 47. With the extreme values included, $t = 1.99$ and $P = 0.0746$, and without the extreme values, $t = 1.8$ and $P = 0.0993$. The samples are clearly too small in this example.

EXAMPLE BOX 5.2

The mechanics of a randomization procedure to compare two groups of data. The artificial data are from Figure 5.2. A copy of the original data is placed in column A (see Figure 5.2 for all data). Column B starts with a copy from column A; column C is filled with random numbers from the function =rand(). Cells C1 and D1 contain the average of the first and second groups, respectively, while E1 contains the test statistic, the absolute mean difference. The objective is to test whether the observed samples could have arisen by chance from a single population. To preserve a copy, the original values are pasted from column A into B and the observed test statistic pasted into D5. The randomization works by sorting columns B and C relative to the column of random numbers (do not include column A in the sorting). This has the effect of randomly reordering the available data into the two groups (inshore and offshore). The test statistic alters accordingly, and each new value is copied by a macro into column D.

Create a macro using Tools/Macro/Record New Macro menu item. Call it Do_Rand. Make sure the Stop Recording toolbar is visible (View/Toolbars) and start by using absolute references. Press <Shift><F9> to recalculate the sheet. Select and copy A5:A24 and paste their values into B5:B24. Copy E1 and paste its value into D5. Select B5:C24 and sort them on column C. Copy E1. Switch to relative references and paste the values into cell D6. Stop recording the macro. Press <Alt ><F11> and maximize the macro window. The modifications necessary to the macro are shown on the next page. Assign the Do_Rand macro to a button created from the Forms toolbar (not the Control Toolbox). If you change the number of iterations in the macro you will also need to change cell D3. Exclude the extreme values by altering C1 to B6:B14, D1 to B15:B23, and D3 to “>=23.1111”, and alter the sort command in the macro.

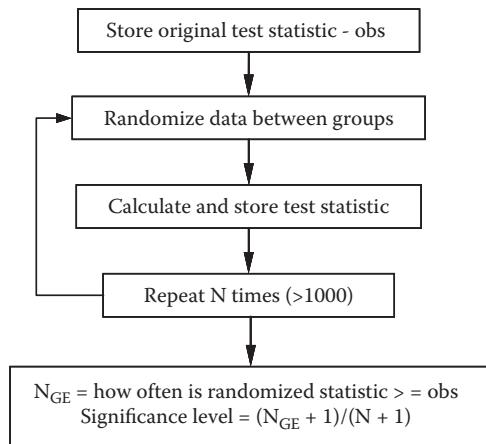
	A	B	C	D	E
1	Do_Rand		=average(B5:B14)	=average(B15:B24)	=abs(C1-D1)
2					
3			P =	=countif(D5:D1004,”>=47”)/1000	
4	Original	Values	Randomize Rows		
5	272	272	=rand()		
6	114	114	=rand()		
7	112	112	=rand()		
8	100	100	Copy down		
9	80	80	To row 24		
10	63	63	0.729468		
11	63	63	0.450439		
12	33	33	0.023943		
13	Continue down, data from Figure 5.2				

continued

EXAMPLE BOX 5.2 (continued)

The macro contents as recorded following the directions in the first part of this example box. You will need to add the lines and changes shown in italics. The only tricky bit is the replacement of the step six rows up from the bottom in the ActiveCell.Offset statement to become the dynamic $4 + i$, thereby using the counter variable to identify the pasting location for the results from the randomizations. To conduct the randomizations without the extreme values, alter the calculations for the group averages and alter the select command just prior to the sort to read Range("B6:C23").Select. This isolates the extreme values and the results should be rather different. Try modifying the macro by omitting commands such as the Application.ScreenUpdating=False. How many replicates are needed to obtain consistent results?

```
Sub Do_Rand()
    ' Do_Rand Macro
    Range("A5:A24").Select
    Selection.Copy      ' copy original data
    Range("B5").Select
    Selection.PasteSpecial Paste:=xlPasteValues
    Range("E1").Select
    Selection.Copy      ' store the original test statistic
    Range("D5").Select
    Selection.PasteSpecial Paste:=xlPasteValues
    ' unnecessary defaults removed
    Application.CutCopyMode = False
    Application.ScreenUpdating = False      ' for speed
    For i = 1 To 999 ' plus the original = 1000
        Range("B5:C24").Select
        Selection.Sort Key1:=Range("C5"),
            Order1:=xlAscending, Header:=xlGuess, _
            OrderCustom:=1, MatchCase:=False,
            Orientation:=xlTopToBottom
        Range("E1").Select
        Selection.Copy ' copy and store test replicates.
        ActiveCell.Offset(4 + i, -1).Range("A1").Select
        ' use counter to identify cells.
        Selection.PasteSpecial Paste:=xlPasteValues
    Next i
    Range("A1").Select ' returns to top of sheet
    Application.ScreenUpdating = True
End Sub
```

**Figure 5.3**

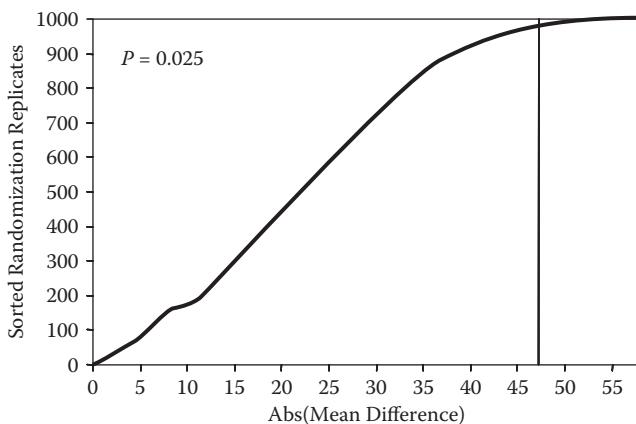
Algorithm for conducting a randomization test and for calculating the consequent significance test. One always includes the original test statistic value; this prevents a probability of zero occurring.

The group allocations (inshore/offshore) of the sample observations were randomized one thousand times and the mean difference was recalculated (algorithm shown in Figure 5.3). The randomization test found that the original mean difference only occurred twenty-five times out of one thousand, so evidence of a real difference exists (Figure 5.4). If this analysis is repeated, then a number slightly different from twenty-five might arise, but a significant difference should still be found. It is the weight of evidence that matters, not whether we have a difference significant at 5%, 1%, or whatever. The probability value indicates how likely it was to obtain a value like the observed test statistic. When outliers in the data are ignored (effectively removed from the data set), the randomization test agrees very closely with the conventional t test.

When the algorithm in Figure 5.3 is followed, one obtains N randomized replicate values. When these are sorted in ascending order, they may be plotted to give a visual representation of the distribution of values (Figure 5.4, Example Box 5.2).

5.2.5 Selection of a Test Statistic

With the release from the requirement of having one's test statistic adhere to a theoretical probability distribution there comes the freedom to select the most appropriate statistic. A test statistic should be chosen because its value is sensitive to the substantive theory being tested (i.e., the hypothetical property being checked or compared). However, some researchers see this freedom as a disadvantage because with the same sample, different test

**Figure 5.4**

One thousand sorted randomization replicates of the absolute mean difference between the groups in Figure 5.2, using the algorithm in Figure 5.3. The outer vertical line is at 47, the original mean difference. Including the original 47, there were twenty-five replicates that ≥ 47 (i.e., lie on or outside 47); therefore, $P = 0.025$. With the extreme values excluded the P value tends to be more like 0.094 (similar to the parametric t test). More replicates would lead to a smoother curve.

statistics can give different levels of significance. They are mistaken in thinking this invalidates the process. Rather, it emphasizes that one should be careful when selecting and using a nonstandard test statistic.

Basu (1980) was aiming to criticize Fisher and took as an example a simple data set of five values with which it was desired to determine whether the expected population value was significantly different from zero. The data were a set of five numbers, the values of which could have been either positive or negative but were, in fact, (1, 2, 3, 4, 7), which have a mean of 3.4. Basu (1980) argued that the question of whether this is significantly different from zero can be tested by a randomization test. He states that the significance of this test (is the sample mean > 0 ?) can be determined by comparing the mean with all the means possible from the thirty-two possible unique combinations of $(\pm 1, \pm 2, \pm 3, \pm 4, \pm 7)$. It is quickly shown that a mean of 3.4 is the largest value out of all possible values with the data available, and so is significant at the 1/32 level ($P = 0.0313$). However, the median is 3, and when used as the test statistic, there are four combinations, namely, $(\pm 1, \pm 2, 3, 4, 7)$, with a median as high as 3, implying a significance of $4/32 = 1/8 = 0.125$, which is not generally recognized as being significant. This disparity between the mean and median works for any set of five positive numbers tested in this way. In the end, this does not imply that the randomization procedure is not workable, but instead that this particular test statistic, the median, can be unstable and should not be used for such purposes with such limited data (Example Box 5.3).

EXAMPLE BOX 5.3

An example (from Basu, 1980) of a randomization procedure to compare two test statistics. Column B is filled with the random number generator =rand(). Cells C1 and D1 contain the average and median of the top 5 cells (A5:A9). The objective is to test whether the collection shown is significantly different from zero when the values can be ($\pm 1, \pm 2, \pm 3, \pm 4, \pm 7$). The observed values of the two test statistics are copied as values into C5 and D5. The randomization works by sorting columns A and B on the column of random numbers (keep a copy of the raw data and its order somewhere safe on the worksheet). This has the effect of randomly reordering the available data into the two groups (used and unused). The test statistics alter accordingly, and these new values are copied down below the starting observed values. After sufficient replicates we can count the number that are the same as or greater than the original observed values. Create a macro using Tools/Macro/Record New Macro menu item. Call it Do_Randz and start by using absolute references. Select C2:D2 and delete the contents. Press <Shift><F9>. Select A5:B14 and sort them on column B. Copy C1:D1. Switch to relative references and paste the values into cell C6 (and D6). Switch to absolute references. Select C2 and type =countif(C5:C1004,">=3.4"), and select D2 and type =countif(D5:D1004,">=3"). Stop recording the macro. Press <Alt><F11> and maximize the macro window. The modifications necessary to the macro are shown on the next page. Assign the Do-Randz macro to a button created from the Forms toolbar. If you change the number of iterations, you will also need to change cells C3 and D3.

	A	B	C	D	E
1			=average(A5:A9)	=median(A5:A9)	
2		Do_Rand		1	10
3			=C2/1000	=D2/1000	
4	Values	Reorder			
5	7	=rand()	3.4	3	
6	4	=rand()			
7	3	=rand()			
8	2	Copy Down			
9	1	To Row 14			
10	-1	0.729468			
11	-2	0.450439			
12	-3	0.023943			
13	-4	0.97243			
14	-7	0.312233			

continued

EXAMPLE BOX 5.3 (continued)

The macro contents as recorded following the directions in the first part of this example box. You will need to add the lines and changes shown in italics. You can either delete the struck-out text or leave it, whichever you prefer. If you decide on more than one thousand iterations, then you will need to alter the COUNTIF statements to reflect your choice. The only tricky bit is the replacement of the step ten rows up from the bottom in the ActiveCell.Offset statement to become the dynamic $4 + i$, thereby using the counter variable to identify the pasting location for the results from the randomizations. Try running the macro and comparing the significance of the comparison with a mean of zero when using the average and when using the median. There is a clear difference. In the text, complete evaluations of all possible combinations were discussed. In small discrete cases like this, complete evaluation is a reasonable option, but with larger numbers of observations a complete evaluation becomes onerous and a random sampling provides sufficient resolution (Manly, 1997).

```

Sub Do_Randz()
  ' Do_Randz Macro
  Dim i As Integer                               ' Not strictly needed
  '
  Application.ScreenUpdating = False   ' vital for sanity
  Range("C2:D2").Select
  Selection.ClearContents                      ' saves recalculating
  For i = 1 To 1000                            ' usually >=1000
    ActiveSheet.Calculate                     ' new random numbers
    Range("A5:B14").Select
    Selection.Sort Key1:=Range("B5"), Order1:=xlDescending,
      Header:=xlGuess, _
      OrderCustom:=1, MatchCase:=False,
      Orientation:=xlTopToBottom
    Range("C1:D1").Select
    Selection.Copy
    ' Replace 5 with 4 + i so it reads:
    ActiveCell.Offset(4 + i, 0).Range("A1").Select
    Selection.PasteSpecial Paste:=xlPasteValues,
      Operation:=xlNone, SkipBlanks:=_
      False, Transpose:=False      ' defaults can be deleted
  Next i
  Range("C2").Select
  Application.CutCopyMode = False

```

continued

EXAMPLE BOX 5.3 (continued)

```

ActiveCell.FormulaR1C1 = "=COUNTIF(R[3]C:R[1004]
C,"">=3.4""")"
Range("D2").Select
ActiveCell.FormulaR1C1 =
    "=COUNTIF(R[3]C:R[1004]C,"">=3""")".
Range("A1").Select           ' returns to top of sheet
Application.ScreenUpdating = True
End Sub

```

Examples of nonstandard test statistics could include the differences between parameter estimates of two growth curves ($K_1 - K_2$, or $L_{\infty 1} - L_{\infty 2}$, etc., although a randomization test to compare growth curves should not focus on single parameters and would have other complications; see later example in Chapter 9). Other examples could include the comparison of parameters from other models, such as stock recruitment relationships. Such direct comparisons would not be possible with traditional statistics. One can investigate questions that were previously untestable. For example, Lento et al. (1997) examined haplotype diversity across the geographical range of southern fur seal species using a randomization test for testing the reality of apparent genetic structure between populations. This tests whether the H_{st} value (a measure of the diversity and evenness of genetic variation between populations) provides evidence of geographical structure.

Multivariate comparisons are also possible (Anderson et al., 2008) and are limited only by imagination. Having said that, one must be extremely careful to determine exactly which hypothesis is being tested by the test statistic developed; when in doubt, be conservative.

5.2.6 ideal Test Statistics

Ideally one should select the test statistic that has the greatest statistical power for the situation being studied. This relates to the two types of error (Table 5.1). Making decisions under circumstances of uncertainty is very much concerned with the different types of statistical inference error it is possible to make. The implications of making each type of error in a particular situation should be made explicit before deciding on a test statistic.

If the test had been about the effects of fishing and the null hypothesis that fishing had negligible effects was incorrectly accepted, this would be a type II error that could have dangerous implications. No mitigating management actions would be implemented in the false belief that the stock was healthy. Conversely, if it were incorrectly concluded that stock damage was accruing when it was not (type I error), then managers may unjustifiably reduce the potential earnings of fishers (null hypothesis would be that no

TABLE 5.1
Type I and Type II Error Types

	No Differences Exist Null True	Differences Exist Null False
Null Accepted	OK	Type II error
Null Rejected	Type I error	OK

Source: After Sokal and Rohlf, 1995.

stock damage was detectable and this is mistakenly deemed false). It is hard to escape the conclusion that in the past more type II errors than type I errors have been made in fisheries management.

The *significance* of a test is the probability of making a type I error. Because we would expect a particular test statistic value to arise about one time in twenty at a probability of 0.05, accepting a significance level of 5% implies that one time in twenty we are likely to be claiming to have found a significant difference between groups where one does not exist (type I error). This is why a difference that is significant at the 5% level is less convincing than one at the 0.1% level.

The *power* of a test is the complement of the probability of making a type II error. To make a type II error is to claim no differences when differences exist; therefore, the complement of this probability is that of deciding when differences exist (the complement of δ is $1 - \delta$). In short, the power of a test is the probability of making the correct decision.

In practice, one would fix the significance level as small or large as is acceptable and then choose a statistic that maximizes the power of the test. A test is said to be *unbiased* if in using the test one is more likely to reject a false hypothesis than a true one (Good, 1994).

5.3 Randomization of Structured Data

5.3.1 introduction

The fact that randomization tests are restricted to tests that are basically comparisons between groups may be considered a major limitation; for example, they cannot be used for parameter estimation. On the other hand, they are very good at comparison tests.

Not every comparison is one of means; sometimes we would wish to compare variation between samples. It turns out that simple randomization tests of a mean difference between two samples can be influenced by differences in variation, particularly if this is related to sample size. For comparisons of variation, Manly (1997) recommends that one should randomize

the residuals of the two samples instead of the original data values. That effectively standardizes the means to zero and concentrates the test upon the variation within each sample.

Many comparisons are of more than two groups, and the conventional approach is to analyze these using ANOVA. Randomization tests have been used in conjunction with ANOVA for a few decades. They are best used when the assumptions of ANOVA fail badly. The basic rule is that with unbalanced and highly nonnormal data, one should use a randomization procedure to determine the significance of one's analyses.

With more complex ANOVA models, such as three-way, perhaps with nested factors, or repeated measures, there is some debate in the literature over the correct procedure to use in a randomization test. The question at issue is whether one should just randomize one's data across all categories and treatments (Manly (1997) says yes, Edgington (1987) emphatically says no), or whether there should be some restrictions placed upon what is randomized (randomize the treatments and categories separately). Manly also claims that one can test for interactions as one would normally, while Edgington claims the contrary and says one cannot test interactions. Edgington (1995) continues the discussion and provides many insights into the analysis of structured data. Investigations into the most efficient method of conducting randomization tests on structured data are an open field in need of further research (Anderson and Legendre, 1999). The question that tends to be addressed when considering structured data is whether one should randomize the raw data, subsets of the raw data, or residuals from the underlying model. There is no simple answer to this, as the debate between Manly and Edgington demonstrates.

What this all means is that when one's data are structured or nonlinear (often the case with fisheries models and relationships), care needs to be taken in deciding what components should be randomized during a test. Anderson and Legendre (1999, p. 302) capture the present situation when they conclude the following:

Obtaining empirical measures of type I error or power allows direct practical comparisons of permutation methods. Current theoretical comparisons of the methods cannot provide us with complete information on how the methods will compare in different situations in practice.

5.3.2 More Complex examples

Consider the problem of comparing growth curves (this will be considered in detail in Chapter 9, on growth). If one wanted to compare age length data from two populations of fish, then one might fit two von Bertalanffy curves and wish to determine whether any of the parameters of the two curves are significantly different. At present one would generally use a likelihood ratio test (Kimura, 1980; see Chapter 9), but to avoid some of the assumptions

concerning underlying distributions, one could utilize a randomization test. However, it is not immediately clear what one should randomize.

One could randomize the available data pairs (ages plus associated lengths) between the two populations, keeping the number of observation pairs in each sample the same as in the original data. However, by chance many of the older animals may be collected in one population and many of the younger in the other; this would obviously distort any growth curve fitted to these randomized data. On the other hand, this randomization design could be used when testing whether the proportional age composition or length composition of the different data sets was significantly different.

If one wanted to test the difference between the average growth curves for the two samples, then one requires a slightly more complicated scheme of randomization. The original data sets need to be stratified, in this case into discrete ages, and then the data should be randomized between populations but within age strata, thereby maintaining the original numbers of individuals within each age class for each population. In this way the underlying age structures of the two populations could be maintained while the dynamics of growth are compared. In this case, it would be important to make sure that every age class was represented in each data set, though the numbers in each age class would not need to be the same. An alternative approach, which should produce equivalent results, would be to randomize ages between populations but within length classes. This example will be considered explicitly when we consider the comparison of growth curves in Chapter 9.

6

Statistical Bootstrap Methods

6.1 The Jackknife and Pseudovalue

6.1.1 introduction

In this chapter, we will describe the use of the bootstrap to generate estimates of bias, standard errors, and confidence intervals around parameter estimates. We will also include a short treatment on the jackknife, which predated the bootstrap as a method for generating estimates of bias and standard errors around parameter estimates. While the jackknife and bootstrap share some common uses, they are based on very different principles of resampling.

6.1.2 Parameter estimation and Bias

A random sample from a population may not necessarily be representative of the whole population (in the sense of reflecting all of the properties of the sampled population). For example, a sample from a normal random deviate ($N(0,1)$, i.e., mean = zero, variance = 1) could have values almost solely from one arm of the bell-shaped curve (Figure 6.1), and in this way the sample would not represent the full range of possible values.

Such a sample (Figure 6.1) could well be random (and indeed was) but might also come about because the sampling is not strictly random. Truly random samples can be difficult to arrange; for example, the sample in Figure 6.1 only arose after repeated trials. But without the samples being truly random, there is a possibility that the sample could produce biased estimates of such population parameters as the mean and variance or other parameters with less well-known behaviour. There can also be other sources of bias. With the example above, a visual inspection is enough to inform us that our sample is likely to give poor estimates of such statistics. But what can be done when we are unsure of the exact probability density function of the population from which we have a sample? One obvious answer is to take a larger sample, or replicate samples, but this is frequently not possible for reasons of time, funding, or circumstances.

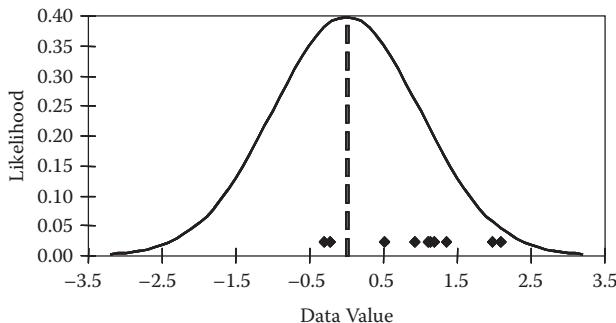


Figure 6.1

The solid line shows the expected distribution from a standard random normal deviate of mean = 0 and variance = 1. The expected mean of samples from this distribution is shown as the dashed line. However, the diamonds are a random sample of ten having a sample mean of 0.976 and variance of 0.642.

An early solution to the investigation of bias, termed the half-sample approach (because it split the original data randomly into two equal-sized groups), gave unreliable estimates of the statistic of interest and its variance (Hinkley, 1983). Quenouille (1956) produced a relatively sophisticated extension of this half-sample idea in an effort to estimate bias. Tukey (1958) went a step further by generalizing Quenouille's particular approach, calling it the jackknife, and recommending it be used to produce estimates of parameters along with approximate confidence limits.

The jackknife method is relatively straightforward. Assuming one has a random sample (independent and identically distributed (iid)) of n values x_1, x_2, \dots, x_n , the sample mean is

$$\bar{x} = \frac{\sum x_i}{n} \quad (6.1)$$

This is also an unbiased estimate of the mean of the population from which the sample was taken. The jackknife methodology subsets the data sequentially by calculating the required statistic with one original value missing each time. In a data set of n values there will be n subsets of $n - 1$ data points (Table 6.1). Thus, for the sample mean minus the j th value,

$$\bar{x}_{-j} = \frac{\left[\left(\sum_{i=1}^n x_i \right) - x_j \right]}{(n-1)} \quad (6.2)$$

where x_j is the j th observation out of the n values. Equations 6.1 and 6.2 are related thus:

TABLe 6.1

An Illustration of the Generation and Use of Jackknife Samples and Replicate Observations

	Original	Data Series	Systematically Minus One Observation			
	1		1	1	1	1
	2		2	2	2	2
	3		3	3	3	3
	4		4	4	4	4
	5		5	5	5	5
Average	3	Mean-j	3.5	3.25	3	2.75
StDev	1.581	StDev-j	1.291	1.708	1.826	1.708
n	5		4	4	4	4
PV Mean	3	PV for Mean	1	2	3	4
PV Mean	1.647	PV for StDev	2.742	1.074	0.603	1.074
						2.742

Note: The pseudovalues when estimating the mean are simply the original data values, while those when estimating the standard deviation are not directly related to the data values. The mean is an unbiased estimator of a sample mean, hence the mean of the pseudovalues for the mean equals the original sample mean. The sample is not taken from a normal distribution and contains some consequent bias when estimating the standard deviation. This is reflected in the difference between the sample StDev (1.581) and the Mean of the StDev pseudovalues (1.647) (Example Box 6.1).

$$(n-1)\bar{x}_{-j} = \left(\sum_{i=1}^n x_i \right) - x_j = n \frac{\left(\sum_{i=1}^n x_i \right)}{n} - x_j \quad (6.3)$$

which, when we convert the sum of x over n to the average of x , gives us

$$(n-1)\bar{x}_{-j} = n\bar{x} - x_j \quad (6.4)$$

and then, rearranging:

$$x_j = n\bar{x} - (n-1)\bar{x}_{-j} \quad (6.5)$$

which is simply a way of showing how the x_j values relate to the sample mean and the mean with the x_j values removed. Equation 6.5 is important because it is the basis for generating the pseudovalues upon which the jackknife calculations are based; we thus go one step further than a simple resample.

The jackknife estimate of the mean is simply the mean of these x_j values, known as pseudovalues, which is clearly the same as the original unbiased mean estimate:

EXAMPLE BOX 6.1

A simple jackknife example. The five jackknife samples are in columns C to G. The average and standard deviation of all columns is estimated in rows 8 and 9 with the count in row 10 (copy C8:C12 across to column G and into column B). These are used with Equation 6.5 to create the required pseudovalues for the mean and standard deviation in rows 11 and 12. By putting =average(C11:G11) and =average(C12:G12) into D14 and D15 we generate the jackknife estimates of the two parameters. Try altering the data in column B to see the impact on the estimates.

	A	B	C	D	E	F	G	
1		Original		JK1	JK2	JK3	JK4	JK5
2		1			1	1	1	1
3		2		2		2	2	2
4		3		3	3		3	3
5		4		4	4	4		4
6		5		5	5	5	5	
7								
8	Mean	3	=average(C2:C6)	3.25	3	2.75	2.5	
9	StDev	1.5811	=stdev(C2:C6)	1.708	1.826	1.708	1.291	
10	Count	5	=count(C2:C6)	4	4	4	4	
11	PV Mean		=(\$B\$10*\$B8)-(C\$10*C8)	2	3	4	5	
12	PV StDev		=(\$B\$10*\$B9)-(C\$10*C9)	1.074	0.603	1.074	2.742	
13								
14	Mean of pseudovalue Mean Values			3				
15	Mean of pseudovalue StDevs			1.647				

$$\tilde{x} = \frac{\sum x_j}{n} \quad (6.6)$$

As Manly (1991, p. 25) said, "Obviously, this is not a useful result if the sample values are known in the first place. However, it is potentially useful in situations where the population parameter being estimated is something other than a sample mean." These other parameters might be a standard error or measure of kurtosis or skewness, or some other statistic or model parameter.

Analogous to the jackknife estimate of the mean, the jackknife estimate of standard error of the parameter using the pseudovalues would be either option in Equation 6.7 (i.e., the standard deviation of the pseudovalues divided by root n). Thus,

$$\tilde{s}_{jack} = \sqrt{\frac{\sum (x_j - \tilde{x})^2}{(n-1)}} / \sqrt{n} \quad \text{or} \quad \sqrt{\frac{\sum (x_j - \tilde{x})^2}{(n-1)n}} \quad (6.7)$$

If other population parameters, such as the variance, were estimated, then the equivalents to the x_j pseudovalues would not necessarily be known. It is, however, possible to generalize the jackknife procedure to such population parameters. Given a population parameter, θ , which is estimated as a function of a sample of n values of x_i ,

$$\hat{\theta} = f(x_1, x_2, \dots, x_n) \quad (6.8)$$

Just as before, there are n estimates of this θ with the j th observation removed, and just like Equation 6.4, we can define the set of pseudovalues θ_j (Efron and Tibshirani, 1993) to be

$$\theta_j = n\hat{\theta} - (n-1)\hat{\theta}_{-j} \quad (6.9)$$

These θ_j values act in the same manner as the x_j values when estimating the mean. To produce the jackknife estimate of the parameter θ ,

$$\tilde{\theta} = \frac{\sum \theta_j}{n} \quad (6.10)$$

If θ is the sample mean, then the pseudovalues are exactly the same as the x_j values, but with other parameters they become rather different from the original data (Table 6.1). If we extend this special case, then we can calculate the jackknife estimate of the standard error of the jackknife replicates as

$$\tilde{s}_{jack} = \sqrt{\frac{\sum (\theta_j - \tilde{\theta})^2}{(n-1)n}} \quad (6.11)$$

This is treating the n pseudovalues as independent data values. Efron and Tibshirani (1993, p. 145) state: "Although pseudo-values are intriguing, it is not clear whether they are a useful way of thinking about the jackknife." Partly, I suggest they are saying this because they are advocates of using bootstrapping for producing better estimates of such parameters.

Some people suggest using such jackknife parameter estimates along with their standard errors to produce jackknife confidence intervals:

$$\tilde{\theta} \pm t_{n-1} \tilde{s}_{jack} \quad (6.12)$$

where t_{n-1} is the percentile value of the t distribution (e.g., 95% value) with $n - 1$ degrees of freedom. Efron and Tibshirani (1993) suggest that confidence intervals produced in this way are not significantly better than cruder intervals based on asymptotic standard errors. It is thought that uncertainty over exactly how many degrees of freedom are involved in jackknife standard errors is part of the problem with this approach.

6.1.3 Jackknife Bias estimation

The jackknife procedure was originally introduced in an effort to estimate and remove bias from parameter estimates. The sample parameter value estimate, $\hat{\theta}$ is compared with the mean of the jackknife pseudovalues of the θ statistic; thus, where the jackknife replicates are defined as a function of the jackknife sample data (note the missing x_j value),

$$\tilde{\theta}_{-j} = f(x_1, x_2, \dots, x_{j-1}, x_{j+1}, \dots, x_n) \quad (6.13)$$

In addition, each jackknife replicate has its complementary pseudovalue as in Equation 6.9, so that the jackknife estimate of bias is defined as

$$\tilde{b}_{jack} = (n - 1)(\tilde{\theta}_m - \hat{\theta}) \quad (6.14)$$

where the mean of the jackknife pseudovalues is

$$\tilde{\theta}_m = \frac{\sum \tilde{\theta}_j}{n} \quad (6.15)$$

Of course, with these formulations one will see that when $\hat{\theta} = \bar{x}$ the estimator is unbiased (assuming a truly random sample).

Exactly what one does once one has an estimate of bias is not clear. The usual reason for its calculation is to correct $\hat{\theta}$ so that it becomes less biased:

$$\bar{\theta} = \hat{\theta} - \tilde{b}_{jack} \quad (6.16)$$

where $\bar{\theta}$ is the bias-corrected estimate of $\hat{\theta}$. However, Efron and Tibshirani (1993, p. 138) finish a discussion of bias estimation thus:

To summarize, bias estimation is usually interesting and worthwhile, but the exact use of the bias estimate is often problematic.... The straightforward bias correction [Equation 6.16] can be dangerous to use in practice, due to high variability in [the bias estimate]. Correcting the bias may cause a larger increase in the standard error.... If the bias is small compared to the estimated standard error [Equation 6.11], then it is safer to use $\hat{\theta}$ than $\bar{\theta}$. If bias is large compared to standard error, then it may be an indication that the statistic $\hat{\theta}$ is not an appropriate estimate of the parameter θ .

This appears to suggest one should never apply Equation 6.16 in practice! It is useful to see if there is bias, but if detected, it appears it is best not to try to correct it (presumably one should try again to obtain an unbiased sample if the bias is too large).

6.2 The Bootstrap

6.2.1 The Value of Bootstrapping

There are a number of analytical strategies for producing estimates of parameters with confidence intervals from samples that have an unknown probability distribution. Efron and LePage (1992) state the general problem thus:

We have a set of real-valued observations x_1, \dots, x_n independently sampled from an unknown probability distribution F . We are interested in estimating some parameter θ by using the information in the sample data with an estimator $\hat{\theta} = t(x)$. Some measure of the estimate's accuracy is as important as the estimate itself; we want a standard error of $\hat{\theta}$ and, even better, a confidence interval on the true value θ .

Since Efron (1979) first discussed the idea of bootstrapping it has become relatively popular, even trendy, at least among statisticians; three reasons have been suggested (Kent et al., 1988):

1. Elegance: The principle behind the bootstrap, that of resampling from the empirical distribution function (as represented by a sample), instead of the actual probability density function, is simple and elegant, and yet very powerful.
2. Packaging: The catchy name *bootstrap* makes it easy for people to recognize the product, though the potential for confusion exists now that parametric resampling, as in classical Monte Carlo simulations, is sometimes included in the term *bootstrapping*.
3. Ease of use (Kent et al., 1988, p. 355): "for the practitioner there is the hope of a fairly automatic and clear methodology that can be used without the need for any thought."

The last reason seems frightening and I would suggest that this latter idea be discouraged vigorously in any analyses; one should always think deeply about one's analyses. I imagine Kent was only implying that such analyses could become routine. Bootstrap resampling is a general form of resampling in that it is resampling with replacement to produce bootstrap samples

Original Sample		Bootstrap Samples				
3	8	5	3	8	3	
5	5	8	11	9	3	
7	→	11	5	5	3	11
8		7	8	7	7	9
9		8	7	7	3	8
11		8	11	11	9	11
Mean	7.17	7.83	7.33	7.33	6.5	7.5

Figure 6.2

An original sample of six numbers with their average. From this are drawn five bootstrap samples, each with a separate average. It is clear that with a sample of size n there are n^n possible bootstrap combinations. Replacement implies it is easily possible for a single observation to appear more than once in the bootstrap sample; it is also possible that some original observations will not occur in the bootstrap samples. The average of the five bootstrap replicates is 7.292 (Example Box 6.2).

of size n . When one resamples with replacement there are many possible arrangements (n^n in fact) of the available data (Figure 6.2, Example Box 6.2).

If one had a sample from a known normal distribution, then there would be no advantage to using a bootstrap method for estimating the standard error of a parameter; “normal” theory would be best. However, in situations where the sampled population cannot be adequately represented by a normal distribution, and especially where the underlying population distribution is unknown, bootstrapping becomes most useful.

6.2.2 empirical versus Theoretical Probability Distributions

In fact, given a sample from a population, the nonparametric, maximum likelihood estimate of the population distribution is the sample itself. Expressed precisely, if the sample consists of n observations $(x_1, x_2, x_3, \dots, x_n)$, the maximum likelihood, nonparametric estimator of the population distribution is the probability function that places probability mass $1/n$ on each of the n observations x_i . Take note that this is not saying that all values have equal likelihood; instead, it implies that each observation has equal likelihood. One expects, some of the time, to obtain the same or similar values in different observations if the population distribution being sampled has a mode.

The implication, first suggested by Efron (1979), is that when a sample contains or is all the available information about a population, why not proceed *as if* the sample really is the population for purposes of estimating the sampling distribution of the test statistic? That is, apply Monte Carlo procedures, sampling with replacement but from the original sample itself, as if it were a theoretical distribution. Sampling with replacement is consistent

EXAMPLE BOX 6.2

A simple bootstrap example (see Figure 6.2). One can generate a bootstrap sample in Excel using the vlookup function (or the offset function). This entails generating random integers that match the numbers in an index list as in column A. The vlookup function uses these index numbers to return the data value next to each respective index. There is nothing to stop the same integer from arising, which will lead to sampling with replacement. In C7 put the function =vlookup(trunc(rand()*6)+1,\$A\$7:\$B\$12,2,false). Use the Excel help to understand this function. The trunc(rand()*6)+1 term will generate random integers between 1 and, in this case, 6. Try typing just this term elsewhere in the sheet and examining its performance each time you press F9 (i.e., recalculate the sheet). Copy C7 down to C12. Then copy C7:C12 across to IV7:IV12. Copy B1 across to IV1. The four averages in C2:C5 are bootstraps with different numbers of replicates (20 to 254). Keep pressing F9 to generate new random numbers and hence new bootstrap samples, and examine the differences between the observed mean and the bootstrap means. Which sample size provides the better estimates? The option of duplicating the parameter calculation either up or down the sheet (perhaps use hlookup instead) can be fast but will generate large worksheets. Plot B2:B5 against A2:A5.

	A	B	C	D	E	F	G
1	n	=average(B7:B12)	5.833	8.833	7.667	7.500	7.833
2	20	=average(C1:V1)	=B1-B2				
3	50	=average(C1:AZ1)	=B1-B3				
4	100	=average(C1:CX1)	=B1-B4				
5	254	=average(C1:IV1)	=B1-B5				
6	Index	Data	BS1	BS2	BS3	BS4	BS5
7	1	3	8	11	9	5	3
8	2	5	3	7	9	8	9
9	3	7	5	8	5	7	8
10	4	8	7	7	7	9	11
11	5	9	3	9	11	5	8
12	6	11	9	11	5	11	8

with a population that is essentially infinite. Therefore, we are treating the sample as representing the total population.

In summary, bootstrap methods are used to estimate a parameter of an unknown population by summarizing many parameter estimates from replicate samples derived from replacing the true population by one estimated from the population (the original sample from the population).

6.3 Bootstrap Statistics

Standard error is a general term for the standard deviation of a summary statistic. So one may have the standard deviation of a sample and a standard error of a sample mean, but one could not have a standard error of a sample. With a sample from a normally distributed variable, one can estimate the standard error of, for example, the mean of a sample of n observations, analytically by using:

$$se_{\bar{x}} = \frac{StDev}{\sqrt{n}} = \sqrt{\frac{\sum (x_i - \bar{x})^2}{(n-1)n}} \quad (6.17)$$

Alternatively, one could take a large number of independent samples from the same population and find the standard deviation of the means of these samples. This latter process is exactly what one does for a bootstrap estimate of the standard error for any parameter. A general approach for producing the bootstrap estimation of the standard error of any parameter θ is as follows:

1. Generate b independent bootstrap samples $x_1, x_2, x_3, \dots, x_b$, each consisting of n data values drawn randomly with replacement from the n values in the original sample (the empirical distribution). Efron and Tibshirani (1993) recommend b to be at least in the range of 25 to 200 for estimating a standard error.
2. Calculate the bootstrap replicate of the parameter or statistic $\hat{\theta}_b$ for each of the b bootstrap samples, x_b . The statistic must be a continuous function of the data (Equation 6.18).

$$\hat{\theta}_b = f(x_b) \quad (6.18)$$

3. Estimate the standard error se_{θ} of the parameter θ by calculating the standard deviation of the b bootstrap replicates (note we are using a standard deviation of multiple samples to estimate a standard error; don't confuse the concepts).

$$se_{\theta} = \sqrt{\frac{\sum (\hat{\theta}_b - \bar{\theta}_b)^2}{b-1}} \quad (6.19)$$

where $\bar{\theta}_b$ is the mean of the bootstrap replicates of θ , which is the bootstrap estimate of the statistic θ :

$$\bar{\theta}_b = \frac{\sum \hat{\theta}_b}{b} \quad (6.20)$$

Such estimates would be called *nonparametric bootstrap* estimates because they are based upon an empirical distribution instead of a theoretical probability distribution. It would be unusual today to use the bootstrap to estimate a standard error. More commonly, the bootstrap is used to generate percentile confidence intervals around parameter estimates for which other methods of obtaining confidence intervals would present difficulties.

6.3.1 Bootstrap Standard errors

Efron and Tibshirani (1993) use a bootstrap to estimate the standard error of a correlation coefficient (a notoriously difficult thing to do). With their example Efron and Tibshirani (1993) suggest that a sample size of between 25 and 200 should be sufficient to calculate standard errors with adequate precision. We have repeated this exercise to determine the repeatability of their results. The example used here is the correlation between catches of tiger prawns and king prawns in the Australian Northern Prawn Fishery across the years 1976 to 1987 (Figure 6.3). The tiger prawns constitute the target in this fishery and the king prawns are a bycatch species.

To determine if the bootstrap standard error estimate improved with increasing numbers of bootstrap replicates, more and more bootstrap replicate samples can be made for each of which the correlation coefficient is calculated (Figure 6.4, Example Box 6.3). The standard error estimates differ between series and with b , the number of bootstrap replicates, but all estimates where b is 200 or greater achieve an acceptable precision. A sample size of twenty-five would appear to be rather low, but two hundred and

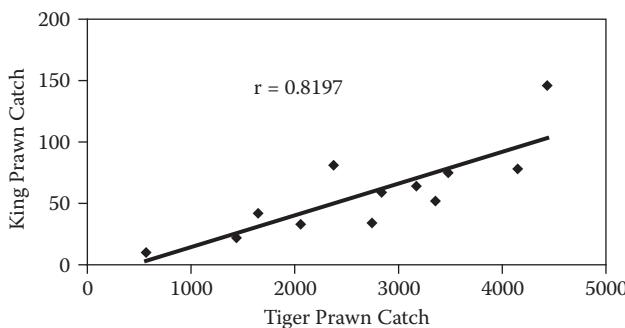
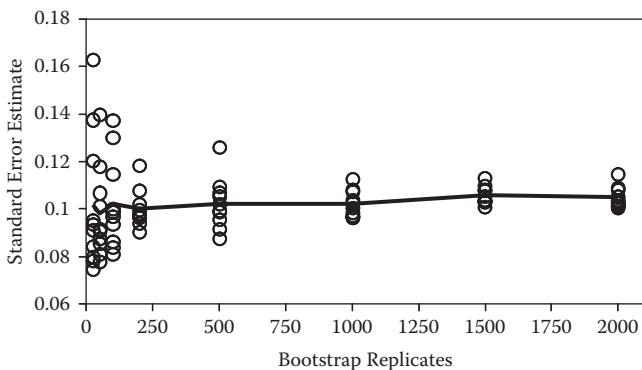


Figure 6.3

Scatterplot relating Australian Northern Prawn Fishery tiger prawn catches, as tonnes, to king prawn catches, between the years 1976 and 1987. The linear regression is king = 0.02585 and tiger = 11.4826.

**Figure 6.4**

Ten estimates of the standard error around the correlation coefficient at each of eight different numbers of bootstrap replicates (25, 50, 100, 200, 500, 1,000, 1,500, 2,000). The solid line is the mean of the estimates. Use Example Box 6.3 to generate an equivalent graph. The overall average standard error was approximately 0.102.

more is clearly enough. Hinkley (1988) suggests that the minimum number of bootstrap samples will depend on the parameter being estimated, but that it will often be one hundred or more. With the large increases in the relative power of computers in recent years, the number of replicate bootstraps to conduct should no longer be an issue for most problems.

6.3.2 Bootstrap replicates

Beyond using the bootstrap to estimate standard errors, it can also provide an estimate of an empirical frequency distribution (Figure 6.5) of possible values for the statistic or parameter in question. The distribution of correlation coefficients derived from the bootstrap replicates is clearly nonnormal with a significant skew.

So far, we have considered exactly what a bootstrap sample is and how it is produced. We have also seen how to determine a bootstrap estimate of a parameter (the average of the bootstrap replicates) and its standard error (standard deviation of bootstrap replicates). However, one of the major areas of research on bootstrapping has been the consideration of different approaches to calculating statistical confidence intervals for estimated parameters (DiCiccio and Romano, 1988; Romano, 1988). With nonnormal populations, these can be difficult to fit in a valid or unbiased way. Using standard errors to generate confidence intervals always leads to symmetrical intervals. If the distribution of the parameter of interest is not symmetric, such confidence intervals would be invalid. The bootstrap provides us with a direct approach that can give rise to excellent approximate confidence intervals. All these direct methods rely on manipulating in some way the empirical frequency distribution of the bootstrap replicates (Figure 6.5).

EXAMPLE BOX 6.3

Bootstrap standard errors around a correlation coefficient between tiger and king prawn catches (cf. Figure 6.3). We will use vlookup again, but this time, because we need to return data pairs, we will have a separate column of random index values (column D) and use them in both vlookup functions in columns E and F, e.g., in E5, =vlookup(D5,\$A\$5:\$C\$16,2,false), and in F5 put =vlookup(D5,\$A\$5:\$C\$16,3,false). Note the only change is the column from which to return data. Copy these down to row 16. Each press of F9 will renew the random numbers in column D, which will lead to new data pairs in columns E and F. In C2 put =correl(B5:B16,C5:C16), which is the original correlation, and in F2 put =correl(E5:E16,F5:F16), which is the bootstrap sample correlation. Record a macro through Tools/Macro/Record New Macro, and call it Do_Boot. While in absolute references copy F2, change to relative references, and paste values into G5. Stop recording. Place a button on the worksheet from the Forms toolbar and assign Do_Boot to it. Edit the macro (via Alt-F11) and make the changes listed in italics to make the macro functional. Change the number of bootstrap replicates by altering C1. Note the answers and determine a reasonable number of replicates to estimate the standard error of approximately 0.102 in G3 (using Equation 6.19). You will need to run each set a number of times (Yr is the year of catch, Tig is tiger prawn catches in tonnes, and King is king prawn catches).

	A	B	C	D	E	F	G
1	TRIALS	500					
2	Original r	0.8197				0.9735	=average(g5:g2004)
3	Original Data pairs						=stdev(G5:G2004)
4	Yr	Tig	King	Bootstrap Index	Tig	King	Bootstraps
5	76	566	10	=trunc(rand()*12)+76	558	2.81	0.930064
6	77	1437	22	=trunc(rand()*12)+76	578	3.03	0.833836
7	78	1646	42		8	661	0.90485
8	79	2056	33		5	666	0.679865
9	80	3171	64		2	635	0.708266
10	81	2743	34		8	661	0.857945
11	82	2838	59		12	575	0.341376
12	83	4434	146		8	661	0.726493
13	84	4149	78		12	575	0.876033
14	85	3480	75		9	651	0.75519
15	86	2375	81		8	661	0.948527
16	87	3355	52		8	661	0.771965

continued

EXAMPLE BOX 6.3 (continued)

Some of the changes needed could be recorded as a separate macro and then copied into this one (e.g., the cell clearing lines just below the Dim statements). The MsgBox will soon lose its novelty and can be turned off by converting it to a comment with a '. Try running this a few times for fifteen replicates without the screen updating turned off (comment out the necessary statements). Plot the bootstrap replicate samples of column E against F and observe how they change.

```

Sub Do_Boot()
    '
    ' Do_Boot Macro
    '

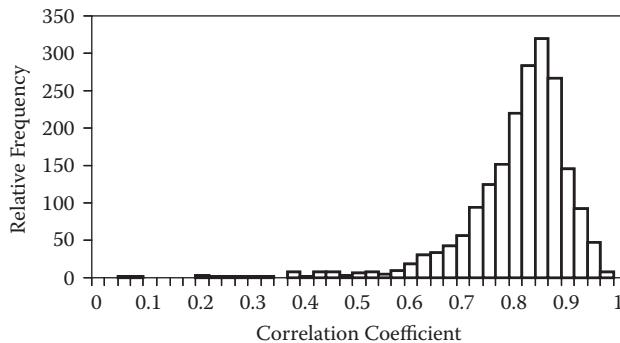
Dim i As Integer, b As Integer
Dim start As Double, endtime As Double
    '
Range("G5").Select
Range(Selection, Selection.End(xlDown)).Select
Selection.ClearContents
Range("G6").Select
Application.ScreenUpdating = False
    start = Timer
    b = Range("C1").Value      ' get the number of replicates
    For i = 1 To b
        ActiveSheet.Calculate
        Range("F2").Select
        Selection.Copy
        ActiveCell.Offset(2 + i, 1).Range("A1").Select
        Selection.PasteSpecial Paste:=xlPasteValues
    Next i
    Range("A1").Select
    endtime = Timer
    Application.ScreenUpdating = True
    MsgBox Format(endtime - start, "##0.000"), vbOKOnly,
        "Bootstrap Complete"
End Sub

```

6.3.3 Parametric Confidence intervals

Where the parameter being estimated is expected to exhibit a normal distribution of expected values (here the central limit theorem may play a part), confidence intervals around the parameter may be obtained from the usual:

$$\text{CI} = \theta \pm t_{n-1,\alpha/2} s e_\theta \quad (6.21)$$

**Figure 6.5**

Frequency distribution of bootstrap replicate values of the correlation coefficient. The observed value was 0.8197. The median value of the illustrated frequency distribution was 0.8423, and the bootstrap estimate of the correlation coefficient was 0.8191, a difference of 0.0006 from the sample estimate (this provides an estimate of any bias).

where θ is the sample parameter estimate, $t_{n-1,\alpha/2}$ is the student's t distribution value for $n-1$ degrees of freedom (where n is b , the number of bootstrap replicates), and $\alpha/2$ is the percentage confidence limits desired; with $\alpha = 0.05$, $100(1 - \alpha)\%$ provides the 95% intervals, where $\alpha/2 = 2.5$ and 97.5. Because the number of replicates in bootstrapping is likely to be high, instead of using the t distribution many statisticians simply replace it with the z value (e.g., 1.96 for the 95% confidence intervals). The bootstrap estimates of standard error can be used in this way to generate confidence intervals. In the example we have been considering the observed correlation coefficient was 0.8197 and the standard error was approximately 0.102 (Figure 6.4). If we used a normal approximation, we would expect the confidence intervals to be $0.8197 \pm 1.96 \times 0.102 = 0.6198$ and 1.0196. Clearly, with a correlation coefficient a value greater than 1 is nonsense and illustrates the problem of using normal theory to estimate confidence intervals for parameters with expectations from nonsymmetrical distributions.

6.3.4 Bootstrap estimate of Bias

If the sample estimate is biased, it is possible to remove this bias before adding and subtracting the requisite z value to find the confidence intervals:

$$\theta - (\bar{\theta}_b - \theta) \pm z_{\alpha/2} s e_\theta \quad (6.22)$$

or, equivalently,

$$(2\theta - \bar{\theta}_b) \pm z_{\alpha/2} s e_\theta \quad (6.23)$$

which is the sample estimate minus the bootstrap bias plus or minus the standard normal distribution for $\alpha/2$ times the bootstrap standard error estimate (standard deviation of the bootstrap replicates).

Of course, if the statistic being considered were far from normal, then Equation 6.23 would produce erroneous results. The example of the correlation coefficients (Figure 6.5) is one where a statistic has an expected distribution that is far from normal. If the estimates are corrected for bias prior to estimating the confidence intervals, the distortion on the confidence intervals becomes slightly greater. Using Equation 6.23 we have $(2 \times 0.8197 - 0.8191) \pm 1.96 \times 0.102 = 0.6204$ and 1.0202 . Thus, the upper limit becomes slightly further removed from 1 (the maximum possible value for a correlation coefficient).

6.4 Bootstrap Confidence Intervals

6.4.1 Percentile Confidence intervals

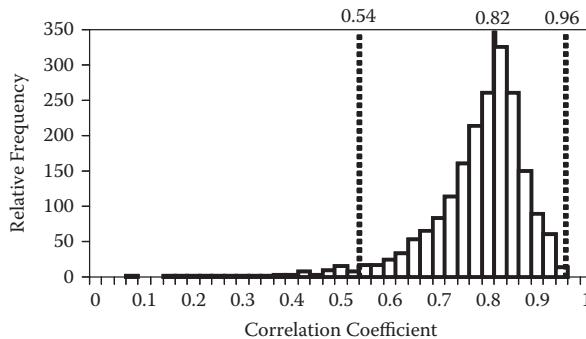
Given b bootstrap replicate samples we can generate b bootstrap estimates of the parameter of interest θ_b . An estimate of the $100(1 - \alpha)\%$ confidence limits around the sample estimate of θ is obtained from the two bootstrap estimates that contain the central $100(1 - \alpha)\%$ of all b bootstrap estimates (Efron, 1979). Thus, the 97.5 and 2.5 percentiles of the two thousand bootstrap estimates of the correlation coefficient, summarized in Figure 6.5, estimate the confidence intervals around the correlation coefficient (Figure 6.6).

With two thousand bootstrap replicates the 95% confidence intervals values would be found at the 50th and at the 1950th position in the sorted bootstrap estimates. In this case, the intervals are between 0.5446 and 0.9567. The bootstrap estimate of the correlation coefficient was very slightly to the left of the sample estimate (0.8191 vs. 0.8197), which shows that the bias in the estimate was small. Note, in this case, the sample estimate is also close to the median value of the bootstrap estimates (Figure 6.6).

In general terms, one would not wish to attempt to fit percentile bootstrap confidence intervals with less than one thousand bootstrap replicates. Even with two thousand replicates the histogram is not as smooth as one could desire for it to be used as a probability density function. However, there is a limit to the precision with which it is useful to estimate these simple bootstrap percentile confidence intervals because they are only ever approximate.

6.4.2 Bias-Corrected Percentile Confidence intervals

Often the bootstrap estimate of the parameter of interest differs somewhat from the observed parameter estimate, indicating that there may be evidence of bias. The validity of any confidence intervals should be improved if they

**Figure 6.6**

Two thousand separate bootstrap estimates of a correlation coefficient grouped into classes of 0.025 with the observed correlation indicated as a solid line and the bootstrap percentile confidence intervals indicated as dotted lines. The 95% bootstrap confidence intervals were at the 51st ($2,000 \times 0.025$) and the 1950th ($2,000 \times 0.975$) sorted bootstrap replicate. The bootstrap estimate of r was 0.8191, while the median was 0.8423. Unlike normal confidence intervals, these confidence intervals are clearly asymmetric and do not suffer from suggesting an upper limit greater than 1. In Excel these can be found using =percentile(g5:g2004,0.025) and =percentile(g5:g2004,0.975).

take into account any bias present. Fitting bias-corrected percentile confidence intervals is slightly different than fitting usual bootstrap percentile intervals around a parameter (Fletcher and Webster, 1996). The difference lies in having first to determine exactly which percentiles should be used after removing any bias that arises because the observed parameter value is not the median of the distribution of bootstrap estimates. Thus, with a slightly biased sample, one might use percentiles such as 0.0618 and 0.992, or perhaps 0.0150 and 0.960 instead of 0.025 and 0.975.

The determination of bias-corrected percentiles is relatively simple (Efron, 1987; Efron and Tibshirani, 1993, provide a justification). After generating the bootstrap sample estimates, one determines F , the fraction of bootstrap replicates that are smaller than the original parameter estimate. Thus, if 56% of the bootstrap replicates were smaller than the original parameter estimate, F would be equal to 0.56. From this fraction, a constant z_0 is calculated to be the probit transform of F :

$$z_0 = \Phi^{-1}(F) \quad (6.24)$$

where Φ^{-1} is the inverse, standard cumulative normal distribution (=norminv(0.56,0,1) in Excel). From Equation 6.24, the appropriate percentiles for the 95% confidence intervals are calculated by the following:

$$\begin{aligned} P_{lower} &= \Phi(2z_0 - 1.96) \\ P_{upper} &= \Phi(2z_0 + 1.96) \end{aligned} \quad (6.25)$$

where Φ is the cumulative normal distribution function. The 1.96 is, of course, the critical value from the inverse normal curve for the 95% confidence intervals. This can be altered appropriately for alternative intervals (e.g., the value would be 1.6449 for 90% intervals). After using Equation 6.25, one would then determine the bias-corrected percentile confidence intervals by taking the values from the bootstrap distribution that align with the calculated upper and lower percentiles.

For an example where 39.8% of bootstrap replicates are smaller than the original parameter estimate, this gives $F = 0.398$ so that $z_0 = -0.2585$, leading to $P_{\text{lower}} = \Phi(-2.4771) = 0.662\%$, and $P_{\text{upper}} = \Phi(1.4429) = 92.54\%$ (using `=normdist(1.4429,0,1,true)` in Excel). Thus, from one thousand ordered values in a bootstrap distribution the 95% confidence intervals would be the 6th and 925th values instead of the 25th and 975th values (using `=percentile(g5:g2004,0.925)`). If there is no bias at all, then $F = 0.5$, which would imply $z_0 = 0$, which would finally lead to the lower and upper bounds being the default of 2.5 and 97.5% (Example Box 6.4).

6.4.3 Other Bootstrap Confidence intervals

We have only considered the simple bootstrap percentile and first-order bias-corrected bootstrap percentile confidence intervals, but many other algorithms exist for generating confidence intervals from bootstrap samples. When using confidence intervals (for example, 90% intervals), one would want them to fail to cover the parameter θ exactly 5% of the time in each direction. There have been many comparative studies conducted on the variety of methods of constructing confidence intervals around a parameter (Efron, 1992; Manly, 1997). Because they use data sets whose properties are known, these studies are able to indicate the strengths and weaknesses of the various methods available. There are two methods that usually perform rather better (generate confidence intervals that work—see Example Box 7.1 in Chapter 7, for an example of how to test for success) than the simple and first-order bias-corrected algorithms considered here; these are named the bootstrap t method and the accelerated bias-corrected percentile methods (Efron, 1987). Both of these extensions are more computer-intensive than the two we have considered here in that they both require the use of a jackknife for best performance (Efron and Tibshirani, 1993; Manly, 1997).

Manly (1997) provided a listing of published biological work using the bootstrap. Generally, in fisheries, the simple percentile confidence interval is most commonly used (Kimura and Balsinger, 1985; Sigler and Fujioka, 1988), though as the first-order bias-corrected percentile intervals involve only a small amount of extra work and the confidence intervals are generally improved, we would recommend that these be used instead. Further examples of the use of the bootstrap will be given when we consider other, more complex models, including the surplus production models that are the simplest stock assessment models available and dynamic age-structured models.

EXAMPLE BOX 6.4

Simple percentile and first-order bias-corrected bootstrap percentile confidence intervals. This example extends the worksheet created in Example Box 6.3. Column G contains one thousand bootstrap replicates of a correlation coefficient with the mean bootstrap estimate in G2 and the standard error estimate in G3. The additions are in columns I, J, and K. The simple percentile intervals are the easiest to implement; in K10 and K11 put the functions =percentile(G5:G1004, 0.975) and =percentile(G5:G1004, 0.025). The values that arise will depend upon the particular bootstrap replicates that are on the sheet, but they will be similar to that shown. J3 contains the estimate of F , the fraction of bootstrap replicates less than the observed value. J4 contains Equation 6.24. J5 and J6 contain the $2z_0 - 1.96$ and $2z_0 + 1.96$, and J7 and J8 contain Equation 6.25, the percentile points where the bias-corrected confidence intervals will be found. In the example sheet, the values were 0.9277 and 0.4140, which have been shifted to the left of the simple percentile intervals in K10 and K11. Run the macro a few times with one thousand bootstrap replicates and notice the impact on the different percentile confidence intervals. Increase the number of replicates to two thousand and modify the equations in J3, J4, and J10:K11. Does the increased number of replicates stabilize the estimated intervals?

	G	H	I	J	K
1					
2	0.81905		Original r	0.819691	
3	0.10225		Fraction F	=countif(G5:G1004,"<"&J2)	
4	Bootstraps		norminv(F)	=norminv(j3/1000,0,1)	
5	0.90599		P_Lower	=2*j4-1.96	
6	0.84306		P_Upper	=2*j4+1.96	
7	0.88260		Percentile L	=normdist(J5,0,1,true)	
8	0.80945		Percentile U	=normdist(J6,0,1,true)	
9	0.77037			Bias-Corrected Intervals	Simple
10	0.84627		Upper95	=percentile(G5:G1004,J8)	0.9567
11	0.86610		Lower95	=percentile(G5:G1004,J7)	0.5446

6.4.4 Balanced Bootstraps

In the process of running a bootstrap procedure the resampling with replacement means it is possible that not all observations in the original sample will be resampled the same number of times across however many replicates are used. While this is not seen as a problem when there are many thousands of bootstrap replicates, if there are only, say, one thousand, then a better

algorithm might be to use a balanced bootstrap. In the balanced bootstrap one first copies the values to be resampled the same number of times as there will be bootstrap replicates; then one resamples at random, without replacement, from within the multiple copies. This process will automatically mean that all observations occur an equal number of times while bootstrapping.

The balanced bootstrap does not appear to have been used very often. It would certainly be easier to use with a single series of data than with more complex models or with structured data. If a model had more than one series of data to be bootstrapped, a balanced design would still be possible but would require some sort of cross-tabulation between data series. For example, two-dimensional balance could be achieved using a classic orthogonal Latin square design. By balancing the use of each observation, the amount of resampling needed to estimate the expectation and other moments of a parameter's distribution, with acceptable accuracy, is reduced by up to fivefold (Hinkley, 1988). However, Hinkley (1988) reports that balanced bootstraps are not so effective for estimating bootstrap percentiles, especially for $p < 0.05$ or $p > 0.95$. This is an area deserving of further research.

6.5 Concluding Remarks

Bootstrapping offers the ability to generate confidence intervals around parameters and model outputs in situations that were previously impossible to approach. The ability to test for bias around a parameter estimate is valuable, but of most value is the ability to estimate the uncertainty around the parameter estimates by estimating standard errors or confidence intervals and the underlying frequency distribution of the parameter of interest.

Where it is valid to use parametric statistics, the best strategy is to use them. However, if one is uncertain what the underlying distribution of a parameter is, then bootstrapping is to be recommended. Fisheries data are generally so variable and uncertain that the debate over the optimum algorithm, while interesting, neglects the fact that the real limitation is most often in the quality of the available data.

7

Monte Carlo Modelling

7.1 Monte Carlo Models

7.1.1 The uses of Monte Carlo Modelling

Monte Carlo models and simulations are computer-intensive methods that can be used to test specific hypotheses and to answer less specific “what if” type questions, including projections into the future. Whichever task is at hand, one requires a simulation model of the fishery that can be compared with nature. It can differ from an assessment model in that it may include hypothetical relationships, parameters, and other modifications. Any modelling task that requires a projection or extrapolation of a model’s implications into the future is best carried out using Monte Carlo simulation techniques. Risk assessment and the more complicated management strategy evaluation are all relatively recent developments that are becoming more commonly applied to fisheries around the world. All use simulation models to explore the implications of manipulating the management of the fishery concerned. The impact of uncertainty concerning any part of a model may also be investigated using simulations.

In this chapter we will consider aspects of modelling that are required when implementing simulations that include hypothetical or unknown components. Like other computer-intensive methods, Monte Carlo simulations require resampling from statistical distributions. In particular, they require resampling with replacement from theoretical probability density functions (pdfs). Detailed examples will be used to illustrate the principles discussed.

Strict Monte Carlo resampling differs from bootstrapping in that the distributions being resampled are parameterized pdfs and are not just empirically determined. Beware of confusion over terminology; some people refer to Monte Carlo resampling as parametric bootstrapping and to bootstrapping as nonparametric bootstrapping. As always, terminology is unimportant as long as one is clear about what is being resampled and how.

7.1.2 Types of uncertainty

A major requirement for developing Monte Carlo simulations is to devise methods for including uncertainty about parameter estimates and other

components of a model. No ecological process is known perfectly, and this constitutes a problem when attempting to create a simulation that adequately captures a system's dynamic behaviour. This appears to be especially true when attempting to understand fishery dynamics. Rather than work entirely with deterministic models, simulations invariably include stochastic elements in which random variation around some model component(s) is included. In this way the implications of uncertainty may be included in a model analysis. There are a number of different types of uncertainty that can influence ecological modelling:

1. The appropriateness of a model. Fundamentally different, independent models can be used to describe the dynamics of a natural system; it is uncertain which model is the best representation.
2. Process error or uncertainty arises where a model has been defined in a deterministic manner but some of the components actually vary randomly through time (for example, virgin biomass is usually defined as representing a constant, but this index of stock productivity is likely to change with environmental conditions).
3. A model of how a particular system operates in nature is accepted, but values for some of the parameters involved are unknown or cannot be independently estimated; these tend to be given fixed values (e.g., natural mortality is often given an assumed constant value in population models).
4. Observation error or uncertainty relates to how precisely a given model's parameters can be estimated given a particular set of data (this is what is estimated when constructing confidence intervals around a set of parameters).
5. Measurement error or uncertainty, where data being put into the model are only measured with error (e.g., ring count estimates from otoliths). This can easily be confounded with observation error.

When conducting a fishery's stock assessment, large parts of the model are often deterministic (process error, type 2 above, is ignored). Parameters are estimated along with some indication of the precision of the parameter estimates (type 4 above; observation error is recognized). However, very often there are parameters, such as natural mortality, that are only poorly known and are not easily estimated. In these cases values for such parameters are often set at an assumed value (type 3 above; uncertainty). The model can be said to be conditioned on such parameters. One of the advantages of Bayesian methodology, as it is used in fisheries (Punt and Hilborn, 1997), is that it is possible to include a prior distribution that attempts to capture our uncertainty for such parameters. A common alternative is to test the sensitivity of the assessment to these constant conditioning parameters (the data are repeatedly refit to the model, and each time the conditioning parameters are given

different values from a predetermined range of values). If there were more than one conditioning parameter, then testing the sensitivity of all possible combinations of values would become more and more difficult as the number of parameters and their ranges increased. Rather than completing such a set of discrete combinations, it would be more efficient to conduct a simulation in which values for the conditioning parameters were selected at random from defined ranges. Such simulations would be Monte Carlo simulations.

By comparing simulated outcomes against observations from nature it is possible to test hypotheses. Simulation models are generally stochastic models because at least some of the variables or parameters have uncertain values. In these cases, the values for the variables or parameters are determined anew during each *run* of the Monte Carlo model, by sampling “with replacement” from a known probability distribution.

7.2 Practical Requirements

7.2.1 The Model Definition

An obvious requirement for Monte Carlo simulation modelling is a formal simulation model. This may closely resemble an assessment model, but in addition it will have a number of unknown components (variables, parameters, or sequence events) that need to be included. The final requirement is to define the expected probability density functions that are to be used to generate values for each uncertain model component.

7.2.2 random Numbers

Fundamental to the process of stochastic simulation modelling is a requirement to obtain random values from under a variety of probability density functions. In Chapter 3, a number of standard pdfs were introduced. Given the parameters of a pdf for a given variable, we saw how to calculate the likelihood for a particular value of that variable. What we now require is a method of inverting that process. We want to be able to randomly select values of the variable concerned once we have selected a parameterized pdf.

There are numerous algorithms for generating random values from given pdfs (Hastings and Peacock, 1975), and modellers who use Monte Carlo simulations tend to collect different techniques for doing this (Press et al., 1989). Fundamental to many methods is the generation of random numbers from a standard uniform variate (i.e., values from 0 to 1 with equal probability). Press et al. (1989) discuss a number of algorithms for generating uniform random numbers.

The pseudorandom number generators used in computers are of variable quality. Such generators are so fundamental to computer-intensive methods that it is a good idea to test any random number generator that you may use. A simple test is to count the number of times the random number generator gives particular values and compare those with the number of times such values would be expected; one could use either a G test or a χ^2 test (Example Box 7.1).

In tests of the efficiency of random number generators, if one chooses a significance level of 5% (i.e., $\chi^2 > 16.919$, for 9 degrees of freedom), the comparison of the frequency of classes of random numbers with their expected values would be expected to fail 5% of the time. The random number generator in Excel (Example Box 7.1) will generate failure rates that average 5%; in some particular tests it is greater than 5%, and in others it is less than 5% (e.g., the average of ten trials of one thousand replicates each using Example Box 7.1 was 0.0504).

7.2.3 Nonuniform random Numbers

The fundamental idea of sampling under a pdf curve is relatively simple, although how it is implemented for each pdf is not necessarily straightforward. For continuous variates the area under a pdf curve must sum to 1. If there is a method for generating random numbers from 0 to 1, then these can be used to generate target areas under a curve. For example, given a normal distribution, $N(0,1)$, i.e., mean zero and variance = 1, then we know that a random number (area under the curve) of 0.05 will give an X variate value of -1.6448, a random area of 0.5 will give a value of 0, and one of 0.9 will give 1.2815 (Figure 7.1). To obtain these inverse pdf values one requires a mechanism by which the pdf curve is integrated until the required random probability is attained (generated from a random number taken between 0 and 1), and then the respective target value of the X variate is determined (Figure 7.1).

It must be remembered that for many statistical distributions there are either direct equations for generating the required random numbers (Hastings and Peacock, 1975), or different, more efficient algorithms for their generation.

If someone wishes to write an independent computer program to conduct a simulation, then a formal algorithm will be necessary once it has been decided which pdf to use for the problem being considered (Press et al., 1989). Fortunately, in Excel many inverse pdfs are provided as built-in functions (Example Box 7.2, Figure 7.2), and one could write other user-defined functions.

How one conducts the integration under the curve will depend upon the probability density function being used (Press et al., 1989). This approach to generating random numbers is, in fact, only one out of many possible. It has only been identified here to assist in the development of intuitions about the process.

EXAMPLE BOX 7.1

A Monte Carlo test of the random number generator function rand(). The =rand() function is copied down as far as A1001. Enter the number of Monte Carlo trials in E15. Select cells C2:C11, enter the array function =frequency(A2:A1001,B2:B11), and press <Ctrl><Shift><Enter>. This counts the number of times a value \leq each respective bin value occurs in the column of random numbers. The χ^2 test is of whether the observed frequencies match the expected and column E has the $(\text{Obs} - \text{Expected})^2/\text{Expected}$. This test should fail one time in twenty at $P = 0.05$. Instead of repeatedly pressing the F9 button, one should generate a macro to count the frequency of successes and failures. The only part of the macro that can be recorded is the activesheet.calculate (as <Shift><F9>). The rest of the algorithm must be added. The ability to write simple programs like this is required for Monte Carlo simulation modelling. Does using bins of 0.05 affect the result? Cell E14 is filled by the macro.

	A	B	C	D	E
1	=count(A2:A1001)	Bin	Observed	Expected	Chi2
2	=rand()	0.1	102	=\$A\$1/10	=(C2-D2)^2/D2
3	=rand()	0.2	97	=\$A\$1/10	=(C3-D3)^2/D3
4	=rand()	0.3	118	Copy down	3.24
5	Copy down	0.4	84	100	2.56
6	0.693034	0.5	107	100	0.49
7	0.502615	0.6	83	100	2.89
8	0.395583	0.7	99	100	0.01
9	0.230871	0.8	114	100	1.96
10	0.598551	0.9	99	100	0.01
11	0.579494	1	97	100	0.09
12	0.421189	Do_Test	Chi2	=sum(E2:E11)	
13	0.705528				
14	0.197339				
15	0.275854		Replicate	1000	

```

Sub Do_Test()           ' attached to button on sheet
    Dim i As Integer, n As Integer ' good practice
    Randomize                   ' resets random number generator
    n = 0                       ' Sets counter to zero
    For i = 1 To 1000
        ActiveSheet.Calculate ' recalculates sheet
    
```

continued

EXAMPLE BOX 7.1 (continued)

```
If Cells(13, 5).Value < 0.05 Then n = n + 1
                                ' no End If as only one line
Cells(14, 5).Value = n / i' interact with worksheet
Cells(15, 5).Value = i
Next i
End Sub
```

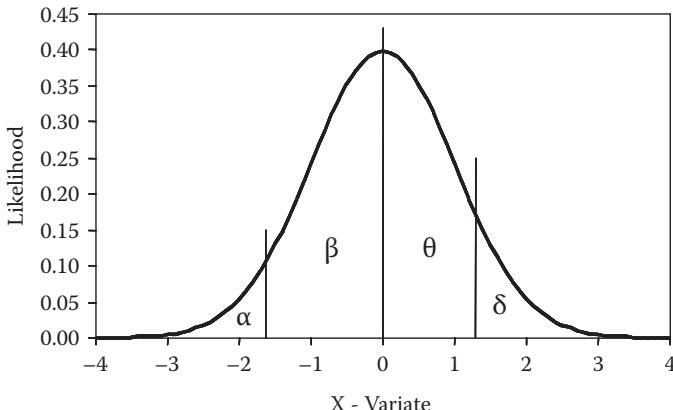


Figure 7.1

Three different values of a variate, X , taken from a standard normal distribution $N(0,1)$, using three different cumulative probabilities: $\alpha + \beta + \theta$. The area under the curve for α was 0.05, for $\alpha + \beta$ was 0.5, for $\alpha + \beta + \theta$ was 0.9, and for $\alpha + \beta + \theta + \delta$ was 1.0. The X values for each of the first three probabilities were -1.6448, 0, and 1.2815, respectively.

7.2.4 Other Practical Considerations

The selection of a suitable probability density function to represent a particular variable or parameter in a simulation is obviously an important step. There are many pdfs that were not considered in Chapter 3 but which are useful in simulations because they are so flexible and general. As usual, one can use whatever is most appropriate as long as one can defend the selection.

Commonly, Monte Carlo replicates are often more time-consuming than randomization or bootstrap replicates, and in the literature it is often found that the number of Monte Carlo replicates are limited. This is risky, as few replicates rarely produce a smooth distribution of expected outcomes. As with the randomizations and bootstraps, the reduction of noise in the results should improve with increasing numbers of Monte Carlo replicates.

EXAMPLE BOX 7.2

The generation of normally distributed random numbers. Instead of using the variance in their normal equations, Microsoft programmers elected to use the standard deviation. This unusual usage possibly derives from them using the standard normal distribution ($N[0,1]$) in which the variance equals the standard deviation. The frequency bins are extended down to B37, generating a range from 1 to 9 in steps of 0.25. Select C5:C37, type =frequency (A5:A1004,B5:B37), and press <Ctrl><Shift><Enter> to enter the array formula. Put the following function into D5 and copy down to D37: $=($C$3/4)*normdist(B5,$B$1,$B$2,false)$. The first term accounts for the relative numbers and the bin sizes. Plot column C against B as a histogram and add column D to the same graph, but make the graph type for that data series a line graph (to mimic Figure 7.2). By repeatedly pressing F9 the random numbers will be recalculated, generating new normally distributed random numbers. Note the differences between the sample mean and standard deviation (C1:C2) and the parameters from which the sample was generated (B1:B2). Note how the graph alters each time and how closely or otherwise it resembles the expected. Try reducing the number of normally distributed random numbers (e.g., delete A105:A1004) and note the impact on the quality of the generated normal distribution. Try altering the value given in B2 and note its impact on the quality of the distribution generated. Clearly, large samples are best when there are many frequency categories. If you implement a χ^2 test on this sheet, remember that the test will be more severe than usual, as there will be many expected frequencies of less than 1, as in D5:D9 (Sokal and Rohlf, 1995). Note the use of rand() in column A. Compare C3 with D3.

	A	B	C	D
1	Mean	5	=average(A5:A1004)	
2	StDev	1	=stdev(A5:A1004)	
3	Count		=count(A5:A1004)	=sum(D5:D37)
4	Inverse Normal Values	Bins	Frequency	Expected
5	=norminv(rand(),\$B\$1,\$B\$2)	1	0	0.017
6	=norminv(rand(),\$B\$1,\$B\$2)	1.25	0	0.044
7	=norminv(rand(),\$B\$1,\$B\$2)	1.5	0	0.109
8	Copy down to row 1004	1.75	0	0.254
9	4.829436	2	0	0.554
10	5.430025	2.25	0	1.137
11	3.227922	2.5	4	2.191
12	4.424067	2.75	4	3.967
13	6.961762	3	7	6.749

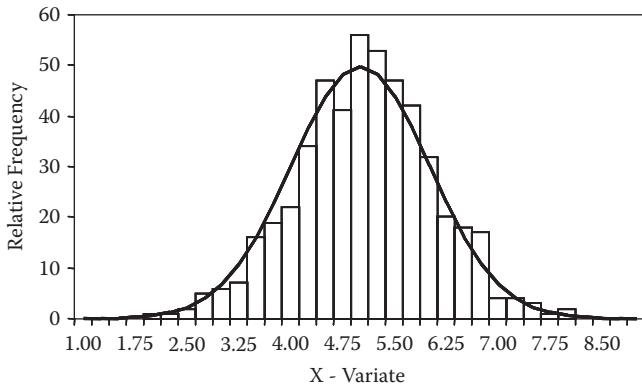


Figure 7.2

A normal distribution generated from five hundred random numbers sampled from under a normal pdf with a mean of 5 and variance of 1. The solid curve denotes the expected relative frequency (Example Box 7.2). Note the imperfections despite there being five hundred random numbers contributing to the frequency distribution. Each sample of five hundred would generate a different relative frequency distribution. This should reinforce the idea that one should try to use as many Monte Carlo replicates as is practically possible.

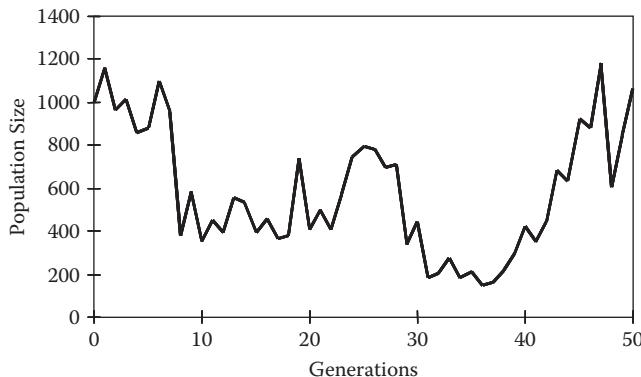
7.3 A Simple Population Model

As a simple example, we will consider a population growing without density dependence:

$$N_{t+1} = rN_t \quad (7.1)$$

where N_t is the population size at time t , and r is the population growth rate. As was seen in Chapter 2, such a population has three possible behaviours, depending on the value of the growth rate r . If $r > 1$, then the population grows exponentially to infinity; if $r = 1$, the population is stable; and if $r < 0$, it declines exponentially to zero. This assumes that the growth rate is a constant. It seems much more likely that a density-independent species will be greatly affected by the environment and the growth rate is likely to vary above and below a value of 1. The question to be answered is whether a population with a randomly varying growth rate (having a mean value of 1 and a given variation σ) would be able to survive. Put another way, we could ask: How often would we expect such a species to go extinct over a given number of generations, and how is that extinction rate influenced by the variability in growth rate? The model becomes

$$N_{t+1} = r_{N(1,\sigma)} N_t \quad (7.2)$$

**Figure 7.3**

A typical population trajectory through fifty generations when the growth rate for Equation 7.2 is set to a mean of 1 and a standard deviation of 0.3. A series of r values greater than 1 would lead to massive population growth, and similarly, a series of values less than 1 would lead to a marked reduction. While variation is low, most model runs do not go extinct and the population trajectory reflects the random walk of the r values around the mean value.

where the $r_{N(1,\sigma)}$ is a random normal deviate having a mean of 1 and a standard deviation of σ ; we also need an artificial lower limit to the r value, say, 0.01 (Figure 7.3).

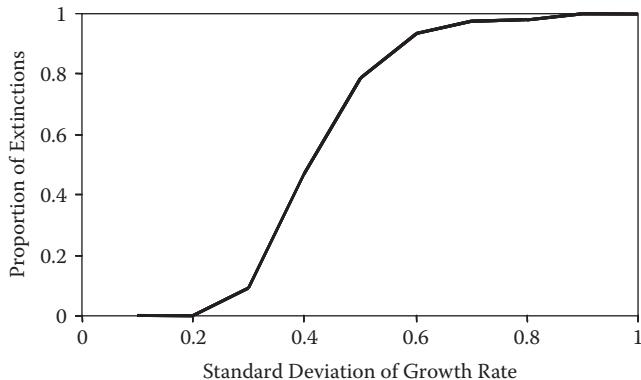
We need to limit the value of r in the simple model to positive numbers because if unconstrained normal random deviates were used, it would be possible to obtain a negative growth rate, which would mean instant extinction. We also need to define extinction; in this case, if the population falls below a single individual (i.e., $N_t < 1$), it can be regarded as extinct.

With the simulation model definition in Equation 7.2 (and the listed assumptions), it would be possible to generate the information necessary to illustrate the relationship between the proportion of simulation runs that go extinct in a given number of generations and the variability of the growth rate (Figure 7.4, Example Box 7.3). In a real exercise, one would also monitor the range and variability of population sizes, along with other measures of the model's performance. Despite the extreme simplicity of this model investigation the power of the method should be clear (Figure 7.4).

7.4 A Nonequilibrium Catch Curve

7.4.1 Ordinary Catch Curve Analysis

A more complex example will illustrate many of the ideas already discussed. As we saw in Chapter 2, if a single cohort were exposed to a constant

**Figure 7.4**

Outcome of ten thousand Monte Carlo replicates of a population growing in a density-independent fashion with a growth rate described by a normal distribution with a mean of 1 and a standard deviation of σ . The graph compares the proportion of model runs that went extinct over fifty generations against the standard deviation of the growth rate.

mortality rate, then the numbers would be expected to decline exponentially following the relationship

$$N_t = N_0 e^{-(M+F)t} = N_0 e^{-Zt} = N_{t-1} e^{-Z}$$
 (7.3)

where N_t is the cohort size at time t , and Z is the instantaneous total mortality rate (natural and fishing combined).

If the total population concerned received constant recruitment and a constant mortality rate each year, then all cohorts would be identical and the numbers in each age class would be expected to decline exponentially. It is possible to follow the fate of a single cohort through a number of years or consider multiple cohorts in a single year; Equation 7.3 would apply in both cases, i.e., whether N_t referred to a cohort or a whole population (Figure 7.5). While it is obviously unlikely that any fished population adheres to any of these conditions (constant recruitment and mortality through time), the logarithmic transform of this relationship is sometimes used to make an estimate of the total mortality:

$$\ln(N_t) = \ln(N_0) - Zt$$
 (7.4)

Given Equation 7.4 and the assumptions of constant recruitment and mortality, a linear regression of the log of numbers-at-age against age should produce a plot with a negative gradient of slope Z . Such an analysis is referred to as a catch curve (Figure 7.6), and by definition these relate to a fishery in equilibrium.

EXAMPLE BOX 7.3

A density-independent population growth model in which the growth rate is described by a normal distribution: $N(1,\sigma)$. Plot the numbers through time (column B) against time (column A) as a connected scattergram to obtain the equivalent to Figure 7.3. By varying the value in B1 and pressing F9 to recalculate the sheet, the population trajectory will alter and may go extinct. If the population goes extinct, then the text in C4 will appear (format it as bold and red).

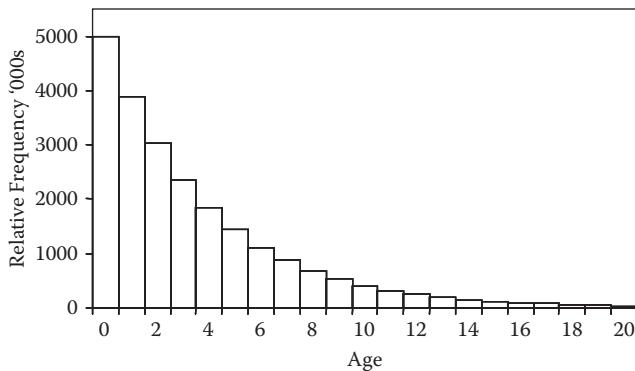
Cell B56 is duplicated in B4 for visual convenience. The use of the max function in column C is to prevent negative deviates being produced. Instead of manually replicating model runs, one could use the macro listed at the bottom of the box. This will run one thousand Monte Carlo replicates and update cell B2 when finished. You could try to extend this macro by adding an outer loop so that it automates the investigation of the relationship between σ and the proportion going extinct (Figure 7.4). Investigate how this population model responds to lognormal random deviates, put =lognorminv(rand(),0,\$B\$1) into C7, copy down, and repeat your analysis. This is computer-intensive work, so try to automate as much as possible.

	A	B	C
1	sigma σ	0.3	<i>Standard deviation of rate of increase</i>
2	Prop	0.30	<i>Proportion going extinct</i>
3	Initial	1000	
4	N50	=B56	=IF(B4=0,"EXTINCT"," ")
5	Time	Nt	Normal Random Deviate
6	0	=B3	
7	1	=IF(B6*C7>1,B6*C7,0)	=max(norminv(rand(),1,\$B\$1),0.01)
8	2	=IF(B7*C8>1,B7*C8,0)	=max(norminv(rand(),1,\$B\$1),0.01)
9	3	=IF(B8*C9>1,B8*C9,0)	=max(norminv(rand(),1,\$B\$1),0.01)
10	4	Copy down to row 56	Copy down to row 56
11	5	1685.231	0.887778
12	6	1765.256	1.047486

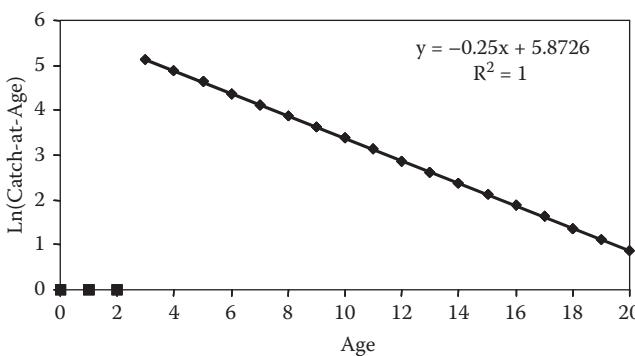
```

Sub Do_Monte()
Dim i As Integer, n As Integer
Randomize
Application.ScreenUpdating = False
n = 0
For i = 1 To 1000
    ActiveSheet.Calculate           ' Only part recordable
    If Cells(4, 2).Value = 0 Then n = n + 1
    Cells(2, 2).Value = n / i
Next i
Application.ScreenUpdating = True
End Sub

```

**Figure 7.5**

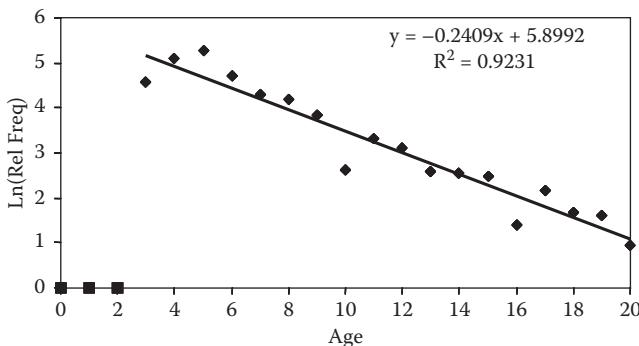
A population in equilibrium with a constant recruitment of 5 million animals and a constant rate of mortality, in this case $Z = 0.25$, being applied instantaneously, leading to an exponential decline. As recruitment is constant, the decline in the total population numbers reflects the decline in each cohort, i.e., there is equilibrium.

**Figure 7.6**

A population in equilibrium with a constant recruitment of 5 million animals and a constant rate of mortality of $Z = 0.25$. The first three year classes are not selected by the fishery and hence are not sampled. The log of the relative frequency of each age class (the relative catch-at-age), plotted against age, generates a straight line whose gradient is an estimate of Z . This is the classical catch curve analysis (Example Box 7.4).

7.4.2 The influence of Sampling error

As well as assuming constant, equilibrium levels of recruitment and mortality, standard catch curve analyses also assume that samples precisely represent the population. Sadly, it is difficult to obtain a sample from a population (in which the fish are measured and aged) that provides a perfect representation of the relative abundance of each age class (the catch-at-age). It is natural to ask what difference sampling error would make to the catch curve analysis. The simplest way of determining this would be to take the perfect sample of

**Figure 7.7**

The same population data as in Figures 7.5 and 7.6 except that the true relative frequencies in a sample of 750 (cf. Figure 7.6) have had random variation added as described in Equation 7.5, with a σ of 15. Note that, in the Monte Carlo replicate illustrated, the linear regression now has a gradient of only 0.241 instead of the true value of 0.25.

size N , which gives rise to the true relative frequencies f_t for each age class t , and then add some random variation to each estimate of the relative frequency. This variability would need to be smaller for the older age classes in absolute terms; else, unrealistically large relative frequencies of older animals would be possible. Also, no frequencies less than 1 should be permitted:

$$\hat{f}_t = f_t + \varepsilon \times \frac{f_t}{\bar{f}} \quad (7.5)$$

where f_t is the true frequency, \bar{f} is the overall mean frequency, \hat{f}_t is the expected frequency, and ε is a normal random variate with mean zero and standard deviation σ (i.e., $N[0, \sigma]$). The last term weights each normal deviate so that the variation around larger true frequencies is greater than around the smaller true frequencies (i.e., we have a constant coefficient of variation and not a constant variance).

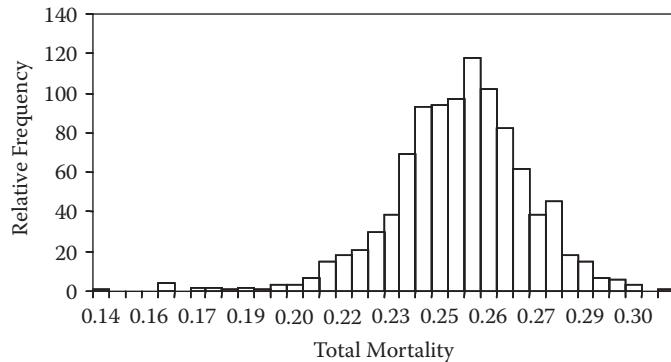
When this is done, the first set of random errors added to the “true” relative frequencies will give rise to a nonperfect straight line with a slightly different gradient from the “true” mortality rate (Figure 7.7, Example Box 7.4).

The actual gradient observed in a single trial has little meaning on its own. However, one can easily imagine taking the same age structure and adding a new set of random errors and repeating the analysis to derive further mortality estimates. If this process were to be repeated many times, we would end up with, say, one thousand Monte Carlo estimates of the Z value. Using these values to form a frequency distribution of outcomes, we could then determine the effect of different degrees of sampling error upon the estimation of Z (Figure 7.8). In addition, as with bootstrapping, we could determine approximate percentile confidence intervals on the estimate of Z (Example Box 7.5).

EXAMPLE BOX 7.4

A classical catch curve analysis with sampling error included. N0 is the constant annual recruitment. B5 contains the age at which fish are first vulnerable to capture. Z is the total mortality (name cell B6 as Z), n is the sample size, and σ_s is the standard deviation of the sampling error. Column D takes the age at first capture into account. Sample size (B8) times the proportion of each age class in the total fished population =IF(D11>0,D11*\$B\$8/\$D\$9,"") is the “perfect sample” in E11:E31. To add sampling error, put =if(isnumber(E11),E11+ (norminv(rand(),0,\$B\$7)*E11/\$E\$9),0) into F11:F31. The total sample may now be smaller or greater than n. The E11/\$E\$9 generates the constant coefficient of variation that prevents excessively large numbers occurring in the older age classes (the lower frequencies). In column H, repeat the formula without the “E11+” to see the range of random variation decreasing with age. In G11 enter =if(F11>1,Ln(F11),0), which prevents the sampled frequency dropping below 1 and produces the required log of catch-at-age. Plot G14:G31 against column A as a scattergram; add a linear trend line to the data to mimic Figure 7.7. Enter =linest(G14:G31,A14:A31) into E1:F1 as an array function (<Ctrl><Shift><Enter>) to produce the catch curve regression. By pressing F9, the rand() functions are recalculated and a new sample will be generated with its associated gradient. You can observe the impact of varying the sampling error variance (in B7) on the quality of the observed catch curve. If you alter the age at first capture you will need to alter E1:E2 and the plot.

	A	B	C	D	E	F	G
1				Gradient	-0.269	5.8317	
2			Z	=abs(E1)			
3							
4	N0	5000000					
5	Age _c	3					
6	Z	0.25					
7	σ_s	15					
8	n	750		Tot Vuln	Average f		
9				=sum(d11:d31)	=average(e11:e31)		
10	Age	Nt		Vuln N	Perfect Sample	+Error	Ln(n)
11	0	=B4		=if(a11>=\$b\$5,b11,0)		0.0	0
12	1	=b11*exp(-Z)		=if(a12>=\$b\$5,b12,0)		0.0	0
13	2	=b12*exp(-Z)		=if(a13>=\$b\$5,b13,0)		0.0	0
14	3	=b13*exp(-Z)		Copy down	167.8	184.1	5.2155
15	4	Copy down		To row 31	130.7	168.5	5.1267
16	5	To row 31		1432524	101.8	93.6	4.5386

**Figure 7.8**

Frequency distribution of a simple Monte Carlo simulation of a catch curve analysis. The hypothetical population had constant recruitment and total mortality but was sampled with random error in the estimates of numbers-at-age (Example Box 7.4). The errors had a constant coefficient of variation instead of a constant variance, which allowed for greater variation at high relative frequencies and lower variation at low frequencies. The distribution of Z estimates is slightly skewed but approximately normal. While the median was 0.24997 (the expected was 0.25), the 2.5 and 97.5 percentiles were 0.205 and 0.286, respectively (55.4% below 0.25 and 44.6% above).

EXAMPLE BOX 7.5

A macro that can be added to Example Box 7.4 to automate the execution of multiple repeats of the Monte Carlo simulation. This will generate a column of estimates of Z that can be summarized using the =frequency function. Implement this and attempt to obtain a version of Figure 7.8.

```
Sub montecarlo()
    Dim i As Integer
    ActiveSheet.Calculate
    Application.ScreenUpdating = False
    For i = 1 To 1000
        Range("D2").Select
        Selection.Copy
        ActiveCell.Offset(i, 9).Range("A1").Select
        Selection.PasteSpecial Paste:=xlPasteValues
    Next i                                         ' turned off
    Application.ScreenUpdating = True
    Range("A1").Select
End Sub
```

The catch curve analysis conducted in Example Boxes 7.4 and 7.5 assumed both a constant annual recruitment and total mortality applied to each recruited age class. Sampling error was added in the form of normal random variation with a constant coefficient of variation. By implementing a Monte Carlo simulation of the fishery and the sampling, we were able to investigate the importance of obtaining a representative sample of the relative catch-at-age.

The Monte Carlo simulation in Example Box 7.4 could also be used to investigate the impact of obtaining a biased catch-at-age sample, or of bias in the ageing methodology (ageing error; Lai and Gunderson, 1987), or other sources of error. By investigating which sources of error exert the greatest impact on the final estimates, researchers can identify weak links in their chain of reasoning and focus their research on reducing uncertainty in those areas.

7.4.3 The influence of recruitment Variability

The assumption of constant recruitment and equilibrium in the catch curve analysis grates against our intuitions about reality. To investigate the significance of this assumption, we could arrange a Monte Carlo simulation where stochastic recruitment variation was included. In this case, the population model would need to be able to step its cohorts through time with each annual iteration having a randomly selected number of recruits. An efficient method of arranging this would be to use some deterministic stock recruitment relationship, such as the Ricker equation (see Chapter 9), and then adding random error (Equation 7.6):

$$\hat{R}_{t+1} = aS_t e^{-bS_t} e^{N(0,\sigma)} \quad (7.6)$$

where \hat{R}_{t+1} is the expected recruitment at time $t + 1$, S_t is an index of the spawning stock size at time t , and a and b are constants of the Ricker equation (a is the recruits-per-spawner at low stock levels, and b relates to how quickly the level of recruits-per-spawner drops as S increases). With most stock recruitment relationships we should use multiplicative lognormal errors (hence the e^{σ}). The spawning stock is the sum of all mature-aged animals. In practice, this would entail calculating the deterministic recruitment expected from a given stock size and including the random variation. The impact of total mortality on each age class would be calculated, and then the results copied and stored, ready for the next iteration (Example Box 7.6).

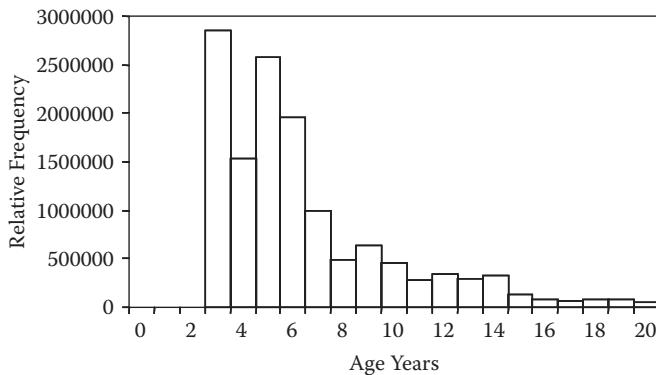
Given such a model, even with no sampling error we would expect to see variation in the relative frequencies of ages in the population. This variation would reflect the nonconstant recruitment to the population. An implication of variable recruitment is that a population is likely to exhibit evidence of strong and weak year classes (Figure 7.9). If this data were used in a catch curve analysis, we would expect to see noise about the hypothetical straight line, even in the absence of sampling error (Figure 7.10, Example Box 7.6).

EXAMPLE BOX 7.6

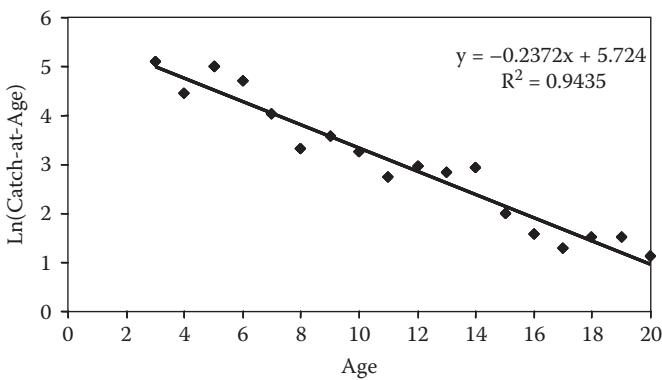
A nonequilibrium, variable recruitment catch curve analysis. This worksheet is identical to that in Example Box 7.4 except in cells A1:B3, B9, B11:B31, and C12:C31. B11:B31 are now just numbers, and C12:C31 now represent the population in column B suffering mortality. Column D now refers to column C, which represents the latest population structure. Otherwise, the worksheet remains the same. Cells A1:B3 contain the Ricker stock recruitment parameters and the stdev of the recruitment variation. Put $=$B$2*D9*exp(-b*D9)*exp(norminv(rand(),0,B3))$ into B9 to calculate the expected recruitment. One could have used $loginv(rand(),0,B3)$ to obtain the same result. D9 represents the spawning stock size that is used in the stock recruitment relationship. Try varying both σ_r and σ_s , and determine the effect on the catch curve analysis. Implement a macro to repeat the analysis one thousand times and construct a relative frequency of Z estimates (Example Box 7.7, Figure 7.11). B11 is filled by the macro from B9. B4 is no longer used.

	A	B	C	D
1	Ricker a	6		Gradient
2	Ricker b	1.826E-07	Z	0.2365
3	σ_r	0.3		
4	N0	5000000		
5	Age _c	3	Step_Model	
6	Z	0.25		
7	σ_s	15		
8	N	750		Mature Pop
9	Recruits	6673370		=sum(D11:D31)
10	Age	Nt	Nt+1	Mature N
11	0	8774442		
12	1	5760803	=B11*exp(-\$B\$6)	=IF(A12>=\$B\$5,C12,0)
13	2	2726971	=B12*exp(-\$B\$6)	=IF(A13>=\$B\$5,C13,0)
14	3	3374618	=B13*exp(-\$B\$6)	=IF(A14>=\$B\$5,C14,0)
15	4	2540555	Copy Down	Copy Down
16	5	1520554	to row 31	to row 31
17	6	1293433	1184209	1184209
18	7	878412	1007327	1007327

A Monte Carlo analysis of catch curves with only recruitment variation leads to a symmetric distribution of total mortality estimates, while recruitment and sampling variation leads to a skewed distribution with much wider percentile confidence intervals (although the median remains centrally located about 0.25). The earlier analysis of sampling variation alone (Figure 7.8)

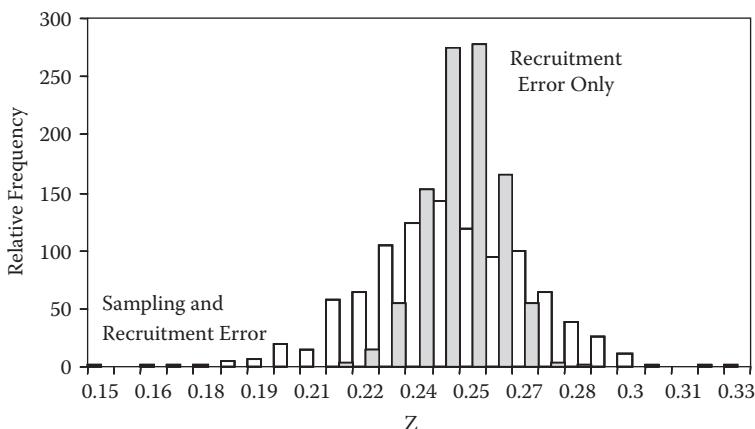
**Figure 7.9**

A nonequilibrium age-structured population model with a constant rate of mortality of $Z = 0.25$ and variable recruitment as in Equation 7.6, with $\sigma = 0.3$. The first three year classes are not selected by the fishery and hence are not sampled. Strong year classes appear evident from three, five, six, and nine years before present (cf. Figure 7.5). If this population were to be sampled, especially if there were sampling error, we would not expect a particularly good fit of a straight line from the log of the relative catch-at-age against age, as required by the standard catch curve analysis (Figure 7.10, Example Box 7.6).

**Figure 7.10**

Catch curve analysis of the data, given in Figure 7.9, from a nonequilibrium population having a total mortality of 0.25 and random recruitment. There was no sampling error. Note the scatter about the regression line and, in this case, the underestimate of the Z value (Example Boxes 7.5 and 7.6). Repeating this analysis many times would permit a characterization of the effect of recruitment variation on the estimation of Z .

indicated that the distribution of the Z estimates only increased its range in a small way after the addition of recruitment variation. With only sampling error, the 95% confidence intervals were 0.205 and 0.286 (Figure 7.8). With both sampling error and recruitment variation, the confidence intervals around the Z estimate were 0.1995 and 0.292 (Figure 7.11). Recruitment variability does not appear as important as the presence of sampling error on the number-at-age.

**Figure 7.11**

The impact of sampling error relative to recruitment variation on the estimation of total mortality using a catch curve analysis (Example Boxes 7.6 and 7.7). The model settings are recruitment variability = 0.3 and sampling variability = 15. The darker columns reflect the catch curve analysis when only recruitment variability is present. The empty bars are where both types of variation are present. The sampling errors dominate the analysis (cf. Figure 7.8).

It would not be valid to draw conclusions after so few investigations. The ranges of variation assumed for the sampling and recruitment error would need to be altered and their interaction more thoroughly determined before any conclusions could be drawn (Example Box 7.7).

7.5 Concluding Remarks

Monte Carlo simulation modelling allows one to investigate many parts of nature that are currently not amenable to direct observation or experiment. Its value in risk assessment and management strategy evaluation is its most important use in fisheries today (Francis, 1992; Smith et al., 2007). Risk assessments involve projecting the stock dynamics forward under different simulated management regimes, and of course, this is beyond experience.

Many skills are needed to conduct such simulation modelling, including knowledge of probability density functions and which to use in what circumstances, as well as a facility with computer programming, in whatever language suits you best. Most important, however, is a need to have an understanding of the present state of knowledge about the system being modelled. Not all simulation models need be realistic, and for those situations a simple mathematical view of the system would be all that was required. However, for a simulation model to be realistic, any hypothetical additions would

EXAMPLE BOX 7.7

A macro and Monte Carlo procedure to add to Example Box 7.6 to automate the simulations and enable percentile analyses of the results. Set the sampling error to 0.001 and the recruitment error to 0.3, and run the Monte Carlo analysis, generate a histogram of the results using the =frequency function, and store the actual numbers away from column K. Then set the sampling error to 15 and rerun the Monte Carlo analysis. Add the Z estimates from this to the histogram already generated to produce something akin to Figure 7.11.

```

Sub Step_Model()
    ' Conducts a single population growth cycle
    Range("C12:C31").Copy
    Range("B12").Select
    Selection.PasteSpecial Paste:=xlValues
    Range("B9").Copy
    Range("B11").Select
    Selection.PasteSpecial Paste:=xlPasteValues
    Application.CutCopyMode = False
    Range("A1").Select
End Sub

Sub Do_Monte_Carlo()
    ' automates simulations for Monte Carlo analyses
    Dim i As Integer
    For i = 1 To 1000
        Application.ScreenUpdating = False
        Step_Model                         ' call the other macro
        Range("D2").Copy
        ActiveCell.Offset(i, 10).Range("A1").Select
        Selection.PasteSpecial Paste:=xlPasteValues ' column K
    Next i
    Range("A1").Select
    Application.ScreenUpdating = True
End Sub

```

need careful construction to ensure biological plausibility. Even if a model has been inappropriately constructed it will still generate the implications of particular actions. Generally, it is better to investigate a range of model structures than rely on a single formulation.

Whenever a simulation model is used and it contains parts that are strictly invention it must not be mistaken for reality; it is only a model. When conducting “what if” trials, we would be testing what would be the

case if the system operated in a particular way. It is important not to forget that even if the results reflected observable nature closely, this would not imply that the particular model being used is a true representation of the operation of nature. As always, while a good fit certainly describes, it does not necessarily explain.

8

Characterization of Uncertainty

8.1 Introduction

Fitting a model to a set of data involves searching for parameter estimates that optimize the relationship between the observed data and the predictions of the model. The parameter estimates are taken to represent some aspect of the world in which we are interested. While it should be possible to find optimum parameter values in each situation, it remains the case that the data used are only a sample. A different sample of the same kind of data would very likely lead to at least slightly different parameter estimates; so the exact value of the estimated parameters is not really the issue. Rather, we want to know how repeatable such estimates are likely to be if we had the luxury of having multiple samples. That is, the parameters are just estimates, and we want to know how confident we can be in those estimates. Some aspects of uncertainty, such as highly variable data leading to parameter estimates with wide confidence intervals, are relatively familiar, and more details will be given here. However, in modelling there are many potential sources of uncertainty, and we need to be aware of them all to avoid drawing stronger conclusions than our data and models should allow.

In this chapter we will explore alternative ways available for characterizing the uncertainty inherent in any modelling situation. Bootstrapping is an excellent method for examining the levels of uncertainty stemming from the available data, but that has already been considered in Chapter 6 and we will not repeat that material. While we will introduce many sources of potential uncertainty, only some of these can be usefully investigated here. Some sources of uncertainty influence the variability of data collected, other sources can influence the type of data available. There are various ways of describing the different types of uncertainty that can influence fisheries models. These are often called sources of error, usually in the sense of residual error rather than as a mistake having been made. Unfortunately, the term *error* has the potential to lead to confusion, so it is best to use the term *uncertainty*.

Francis and Shotton (1997) listed six different types of uncertainty, while Kell et al. (2005) contract these to five; however, they can all be summarized under four headings, some with subheadings, as follows:

- Process uncertainty: Underlying natural random variation in demographic rates (such as growth, interannual recruitment, interannual natural survivorship) and other biological properties and processes. This would be a significant source of residual error between observed and predicted values, so best to call this process uncertainty rather than process error.
- Observation uncertainty: Sampling error and measurement error—samples are meant to represent a population but remain only a sample. Inadequate or nonrepresentative data collection would contribute to observational uncertainty, as would any mistakes or the deliberate misreporting of data (not unknown in the world of fisheries). This is another source of residual errors between observations and predicted values.
- Model uncertainty: Relates to the capacity of the selected model structure to describe the workings of the system dynamics. There can be more than one type of model uncertainty:
 - Different structural models may provide different answers, and uncertainty exists over which is the better representation of nature.
 - The selection of the residual error structure for a given process is a special case of model uncertainty that has already been shown (in Chapter 3) to have important implications for parameter estimates.
 - Estimation uncertainty can be thought of as a form of model uncertainty in that the model structure is not capable of capturing the process dynamics in an unbiased manner.
- Implementation uncertainty: Where the effects or extent of management actions may differ from those intended.
 - Poorly defined management options may lead to implementation uncertainty.
 - Institutional uncertainty: Inadequately defined management objectives leading to unworkable management.
- Time lags between making decisions and implementing them can lead to greater variation. Assessments are often made a year or more after fisheries data are collected, and management decisions often take another year or more to be implemented.

Model uncertainty can be both quantitative and qualitative. Thus, hierarchically structured models could be compared to one another, and the best fitting selected between such models. Such models may be considered to be related but quantitatively different. However, where models are incommensurate, as we have seen, for example, when different residual error structures are used with the same structural model, they can each generate an

optimum fit, and model selection must be based on factors other than quality of fit. Such models do not grade smoothly into each other but constitute qualitatively different descriptions of the system under study. Model uncertainty is one of the driving forces behind model selection. Even where there is only one model developed this has been implicitly selected from many possible models. Working with more than one type of model in a given situation (perhaps a surplus production model along with a fully age-structured model; see later chapters) can often lead to insights that using one model alone would be missed.

Institutional uncertainty is very important in the management of natural resources. The best modelling practices in the world would be pointless if significant implementation uncertainty is present. When discussing an input-controlled fishery, Dichmont et al. (2006) suggested four sources of implementation error: (1) the extent to which management advice is accepted by the decision makers, (2) management decisions fail to be implemented because of different levels of participation in the fishery, (3) restricting fishing mortality may be difficult when a fishery targets multiple species or stocks, and (4) inadequate allowance made for changes in fishing power through time. Time lags between receiving data, generating an assessment, and implementing its recommendations are extremely common in fisheries practice. The extent to which advice is accepted or is effective can be influenced by time delays between advice being given and it being implemented.

Model and implementation uncertainty are both very important in the management of natural resources. However, in this chapter we are going to concentrate on methods that allow us to characterize the confidence with which we can accept the various parameter estimates and other model outputs obtained from given models that have significance for management advice. There are numerous methods for characterizing the uncertainty around any parameter estimates or model outputs. Some methods work best when the underlying data structures are normally distributed, whereas others are more general. We will start with the more classical approaches that relate to estimates of normal standard errors. These lead naturally toward methods that characterize uncertainty by defining the sampling distribution of parameters and outputs and identifying some central percentile range around the distribution's expectation.

8.2 Asymptotic Standard Errors

The classical definition of the 95% confidence intervals around the mean of a sample is given by (Snedecor and Cochran, 1967)

$$\bar{x} \pm t_v \frac{\sigma}{\sqrt{n}} \quad (8.1)$$

where \bar{x} is the mean of the sample, n is the sample size, σ is the sample standard deviation, and t^v is the t distribution with $v = (n - 1)$ degrees of freedom. The term σ represents the variability of the sample about its mean. If we had multiple samples it would be possible to estimate the standard deviation of the group of sample means. The fragment σ/\sqrt{n} is known as the standard error of the variable x , and is one way of estimating the expected standard deviation of a set of sample means when there is only one sample. Classical confidence intervals are distributed symmetrically around the mean or expectation, and this is standard when dealing with normal distributions.

While the classical definition works well with single parameters and normally distributed data, there can be complications when fitting a model if there are multiple and possibly correlated parameters being estimated at once. When multiple parameters are fitted to a model, there are a number of ways in which it is possible to generate estimates of standard errors around each parameter value.

Asymptotic standard errors are produced by estimating the variance-covariance matrix for the model parameters in the vicinity of the optimum parameter set. Essentially the gradient of the maximum likelihood or sum of squares surface at the optimum is used to characterize any relationships between the various parameters, and these are used to generate the variance-covariance matrix. Parts of this are then used in conjunction with the residual variance from the optimum fit to produce the estimates of standard error so that Equation 8.1 can be used to generate approximate confidence intervals. The primary assumptions are that the fitted surface near the optimum is regular and smooth, and that the surface is approximately normal near the optimum. This means the standard errors will be symmetric around the optimal solution, which may or may not be appropriate. As a first approximation, however, asymptotic standard errors provide an indication of the inherent variation around the parameter estimates. The methodology will be illustrated with the data and linear regression describing the relationship between catches of king prawns and tiger prawns used in Chapter 6 (Example Box 6.3).

Formally the variance-covariance matrix is the product of the residual variance and the inverse of the Hessian matrix. The residual variance is simply

$$Sy^2 = \frac{\sum (y - \bar{y})^2}{n - p} \quad (8.2)$$

where the y values are the observed variable (in this case the king prawn catches), \bar{y} is the expected king prawn catch for each time period (predicted

by the regression on tiger prawns), n is the number of sets of observations (in this case twelve data pairs), and p is the number of parameters being estimated (in this case two, a gradient and intercept). The Hessian matrix describes the local curvature or gradient of the sum of squared residual surface. More formally, this is made up of the second-order partial derivatives of the function describing the sum of squared residuals. Given a function with its parameters, e.g., a, b and the linear regression

$$King = f(Tig) = a.Tig + b \quad (8.3)$$

the square Hessian matrix of this function f , with two parameters a and b , would be

$$\mathbf{H}(f) = \begin{Bmatrix} \frac{\partial^2 f}{\partial a^2} & \frac{\partial^2 f}{\partial a \partial b} \\ \frac{\partial^2 f}{\partial a \partial b} & \frac{\partial^2 f}{\partial b^2} \end{Bmatrix} \quad (8.4)$$

The variance-covariance matrix (\mathbf{A}) is estimated by multiplying the elements of the inverse of the Hessian by the residual variance, Equation 8.2:

$$\mathbf{A} = Sy^2 \cdot \mathbf{H}^{-1} \quad (8.5)$$

The estimate of the standard error for each parameter in the set θ is then obtained by taking the square root of the diagonal elements of the variance-covariance matrix:

$$StErr(\theta) = \sqrt{diag(\mathbf{A})} \quad (8.6)$$

We can approximate the elements of the Hessian numerically by making small increments to the optimum parameter estimates and estimating the gradients of the surface at the optimum (this is the method of finite differences). Thus, for each of the n data points, if we use a small increment (e.g., $\Delta = 0.00001$), we would calculate the gradient of the surface of the predicted king catches with respect to the two parameters individually as

$$\frac{\partial K}{\partial a} \approx \left[((a + \Delta)Tig + b) - ((a - \Delta)Tig + b) \right] / (2\Delta) \quad (8.7)$$

and

$$\frac{\partial K}{\partial b} \approx \left[(aTig + (b + \Delta)) - (aTig + (b - \Delta)) \right] / (2\Delta) \quad (8.8)$$

The sums of the squared values and of the cross products of these values are then calculated:

$$\frac{\partial^2 K}{\partial a^2} = \sum^n \left(\frac{\partial K}{\partial a} \right)^2 \quad (8.9)$$

$$\frac{\partial^2 K}{\partial b^2} = \sum^n \left(\frac{\partial K}{\partial b} \right)^2 \quad (8.10)$$

$$\frac{\partial^2 K}{\partial a \partial b} = \sum^n \left(\frac{\partial K}{\partial a} \cdot \frac{\partial K}{\partial b} \right) \quad (8.11)$$

These are substituted into Equation 8.4 and the result inverted (the array function minverse in Excel) and used in Equations 8.5 and 8.6, and then finally in Equation 8.1, to provide confidence intervals around each parameter. These equations are all implemented in Example Box 8.1.

Remember that asymptotic standard errors are quick and convenient but can usually only be regarded as approximate. Nevertheless, they can provide an indication of which parameters are least well estimated and may suggest whether a more detailed examination of uncertainty would be wise.

8.3 Percentile Confidence Intervals Using Likelihoods

There are a number of ways of generating confidence intervals around parameter estimates when the optimum fit is found using a maximum likelihood criterion. It is usually possible to calculate asymptotic standard errors, but there are alternative approaches that can often produce more convincing confidence intervals. Using maximum likelihood, a von Bertalanffy growth curve can be fitted to female Pacific hake (Kimura, 1980; Figure 8.2, Example Box 8.2). A plot of different hypothesized values for the parameter of interest against their respective likelihood (after optimizing the fit of any remaining parameters, e.g., Figure 8.3) demonstrates that as one increments away from the optimum parameter value, the likelihoods decline in a smooth fashion. Such plots of likelihood against the parameter of interest are known as likelihood profiles.

Approximate confidence intervals around parameters may be obtained by generating a likelihood profile, standardizing those likelihoods so they add to 1 (i.e., sum all the separate likelihoods and divide each by the total), and then finding the particular parameter values that encompass the confidence

EXAMPLE BOX 8.1

A linear regression between the bycatch of king prawns and the catch of tiger prawns from the Australian Northern Prawn Fishery in the years 1976 to 1987; data as in Example Box 6.3 (see Figure 8.1). Minimize the sum of squared residual errors in B5 using the solver and varying the two parameters in B2:B3. By plotting column B against column A as data points and adding column C against column A as a line, you should be able to reproduce Figure 8.1.

	A	B	C	D
2	a	0.025854		
3	b	-11.4826		
4				
5	SSQ	=SUM(D11:D22)		
6	n	=COUNT(A11:A22)-2		
7				
8	Sy ²	=B5/B6		StErr
9				
10	Tiger	King	E(King)	Resid ²
11	566	10	=\$B\$2*A11+\$B\$3	=(B11-C11)^2
12	1437	22	=\$B\$2*A12+\$B\$3	=(B12-C12)^2
13	1646	42	=\$B\$2*A13+\$B\$3	=(B13-C13)^2
14	2056	33	41.67	75.22
15	3171	64	70.50	42.26
16	Get data	From Example Box 6.3	Copy down to	Row 22

Generating the asymptotic standard errors requires the parameters to be incremented slightly to estimate a gradient, so place $=((\$B\$2+\$F\$9)*A11+\$B\$3)-((\$B\$2-\$F\$9)*A11+\$B\$3))/(2*\$F\$9)$ into E11, which increments the **a** parameter, and copy down to row 22; put $=((\$B\$2*A11+(\$B\$3+\$F\$9))-(\$B\$2*A11+(\$B\$3-\$F\$9)))/(2*\$F\$9)$ into F11 to increment the **b** parameter and copy down to row 22. Vary the value of delta in F9 to explore the sensitivity of the process to this value. After filling in cells G11:I22, the estimate of the Hessian matrix **H** is formed in E2:F3. Select cells E5:F6, type =MINVERSE(E2:F3), then press all three keys <Ctrl><Shift><Enter> at once to produce the necessary array function needed to invert the Hessian. Cells H2:I3 constitute the variance-covariance matrix and represent Equation 8.5. The matrix in H5:I6 contains the correlation matrix between the parameters. Put =H2/SQRT(H2*H2) into H5 and =I3/SQRT(I3*I3) into I6, both of which

continued

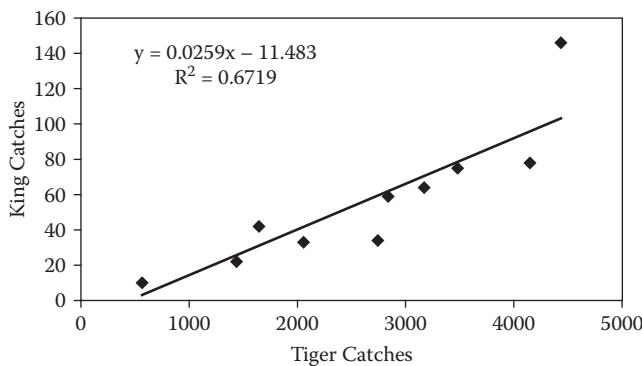
EXAMPLE BOX 8.1 (continued)

should produce 1.0. The cross-correlations are gained from placing =I2/SQRT(H2*I3) into I5 and =H3/SQRT(H2*I3) into H6, which again should be equal. The standard error estimates are produced in E8:F8; the confidence intervals are generated by placing =B2-TINV(0.05,B6)*E8 into H7 and similarly putting =B2+TINV(0.05,B6)*E8 into H9, with =B3-TINV(0.05,B6)*F8 in I7 and =B3+TINV(0.05,B6)*F8 in I9 for the approximate 95% confidence intervals.

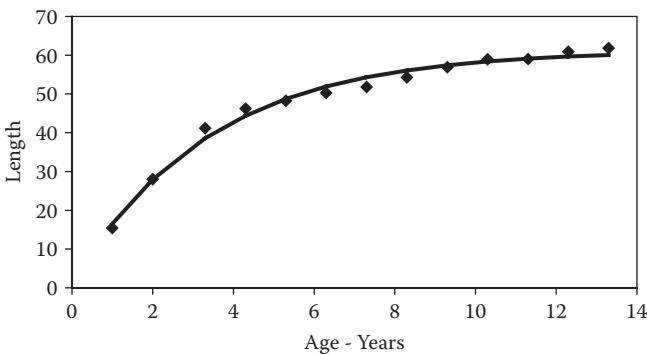
	E	F	G	H	I
1	H			A	
2	=SUM(G11:G22)	=SUM(H11:H22)		=\$B\$8*E5	=\$B\$8*F5
3	=F2	=SUM(I11:I22)		=\$B\$8*E6	=\$B\$8*F6
4	H ⁻¹			a	b
5	7.06E-08	-0.00019		1.0000	-0.9271
6	-0.00019	0.593226		-0.9271	1.0000
7	(S _y ² H ⁻¹) ^{1/2}		Lower95	0.0131	-48.3843
8	=SQRT(H2)	=SQRT(I3)	Estimate	=B2	=B3
9	Delta	0.000001	Upper95	0.0386	25.4190
10	δK/δa	δK/δb	X ²	XY	Y ²
11	566.00	1.000	=E11*E11	=E11*F11	=F11*F11
12	1437.00	1.000	=E12*E12	=E12*F12	=F12*F12
13	1646.00	1.000	=E13*E13	=E13*F13	=F13*F13
14	2056.00	1.000	=E14*E14	=E14*F14	=F14*F14
15	3171.00	1.000	=E15*E15	=E15*F15	=F15*F15
16	2743.00	1.000	=E16*E16	=E16*F16	=F16*F16
17	2838.00	1.000	=E17*E17	=E17*F17	=F17*F17
18	Copy	Down to	Row	22	

intervals required (usually the central 95 or 90% of the total distribution). This approach would only be valid if the increments on the parameter axis are relatively small, so that the likelihood distribution approximates a continuous probability distribution. In addition, the likelihoods at the extremes of the parameter values considered should be negligible. This is an empirical likelihood profile method and is illustrated in Example Box 8.2.

The standardized likelihoods should cumulate to 1, and the 95% confidence intervals may be determined by searching for the 0.025 and 0.975 percentiles of the cumulative distribution (Example Box 8.2). An important difference between likelihood profile confidence intervals and those generated using 1.96 times the asymptotic standard errors is that the latter are forced by their nature to be symmetrical. This is not necessarily the case when using likelihood profile confidence intervals (Figure 8.3). A similar

**Figure 8.1**

The linear regression between king prawn catches and tiger prawn catches, in tonnes, from the Australian Northern Prawn Fishery for the years 1976 to 1987. See Example Boxes 6.3 and 8.1.

**Figure 8.2**

The optimal von Bertalanffy curve fitted to data for female Pacific hake (Kimura, 1980; equal weight given to each data point). Optimum parameters: $L_\infty = 61.22$, $K = 0.296$, $t_0 = -0.057$, and $\sigma = 1.489$ (Example Box 8.2).

process could be applied to each of the model parameters in turn, or even to multiple parameters at once.

8.4 Likelihood Profile Confidence Intervals

An alternative to empirical likelihood profiles is to use a deterministic approximation. Venzon and Moolgavkar (1988) describe a method of obtaining what they call “approximate $1 - \alpha$ profile-likelihood-based confidence intervals.” This simple procedure starts with finding the set of model parameters that generate the maximum likelihood for the data. The method then

EXAMPLE BOX 8.2

Fitting a von Bertalanffy growth curve to length-at-age data for female Pacific hake (Kimura, 1980) using maximum log-likelihood. To calculate the expected lengths in column C, put $=$B$2*(1-exp(-$B$3*(A8-$B$4)))$ into C8 and copy down to C20. Put $=Ln(normdist(B8,C8,$B$5,false))$ in D8 and copy down to D20. Plot column B against A as a scattergram and add column C as a line (cf. Figure 8.2) to observe the relation between age and length. First use the solver to maximize B6 by altering B2:B5. To generate a likelihood profile fill E8:E73 with 57 to 70 in steps of 0.2. To produce the profile, individually copy each of the possible Linf values from column E into B2 and re-solve for the maximum likelihood, but only by varying B3:B5. In other words, for each value of Linf, optimize for the other parameters and save the log-likelihood value in column F next to its respective Linf value. Do this for all the values in column E (a macro to do this is given in the example box continuation, where the final details of producing the likelihood profile are given; cf. Figure 8.3).

	A	B	C	D	E	F	G
1	Parameters						
2	L_∞	61.2250					
3	K	0.2963					
4	t₀	-0.0573					
5	Sig	1.4896					
6	LL	=sum(D8:D20)					=sum(G8:G73)
7	Age	Obs(L)	Ex(L)	Log_L	Linf	Profile	Likelihood
8	1	15.40	16.467	-1.5741	57.0		=exp(F8)
9	2	28.03	27.945	-1.3191	57.2		=exp(F9)
10	3.3	41.18	38.584	-2.8359	57.4		=exp(F10)
11	4.3	46.20	44.390	-2.0555	57.6		=exp(F11)
12	5.3	48.23	48.707	-1.3688	57.8		=exp(F12)
13	6.3	50.26	51.917	-1.9364	58.0		=exp(F13)
14	7.3	51.82	54.304	-2.7081	58.2		=exp(F14)
15	8.3	54.27	56.079	-2.0549	58.4		=exp(F15)
16	9.3	56.93	57.399	-1.3669	58.6		=exp(F16)
17	10.3	58.93	58.380	-1.3856	58.8		=exp(F17)
18	11.3	59.00	59.110	-1.3201	59.0		=exp(F18)
19	12.3	60.91	59.652	-1.6740	...		=exp(F19)
20	13.3	61.83	60.055	-2.0271	to 70		=exp(F20)

continued

EXAMPLE BOX 8.2 (continued)

Development of likelihood profile for the Linf parameter for the von Bertalanffy curve fitted in Example Box 8.1. Copy each of the possible Linf values from column E into cell B2 and re-solve, maximizing the log-likelihood in B6 by varying B3:B5 (do not include B2), copying the optimum maximum log-likelihood from B6 down into column F. Either do this manually or implement the following macro (much of the macro can be recorded and then edited), and then plot column H against column E (cf. Figure 8.3). Compare this with a plot of the log-likelihood in column F.

```

Sub Do_Profile()
For i = 1 To 66
    Range("E7").Select
    ActiveCell.Offset(i, 0).Range("A1").Select
    Selection.Copy
    Range("B2").Select
    Selection.PasteSpecial Paste:=xlPasteValues
    SolverOk SetCell:="$B$6", MaxMinVal:=1, ValueOf:="0",
        byChange:="$B$3:$B$5"
    SolverSolve (True)
    Range("B6").Select
    Selection.Copy
    Range("F7").Select
    ActiveCell.Offset(i, 0).Range("A1").Select
    Selection.PasteSpecial Paste:=xlPasteValues
Next i
End Sub

```

	E	F	G	H	I
6			=SUM(G8:G73)		
7	Linf	Profile	Likelihood	Std Like	Cumulative
8	57	-29.6787	=EXP(F8)	=G8/\$G\$6	=H8
9	57.2	-29.2452	=EXP(F9)	=G9/\$G\$6	=I8+H9
10	57.4	-28.8136	=EXP(F10)	=G10/\$G\$6	=I9+H10
11	57.6	-28.3852	4.7E-13	0.00056	=I10+H11
12	57.8	-27.9617	7.18E-13	0.000855	0.002171
13	58	-27.5448	1.09E-12	0.001298	0.003469
...	Down to
73	70	-31.0395	3.31E-14	3.94E-05	1

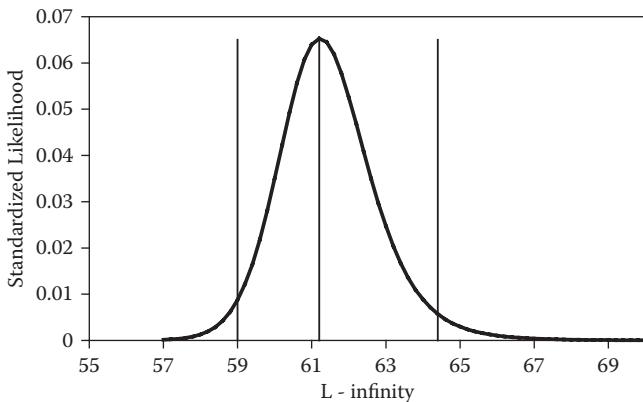


Figure 8.3

Likelihood profile for the L_∞ estimate for the von Bertalanffy curve fitted to data in Example Box 8.2. The outer vertical lines at 59.0 and 64.4 are the closest steps to the 0.025 and 0.975 percentiles enclosing the central 95% around the optimum of 61.2 depicted by the central line. Note the asymmetry of the 95% confidence intervals.

relies on the fact that likelihood ratio tests asymptotically approach the χ^2 distribution as the sample size gets larger (see Chapter 9 for more details on likelihood ratio tests). This means that with the usual extent of real fisheries data, this method is only approximate. Likelihood ratio tests are, exactly as their name suggests, a ratio of two likelihoods, or if dealing with log-likelihoods, the subtraction of one from another, the two are equivalent:

$$\frac{L(\theta)_{\text{Max}}}{L(\theta)} = e^{(LL(\theta)_{\text{Max}} - LL(\theta))} \quad (8.12)$$

where $L(\theta)$ is the likelihood of the θ parameters, the Max subscript denotes the maximum likelihood (assuming all other parameters are also optimally fitted), and $LL(\theta)$ is the equivalent log-likelihood.

The expected log-likelihoods for the actual confidence intervals for a single parameter, assuming all others remain at the optimum, are given by the following (Venzon and Moolgavkar, 1988):

$$2 \times [LL(\theta)_{\text{Max}} - LL(\theta)] \leq \chi^2_{1,1-\alpha}$$

$$LL(\theta) = LL(\theta)_{\text{Max}} - \frac{\chi^2_{1,1-\alpha}}{2} \quad (8.13)$$

where $\chi^2_{1,1-\alpha}$ is the $(1 - \alpha)$ th quantile of the χ^2 distribution with 1 degree of freedom (e.g., for 95% confidence intervals, $\alpha = 0.95$ and $1 - \alpha = 0.05$, $\chi^2_{1,1-\alpha} = 3.84$). For a single parameter θ_i , the approximate 95% confidence intervals are therefore those values of θ_i for which two times the difference between the

EXAMPLE BOX 8.3

Approximate likelihood profile confidence intervals. Extend Example Box 8.2 as below. First use the solver to maximize B6 (the maximum log-likelihood) by changing the parameters in cells B2:B5. Given the optimum parameter estimates, we can calculate the log-likelihood expected at the 95% confidence intervals for Linf. In this instance the optimum LL is -23.6266, and subtracting 1.92 (E4) from that gives -25.5474. Run the solver again, only this time, rather than maximizing the target cell (B6), have the solver vary cell B2 only until the target cell has a value of -25.5474. It may be necessary to slightly vary the value in B2 to start. If the search finds the upper confidence interval, you will need to set the starting value of Linf below the optimum in order that the search will move to the lower confidence interval. Compare the results with the percentile confidence intervals produced in Example Box 8.2. With the true likelihood profiles the other parameters were also optimized rather than staying constant as here.

	A	B	C	D	E
2	Linf	62.20844			
3	K	0.29631			
4	t0	-0.0573	Chi2	=CHIINV(0.05,1)	=D4/2
5	sigma	1.489579			
6	LL	-25.5474			

corresponding log-likelihood and the overall optimal log-likelihood is less than or equal to $3.84 (\chi^2_{1,0.05} = 3.84)$. Alternatively, one can search for the θ_i that generates a log-likelihood equal to the maximum log-likelihood minus half the required χ^2 value (i.e., $LL(\theta)_{\text{Max}} - 1.92$; see Equation 8.13, Example Box 8.3).

As there are often parameter correlations within fisheries models (and many other disciplines), the assumption that keeping other parameters at the value for which the overall optimal fit was obtained will introduce bias such that the interval estimates would tend to be smaller than they should be (Figure 8.4). Strictly, because they hold the other parameters constant at their original optimum, these are slices through the likelihood surface rather than profiles; they are only approximations.

The deterministic likelihood profile method may be applied to more than one parameter to avoid the problem of parameter correlation. The search for values that satisfy Equation 8.13 (e.g., with χ^2 set at 5.99 for two parameters, 2 degrees of freedom; i.e., $LL(\theta)_{\text{Max}} - 2.995$) is somewhat more complicated, but Excel's solver could be set to search for the requisite values if it were started in the correct direction. A quick and simple method for doing this in Excel is to use a table function to calculate the log-likelihood for many combinations

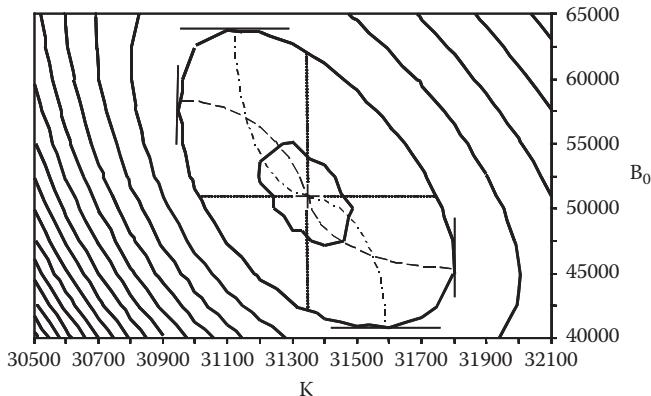


Figure 8.4

Maximum likelihood contours for two parameters from a surplus production model of northern Australian tiger prawns from the Gulf of Carpentaria (see Chapter 11). With no parameter correlations the contours would be perfect circles. The second central ellipse here represents the 95% confidence intervals. The vertical and horizontal fine lines inside this ellipse indicate the approximate likelihood confidence intervals for single parameters (holding the other parameters constant), while the S-shaped dashed lines illustrate the true two-parameter likelihood profile confidence intervals that are wider than the single-parameter intervals.

of the two parameters, and then plot a contour diagram, adjusting the interval in the contours so that one contour matches the required $LL(\theta)_{\text{Max}} - 2.995$ (Figure 8.4).

Clearly, when considering more than one parameter, the confidence intervals become wider (Figure 8.4). This only occurs if there is any correlation (covariance) between the parameters. If there were no parameter correlation, then there would be no interference between the parameters and the confidence intervals would be unbiased and circular.

The empirical likelihood profile method produced confidence intervals that were asymmetric around the optimal value (58.9 to 61.2 to 64.4; a ratio of 1:1.47), whereas the deterministic approximation tends to be symmetric (60.24 to 61.2 to 62.21; a ratio of 1:1). Both methods are approximations, but the deterministic approximation has more assumptions and tends to produce narrower or underestimated confidence bounds.

8.5 Percentile Likelihood Profiles for Model Outputs

While the generation of likelihood profiles for model parameters is relatively straightforward, generally the interest in stock assessment models relates to model outputs that are not directly estimated as parameters. For example, an

assessment model might estimate stock biomass, or the maximum sustainable yield, or some other performance measure that is an indirect output from a model. Generating a likelihood profile for such model outputs can be produced by adding a penalty term to the log-likelihood that constrains the likelihood to the optimal target, as in Equation 8.14. In this way, the impact on the log-likelihood of moving away from the optimum can be characterized.

$$LL = LL + w \left(\frac{\text{output} - \text{target}}{\text{target}} \right)^2 \quad (8.14)$$

where LL is the log-likelihood, output is the variable of interest, target is the optimum for that variable, and w is a weighting factor. The weighting factor should be as large as possible to generate the narrowest likelihood profile while still being able to converge on a solution.

As an example, we will use a simple surplus production model similar to those introduced briefly in Chapter 2 and examined in detail in Chapter 11 (Example Box 8.4). These models are sometimes referred to as biomass dynamic models (Hilborn and Walters, 1992) because the stock dynamics are usually represented solely in terms of changing levels of biomass. Thus, the biomass at time $t + 1$ derives from the biomass at time t multiplied by some composite terms reflecting reproduction and growth, minus whatever catch has been taken.

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K} \right) - C_t \quad (8.15)$$

where B_t is the stock biomass at time t , r is the intrinsic rate of natural increase, K is known as the carrying capacity, and C_t is the catch taken in period t . The model can be fitted to catch rate data using the relationship

$$\frac{C}{E} = qB_t e^{\varepsilon} \quad (8.16)$$

where C/E is the catch rate data and q is the catchability coefficient (defined as the proportion of the exploitable stock biomass taken with one unit of effort). Given a time series of catches and catch rates, it is possible to suggest a time series of stock biomasses that is consistent with the data, and conclusions can be drawn about the productivity of the resource. Equations 8.15 and 8.16 represent a simple nonequilibrium version of a model first proposed by Schaefer (1954, 1957). For our purposes here, we also need to know that the maximum sustainable yield may be estimated once the model is fitted, using (see Chapter 11)

$$MSY = \frac{rK}{4} \quad (8.17)$$

EXAMPLE BOX 8.4

A nonequilibrium Schaefer surplus production model fitted to abalone data from the southwest of Tasmania (Table 8.1). Copy the data into columns A to C, down to row 33. In D11 put Equation 8.15 as $\text{MAX}(\text{D}10+\$B\$2 * \text{D}10 * (1-(\text{D}10/\$B\$3)) - \text{B}10, 100)$, and copy down to D33. The max function ensures that the stock biomass cannot go extinct when using the solver. In E10 put $=((\text{D}10+\text{D}11)/2) * \$B\$5$, the mid-year biomass in a given year multiplied by the estimate of q , and copy down to E32 (in E33 put $=\text{D}33 * \$B\5). In F10 put $=\text{Ln}(\text{C}10/\text{D}10)$ to generate the contributions to the q estimate. In G10 put $=(\text{Ln}(\text{C}10) - \text{Ln}(\text{E}10))^2$ to generate the residuals for lognormal random errors. Select F10:G10 and copy down to row 33. Complete the worksheet by putting $=\text{exp}(\text{average}(\$F\$10:\$F\$33))$ into B5 to calculate the closed form of q (see Equation 8.21). Count the number of observations by putting $=\text{count}(\text{C}10:\text{C}33)$ into B7, and to estimate the standard deviation of the residuals put $=\text{sqrt}(\text{sum}(\text{G}10:\text{G}33)/\text{B}7)$ into B8 (see Equation 3.17). Plot columns C and E against column A (use different colours) to replicate something like Figure 8.5. The parameters shown are close to optimum. Put $=-(\text{B}7/2) * (\text{LN}(2 * \text{PI}()) + 2 * \text{LN}(\text{B}8) + 1)$ into B6 to gain the log-likelihood (Equation 11.25 and Appendix 11.3). Maximize B6 using the solver and changing B2:B4. In the solver options, turn on automatic scaling, increase the required precision, and decrease the convergence limits. Cells C1:G7 relate to the MCMC to be developed later (Example Box 8.5). In E5 put $=\text{NORMINV}(\text{RAND}(), 0, 1)$ and the other numbers in C1:E5 are constants.

	A	B	C	D	E	F	G
1		Param	Scale	Iteration	15000	Bcurr	$=\text{D}33$
2	re	0.39065	0.025	N	15000	Bcurr/K	$=\text{G}1/\text{B}3$
3	Ki	8844.976	2.5	np	3	MSY	$=\text{B}2 * \text{B}3 / 4$
4	B0	3170.305	2.5	Step	1	Output	
5	qi	0.000373	0.0148	Norminv	-1.0680		
6	LL	41.7623					
7	n	24				Weight w	0
8	σ	0.04247					
9	Year	CatchT	CE	Model B	E(CE)	Expt_q	$\text{Ln}(\text{I}-\text{I})$
10	1985	1018.884	1.00000	$=\$B\4	1.1414	-8.0616	0.0175
11	1986	742.347	1.0957	2946.982	1.1042	-7.8968	0.0001
12	1987	868.023	1.1303	2971.163	1.0908	-7.8742	0.0013
13	1988	715.104	1.1466	2873.924	1.0806	-7.8266	0.0035
	Extend	Down to	Row 33				

continued

EXAMPLE BOX 8.4 (continued)

Development of a likelihood profile for the MSY parameter for the surplus production model fitted in Example Box 8.4. Put potential values of MSY into H10:H55 (650:1,100 in steps of 10). Alter the log-likelihood in B6 to become $=-(B7/2) * (\ln(2*\pi()) + 2*\ln(B8)+1) + G7*((G3-G4)/G3)^2$. Copy each MSY value in turn from column H into cell G4 and re-solve, maximizing the log-likelihood in B6 by varying B2:B4, copying the optimum maximum log-likelihood from B6 down into column I. Either do this manually or implement the following macro and then plot column K against H (cf. Figure 8.6). Try different weights in G7. Once you complete the MCMC section below and develop a marginal posterior for the same MSY, you will see that a weight of 100 is satisfactory in this case. The profile likelihoods in column K should sum to 1.0. If they are cumulatively summed (in column L), it is possible to search for the MSY trials that most closely correspond to the 0.025 and 0.975 percentiles, as in Figure 8.6. The optimum values are stored in J3:J5 for reference.

```

Sub Profile()
    Application.ScreenUpdating = False
    For i = 1 To 46      ' or however many trials you decide
        Range("H9").Select
        ActiveCell.Offset(i, 0).Range("A1").Select
        Selection.Copy
        Range("G4").Select
        Selection.PasteSpecial Paste:=xlPasteValues
            ' other terms deleted for brevity
        SolverOk SetCell:="$B$6", MaxMinVal:=1, ValueOf:="0",
            ByChange:="$B$2:$B$4"
        SolverSolve (True)
        Range("B6").Select
        Selection.Copy
        Range("I9").Select
        ActiveCell.Offset(i, 0).Range("A1").Select
        Selection.PasteSpecial Paste:=xlPasteValues
    Next i
    Range("A1").Select
    Application.ScreenUpdating = True
End Sub

```

continued

EXAMPLE BOX 8.4 (continued)

	F	G	H	I	J	K
1	Bcurr	5344.535				
2	Bcurr/K	0.5687			Optimum	
3	MSY	882.5			0.39065	
4	Output	650			8844.976	
5					3170.305	
6						
7	Weight w	100				
8					=SUM(J10:J55)	
9	Expt_q	Ln(I-I)	MSY	LL	Likelihood	Profile
10	-8.1197	0.0119	650	48.23374	=EXP(-I10)	=J10/\$J\$8
11	-7.9644	0.0001	660	47.65001	=EXP(-I11)	=J11/\$J\$8
12	-7.9473	0.0019	670	47.09313	3.5295E-21	0.000329

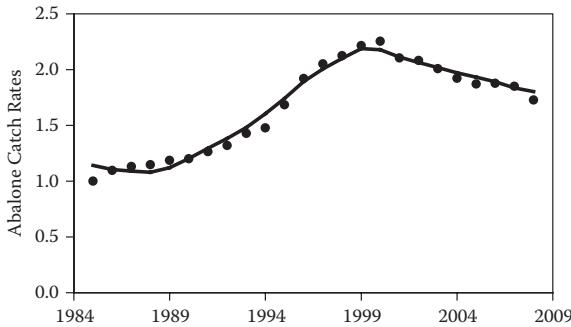
TABLe 8.1

The Abalone (*Haliotis rubra*) Catch and Catch Rates, CE
 (Standardized by Diver, Month, and Reporting Block) for the Years
 1985 to 2008, from the Southwest of Tasmania (see Figure 8.5)

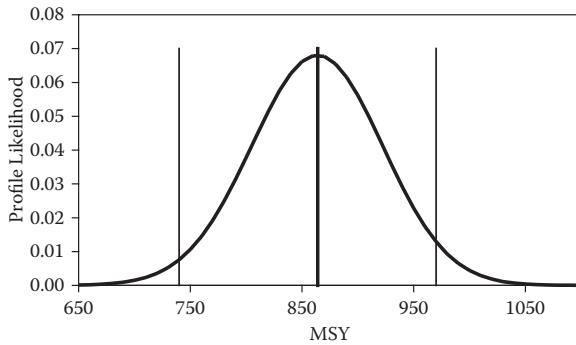
Year	Catch t	CE	Year	Catch t	CE
1985	1018.884	1.0000	1997	657.496	2.0515
1986	742.347	1.0957	1998	480.660	2.1244
1987	868.023	1.1303	1999	645.049	2.2148
1988	715.104	1.1466	2000	960.741	2.2531
1989	585.651	1.1873	2001	940.434	2.1051
1990	532.214	1.2018	2002	911.717	2.0820
1991	566.507	1.2652	2003	954.589	2.0087
1992	611.126	1.3199	2004	935.142	1.9226
1993	548.256	1.4284	2005	940.138	1.8703
1994	499.406	1.4772	2006	951.849	1.8776
1995	478.919	1.6853	2007	1030.043	1.8496
1996	427.787	1.9195	2008	984.599	1.7271

In addition, we need a number of other equations to anchor the dynamics to a fishery and to fit the model. Assuming that the error in Equation 8.16 is multiplicative and lognormal with a constant variance (i.e., $I_t = qB_t e^\varepsilon$, where $\varepsilon = N(0, \sigma^2)$), then the estimates of the model parameters (B_0 , r , q , and K) are obtained by maximizing the appropriate likelihood function:

$$L(\text{data} | B_0, r, K, q) = \prod_t \frac{1}{I_t \sqrt{2\pi\hat{\sigma}}} e^{-\frac{(\ln I_t - \ln \hat{I}_t)^2}{2\hat{\sigma}^2}} \quad (8.18)$$

**Figure 8.5**

Standardized catch rates for abalone from southwest Tasmania with the predicted catch rates from the simple surplus production model in Example Box 8.4. Data from Table 8.1.

**Figure 8.6**

The estimated likelihood profile for MSY for abalone from the southwest of Tasmania, as determined in Example Box 8.4.

where $L(\text{data} | B_0, r, K, q)$ is the likelihood of the data given the parameters, the product is overall years (t) for which CPUE data are available, and (Neter et al., 1996, p. 34)

$$\hat{\sigma}^2 = \sum_t \frac{(\ln I_t - \ln \hat{I}_t)^2}{n} \quad (8.19)$$

and n is the number of observations (maximum likelihood estimate of the variance uses n rather than $n - 1$). A simplified version of the same maximum likelihood equation is

$$LL = -\frac{n}{2} (\ln(2\pi) + 2\ln(\hat{\sigma}) + 1) \quad (8.20)$$

(see Appendix 11.3 for its derivation).

The catchability, q , simply scales the catch rates to match the units of the estimated biomass levels and, in this case, assumes a linear relationship between catch rates and exploitable stock size. An estimate of q , which maximizes Equation 8.18, is given by the geometric average of the time series of individual q estimates (see Appendix 11.2 for the derivation); thus,

$$\hat{q} = e^{\frac{1}{n} \sum \ln\left(\frac{I_t}{B_t}\right)} \quad (8.21)$$

Alternatively, one could estimate the q value directly using the solver, but the value thus determined should differ from that derived from Equation 8.21 by only a small fraction. Such closed-form estimates, as in Equation 8.21, are valuable because, on average, the model tends to be quicker to fit and more robust when it has fewer directly estimated parameters.

A surprising thing here is that such a simple model can generate seemingly reasonable management advice. It is also surprising that catch rates appear to be meaningful for an abalone species, which because of their aggregated nature and the hand-collected nature of the fishery are notorious for having hyperstable catch rates. However, in Tasmania, catch rates do appear to be informative, although in this example no attention has been given to any improvements in fishing methods. The advent of global position receivers and other practical methods used in this diver fishery has undoubtedly improved catch rates for a given number of hours underwater. What this means is that the catchability, or the effectiveness of a unit of effort, is likely to have increased through time so that, for example, catch rates in the 2000s are of a different quality than those in the 1990s. Such “effort creep” or “technology creep” has the effect of biasing such analyses high so that they become more risk prone. Keep in mind that this simple model is designed simply to illustrate the methods and not to provide specific management advice. Rather, more details than we need here are required to provide usable advice while capturing more of the uncertainty in the system and data.

8.6 Markov Chain Monte Carlo (MCMC)

Parameter optimization can be envisaged as finding the location of the maximum likelihood on the multidimensional likelihood surface implied by a model and a given data set. If the likelihood surface is very steep in the vicinity of the optimum, then the uncertainty associated with those parameters would be relatively small. Conversely, if the likelihood surface was comparatively flat near the optimum, this would imply that similar likelihoods could be obtained from rather different parameter values, and the uncertainty around those parameters would be relatively high. If we assume that

the likelihood surface is multivariate normal in the vicinity of the optimum, then we could use asymptotic standard errors to define confidence intervals around parameter estimates. However, for many variables and model outputs in fisheries that might be a very strong assumption. Ideally, we would use methods that independently characterized the likelihood surface in the vicinity of the optimum solution. If we could manage that, we could use the equivalent of percentile methods to provide estimates of the confidence intervals around parameters. It would be possible to produce a likelihood profile for two parameters at once using the solver as described in the previous section. However, this would be clumsy and become impractical if there were more than two parameters. What is required is a way of integrating across many dimensions at once to generate a multidimensional likelihood profile. Fortunately, there are numerous methods for doing this (Gelman et al., 2004) including Sampling Importance Resampling (SIR) and Markov chain Monte Carlo (MCMC). Here we will focus on the use of a MCMC method. This approach has become much more common with the expansion in the use of Bayesian statistics that has occurred in fisheries modelling (Punt and Hilborn, 1997). As described in Chapter 3, when using Bayesian methods, a common problem is to characterize a multidimensional posterior distribution. If the prior information is omitted from a Bayesian analysis (as a strategy for providing truly uninformative priors), it becomes equivalent to a multidimensional likelihood profile. There are numerous alternative algorithms for conducting an MCMC, but we will focus on a relatively flexible approach called the Gibbs sampler (which is formally termed alternating conditional sampling).

An MCMC uses a Markov chain to trace over the multidimensional likelihood surface. A Markov chain describes a process whereby each state is determined probabilistically from the previous state. A random walk would constitute one form of Markov chain, and its final state would be a description of a random distribution. However, the aim here is to produce a Markov chain whose final state, the so-called stationary distribution, provides a description of the target or posterior distribution. The Markov chain starts with some combination of parameter values and the model being used that defines a location in the likelihood space. Depending on the set of parameter values, the likelihood can obviously be small or large. The MCMC process entails iteratively stepping through the parameter space following a set of rules based on the relative likelihood of each candidate parameter set to determine which steps will become part of the Markov chain, that is, which steps will be accepted and which rejected. Each step of the process entails the production of a new candidate set of parameter values, which is done stochastically (hence Markov chain) and, in the Gibbs sampler, one parameter at a time (Casella and George, 1992). Each of these new candidate sets of parameters, combined with the available data and the model, defines a new likelihood. Whether this new parameter combination is accepted as the next step in the Markov chain depends on how much the likelihood has been

changed. In all cases where the likelihood increases the step is accepted. But where the likelihood decreases it can still be accepted if the ratio of the new likelihood relative to the old likelihood is larger than some uniform random number (between 0 and 1). Thus, a Markov chain can be generated if the likelihood of an initial set of parameters θ_t given a set of data x can be defined as follows:

$$L_t = p(\theta_t | x) \quad (8.22)$$

If we then select a new trial or candidate parameter set θ^* by randomly incrementing one of the parameters in θ_t ($\theta^* = \theta_t + \Delta\theta_i$), this will alter the implied likelihood:

$$L^* = p(\theta^* | x) \quad (8.23)$$

If the ratio of these likelihoods is greater than 1, then the jump from θ_t to θ^* is accepted into the Markov chain.

$$r = \frac{L^*}{L_t} = \frac{p(\theta^* | x)}{p(\theta_t | x)} > 1.0 \quad (8.24)$$

Alternatively, if the ratio is less than 1, then the jump is only accepted if the ratio r is greater than a newly selected uniform random number:

$$\theta_{t+1} = \begin{cases} \theta^* & \text{if } r > U(0, 1) \\ \theta_t & \text{otherwise} \end{cases} \quad (8.25)$$

Strictly, only Equation 8.25 is required because where the new likelihood is greater than the original it will satisfy the top clause of Equation 8.25, but both are given to improve the clarity of the algorithm. If the candidate parameter set is rejected, it reverts to the original and the cycle starts again with a new trial parameter set. As the Markov chain develops it should trace out a multidimensional volume in parameter space. After sufficient iterations it should converge on the stationary distribution.

The jumping distribution defines how each parameter is incremented when adopting new candidate parameter sets. There are many options available, but commonly, for each parameter in turn in the set θ , a standard normal random deviate $N(0,1)$ is generated, and this is scaled, α_i , to suit the scale of the parameter, i , being incremented.

$$\theta^* = \theta_{t,i} + N(0, 1) \cdot \alpha_i \quad (8.26)$$

This scaling by α_i is important because if the jumps in parameter space are too large, then the outcome may be unstable, but if they are too small, it may take an enormous number of iterations to converge on a stationary distribution. There is an element of trial and error in this procedure with no fixed or simple rule as to what scaling factor to use. The acceptance rate of the new candidate values is an indicator of the efficiency of the performance. A simple rule of thumb might be to scale the normal random deviate to approximate between 0.5 and 1.0% of the original parameter value. There are other MCMC algorithms that vary multiple parameters at each iteration; however, if there are parameter correlations, this can complicate the selection of new candidate parameter sets. Cycling through each of the parameters in θ in turn, using something like Equation 8.26, is relatively simple and is known as the Gibbs sampler (Example Box 8.5). There are numerous algorithms for conducting Markov chain Monte Carlo simulations with a growing literature devoted to this subject (Gelman et al., 2004).

An example MCMC run, using Example Boxes 8.4 and 8.5, illustrates that while the individual parameters might show evidence of serial correlation within the MCMC, the model output used (MSY estimate) produces the desired “hairy caterpillar” that indicates an acceptable result (Figure 8.7). That there is a strong correlation between the r and K parameters was explained in Chapter 2. This means that the negative correlation between these two parameters effectively cancels out any serial correlation in the MCMC runs when we consider the MSY output (which is a combination of both the r and K parameters; Figure 8.7).

Rather than simply using graphical indicators (as in Figure 8.7), diagnostic statistics should be used to indicate whether convergence to a stationary distribution has occurred. There are many available, but here we will only mention some simple strategies. As with any nonlinear solver, it is a good idea to start the Gibbs sampler from a wide range of initial values (the output illustrated in Figure 8.7 was generated by starting the Gibbs sampler at the optimum solution). Any diagnostic tests for identifying whether the MCMC has achieved the target stationary distribution would literally consider the convergence of the different Markov sequences. Of course, it would be necessary to discard the so-called burn-in phase before making any comparisons. The burn-in phase is where the Markov chain is traversing the likelihood space before it starts to characterize the posterior distribution. Gelman et al. (2004) recommend the conservative option of discarding the first half of each sequence, but the actual fraction selected should be determined by inspection. The simplest diagnostic statistics involve comparing the means and variances of either different sequences, or different portions of the same sequence. If the mean values from different sequences (or subsets of a sequence) are not significantly different, then the sequence(s) can be said to have converged. Similarly, if the within-sequence (or subset of a sequence) variance is not significantly different from the between-sequence, then convergence can be identified. Using a single sequence may appear convenient,

EXAMPLE BOX 8.5

The macro needed implements a Gibbs sampler to run a MCMC using the Excel sheet set out as in Example Box 8.4. You could delete the parts of the worksheet relating to the likelihood profile (or set the weight in G7 to zero). The i is just a counter used in the macro, N is the number of iterations of the Markov chain, np is the number of parameters, and step is how often a candidate parameter set should be considered for acceptance. In Example Box 8.4, Norminv in E5 is a standard normal variate, and the scales are the multipliers used to adjust each normal random deviate to suit the scale of the parameter being varied; see Equation 8.22. The output is placed in B40:F15040.

```

Sub Do_MCMC()
Dim N, np, step, Count, i, j As Integer
Dim func0, func1, trial As Double
Dim Scales(4), pars(4), trialpar(4), arate(4) As Double
    Range("B40:F15040").Select
    Selection.ClearContents
    Range("A1").Select
N = Cells(2, 5).Value      ' iterations in the MCMC
np = Cells(3, 5).Value      ' number of parameters
step = Cells(4, 5).Value      ' how often to store results
For i = 1 To np            ' Get the parameters and scales
    Scales(i) = Cells(1 + i, 3).Value
    pars(i) = Cells(1 + i, 2).Value
Next i
func0 = Cells(6, 2).Value  ' posterior
Count = 1
For j = 1 To N * step      ' Start the MCMC loop
    For i = 1 To np ' loop through parameters
        Calculate
        trial = pars(i) + Cells(5, 5).Value * Scales(i)
        Cells(1 + i, 2).Value = trial
        func1 = Cells(6, 2).Value      ' New log-likelihood
        If (Rnd < Exp(func1 - func0)) Then ' Equ 8.24
            trialpar(i) = trial
            func0 = func1
            arate(i) = arate(i) + 1
        Else: trialpar(i) = pars(i)
        End If
    Next i           ' End of Gibbs sampler
End Sub

```

continued

EXAMPLE BOX 8.5 (continued)

The rest of the macro needed implements a Gibbs sampler to run a MCMC using the Excel sheet set out as in Example Box 8.4.

```

If ((j Mod step) = 0) Then
    Cells(1, 5).Value = Count
    For i = 1 To np
        Cells(Count + 40, 1 + i).Value = trialpar(i)
        pars(i) = trialpar(i)
    Next i
    Cells(Count + 40, np + 2).Value = func0
    msy = Cells(3, 7).Value
    Cells(Count + 40, np + 3).Value = msy
    Count = Count + 1
End If
If ((j Mod 100) = 0) Then           ' controls screen
    Application.ScreenUpdating = True
    Application.ScreenUpdating = False
End If
Next j ' End of MCMC
For i = 1 To np
    Cells(40, 1 + i).Value = arate(i) / N
Next i
End Sub

```

In the example run illustrated in Figure 8.7, the MSY values ranged from 655.08 up to 1,094.35 (this will differ from run to run). In cell J45 put =min(F41:F15040) and in J46 put =max(F41:F15040). The marginal distribution can be generated (for each variable) by finding the range and setting up a series of bins, in this case 650 to 1,100 in steps of 10. In cell K48 place =countif(\$F\$41:\$F\$15040,">="&J48)-countif(\$F\$41:\$F\$15040,">="&J49) and copy down to row 92 to give the relative frequency of occurrence of the different MSY values. In K46 put =sum(K48:K92), to ensure all 15,000 are captured. In cell L48 put =K48/\$K\$46 and copy down to row 92. Copy the final likelihood profile from the first use of Example Box 8.4 into M47:M93. Plot L48:L92 against J48:J92. Add M48:M92 to this graph. Put =percentile(\$F\$41:\$F\$15040, 0.025) into cell N48, and in N49 put =N48. In N50 put =median(F41:F15040), and in N52 put =percentile(\$F\$41: \$F\$15040,0.975). Add the groups in N48:O49, in N50:O51, etc., to the graph to mimic Figure 8.8. Compare a graph with fifteen thousand iterations with one of five thousand iterations.

continued

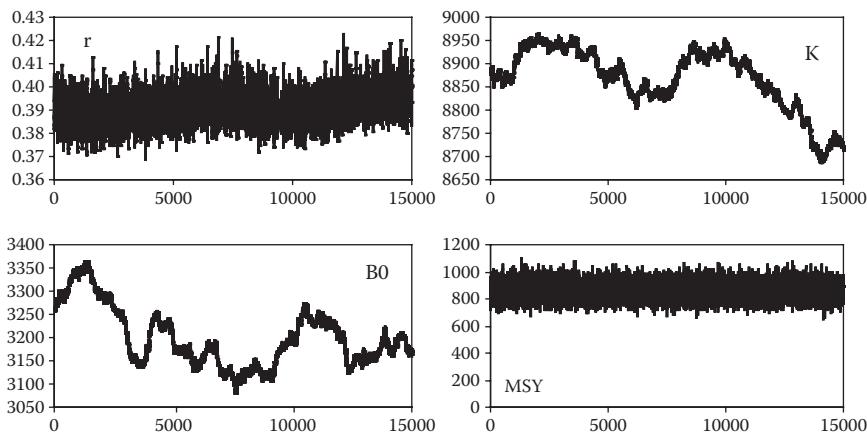
EXAMPLE BOX 8.5 (continued)

	J	K	L	M	N	O
45	655.0839					
46	1094.346	15000				
47	MSY	Freq	Prop	Profile		
48	650	1.00	0.00007	0.00011	752.5	0
49	660	2.00	0.00013	0.00019	=N48	0.075
50	670	3.00	0.00020	0.00033	868.4	0
51	680	4.00	0.00027	0.00056	=N50	0.075
52	690	6.00	0.00040	0.00092	984.5	0
53	700	15.00	0.00100	0.00149	=N52	0.075
54	710	35.00	0.00233	0.00233		
55	720	61.00	0.00407	0.00354		
56	Extend	Down to	Row 93	...		

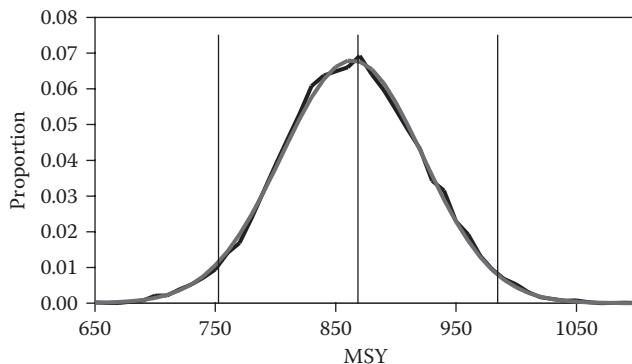
but if convergence is relatively slow and this was unknown, then relying on a single sequence may provide incorrect answers. The title of Gelman and Rubin (1992) states the problem clearly: “A single sequence from the Gibbs sampler gives a false sense of security.” Suffice to say that it is better to use multiple starting points to give multiple sequences along with an array of diagnostic statistics and graphics to ensure that the conclusions that one draws from any MCMC simulation are not spurious (Gelman et al., 2004). Such approaches are termed computer-intensive for a good reason.

The marginal distribution of the MSY (Example Box 8.5, Figure 8.8) is not completely smooth but forms a close approximation to the likelihood profile generated for the MSY in Example Box 8.4 (with a weight of 100 given to the penalty term; Figure 8.8). To obtain a smoother marginal distribution, more than fifteen thousand iterations of the MCMC would be required. In the example illustrated the MCMC was started with the maximum likelihood optimum parameter set; if it had been started elsewhere, an initial burn-in period would have been required, which should be omitted from the marginal distribution as not representing plausible parameter combinations.

In a Bayesian framework the MCMC can be used to characterize the posterior distribution. In this case, when estimating the log-likelihood value for each new trial parameter value it would also be necessary to include the prior probability for each of the parameter values. If the MCMC is used to fit the model, then because it would be unlikely that the MCMC could start near the optimum parameter set, there would need to be some, often long, burn-in series aimed at moving the parameter combinations into the vicinity of the main posterior distribution. With multiparameter models

**Figure 8.7**

Outputs from the Gibbs sampler in Example Boxes 8.4 and 8.5. The top left is the Markov chain for the r parameter, the top right is the K series, the bottom left is the B_0 series, and the bottom right is the model output MSY series.

**Figure 8.8**

The marginal frequency distribution of fifteen thousand iterations of the Gibbs sampler for MSY from Example Box 8.5 (left-hand Y axis). The smooth fine line is the likelihood profile from Example Box 8.4 with a weight of 100 (right-hand Y axis). The verticals represent the 95% confidence intervals and the median.

the number of iterations required can become enormous, and so this is invariably a very slow process.

In a real analytical situation the use of Excel to run an MCMC would be very slow and inefficient, and it is not recommended for anything except perhaps very small jobs (or, as here, for learning the principles). The algorithm and implementation expressed in Example Box 8.5 can be generalized to most problems, but this would not be sensible in Excel. As a means of understanding the process of stepping through a Markov chain, Excel is

excellent, but for any serious undertaking, one should be realistic and at least use R or WinBugs (both of which are freely available). However, if the algorithm expressed by Equations 8.23 to 8.26 and as code in Example Box 8.5 is compiled into some executable language, the analysis will run much more quickly. With stock assessments involving many parameters it is not uncommon to run millions of iterations to adequately describe the marginal distributions of the outputs of interest, and under such circumstances some serious computing can be required.

8.7 Concluding Remarks

Exactly how one decides to characterize the uncertainty around parameter estimates or model outputs depends on the circumstances and the properties of the model involved. In addition to the methods listed in this chapter, it is also possible to use bootstrapping methods, as described in Chapter 6. Keep in mind that it appears to be more common to underestimate uncertainty than to overestimate it. How such estimates of uncertainty are used varies greatly. But at least it means that it becomes possible to attribute levels of relative risk to different management decisions.

9

Growth of Individuals

9.1 Growth in Size

9.1.1 uses of growth information

Ignoring immigration and emigration, stock production is a mixture of recruitment of new animals to the population and the growth of the individuals already in the population. This is one reason there is a huge literature on the growth of individuals in fisheries ecology. In addition, many aspects of a species' life history characteristics tend to be reflected in how it grows. Thus, long-lived species tend to be relatively slow growing, while short-lived species tend to grow more quickly (though exceptions exist; Ziegler et al., 2007). In this chapter, we will ignore the biology of growth and focus instead on the mathematical description of growth.

In ecology and fisheries, it is very common to gather information about how organisms grow in size (especially in terms of length- or weight-at-age). Besides recruitment of juveniles, increases in the stock biomass vulnerable to fishing come about by the growth of individuals already recruited to the stock. This aspect of production is used in many stock assessment analyses. For example, as discussed in Chapter 2, yield-per-recruit analyses ask: What average or minimum size or age at first capture leads to the optimal yield? This is a trade-off between the loss of biomass through the natural mortality of individuals and the gain to biomass through the growth of individuals. Without this sort of information and analysis there is a risk of growth overfishing (taking too many fish when they are still too small for optimum yield). Ecologically, growth information can also provide insights into how a species interacts with its environment. Mathematical relationships between age, length, and weight are often used to translate the outputs of models based upon animal numbers into outputs based upon biomass.

The literature on individual growth is too extensive (Summerfelt and Hall, 1987) to permit here anything other than a brief review of the most important aspects from a stock assessment point of view. In this chapter, we will introduce various models of individual growth and the methods used to estimate their parameters for particular populations. Very commonly, it is

useful to be able to compare growth curves (indeed, any set of nonlinear relationships). Strategies and methods for making such comparisons are also addressed in this chapter, including a randomization test that may improve matters when the ageing data are suboptimal.

9.1.2 The Data

Generally, data in studies of growth consist of estimates and measurements of age, size (often length or width), and weight. However, tagging data can also be collected and those, generally, consist of the dates of tagging and recapture, the initial length at tagging, and the length at recapture. It is unusual to have the age of the individuals in tagging studies. Different methods are required for fitting growth models to these two distinct types of data. It is also possible to describe the average growth within a population by following a series of model progressions assumed to represent cohorts through known time periods (using multiples of Example Box 3.14).

We are interested in the relationships formed between all three possible combinations of direct data: age vs. length, age vs. weight, and length vs. weight. Of these, the latter usually has the simplest model and is usually the most straightforward to fit to raw data. Obtaining data relating to length or weight is relatively simple, although weight may be affected by many things other than length (maturity and gonad development stage, gut contents, freshness, free water content, etc.). Obtaining data relating to age tends to be far more problematical.

Many methods have been suggested for ageing aquatic organisms, and the approach that best suites a particular species depends upon many factors. Many species do not grow at a uniform rate throughout the year. Instead, there tends to be a slowing of growth in the winter or less productive months. This can be relatively unmarked in tropical areas but tends to be very clear in cooler or freshwater environments. Many body parts can be affected by this differential growth, and these effects can be used to age the fish. Literal growth rings (analogous to annual tree rings) can be found in such body parts as the scales, the vertebrae, and fin-ray spines, but especially in the various ear bones known as otoliths (Summerfelt and Hall, 1987). As well as annual rings, there have been developments using daily growth rings. Analogous rings can be found in some invertebrates, and although these may not necessarily be annual, they can also be used to age the animals concerned (Moltschaniwskyj, 1995).

There is an enormous literature concerning the development and structure of otoliths. However, here all we need to know is that when a fish to be aged is captured, it is first measured for length and weight, and then commonly its otoliths are removed (this can be a highly skilled art when done properly). There are a number of ways in which the otoliths (or other structures to be aged) can be treated to make the yearly rings more visible, but whatever method is used, the aim is to determine the age of the fish in years or

fractions of years. Using such methods relies upon many assumptions, the most important being that the rings can be clearly identified and that they are, in fact, annual; this latter can be validated using tagging experiments or a variety of other techniques (Summerfelt and Hall, 1987).

9.1.3 Historical usage

A variety of mathematical descriptions have been applied to growth. At the start of the twentieth century various people assumed either a constant proportional increase (equivalent to exponential growth) or a linear increase in size with age. In the 1930s the observed size-at-age was used, and later still, Ricker is reported as assuming an exponential increase in weight (Smith, 1988). In the 1950s, there was a search for a general mathematical model of growth with a biological basis, i.e., an explanatory model. Beverton and Holt (1957) introduced the idea of von Bertalanffy growth curves to fisheries. This was an approach in which growth was defined as the balance between positive and negative processes within organisms. Von Bertalanffy derived an equation that could be used to predict the length of an organism as a function of its age (von Bertalanffy, 1938). The cube (or close approximation to the cube) of this equation could then be interpreted as the weight of an organism in relation to age (changes in one dimension being reflected in three dimensions). The validity of applying this model to the average growth of collections of individuals, when it was designed to describe the growth of single individuals, was not attended to at the time (Sainsbury, 1980).

A common alternative to the von Bertalanffy equation is simply to have a lookup table of mean lengths (or weights) at a given age or the proportional distribution of numbers at different sizes for given ages. If sufficient information is available, such age-length keys permit estimates of the uncertainty around each mean length-at-age value. However, an empirical table does not readily permit interpolation of missing or underrepresented ages, so most models use some mathematical representation of average individual growth. Not all growth equations currently used have interpretable parameters; there are even examples of the use of polynomial equations to describe growth in fish empirically (Roff, 1980).

9.2 Von Bertalanffy Growth Model

9.2.1 Growth in Length

Despite a wide array of criticisms, the growth model of length with age most commonly used in fisheries remains the three-parameter equation developed by von Bertalanffy (1938):

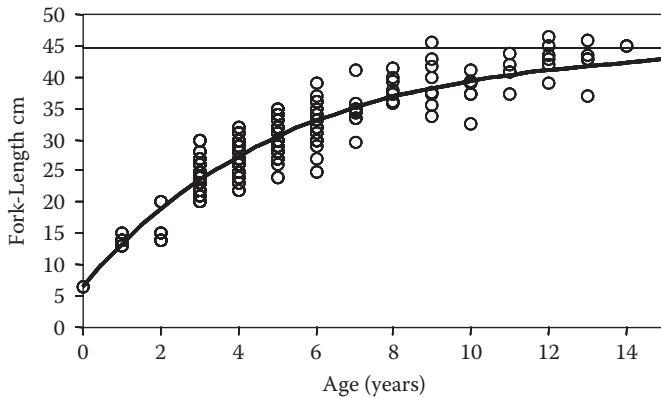


Figure 9.1

Von Bertalanffy growth curve for fish length against age, from a 1985 sample of snapper, *Pagrus auratus*, from the Bay of Plenty, New Zealand. The parameters are $L_\infty = 44.79$, $K = 0.196$, and $t_0 = -0.81$. The L_∞ asymptote is illustrated by the fine horizontal line. Some points lie above this line because, with Equation 9.1, L_∞ is interpreted as the average length at the maximum age. Notice also that most data occur where the curve is turning over (ages 3 to 6), that there are only few data points for the youngest ages, and the number of observations are also reducing for older fish; this is typical of many data sets. This lack of data points for the younger and older animals can distort or bias all of the estimated parameters (L_∞ and K should be bigger, while the t_0 value should be closer to zero).

$$L_t = L_\infty \left(1 - e^{-K[t-t_0]}\right) + \epsilon \quad (9.1)$$

where L_t is the length-at-age t , L_∞ (pronounced L -infinity) is the asymptotic average maximum body size, K is a growth rate coefficient that determines how quickly the maximum is attained, and t_0 is the hypothetical age at which the species has zero length (t_0 fixes the position of the curve along the x axis, and can affect the steepness of the curve; see Figure 9.1). It should be remembered that t_0 is an extrapolation from available data and can be difficult to interpret. The epsilon (ϵ) denotes the belief that residuals would be distributed normally about the expected growth line. When fitted using least squared residuals, this curve represents the average growth of the population members.

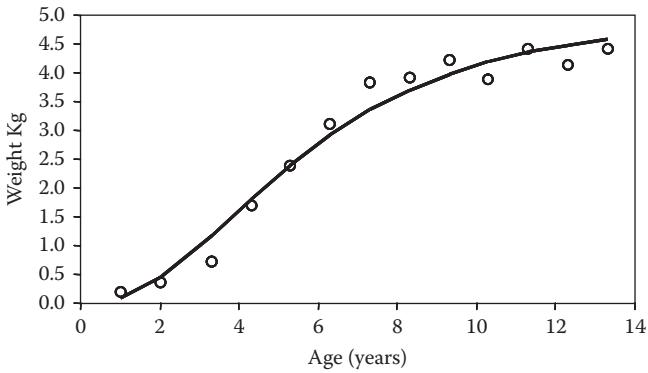
Continuous and serial spawning species add variation into the length-at-age relationship. To some extent the t_0 parameter glosses over uncertainties relating to the date of spawning and metamorphosis from larval forms to juveniles.

The parameter values derived from a single sample may not provide an adequate description of the growth properties of the sampled population (Figure 9.1). The L_∞ and t_0 parameters are at the extremes of the curve, and this is where the data tend to be least adequate. As with all things, care must be taken to obtain a representative sample. The curve may be fitted to raw data using nonlinear least squares methods (Example Box 9.1). Whether the

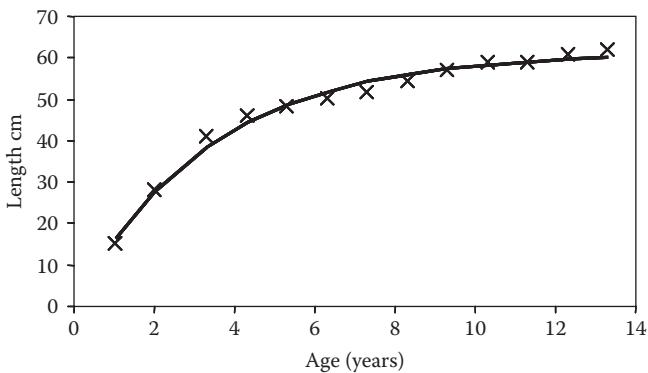
EXAMPLE BOX 9.1

Fitting length- and weight-at-age von Bertalanffy growth curves to length data for female Pacific hake (Kimura, 1980). The weight-at-age data were invented. To calculate the expected lengths in column D, put $=\$B\$1*(1-exp(-\$B\$2*(A5-\$B\$3)))$ into D5 and copy down to D17. Similarly, in F5 put $=\$F\$1*(1-exp(-\$B\$2*(A5-\$B\$3)))^\$F\2 and copy down to F17. Finally, put =average(D5:D17) into cell F3. Plot column C against A as a scattergram and add columns A against F as a line (cf. Figure 9.2) to observe the relation between age and weight. In addition, plot column B against A as a scattergram and add column D to the graph to relate length and age (cf. Figure 9.3). First use the solver to minimize D1 by altering B1:B3 (the values given here are close to but not the optimum). Then, minimize D2 by varying cells F1:F2. Copy and store the values from A1:F3 to the right of the workings below. Then minimize the total sum of squared residuals in D3 by varying B1:B3 and F1:F2 together (B1:B3,F1:F2). Do the answers differ? If you believe the variance of the residuals around the curve increases with age, we could use a constant coefficient of variation and not a constant variance. This means we need to increase the weight of the residuals for the smaller fish and decrease it for the larger. To do this, put $=(\$F\$3/D5)*(B5-D5)^2$ into E5, copy down, and re-solve. The curve fits the younger ages more closely than the older ages (the residuals are allowed to spread more widely with age).

	A	B	C	D	E	F	G
1	L_{∞}	61.2	SSq_L	=sum(E5:E17)	W_{∞}	4.85	
2	K	0.3	SSq_W	=sum(G5:G17)	b	3.078	
3	T_0	-0.06	Tot_SSq	=D1+D2	Avg Ex(L)	48.853	
4	Age	Obs(L)	Obs(W)	Ex(L)	SSqL	Ex(W)	SSqW
5	1	15.40	0.20	16.671	$=(B5-D5)^2$	0.0883	$=(C5-F5)^2$
6	2	28.03	0.35	28.212	$=(B6-D6)^2$	0.4466	$=(C6-F6)^2$
7	3.3	41.18	0.72	38.865	$=(B6-D6)^2$	1.1978	$=(C7-F7)^2$
8	4.3	46.20	1.70	44.654	Copy down	1.8370	Copy down
9	5.3	48.23	2.40	48.942	To row 17	2.4366	To row 17
10	6.3	50.26	3.12	52.119	3.4571	2.9574	0.0265
11	7.3	51.82	3.82	54.473	7.0378	3.3883	0.1864
12	8.3	54.27	3.93	56.216	3.7886	3.7336	0.0607
13	9.3	56.98	4.22	57.508	0.3342	4.0042	0.0466
14	10.3	58.93	3.88	58.465	0.2163	4.2129	0.1109
15	11.3	59.00	4.42	59.174	0.0302	4.3723	0.0023
16	12.3	60.91	4.13	59.699	1.4666	4.4929	0.1317
17	13.3	61.83	4.42	60.088	3.0345	4.5837	0.0268

**Figure 9.2**

Von Bertalanffy growth curve of inverted mean body weights against age in years for female Pacific hake (length and age data from Kimura, 1980; see Example Box 9.1). The shape of such curves is typically sigmoidal, which contrasts with that for growth in length ($w_\infty = 4.85$ and $b = 3.078$).

**Figure 9.3**

The optimal von Bertalanffy curve fitted to data for female Pacific hake (Kimura, 1980). The curve may be fitted using simple least squares with a constant variance for the residuals for all ages, or using weighted least squares to give rise to a constant coefficient of variation (Example Box 9.1).

least squares assumption of a constant variance of lengths across all ages is valid should always be considered.

9.2.2 Growth in Weight

The relation between observed length (L_t) and predicted weight (w_t) for many animals is best described by a power function:

$$\hat{w}_t = aL_t^b \quad (9.2)$$

where b is the allometric growth parameter and a is a scaling constant. The residual errors for such a curve can be either normal, ϵ , or lognormal, e^ϵ . If normal random errors are used, then how the variance changes with length would most likely need to be explicitly modelled, which would usually require maximum likelihood methods. By combining Equations 9.1 and 9.2, and defining the asymptotic maximum expected weight to be w_∞ , we can produce the von Bertalanffy growth equation for body weight:

$$\hat{w}_t = w_\infty \left[1 - e^{-K[t-t_0]} \right]^b \quad (9.3)$$

which is identical in form to the equation for length, Equation 9.1, but replacing L_∞ with the equivalent of Equation 9.2 at L_∞ (i.e., $w_\infty = a \cdot L_\infty^b$) and the addition of the allometric growth parameter b (the two equations are identical if a and b are set to 1). As an approximation the constant b is often set equal to 3. The shape of the two curves is clearly different (cf. Figures 9.1 and 9.2). The curve describing growth in length has a rapid increase that slows down to reach the asymptote at the L_∞ . The curve describing growth in weight, however, can have two inflections producing a sigmoidal curve (Figure 9.2, Example Box 9.1).

As with the von Bertalanffy curve of length-at-age, one can use nonlinear least squares to fit this curve to a data set (Figure 9.2, Example Box 9.1). Of course, if the residuals were deemed to have a distribution that is anything other than a normal or lognormal distribution (this would be uncommon), then one would need to use maximum likelihood methods (Haddon et al., 2008). Where there may be a modification from the standard least squares strategy is with the variance of the residuals. It is possible that the variance of the residuals is not constant but increases with age. If this were so, it is possible to use residuals having a constant coefficient of variation rather than a constant variance (Example Box 9.1); this would be weighted least squares.

9.2.3 Seasonal growth

The growth of many organisms in highly seasonal waters does not necessarily proceed at the same rate throughout the year. Growth rings in otoliths and other hard parts come about through differences in the metabolism and growth rate of the species concerned. In the tropics, with reduced seasonal variation in the environment, annual rings are difficult to detect because growth is more continuous. This is one reason why age-related fisheries techniques can be less useful in tropical regions than in temperate or boreal systems (although there has been some progress using daily growth rings; Choat and Axe, 1996).

In nontropical regions, especially in freshwater systems, differences in growth rate within a year are sometimes so marked that modifications are required to growth models so that seasonal variation can be described

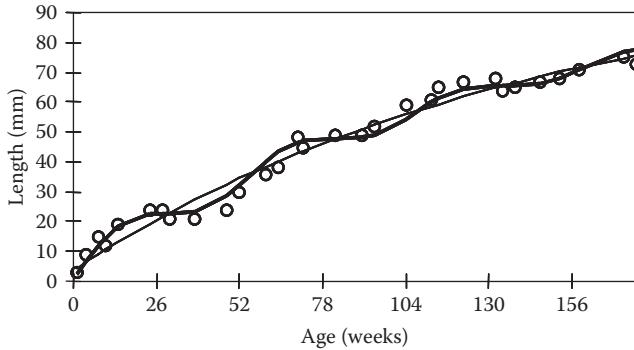


Figure 9.4

Data extracted from Pitcher and Macdonald (1973) for minnows. Note the x axis is in weeks and covers just over three years. The thick curve is from Equation 9.4, with $L_{\infty} = 106.89$, $t_0 = -5.2$, $K = 0.00768$, $C = 0.06$, and $s = 4.007$. The fine nonoscillatory curve is the same von Bertalanffy curve without the imposed oscillation (Example Box 9.2). Both t_0 and s are in units of weeks.

adequately. Once again, many different models have been proposed. Pitcher and MacDonald (1973) proposed a modification to the von Bertalanffy curve to include seasonality:

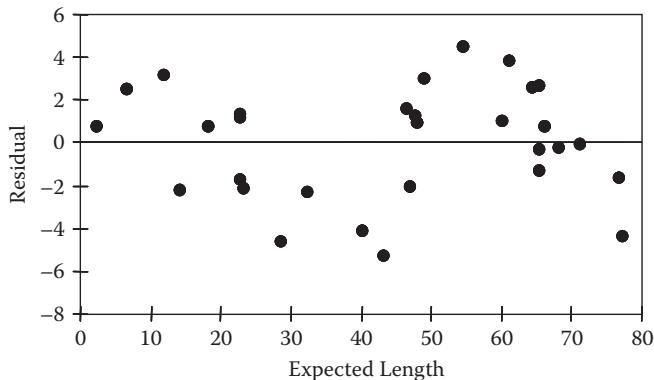
$$L_t = L_{\infty} \left(1 - e^{- \left[C \sin \left(\frac{2\pi(t-s)}{52} \right) + K(t-t_0) \right]} \right) \quad (9.4)$$

where C is related to the magnitude of the expected oscillations above and below the nonseasonal growth curve, s is the starting point in time for the sine wave (relates to the phase of the oscillation), and the other constants, K , L_{∞} , and t_0 , are defined as before (Figure 9.4). The variable t is the age at length L_t . The value of 52 in Equation 9.4 indicates that the timescale of events is that of weeks (thus, s , t , and t_0 will be measured in weeks). In effect, this equation is the von Bertalanffy curve with a sine wave added.

By changing the period to twelve, and adjusting the units of the parameters s , t , and t_0 , one could just as easily work with months (though obviously with less precision). Such seasonal adjustments to the growth model are less likely to be necessary in tropical areas, and are more likely to be required in freshwater environments where temperatures and the productivity of the habitat are highly seasonal.

As with all curve fitting, it is a good idea to examine the residuals after the optimum fit has been determined (Figure 9.5). When this is done with the minnow data, it is clear that the optimum fit is missing an obvious cycle in the data.

The pattern in the residuals approximates another sinusoidal wave, so one possible solution would be to add a further sine wave to the model and

**Figure 9.5**

The residuals remaining after an optimum fitting seasonal growth curve has been fitted to the data in Table 9.1 (Figure 9.4). There remains a clear sine wave in the data. Inspection of Figure 9.4 suggests that it has a period of about two years, so it may be worthwhile to add a further sine wave to the model (Example Box 9.2).

refit to the data. Whether this pattern in the residuals reflects some natural phenomenon not noticed when the data were being collected would require further investigation.

The equation would become

$$L_t = L_{\infty} \left(1 - e^{-\left[C_1 \sin\left(\frac{2\pi(t-s_1)}{52}\right) + C_2 \sin\left(\frac{2\pi(t-s_2)}{p}\right) + K(t-t_0) \right]} \right) \quad (9.5)$$

where p is the period of the second cycle, and the other parameters are as before, only duplicated for each cycle (Example Box 9.2).

The addition of a further cycle to the model may appear arbitrary but illustrates a vital issue when attempting to model a natural process. The objective is generally to obtain the optimal balance between generating a realistic model of a process while at the same time obtaining an optimal fit to the data using the smallest number of parameters to do so. A regular pattern in the residuals indicates a trend remains undescribed by the model. Therefore, decisions need to be made about changing the model (usually to make it more complicated). Generally, one would only accept a more complex model if some criterion, such as Akaike's information criterion (Burnham and Anderson, 2002) indicated that the improvement in the quality of fit outweighed the inclusion of an increased number of parameters. The second sine wave presumably represents a cycle of longer period than the annual cycle of seasons. In this way, the model has indicated a valuable research direction to be followed in future work (Example Box 9.2).

EXAMPLE BOX 9.2

A seasonal varying growth curve fitted to data extracted from Pitcher and MacDonald (1973) for minnows (Figure 9.4, Table 9.1). The data need to be copied into columns A and B, down to row 36. The model is relatively complicated being Equation 9.5; put the following into C7 and copy down to C36: $=\$B\$1*(1-exp(-(\$B\$4*sin((2*pi())*(A7-\$B\$5))/52)+\$E\$1*sin((2*pi())*(A7-\$E\$2))/\$E\$3)+\$B\$2*(A7-\$B\$3)))$. When the amplitude parameters C_1 and C_2 are set to zero, then the sine wave terms collapse to zero, leaving the basic von Bertalanffy growth curve. Remember that each of the time-related parameters are in weeks. Plot column B against A as a scattergram and add column C to it as a thick line. Add column F to this as a thin line to mimic Figure 9.4. Minimize F5 by altering cells B1:B5. Then plot the residuals as column D against C to mimic Figure 9.5. Once the pattern in the residuals is apparent, refit the model but this time alter cells B1:B5, E1:E3. Observe the impact of this on the total sum of squares and on the residuals. Is there still a pattern in the residuals? Is there anything suggestive about the estimated period for the second curve? By how much does the SSQ get smaller? Is it worth adding three more parameters for the improved quality of fit? Look ahead to Equation 9.18 and put $=F4*Ln(F5/F4)+2*5$ into F1 to calculate the Akaike information criterion. The $2*5$ indicates five parameters, when you fit both cycles that would use eight parameters, leading to $2*8$, so the addition of the second cycle would need to reduce the first term by at least six for the bigger model to be preferable.

	A	B	C	D	E	F
1	L_{∞}	106.9		C_2	0	
2	K	0.0068		S_2	-20	
3	t_0	-5.2		Period2	70	
4	C_1	0.06			N	=count(E7:E36)
5	s_1	4.0			SSQ	=sum(E7:E36)
6	T	Obs_L _t	Model	Resid	Resid ²	Nonseasonal
7	1	3	2.19	=B7-C7	=D7^2	$=\$b\$1*(1-exp(-\$b\$2*(a7-\$b\$3)))$
8	4	9	6.46	=B8-C8	=D8^2	$=\$b\$1*(1-exp(-\$b\$2*(a8-\$b\$3)))$
9	8	15	11.84	=B9-C9	=D9^2	$=\$b\$1*(1-exp(-\$b\$2*(a9-\$b\$3)))$
10	10	12	14.24	Copy	Down	Copy down to row 36
11	14	19	18.18	To	Row 36	13.056
12	24	24	22.64	1.363	1.857	19.210
13	28	24	22.78	1.221	1.491	21.557

TABLe 9.1

A Subset of Length-at-Age Data for Minnows Measured from a Figure in Pitcher and Macdonald (1973)

Weeks	Obs L	Weeks	Obs L	Weeks	Obs L
1	3	52	30	114	65
4	9	60	36	122	67
8	15	64	38	132	68
10	12	70	48	134	64
14	19	72	45	138	65
24	24	82	49	146	67
28	24	90	49	152	68
30	21	94	52	158	71
38	21	104	59	172	75
48	24	112	61	176	73

Note: The ages are in weeks and the lengths are in millimeters. These data are illustrated in Figure 9.4 and used in Example Box 9.2.

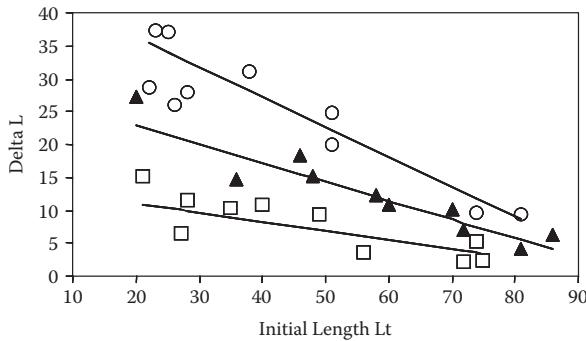
9.2.4 Fitting to Tagging Data

So far, we have only considered fitting the von Bertalanffy curve to data where one has each fish's length at particular ages. Obviously, for this, one would need to be able to age the fish accurately. But there are other forms of data available that can be used to fit a von Bertalanffy curve. When one conducts a tagging experiment, it is common to obtain lengths when animals are first tagged and to remeasure them on recapture with the time interval between recaptures known. If the von Bertalanffy curve could be reformulated in terms of size increments after a given time from a given initial size, it would be possible to use such data to fit the growth curve.

Fabens (1965) transformed the von Bertalanffy curve so it could be used with the sort of information obtained from tagging programs (see Appendix 9.1 for the full derivation). By manipulating the usual von Bertalanffy curve (Equation 9.1) Fabens produced

$$\begin{aligned}\hat{\Delta L} &= (L_{\infty} - L_t)(1 - e^{-K\Delta t}) \\ \hat{\Delta L} &= L_{t+\Delta t} - L_t\end{aligned}\quad (9.6)$$

where, for an animal with an initial length of L_t , $\hat{\Delta L}$ is the expected change in length through the period of Δt . By minimizing the squared differences between the observed ΔL and the expected $\hat{\Delta L}$ for each point, using Equation 9.6, estimates can be derived for the K and L_{∞} parameters. The average length at a known age would be required to include an estimate of t_0 , so often, no estimate can be generated and the exact location of the growth curve along an age axis is not determined. In these cases, the t_0 parameter is often set to zero (Figure 9.6, Example Box 9.3).

**Figure 9.6**

Plot of artificial data for tag returns from three different time intervals (squares = 170 days, filled triangles = 385 days, and circles = 690 days); each time interval has its own expected ΔL for a given starting length L_t illustrated by the three solid lines. If the lines were projected, they would meet the x axis at L_∞ (Table 9.2, Example Box 9.3).

9.2.5 extensions to Fabens Method

The use of the Fabens method appears straightforward (Example Box 9.3), but there are difficulties that are easily overlooked. Sainsbury (1980) pointed out that, as originally developed, both Equations 9.1 and 9.6 relate to the growth of individuals and thus do not predict the average length-at-age t or the average growth increment for a given initial length and time passed, Δt . Instead, it is just assumed that these curves can be applied to collections of individuals. This ignores the fact that there will be variation in the growth of individuals.

An inspection of the distribution of the length increments relative to the initial size at tagging (Figure 9.6) indicates that the variation around the expected length increments appears to be greater at the smaller initial lengths, L_t . Thus, as the expected ΔL declines with increasing initial size, the variability of the residuals appears to decline. One could use either a weighted least squares approach to fitting the model (having a constant coefficient of variation instead of a constant variance), or one could use a maximum likelihood method and directly estimate the variance. Francis (1988a) described just such a maximum likelihood approach that fitted the model to the data assuming the residuals were distributed normally, and he suggested a number of different functional forms for the relationship between residual variance and expected ΔL . Thus, normal errors are used, but the variance of the residuals is determined separately. Using ordinary normal random errors (i.e., constant variance) would provide identical answers to a least squares approach. The negative log-likelihood in this case would be

$$-veLL = -\sum \ln \left(\frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(\Delta L - \bar{\Delta L})^2}{2\sigma^2}} \right) \quad (9.7)$$

EXAMPLE BOX 9.3

The Fabens method of fitting a growth curve to tagging data extended using ideas from Francis (1988a). The t_0 is redundant (but could be used to plot a growth curve from a length-at-age perspective). Enter the data from Table 9.2 into columns A to C, down to row 35. In E4 put =sum(H6:H35). To obtain the number of years at liberty put =A6/365.25 into D6. In E6 put =(\$B\$1-B6)*(1-EXP(-\$B\$2*D6)). Copy D6:E6 down to row 35. In column H put =-Ln(normdist(C6,E6,G6,false)) and copy down to row 35 to obtain the negative log-likelihoods. The first model fit can be generated using least squares by getting the solver to minimize B4 while changing B1:B2. Record the answer somewhere else on the sheet. If you were to put =E\$3 into cell G6 and copy down, you could obtain the same result via maximum likelihood as from least squares, by minimizing E4, by changing (B1:B2, E3). This is not particularly stable and you may need to try a number of starting points to obtain an answer. If it does fail and generate a #NUM error, look for the reason why it happened. Alternatively, you could put =E\$1*E6 into G6 and copy down to obtain Equation 9.8, the linear relation between residual standard deviation and the expected ΔL (minimize E4 by modifying B1:B2, E1). Finally, try the two other residual structures: =E\$1*E6^\$E\$2 and =E\$2*(1-exp(-\$E\$1*E6)). Compare the parameter estimates and the total log-likelihood. Which is the best fitting model? Examine the residuals in a graphical plot. Compare the various fits using the likelihood ratio test or using Akaike's information criterion ($AIC = 2LL + 2p$), where LL is the negative log-likelihood and p is the number of parameters. The smallest AIC wins.

	A	B	C	D	E	F	G	H
1	L_{∞}	100.39		Nu	0.5			
2	K	0.31		tau	0.5			
3	t0	0		Sigma	3			
4	SSq	=sum(F6:F35)		-veLL	75.5175			
5	ΔT	Lt	ΔL	ΔT Yrs	E(ΔL)	Resids²	StDev	LL
6	170	21	15.1	0.465	10.62	$=(C6-E6)^2$	3.00	3.133
7	170	27	6.4	0.465	9.82	$=(C7-E7)^2$	3.00	2.666
8	170	28	11.5	0.465	9.68	$=(C8-E8)^2$	3.00	2.201
9	170	35	10.3	0.465	8.75	Copy down	3.00	2.151
10	170	40	10.8	0.465	8.08	To F35	3.00	2.429
11	170	49	9.4	0.465	6.87	6.379	3.00	2.372

TABLE 9.2Artificial Example Tagging Data Simulated from $L_\infty = 100$ and $K = 0.3$

Δt	L_t	ΔL	Δt	L_t	ΔL	Δt	L_t	ΔL
170	21	15.1	385	20	27.2	690	22	28.6
170	27	6.4	385	36	14.8	690	23	37.3
170	28	11.5	385	46	18.3	690	25	37.2
170	35	10.3	385	48	15.2	690	26	26.1
170	40	10.8	385	58	12.2	690	28	27.9
170	49	9.4	385	60	10.8	690	38	31
170	56	3.6	385	70	10.2	690	51	24.7
170	72	2.1	385	72	7.1	690	51	19.9
170	74	5.2	385	81	4.1	690	74	9.7
170	75	2.3	385	86	6.2	690	81	9.3

Note: Each set of three relates to different days at liberty, Δt , L_t relates to the initial size at tagging, and ΔL is the change in length during Δt . These data are illustrated in Figure 9.6 and are used in Example Box 9.3.

where σ^2 is the constant variance of the residuals between the observed and expected ΔL values. Francis (1988a) provided a number of different formulations for describing this variance, including an inverse linear relationship between the standard deviation and the expected ΔL :

$$\sigma = v(\hat{\Delta L}) \quad (9.8)$$

where v (nu) is a constant multiplier on the expected ΔL , and would need to be estimated separately. The likelihood becomes

$$L(\Delta L | Data) = \sum_i \left(\frac{1}{\sqrt{2\pi}v\hat{\Delta L}} e^{-\frac{(\Delta L - \hat{\Delta L})^2}{2(v\hat{\Delta L})^2}} \right) \quad (9.9)$$

Francis (1988a) also suggested exponentially declining residual standard deviations:

$$\sigma = \tau(1 - e^{-v\hat{\Delta L}}) \quad (9.10)$$

where τ is an extra estimable constant. Finally, Francis (1988a) suggested that the residual standard deviation might follow a power law:

$$\sigma = v\hat{\Delta L}^\tau \quad (9.11)$$

Francis (1988a,b) took his extensions of the Fabens method further with suggestions for how to account for consistent bias in the measurement of length,

with additions to the model to estimate seasonal variation in growth rates and to account for outlier contamination. All of these extensions constitute valuable improvements over the simple Fabens method. With each different formulation of the relationship between the variance of the residuals and the expected ΔL , the constants τ and v would change in their interpretation. As seen before, the parameter estimates obtainable from the same model can vary if different error structures are assumed (Example Box 9.3).

Unfortunately, how we select which error structure is most appropriate is not a question that is simple to answer. One could use a likelihood ratio test (see Equation 9.21) to compare the quality of fit obtained with the different numbers of parameters. Thus, if there were an improvement to the log-likelihood of the order of 1.92 (a χ^2 value of 3.84 divided by 2) from fitting the model using Equation 9.11 instead of Equation 9.8 (adding a parameter), this would constitute a statistically significant improvement. However, ideally, one would have other reasons for preferring one error structure over another for the residual variance.

9.2.6 Comparability of growth Curves

The Fabens version of the von Bertalanffy equation derives directly from the classical equation (Appendix 9.1), and yet the parameters generated from size-at-age data have been given different interpretations than those generated from tagging data (Sainsbury, 1980; Francis, 1988b). This may appear paradoxical until it is realized that the curves are being fitted using very different residual error structures.

With size-at-age data, the residuals are between observed size-at-age and expected size-at-age in a snapshot sample from the population. With tagging data the residuals are between the observed size increment and the expected for possibly different time intervals, for data collected at least some time after the initial observations. The net result is that the estimation of L_∞ tends to be biased upwards with tagging data, while the reverse seems true for the size-at-age data. That the estimates of the parameters obtained from length-at-age data and from tagging data are different (as claimed by Sainsbury, 1980; Francis, 1995) can be seen directly by simulating a population where the individuals each grow with their own particular von Bertalanffy growth parameters. If a population is set up with individuals each having their own L_∞ and K values (assume a t_0 of zero) varying normally about overall mean parameter values, then this hypothetical population could be sampled for both size-at-age data and time increment growth data. Note that the same population is being sampled. If there were no difference between the two methods, then, on average, we would expect their parameter estimates to coincide (Figure 9.7). In fact, the parameter estimates do not coincide and both show biases, with the tagging approach appearing to be more biased than the size-at-age approach. Clearly, care must be taken if comparisons are to be made between growth curves estimated differently.

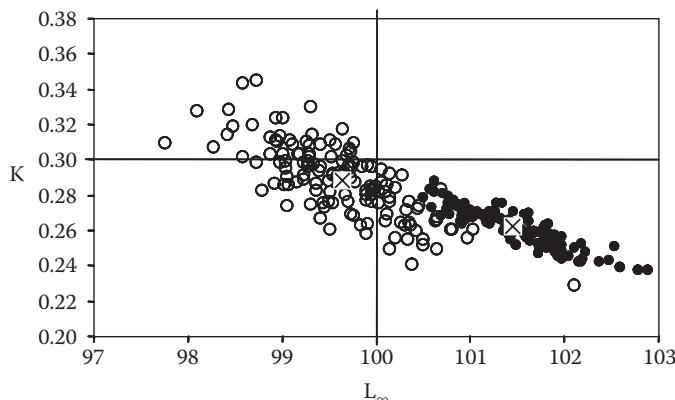


Figure 9.7

Growth curve parameters estimated from two hundred Monte Carlo simulations of sampling a single hypothetical population of individuals, each individual with its own von Bertalanffy growth parameters. Growth curves were fitted as with size-at-age data (open circles) and tagging data (small, solid circles). The two crosses indicate the mean of each set of parameter estimates. The mean values for L_∞ and K were 100 and 0.3, respectively, as indicated by the crossed lines. Generally, the estimates from tagging data were biased high for the L_∞ and low for the K parameter. From size-at-age data, both parameter estimates were biased slightly low.

9.2.7 growth from Modal Progression

If the size distribution of a population is measured through time, then the average growth of the animals surviving through time can be estimated in the form of a growth curve. Such curves would not be directly comparable to growth curves estimated using size-at-age or tagging data. Modal progression relates to the average growth of a surviving population, whereas the other two methods relate to the growth of individuals. If there are any size-selective mortality processes occurring, then the growth curve produced using modal analysis will differ significantly from the other methods. Nevertheless, modal analysis has been used for a long time in fisheries science (Fournier and Breen, 1983) and has the advantage that the collection of data is simple and cheap.

Example Box 3.14 illustrates how to fit modes directly to length frequency data. Given a time series of such data, a growth curve can be fitted by including growth curve parameters that give rise to predicted mean lengths at time instead of estimating these modal means directly. The modal means are taken to represent different cohorts growing within the population.

This approach to describing average population growth is most useful with juvenile and small animals. Generally, as animals become mature, their growth tends to slow significantly and any modes begin to overlap and become difficult to distinguish correctly. Nevertheless, modal analysis remains a useful approach for characterizing early growth.

9.3 Alternatives to Von Bertalanffy

9.3.1 A generalized Model

Virtually every fishery paper concerned with growth uses the von Bertalanffy growth equation, but this does not mean that it is the only possible growth function or even necessarily the best in a given situation.

A very general model has been proposed by Schnute and Richards (1990). This starts as a four-parameter model of growth, which generalizes the classical logistic model, as well as those by Gompertz (1825), von Bertalanffy (1938), Richards (1959), Chapman (1961), and Schnute (1981). It also generalizes the Weibull (1951) distribution, which has been used with applied problems. All of these papers contain equations, which could easily be used as alternatives to the von Bertalanffy growth function (VBGF). They all share the property of permitting a description of increasing size, leading to an asymptotic maximum, but have alternative shapes, depending on their parameters. Schnute and Richards's (1990) model has the form

$$y^{-b} = 1 + \alpha e^{-ax^c} \quad (9.12)$$

By altering the parameters (a , b , c , and α), and the formal structure of the model, Equation 9.12 can take the form of many of the popular growth models (Figure 9.8). For example, if $b = c = 1$, then Equation 9.12 becomes the classical logistic relationship

$$y = \frac{1}{1 + \alpha e^{-ax}} \quad (9.13)$$

Schnute and Richards (1990) implicitly assumed that the y variable was scaled in units of y_∞ . If this asymptote is included, the model finishes with five parameters and becomes extremely flexible:

$$y_t = y_\infty \left(1 + \alpha e^{-at^c} \right)^{-\frac{1}{b}} \quad (9.14)$$

where the parameters are as before, t is age, and y_∞ is the average maximum value of the variable y . When parameter $c = 1$, the model becomes equivalent to Schnute's (1981) generalized growth model. The Schnute and Richards (1990) model generalizes the Schnute (1981) model when the age t is replaced with t^c :

$$Y_t = \left[y_1^b + \left(y_2^b - y_1^b \right) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b} \quad (9.15)$$

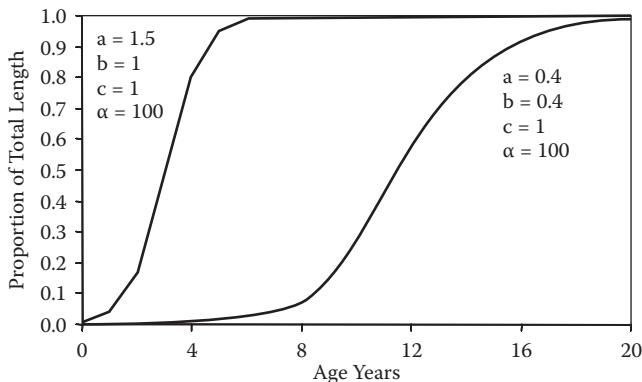


Figure 9.8

Two curves generated by substituting different sets of values for α , a , b , and c , in Equation 9.12. The general equation generates a curve of relative size against age. Construct a worksheet to illustrate this growth curve.

where t is age, y_i is the size-at-age τ_i , and the other parameters are as before. Once again, by varying the various parameters, a wide range of curves can be generated, some of which are not necessarily asymptotic. Schnute's (1981) model appears to have been used more in the literature than the more general Schnute and Richards (1990) model (Gillanders et al., 1999, although strictly, they used Francis's (1995) mark-recapture analogue to Schnute's Equation 9.15; Ziegler et al., 2007). Different model designs are still being developed (Francis, 1995; Wang and Thomas, 1995). This area of research remains open for further development (Haddon et al., 2008).

9.3.2 Model Selection—AIC and BIC

With four parameters, Equation 9.12 has one more parameter than most other growth models, which is one reason why it can embody so many models with fewer parameters as special cases. Such an equation is mathematically general and is useful for providing a unified analytical framework for a diverse literature. Knowing that all these growth models constitute special cases of a single general model should make it clear that they may be regarded solely as descriptions of growth with no explanatory power. This is a very valuable lesson. What it means is that even if we manage to obtain a very good fit of a particular growth model to a data set, the interpretation of its parameters is not necessarily meaningful. For example, just because a model implies an asymptotic maximum mean length (because it calculates one) does not force the species concerned to actually have such a maximum. We will discuss this point further when considering the many criticisms directed against von Bertalanffy curves.

Whether one would use Schnute and Richards's (1990) general model when selecting an equation to describe growth, instead of one of the special

cases, is a difficult question to answer. The special cases might be preferred to the general equation because having fewer parameters, fitting them to real data might be more straightforward, as would using them in an assessment model. However, if these growth models truly are just descriptive black boxes, having an input to provide a particular output, then, with available computing power, it would make very little difference which equation was used. Presumably, one should use the equation that provides the best description of the growth process being described. Unfortunately, deciding what constitutes "best" is not as simple as one might hope. If one simply wants the closest description of one's growth data (according to some criterion such as likelihood ratio or AIC), then one could try fitting a wide range of models and error structures and proceed with the one producing the best fit. As mentioned before, the AIC attempts to balance the trade-off between improving the quality of fit for a model and minimizing the number of parameters used. The AIC is calculated using

$$AIC = 2LL + 2p \quad (9.16)$$

where LL is the negative log-likelihood and p is the number of parameters. The model fit with the smallest AIC provides the best trade-off between fit and number of parameters. An alternative is the so-called Bayesian information criterion (BIC), which includes the natural log of the sample size (N) in its calculation (Burnham and Anderson, 2002). Where the sample size is greater than seven ($(\ln(7.389) = 2)$ the BIC tends to penalize the addition of parameters more than the AIC (Haddon et al., 2008).

$$BIC = 2LL + p \ln(N) \quad (9.17)$$

Burnham and Anderson (2002) provide an alternative when using least squared residuals:

$$AIC = N \ln(\hat{\sigma}^2) + 2p \quad (9.18)$$

where $\hat{\sigma}^2$ is the maximum likelihood estimate of the variance

$$\hat{\sigma}^2 = \frac{\sum \epsilon^2}{N} \quad (9.19)$$

where ϵ^2 is the sum of squared residuals. However, if one really wants to obtain biologically sensible interpretations when fitting a model, then model selection cannot be solely dependent upon quality of statistical fit. Instead, it should reflect the theoretical viewpoint (for example, of growth) that is being considered for reasons independent of its statistical fit to data.

9.3.3 Polynomial equations

Polynomial functions, of three or four parameters, have been suggested as alternatives to the von Bertalanffy growth function. These polynomials are explicitly empirical, as there is little to be gained from trying to interpret the parameters. Comparisons between curves would be reliant on them each having the same number of parameters. However, Chen et al. (1992) made an explicit comparison of a variety of polynomials against the VBGF and concluded that the VBGF performed better than any of the polynomial equations considered. In the process of doing this, they also suggested a neat way of comparing growth curves of any type (see later) to determine whether they differed statistically.

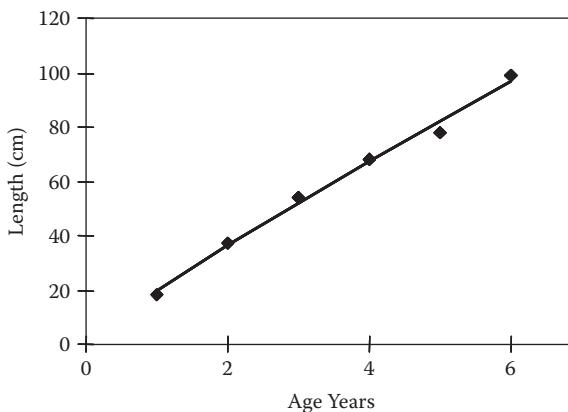
If all that is required is a description of how growth has occurred, there is no reason not to use polynomial equations. However, while the interpolation of growth within the range observed is possible, attempts to extrapolate beyond the observed data could possibly lead to large errors.

9.3.4 Problems with the von Bertalanffy growth Function

With the wide range of alternative growth equations available, the ongoing use of the VBGF to represent fish growth has been questioned by a number of people. Knight (1968) criticized the VBGF as often being more like fiction than a useful model of growth. His major complaint was that L_{∞} was generally estimated through extrapolation, and sometimes extreme extrapolation (Figure 9.9).

The estimation of L_{∞} is especially a problem with fish species that do not exhibit an asymptotic maximum length (Figure 9.9). The best fit von Bertalanffy curve to the minimal data provided by Knight (1968) suggests an L_{∞} of 453 cm, that is, a cod 4.5 meters in length, which is biological nonsense. The validity of such extrapolation depends almost completely on the appropriateness of the assumptions of the von Bertalanffy model of growth for the species concerned. Roff (1980) was critical of a number of people, including Beverton and Holt (1957), who applied the curve in an apparently unthinking manner. He also emphasized its inapplicability to fish species that do not appear to have an asymptotic maximum length. The same argument against extrapolation could have been expressed about the estimation of t_0 .

Roff (1980) reviewed the problems associated with using the VBGF and suggested that people stop using it and turn to different functions instead. To his credit, Roff (1980) did not advocate any particular equation but stated that the choice should be dictated by circumstances. He also pointed out that the equation was very hard to fit to data in a statistically satisfactory manner, meaning, presumably, either that there was no simple or deterministic way of fitting the curve or that the comparison of growth curves was difficult. It is common to fit growth curves even with little data available for younger and older animals, and when the sampled population is fished and has a

**Figure 9.9**

Plot of the growth of Atlantic cod through the first six years of life. (After Knight, 1968.) Shows the best von Bertalanffy curve fit with $K = 0.0391$, $t_0 = -0.126$, and $L^\infty = 453$ cm, which is clearly an exaggeration of possible reality.

legal minimum size. In these cases, the data are not really representative of the population, and care must be taken with the generality of any resulting curves and comparisons with other populations.

Very obviously, there are many problems with using the VBGF; nevertheless, fisheries scientists continue to use it in their models. Given a model, although fitting the curve is no longer the technical problem it was, there is rarely any discussion about how the residuals are expected to be distributed about the expected curve. Generally, they are assumed to be normal random and additive, but there is rarely consideration of whether they are symmetrical or otherwise, or whether the variance of the residuals is constant or varies with size. Analytical and statistical computer programs routinely have procedures for generating nonlinear fits to particular models (e.g., SAS, R, Excel's nonlinear solver). Putting aside Sainsbury's (1980) and Francis's (1988a,b) problem of different concepts having the same name, the major difficulty is that of statistically comparing growth curves, for example, from different stocks or sexes of the same species.

9.4 Comparing Growth Curves

9.4.1 Nonlinear Comparisons

Because of the nonlinear nature of the von Bertalanffy growth function (VBGF), we cannot use a standard analysis of covariance with which we might usually compare regression lines. Many early methods of comparing

growth curves relied upon linearizing the VBGF and comparing the linear regressions produced. These methods often only produced approximate fits of the VBGF to the data and will not be discussed further. Misra's (1980) approach was rather more complicated but still used a linearized reparameterization of the VBGF, fitting it to data using multiple regression, and tested for differences between growth curves using ANOVA on the separate parameters. Alternatively, Bernard (1981) used a multivariate test, Hotelling's T , to compare all three VBGF parameters at once.

A summary and consideration of methods was provided by Cerrato (1990), who compared the ability of the t , univariate χ^2 , likelihood ratio, and Hotelling's T tests to provide valid comparisons of VBGF curves. The last two methods are generally considered better than the others, not least because they consider all parameters at once. Because there are strong correlations between the parameters of the von Bertalanffy equation, one should never compare individual parameters in isolation.

Cerrato (1990, p. 416) provided a clear statement of the problems faced when attempting to compare nonlinear growth curves using the likelihood ratio or Hotelling's T tests:

Both approaches are approximate ones. They are taken from linear statistical theory, and their validity when applied to the von Bertalanffy equation depends on the degree of bias and non-normality in the parameter estimates caused by the non-linearity of the model. In addition, both are characterized in terms of asymptotic properties for which no exact small sample theory exists. Finally, at least as commonly practised, both approaches handle unequal and unknown error variances in an approximate way.

Despite these problems, Cerrato (1990), in an empirical test, found that the likelihood ratio comparison most often, and most accurately, reflected the true state of affairs and recommended that this should be the approach of choice. Moulton et al. (1992) went slightly further in that they recommended reparameterizing the VBGF as recommended by Francis (1988a,b), and then using the likelihood ratio for comparative tests between the reparameterized curves.

9.4.2 An Overall Test of Coincident Curves

A method of comparing a number of curves at once was proposed by Chen et al. (1992) and is called the analysis of residual sum of squares (AoRSS). The method is different from the likelihood ratio approach, but it is useful in itself, and because there are analogies between the two approaches, the AoRSS is a useful way to introduce the principle behind likelihood ratios. Only curves fitted using the same residual error structures can be compared using these methods.

The analysis of residual sum of squares is a total comparison, meaning that it does not compare the parameters separately but simply tests whether two or more curves are statistically different (are coincident curves). A linear version of this test was described by Zar (1984) as an overall test for coincident regressions. Equation 9.20 is simply an extension to the nonlinear case. There are four steps to the AoRSS:

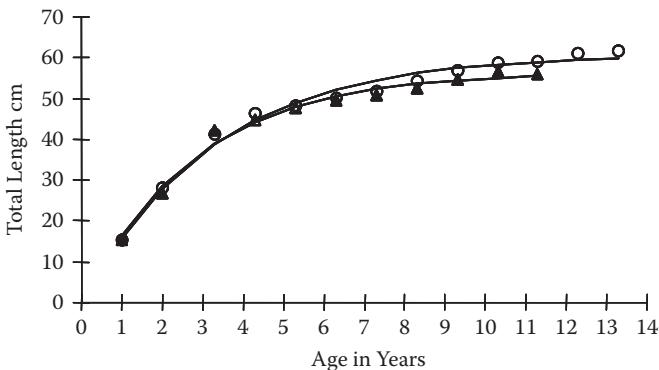
1. For each data set i , fit a curve and calculate the sum of squared residuals, RSS_i , and an associated degree of freedom, DF_i .
2. The resultant RSS_i and DF_i for each curve are added to give the ΣRSS_i and ΣDF_i .
3. Data for all curves are pooled, a new curve is fitted to the combined data, and the total or pooled RSS_p and DF_p are calculated.
4. Using these statistics, an F statistic is calculated as in Equation 9.20:

$$F = \frac{\frac{RSS_p - \sum RSS_i}{DF_p - \sum DF_i}}{\frac{\sum RSS_i}{\sum DF_i}} = \frac{\frac{RSS_p - \sum RSS_i}{3.(K-1)}}{\frac{\sum RSS_i}{N-3.K}} \quad (9.20)$$

where F is the F statistic with $3.(K-1)$ and $(N-3.K)$ degrees of freedom, K is the number of curves being compared, and N is the total or pooled sample size. This test can be applied to all classes of curve, not just the VBGF. This is a test of the hypothesis that the curves being compared are all equivalent descriptions of the data available; an example may serve to make this clear.

Kimura (1980) provides a table of age length data relating to Pacific hake with separate data for both males and females (Figure 9.10, Table 9.3). The question is whether the male and female Pacific hake exhibit different growth throughout their lives. In this case $K = 2$ and $N = 24$.

As listed above, one first has to find the best fitting curves for the males and females separately. For the von Bertalanffy curve this leads to: females, $L_\infty = 61.23$, $K = 0.2963$, and $t_0 = -0.0573$, with 10 df, and $RSS = 48.224$; males, $L_\infty = 55.98$, $K = 0.3856$, and $t_0 = 0.1713$, with 8 df, and $RSS = 19.423$. Then the male and female data are treated as one population and the pooled growth curve fitted, which leads to $L_\infty = 59.29$, $K = 0.3205$, and $t_0 = 0.0104$, with 21 df, and $RSS = 79.764$. When these figures are substituted into Equation 9.20, the resulting $F = 3.915$ is just significant ($P = 0.0258$). This analysis certainly indicates that the two curves (Figure 9.10) are different but does not indicate in which way. A different test would be necessary if more details were required.

**Figure 9.10**

Average length-at-age for the Pacific hake for females (circles; $L_\infty = 61.23$, $K = 0.296$, and $t_0 = -0.057$) and males (triangles; $L_\infty = 55.98$, $K = 0.386$, and $t_0 = 0.171$). (Data from Kimura, 1980.) The lines illustrated are the maximum likelihood best fitting curves (Table 9.3, Example Box 9.6).

TABLE 9.3

Average Length-at-Age for Male and Female Pacific Hake from the U.S. West Coast

Age Years	Female Sample Size	Female Mean Length, cm	Male Sample Size	Male Mean Length, cm
1.0	385	15.40	385	15.40
2.0	36	28.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91	-	-
13.3	6	61.83	-	-

Source: Data from Table 1 in Kimura, 1980.

Note the change to the years of age after age 2.

9.4.3 Likelihood ratio Tests

The general principle when using the AoRSS involves comparing the outcome (RSS_p) of the hypothesis that all the curves are coincident (each data set is effectively a sample from the same population) with the outcome ($\sum \text{RSS}_i$) of the hypothesis that all data sets are from independent populations

(Example Box 9.4). The method of likelihood ratios does something very similar in that it sets up the outcome of the hypothesis of two or more independent curves as a base case against which to compare all alternative hypotheses. For the von Bertalanffy curve the alternative hypotheses would be: (1) that all curves were coincident, as with the AoRSS test, (2) that the L_∞ values were equal, (3) that the K values were equal, (4) that the t_0 values were equal, (5) that the L_∞ and K values are equal, (6) that the L_∞ and t_0 values are equal, and finally, (7) that the K and t_0 values are equal. Strictly, if the test of coincident curves (hypothesis 1) were not rejected, one would not need to test hypotheses 2 to 7.

However, if one were testing multiple curves for equivalence and the test of coincident curves proved false, then one would have to proceed by making subsequent pair-wise comparisons between individual growth curves to discover the details of which aspects of the curves in question differed.

The standard description of the likelihood ratio methodology was given by Kimura (1980), who dealt exclusively with the von Bertalanffy growth curve. The method is more general than this, however, and can be applied to comparing any nonlinear equations fitted to data as long as the residuals used are additive and normally distributed (Barrett et al., 2007). The necessity for this restriction is illustrated in the derivation of the method (see Appendix 9.2). The important thing for our discussion is to determine how to calculate the likelihoods for each hypothesis to be compared. The test calculates a statistic that is compared with the χ^2 distribution with degrees of freedom equal to the number of constraints (i.e., the number of parameters being assumed equal). The method turns out to be extremely simple, and to start with the conclusion, the test is based on the following equation:

$$\chi_k^2 = -N \times \ln \left(\frac{\sum RSS_i}{RSS_p} \right) = -N \times \ln \left(\frac{RSS_\Omega}{RSS_\omega} \right) \quad (9.21)$$

where k is the degrees of freedom (equals the number of constraints placed upon the fit), N is the total number of observations from both curves combined, RRS_Ω is the total sum of squared residuals derived from fitting both curves separately (i.e., the minimum sum of squares from each curve added together), and RRS_ω is the total sum of squared residuals derived from fitting the curves with one of the hypothesized constraints (e.g., the K s are equal, or the L_∞ s are equal; hypotheses 1 to 7 above). The base case (RRS_Ω) will always provide the smallest residual sum of squares because it has the largest number of independent parameters (all parameters are assumed to be independent). When any of the possible constraints are tested, the number of independent parameters will obviously decrease so the fit will be somewhat less precise. The question to be answered in each test is whether the decline in fit (i.e., the difference between the two residual sums of squares) is greater than would

EXAMPLE BOX 9.4

The implementation of the analysis of residual sum of squares. The data are in Table 9.3. Put =sum(H14:H24) into C5. In cell B6 put =count(B14:B26)-3 or the female df, in C6 put =count(F14:F26)-3, and in D6 put =count(B14:B26, F14:F26)-3. In B10 put =abs((C8-B8)/(C9-B9))/(B8/B9), and in C10 put =abs((C8-B8)/(3*(2-1)))/((B8/(24-(3*2)))); they should give the same F value. In B11 put =fdist(B10,3,B9). To calculate the expected lengths put =\\$B\$2*(1-exp(-\\$B\$3*(A14-\\$B\$4))) into C14 and =(B14-C14)^2 into D14. Copy C14:D14 down to row 26. Similarly, put =(F14-G14)^2 into cell H14 and put =\\$C\$2*(1-exp(-\\$C\$3*(E14-\\$C\$4))) into G14, and copy G14:H14 down to row 24. Using the solver, in turn, minimize B5 by altering B2:B4, and C5 by altering C2:C4. Copy B5:C6 into F2:G3 as values. Put =D2 into B2 and C2, and copy down to row 4. Then minimize cell D5 by altering D2:D4; copy D5:D6 into H2:H3, and the answer should be determined. Plot column B against A as points and add column C as a line; add columns E and F as points and column G as a further line to mimic Figure 9.10.

	A	B	C	D	E	F	G	H
1		Female	Male	Total		Female	Male	Total
2	Linf	61.233	55.978	59.294	SSq	28.800	19.423	79.765
3	K	0.296	0.386	0.320	df	10	8	21
4	t0	-0.057	0.171	0.010				
5	SSQ	=sum(D14:D26)	19.423	=B5+C5				
6	df		10	8	21			
7		Individual	Pooled					
8	SSQ	=F2+G2	=H2					
9	df	=F3+G3	=H3					
10	F	3.924	3.924					
11	P	0.026						
12	Fem	Fem	Fem	Fem	Male	Male	Male	Male
13	Age	Length	E(L)	Resid2	Age	Length	E(L)	Resid2
14	1	15.4	16.47	1.14	1	15.4	15.31	0.01
15	2	28.03	27.94	0.01	2	26.93	28.32	1.94
16	3.3	41.18	38.58	6.73	3.3	42.23	39.22	9.03
17	4.3	46.2	44.39	3.27	4.3	44.59	44.58	0.00
18	5.3	48.23	48.71	0.23	5.3	47.63	48.23	0.36

be expected by chance. If the χ^2 value calculated from Equation 9.21 is not significant, then the decline in the quality of fit is assumed to be no more than if the parameters being compared were random selections from the same origin (i.e., those parameters are not significantly different).

Equation 9.21 is relatively simple to calculate because, as with the AoRSS method, it only requires the calculation of various sums of squares. Kimura's (1980) paper provides a brief description of why we can successfully use the specified residual sum of squares as likelihood estimates in this likelihood ratio test (demonstrated in detail in Appendix 9.2). In practice, the likelihood ratio requires separately calculating the total residual sum of squares for the base case and for the hypothesis of interest (e.g., the K values are equal) and substituting the values into Equation 9.21. The likelihood ratio is then compared with a table of the χ^2 distribution with k degrees of freedom (k is the number of constraints placed upon the fit; Example Box 9.5).

9.4.4 Kimura's Likelihood ratio Test

Kimura (1980) provided a set of test data and the analytical outcomes so that anyone attempting to implement a likelihood ratio test would be able to ensure the computer program worked. He provided data relating to the average length-at-age for Pacific hake for each sex with the objective of determining whether the two sexes differed significantly in their overall growth pattern (Table 9.3, Figure 9.10). The data were used in the AoRSS statistic example above and the curves were not found to be coincident. We will use the likelihood ratio test to determine how the curves differ (Example Box 9.5).

The method is simple. First, find the best fitting separate curves for each data set separately. Then, in sequence, compare the total residual sum of squares from this base case with that obtained by adding various constraints. Perhaps the best order in which to impose these tests is to first assume the hypothesis that both data sets can best be described by a single line (coincident curves). If this indicates that a significant difference exists, then one should sequentially assume that single parameters are the same between the two lines and determine whether significant differences arise. If differences are found, then one would conclude that evidence exists that the curves do differ and be able to identify which parameters are different between the curves for each data set (Table 9.3).

When the likelihood ratios were calculated for Kimura's data, a difference between the curves was indicated by the comparison of the base case with the assumption of the same curve fitting both data sets. With the more detailed analyses, a difference between the L_∞ was strongly indicated, while there was some slight evidence that the K parameter might be different; however, there was no indication that the t_0 parameters differed significantly (Table 9.4).

EXAMPLE BOX 9.5

Kimura's (1980) likelihood ratio test. Copy the data from Table 9.3 into columns B and C, female data followed by the male. In D14 put $=$B$1^* (1-\exp(-$B$2*(B14-$B$3)))$ and copy down to D26. In D27 put $=$B$4^* (1-\exp(-$B$5*(B27-$B$6)))$ and copy down to D37. In B8 put =sum(E14:E26) and in C8 put =sum(E27:E37). Put =count(B14:B26) into B12 and =count(B27:B37) into C12. In D12 put =B12+C12 for the total N. In D9 calculate the likelihood ratio $=-D12*\ln(F8/D8)$. In D10 manually put the degrees of freedom = number of constraints being considered. In D11 put =chidist(D9,D10). In D9, note the reference to F8, which is merely the stored result of minimizing D8 by altering B1:B6 and storing B1:B6 into F2:F7 and B8 into F8 as values. This sets up the sheet ready for hypothesis testing. To test for coincident curves, put =B1 into B4 and copy down to B6. This sets the same parameters for both data sets. Then minimize D8 by altering B1:B3. Copy the answers as values from B1:B6 and from D8:D11 into G2:G11 for later reference. To test if the L_∞ are different put =B1 into B4 and minimize D8 by altering (B1:B3,B5:B6). Remember to alter the degrees of freedom in D10 to 1. Copy the results to the right of column G. Try the other hypotheses by similar manipulations of which cells are set equal to which and by altering the cells to be altered by the solver. Try changing the analysis by restricting the sum of squares residuals for females to the first 11, like the males, by putting =sum(E14:E24) into B8 and =count(C14:C26) into B13. Are the results of the analysis the same?

	A	B	C	D	E	F	G
1	$L_{\infty-f}$	61.23			Results	BaseCase	Coincident
2	$K-f$	0.296			$L_{\infty-f}$	61.2331	59.2938
3	T_0-f	-0.057			$K-f$	0.2963	0.3205
4	$L_{\infty-m}$	55.98			t_0-f	-0.0573	0.0104
5	$K-m$	0.386			$L_{\infty-m}$	55.9779	59.2938
6	T_0-m	0.171			$K-m$	0.3856	0.3205
7		Female	Male	Total	t_0-m	0.1713	0.0104
8	SSQ	28.800	19.423	=B8+C8	SSQ	48.2238	79.7645
9			χ^2	0	χ^2		12.077
10			df	3	Df		3
11			P	1	P		0.0071
12	Count	13	11	24			
13		Age	Length	E (L)	Resid2		
14	Fem	1	15.4	15.54	$=(C14-D14)^2$		
15	Fem	2	28.03	27.70	$=(C15-D15)^2$		
16	Fem	3.3	41.18	38.76	Copy down		
17	Fem	4.3	46.2	44.68	To row 37		

TABLe 9.4

Likelihood Ratio Test for the Pacific Hake Data from Table 9.3

	BaseCase	Coincident	=Inf	=K	=t0
$L_{\infty}f$	61.233	59.294	59.404	60.140	60.767
Kf	0.296	0.320	0.337	0.330	0.313
t_0f	-0.057	0.010	0.087	0.095	0.057
$L_{\infty}m$	55.978	59.294	59.404	57.435	56.454
Km	0.386	0.320	0.297	0.330	0.361
t_0m	0.171	0.010	-0.111	-0.021	0.057
RSS _ω	48.224	79.765	71.602	56.337	50.758
χ^2	—	12.077	9.487	3.732	1.229
df	—	3	1	1	1
P	—	0.0071	0.0021	0.0534	0.2676

Source: Data from Kimura, 1980.

Note: The top three rows of parameters relate to the female fish, while the middle set of parameters refer to the male fish. The base case is where two separate curves are fitted independently, the coincident column is where the lines are assumed identical, and the remaining three columns are where the listed parameter is assumed equal between the two lines. RSS_ω refers to the total residual sum of squares for both curves together given the constraint ω. In the BaseCase column, the 48.224 refers to the unconstrained RSS_ω, against which all the RSS_ω are compared. N in all these cases is 24, 13 females and 11 males (Example Box 9.5, Figure 9.10).

9.4.5 Less than Perfect Data

Unfortunately, it is quite common with real fisheries to only obtain ageing data from a sample of fish obtained from commercial operations. Such a sample may be influenced by the existence of a legal minimum length, and there may be low numbers of animals taken in the younger or older age classes. Finally, with size-selective fishing, the larger, faster growing fish of all ages may have been differentially removed from the population through fishing pressure (Figure 9.11).

Growth curves fitted to samples from a commercial fishery can have many biases, and the parameters obtained may be very wide of the values obtained from a more representative sample (Figure 9.11). However, if such data are all that is available, it would be useful to know whether it was valid to compare growth curves derived from such imperfect data.

For example, in Example Box 9.5 two curves are compared where one data set covered the ages 1 to 13.3 while the other only covered ages from 1 to 11.3 years. In that example, a significant difference was found between the two curves, driven primarily by differences in the L_{∞} parameter. However, if the comparison is restricted to the first eleven data points in both data sets, the hypothesis that the two curves are coincident is not proved incorrect (this can be tried in Example Box 9.5). However, in that example only average length-at-age data were used; in reality, one would now use the unsummarized data, so the results may differ, but the methods remain the same.

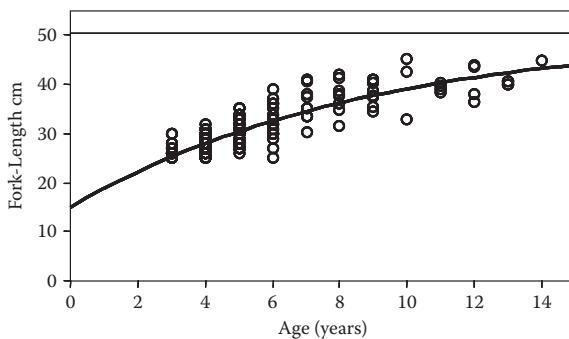


Figure 9.11

The same data as in Figure 9.1, for snapper, *Pagrus auratus*, from the Bay of Plenty, New Zealand, but with all animals less than 25 cm excluded as being below the legal size, and fewer older animals, as taken by the commercial fleet. Instead of $L_{\infty} = 44.79$, $K = 0.196$, and $t_0 = -0.81$, the best fitting von Bertalanffy growth curve was for $L_{\infty} = 50.45$, $K = 0.115$, and $t_0 = -3.06$; the L_{∞} line is now well above the data and the t_0 is obviously unrealistic. Clearly, there are many potential impacts of limiting the data in this way. It also makes drawing conclusions from curve comparisons dangerous.

The von Bertalanffy curve is strongly determined by the values for L_{∞} and t_0 , which are at the extremes of the curve and usually have the least data. This is why so many people have spent time trying to reparameterize the curve (Sainsbury, 1980; Frances, 1988a,b) to have parameters closer to the data from which they are estimated. If the data we use to construct growth curves is biased or not representative (e.g., samples from commercially caught fish), then extra care needs to be taken when comparing growth curves. When comparing growth curves derived from nonrepresentative data, it seems intuitively reasonable to conduct tests only over equivalent ranges of data. Thus, if we were to compare the data from Figures 9.1 and 9.11, we would be likely to find differences. But if we restricted the data from Figure 9.1 to those sizes greater than 25 cm and ages greater than 2, we would be much more likely to find no differences (because, along with removing some of the older animals, that was how the data in Figure 9.11 were generated). We are assuming there are no errors in the ageing, so we should only compare ages with like ages. If there is an obvious difference, such as a legal minimum length influencing only one of the samples, then this must also be taken into account.

What these suggestions mean is that we are not comparing complete growth curves but, instead, the growth of the species over the ranges of ages (or lengths) for which we have data in each of the data sets being compared. Obviously, when reporting such comparisons, it is vital to be explicit about exactly what was compared with what.

9.4.6 A randomization Version of the Likelihood ratio Test

When low-quality data are compared, the assumption that the likelihood ratio adheres to the χ^2 distribution becomes invalid and alters the risk of

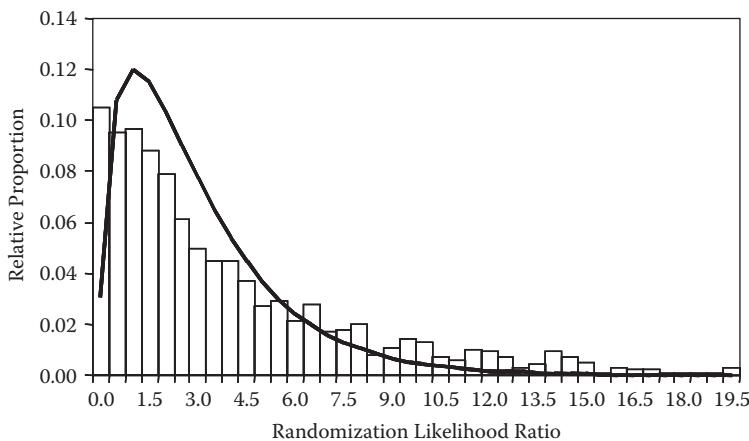
type I errors (claiming a difference where one does not exist) and type II errors (claiming no difference when one exists). If, in Example Box 9.7, one restricts the comparison of curves to ages 1 to 11.3, the coincident curve comparison indicates no statistical difference ($\chi^2 = 6.398, P = 0.0938, \text{df} = 3$). However, if one then continued and compared the two curves with the L_∞ constrained to be identical, a slightly significant difference is found ($\chi^2 = 4.359, P = 0.0368, \text{df} = 1$). Thus, one test concludes no difference while the other concludes a difference exists. An assumption in the analysis, that the likelihood ratio will approximate the χ^2 distribution, appears to be failing.

With inadequate data, instead of using the likelihood ratio test as it stands, it is possible to arrange the data so that we can generate a randomization version of the likelihood ratio test that will generate its own empirical sampling distribution for the test statistic. What is being suggested is that the length-at-age data need to be randomized in some way between the two groups to test the hypothesis that the two data sets are equivalent to two random samples from the same statistical population. This has previously been suggested by Weinberg and Helser (1996), where they made the comparisons by randomizing age and length data pairs between different populations of surfclams. Unfortunately, with their design of randomization, if there are low numbers of the extreme age classes, it would be quite possible to include tests where all the younger or older individuals were selected by chance into one of the randomized data sets. This would have the effect of overestimating the number of times large likelihood ratios would be expected to occur. This design appears to be including a comparison of the proportional catch-at-age as well as the growth curves from the two populations. If the data sets were large and the numbers at age were relatively evenly distributed, this may not be a great problem.

With Kimura's (1980) data (for ages 1 to 11.3), when a randomization test is conducted in the manner described above, the test of coincident curves suggests that likelihood ratios greater than that observed (6.3986) occurred 223 times out of 1,000 (i.e., a $P = 0.223$), which is overly conservative. If we were to plot the proportion of the different likelihood ratio χ^2 values along with the hypothetical proportions from the χ^2 distribution, we would be able to see how closely the empirically determined statistic mimics the hypothetical (Figure 9.12, Example Box 9.6).

Clearly, the randomization of data pairs between the sexes would lead to a greater number of type II errors than expected. The test is too conservative and would have trouble detecting a difference even when one existed. If we are to use a randomization test, some other randomization schema would need to be adopted.

The ages are assumed to have been measured without error, and each age has an associated range of lengths observed in each population; in the Kimura example this is reduced to just a single length per age per sex, but with real data there would be a number of observations per age class.

**Figure 9.12**

A comparison of the relative proportion of different χ^2 values obtained from a randomized likelihood ratio test (open columns) with the expected proportions derived from the χ^2 distribution (solid curve). The test was of whether the growth curves for Pacific hake were coincident for males and females when the ages being compared were restricted to ages 1 to 11.3 (Table 9.2, Figure 9.12, Example Box 9.6). The randomization test, in this case, involved the randomization of age and length data pairs between the two sexes (not recommended if relative numbers are uneven or proportional catch-at-age is variable). If the critical value chosen is 0.05, then the empirical statistic would require a larger likelihood ratio than the true χ^2 . In other words, the empirical statistic would claim not to have found a difference more often than it should (Example Box 9.6).

This structure to the data should be recognized, and instead of randomizing data pairs, the randomizations should be of lengths within age classes between sexes. Thus, for each randomization test one would need to conduct the same number of randomizations of data as one had age classes. With the Kimura data this would entail conducting eleven randomizations before fitting the models, one for each age class. In that case it would be merely deciding which data point was associated with which age. Clearly, this routine would be more complicated to implement (Example Box 9.7) than randomizing data pairs, and the Kimura data are an extreme case.

By randomizing within age classes but between sexes, the randomization test can avoid problems with the relative number of observations present in each age class. These now remain the same as in the original data set, and the proportional age structure of each data set remains the same as the original. The only thing that changes is the distributions of lengths at age in each of the two data sets. In fact, with the Kimura data there are only ten pairs of data points that differ, as the data for the one-year-old fish are the same for both sexes. By having so few data points that differ, the randomization test is relatively limited in the number of likelihood ratio values it can produce randomly. The upper and lower limits and the relative distribution did not alter after the first four thousand replicates (Figure 9.13).

EXAMPLE BOX 9.6

The simplistic randomization algorithm can be introduced into Example Box 9.5 by adding some columns to the right of the calculations. Start in row 1. In one column put a series of =rand(); next to that put the female data pairs of age and length for containing ages 1 to 11.3, and under the female data put the male data for ages 1 to 11.3. Conduct the randomization as illustrated in Chapter 5. Sort the three new columns on the column of random number to randomize the data pairs between the two sexes. Then copy, as values, the randomized ages and associated lengths into columns B and C of Example Box 9.5. Repeat that at least one thousand times, conducting the likelihood ratio test each time, and recording the χ^2 value each time, perhaps into column K. Put =countif(\$K\$1:\$K\$1000,">="&M1)-countif(\$K\$1:\$K\$1000,">="&M2) in N2 and copy down to count the frequency of randomization χ^2 values into column N, using the bins defined in column M. Convert the cumulative χ^2 distribution into the standard distribution as shown in columns O and P. Plot columns P and Q against column L to mimic Figure 9.12. If you do more than one thousand replicates, be sure to alter columns N and Q.

L	M	N	O	P	Q
Average Class	0	Obs Freq	χ^2 Cumulative	χ^2	Prop Freq
=average(M1:M2)	1	197	=chidist(L2,3)	=1-O2	=N2/1000
=average(M2:M3)	2	173	=chidist(L3,3)	=O2-O3	=N3/1000
	2.5	144	0.4753	=O3-O4	=N4/1000
	3.5	73	0.3208	0.1545	0.073
	4.5	51	0.2123	0.1085	0.051

There are clearly some distortions away from the ideal χ^2 distribution for the test statistic. It illustrates that the reliance of the likelihood ratio test on the χ^2 statistic is only approximate, especially when the data are not as representative as one would wish them to be. When the data used are of better quality (Figure 9.1), then the match between the empirical distribution and the hypothetical ideal can become closer.

9.5 Concluding Remarks

The study of individual growth is fascinating for many people, and this can lead them to draw strong conclusions from the form of the equations

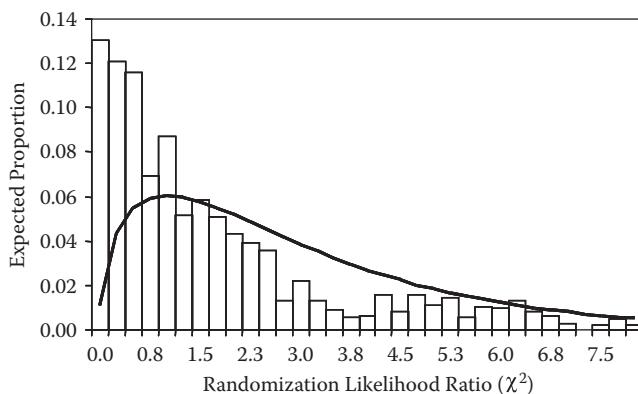
EXAMPLE BOX 9.7

A randomization of Kimura's (1980) Pacific hake data. The age data are set out into eleven columns with columns of random numbers (=rand()) beside them. Row 41 relates to female lengths and row 42 to males. The test first randomizes the row in which each data point sits. The age-structured data are reconstituted in columns A and B. How the age length data are reconstructed can vary, but in the end one must be able to copy and paste the values into the required cells (C14:C35) prior to conducting the likelihood ratio test (assumes the females aged 12.3 and 13.3 have been removed). Age 1 is unchanged. For the rest, one first has to randomize the lengths between sexes within ages. Of course, one would create a macro to do all of the separate sorts, first D41:E42 on column D, then F41:G42 on column F, and so on. Once completed, the data in columns A and B would have been randomized. These data are copied and pasted as values into the correct cells for the likelihood ratio test to proceed. All this is repeated at least one thousand times and the results compared with the original analysis (Figure 9.13).

	A	B	C	D	E	F	G
40	Age	Length	Age 1	Age 2	Age 2	Age 3.3	Age 3.3
41	1	=C41	15.4	=rand()	28.03	=rand()	41.18
42	2	=E41	15.4	=rand()	26.93	=rand()	42.23
43	3.3	=G41					
44	4.3	=I41					
45	5.3	=K41					
46	6.3	=M41					

used to describe the growth of their favourite organism. Hopefully, it has been shown that growth equations are principally just descriptions of how growth proceeds; they are not explanations for the process of growth. Just because the equation has an asymptote does not imply that the fish species has such a thing. The move toward reparameterized growth curves should assist in avoiding this error.

Comparisons between growth curves are difficult to conduct in a valid manner, and care must be exercised in any conclusions drawn from such tests. In many publications, the data presented constitute only a subsample of the true population. While this is better than no data, it should be recognized for what it is, which is a potentially nonrepresentative sample from the population. The difficulties of sampling marine populations are such that this will be a persistent problem for fisheries biologists. It is quite possible to obtain representative samples of what is caught by commercial fishers. This must be recognized, and its implications for comparisons of growth between different populations

**Figure 9.13**

A comparison of the relative proportion of different χ^2 values obtained from a randomized likelihood ratio test (open columns) with the expected proportions derived from the χ^2 distribution (solid curve). The test was of whether the growth curves for Pacific hake were coincident for males and females when the ages being compared were restricted to ages 1 to 11.3 (Table 9.2, Figure 9.12, Example Box 9.7). The randomization test, in this case, involved the randomization of length data within ages but between sexes. Despite the distortions below a ratio of 5.0, the cumulative distribution leads to similar decisions when comparing the two curves. The empirical distribution suggests that there is some evidence that the curves are not coincident (Example Box 9.7).

should be considered before such comparisons are made. The randomization test suggested in this chapter is complex to implement (but is possible even in Excel), but it permits one to conduct the test required while testing the validity of the assumption of the test statistic being equal to the χ^2 statistic. Where the representativeness of the data is at all suspect, it is recommended that some version of the randomization test be implemented. With a great deal of data this can be relatively slow, but it is a case of computer-intensive statistics answering the questions for which answers are needed.

Appendix 9.1: Derivation of the Fabens Version of the von Bertalanffy Growth Equation

This is the version that is used when attempting to estimate the growth curve parameters from tagging data. With such data, one tends to have the dates of tagging and recapture, the initial length at tagging, and the length at recapture. It would be unusual to have the age of the tagged organisms. Hence, the standard length-at-age formulation cannot be used. Instead, we need an equation that generates an expected length increment in terms of the von Bertalanffy parameters, the length at time t (not age t), and the

elapsed time, Δt . The standard formulation of the von Bertalanffy growth equation is given by Equation A9.1:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \quad (\text{A9.1})$$

where L_t is the length at time t , L_∞ is the average maximum length of individuals in the population, K is a growth rate parameter, t is the age of the animals, and t_0 is the hypothetical age at length zero. The brackets can be expanded thus:

$$L_t = L_\infty - L_\infty e^{-K(t-t_0)} \quad (\text{A9.2})$$

The expected length of an animal of age t after the passage of time, Δt , is given by Equation A9.3:

$$L_{t+\Delta t} = L_\infty - L_\infty e^{-K(t+\Delta t-t_0)} \quad (\text{A9.3})$$

Extract the Δt term from the exponential term:

$$L_{t+\Delta t} = L_\infty - L_\infty e^{-K(t-t_0)} e^{-K\Delta t} \quad (\text{A9.4})$$

The change in length over the time Δt is simply the difference between Equations A9.4 and A9.2:

$$\Delta L = L_{t+\Delta t} - L_t = L_\infty - L_\infty e^{-K(t-t_0)} e^{-K\Delta t} - L_\infty + L_\infty e^{-K(t-t_0)} \quad (\text{A9.5})$$

The order of the two exponential terms can be reversed:

$$\Delta L = L_\infty - L_\infty + L_\infty e^{-K(t-t_0)} - L_\infty e^{-K(t-t_0)} e^{-K\Delta t} \quad (\text{A9.6})$$

The $L_\infty e^{-K(t-t_0)}$ term can be extracted:

$$\Delta L = \left(L_\infty - L_\infty + L_\infty e^{-K(t-t_0)}\right) \left(1 - e^{-K\Delta t}\right) \quad (\text{A9.7})$$

The final change is to recognize that, in the first brackets, the second and third terms combined are equivalent to the standard von Bertalanffy equation (Equation A9.2):

$$\Delta L = \left(L_\infty - \left(L_\infty - L_\infty e^{-K(t-t_0)}\right)\right) \left(1 - e^{-K\Delta t}\right) \quad (\text{A9.8})$$

so we can substitute an L_t to leave the standard Fabens version of the von Bertalanffy growth equation:

$$\Delta L = (L_\infty - L_t) \left(1 - e^{-K\Delta t}\right) \quad (\text{A9.9})$$

Appendix 9.2: Derivation of the Maximum Likelihood Estimator for the von Bertalanffy Curve

Kimura (1980) starts by writing out the maximum likelihood estimator for a von Bertalanffy curve. We will do the same here, but with a few more details to ensure clarity of exposition. With the usual notation the length of the u th individual at age t_u is defined as

$$L_u = L_\infty \left(1 - e^{(-K(t_u - t_0))}\right) + \varepsilon_u \quad (\text{A9.10})$$

Let L_∞ be the, possibly hypothetical, asymptotic length; K the constant relating to the rate of growth; t_0 the hypothetical age at length zero; and the ε_u s the independent, additive, normal random errors ($N(0, \sigma^2)$). For brevity in the following equations, the expected values of L_u can be regarded simply as a function of L_∞ , K , and t_0 :

$$\hat{L}_u = f(L_\infty, K, t_0, t_u) \quad (\text{A9.11})$$

In the following description, the $f(L_\infty, K, t_0, t_u)$ referred to is the von Bertalanffy equation, but it should be noted that the argument holds irrespective of which growth or nonlinear equation is used and compared. It should be remembered that there is more than one way in which the von Bertalanffy curve can be estimated (e.g., to individual fish data, to mean lengths at age, with or without constant variance), and this will influence the form of the residuals used. Of course, one can only compare like with like. As Kimura states, the optimum way to fit a von Bertalanffy curve to a set of data is to use a maximum likelihood estimator, and because we would be using normal random errors, this means the likelihood function would derive from the normal distribution:

$$L(L_u | L_\infty, K, t_0, \sigma^2) = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-[L_u - f(L_\infty, K, t_0, t_u)]^2}{2\sigma^2}\right)} \quad (\text{A9.12})$$

which is the likelihood of the single observation L_u . This is simply the usual normal distribution equation with the observed and expected lengths at t_u as the numerator in the major term. Note that the term involving the observed and expected values is identical to that which would be used in a least squares estimation. Given N different observations of age and length, the overall likelihood \tilde{L} is obtained by multiplying N by the separate likelihoods:

$$L(\tilde{L} | L_\infty, K, t_0, \sigma^2) = \prod_{i=1}^{i=N} \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-[L_i - f(L_\infty, K, t_0, t_i)]^2}{2\sigma^2}\right)} \quad (\text{A9.13})$$

This can be simplified by noticing that if we raise the $1/[\sigma\sqrt{2\pi}]$ term to the power N , square it, and invert it, we can take it outside of the product and the remaining product can be converted to a summation term:

$$L(\tilde{L}|L_{\infty}, K, t_0, \sigma^2) = (2\pi\sigma^2)^{-N/2} \prod_{i=1}^N e^{\left(\frac{-(L_i - f(L_{\infty}, K, t_0, t_i))^2}{2\sigma^2}\right)} \quad (\text{A9.14})$$

Equation A9.14 is a form that can be used for making maximum likelihood comparisons. However, Equation A9.14 can be simplified by using log-likelihoods that serve to replace the product with a summation. This acts to reduce the chance of rounding errors occurring due to the very small likelihoods that can arise. The logarithmic transformation also has the effect of reducing the e term to its exponent. To make the impact of the transformation explicit, note that

$$\begin{aligned} \ln\left(\prod_{i=1}^N \frac{1}{\sqrt{2\pi\sigma^2}}\right) &= \ln\left(\left(\frac{1}{\sqrt{2\pi\sigma^2}}\right)^N\right) \\ &= \ln\left((2\pi\sigma^2)^{-N/2}\right) = -\frac{N}{2} \ln(2\pi\sigma^2) \end{aligned} \quad (\text{A9.15})$$

and that

$$\begin{aligned} \ln\left(\prod_{i=1}^N e^{\left(\frac{-(L_i - f(L_{\infty}, K, t_0, t_i))^2}{2\sigma^2}\right)}\right) &= \sum_{i=1}^N \frac{-(L_i - f(L_{\infty}, K, t_0, t_i))^2}{2\sigma^2} \\ &= \left(-\frac{1}{2\sigma^2} \sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2\right) \end{aligned} \quad (\text{A9.16})$$

We can then see that the log-likelihood estimator is the combination of Equations A9.15 and A9.16:

$$\text{LL}(\tilde{L}|L_{\infty}, K, t_0, \sigma^2) = -\frac{N}{2} \ln(2\pi\sigma^2) - \frac{\sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2}{2\sigma^2} \quad (\text{A9.17})$$

The maximum likelihood estimate of σ^2 , denoted $\hat{\sigma}_\phi^2$, is obtained from the log-likelihood estimator by calculating the partial derivative with respect to σ^2 , and equating that to zero. Using Equation A9.17,

$$\frac{\partial \text{LL}(\tilde{L}|L_\infty, K, t_0, \sigma_\phi^2)}{\partial \sigma_\phi^2} = -\frac{N}{2\sigma_\phi^2} + \frac{\sum_{i=1}^N [L_i - f(L_\infty, K, t_0, t_i)]^2}{2(\sigma_\phi^2)^2} = 0 \quad (\text{A9.18})$$

which leads by algebra to

$$\sum_{i=1}^N [L_i - f(L_\infty, K, t_0, t_i)]^2 = \frac{2(\sigma_\phi^2)^2 N}{2\sigma_\phi^2} \quad (\text{A9.19})$$

and, thereby,

$$\sigma_\phi^2 = \frac{\sum_{i=1}^N [L_i - f(L_\infty, K, t_0, t_i)]^2}{N} \quad (\text{A9.20})$$

The numerator in this relation is the sum of squared residuals; thus, the problem of maximum likelihood estimation for the von Bertalanffy curve is reduced to finding the least square estimates of L_∞ , K , and t_0 (Kimura, 1980). N is used instead of $N - 1$ because this is a maximum likelihood estimate of variance. The exact details of the structure of the numerator (the structure of the residuals) will be related to the form of the data available. As described in Chapter 3 on parameter estimation, this is a general property of the maximum likelihood estimator for any linear or nonlinear equations that are fitted using additive, normal random errors. The form of Equation A9.20 is that required for the determination of the likelihoods of different hypotheses to be compared. This is done by substituting the maximum likelihood estimate of the variance, i.e., Equation A9.20, into Equation A9.16, which is equivalent to Equation 9.30 in the main text:

$$\begin{aligned} L(\tilde{L}|L_\infty, K, t_0, \sigma^2) &= (2\pi\hat{\sigma}^2)^{-\frac{N}{2}} e^{\left(\frac{-\sum(L_i - f(L_\infty, K, t_0, t_i))^2}{2\sum(L_i - f(L_\infty, K, t_0, t_i))^2/N} \right)} \\ &= (2\pi\hat{\sigma}^2)^{-\frac{N}{2}} e^{\left(\frac{-N}{2} \right)} \end{aligned} \quad (\text{A9.21})$$

When comparing two or more curves using likelihood ratios, one first sets up the general model against which all alternative simplified hypotheses are to be tested. This statistic is determined by comparing the ratio of the two likelihoods (Kimura, 1980):

$$\Lambda = \frac{\left(2\pi\hat{\sigma}_{\omega}^2\right)^{-\frac{N}{2}} e^{\left(\frac{-N}{2}\right)}}{\left(2\pi\hat{\sigma}_{\Omega}^2\right)^{-\frac{N}{2}} e^{\left(\frac{-N}{2}\right)}} = \left(\frac{\hat{\sigma}_{\Omega}^2}{\hat{\sigma}_{\omega}^2}\right)^{\frac{N}{2}} \quad (\text{A9.22})$$

Kimura (1980) states that under the hypothesis that the linear constraint ω is true (e.g., the K_s are equal), the test statistic

$$-2\ln(\Lambda) = -2\ln\left(\left(\frac{\hat{\sigma}_{\Omega}^2}{\hat{\sigma}_{\omega}^2}\right)^{\frac{N}{2}}\right) = -2\frac{N}{2}\ln\left(\frac{\hat{\sigma}_{\Omega}^2}{\hat{\sigma}_{\omega}^2}\right) = -NL\ln\left(\frac{\hat{\sigma}_{\Omega}^2}{\hat{\sigma}_{\omega}^2}\right) \quad (\text{A9.23})$$

will have, asymptotically, a χ^2 distribution. This means that the larger the sample size, the more likely the conclusions are to be valid. However, it should be clear that Equation A9.22 is equivalent to Equation 9.21 (the N_s inside the brackets cancel to leave the RSS_x), leading to Equation 9.23.

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 recruitment 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

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.

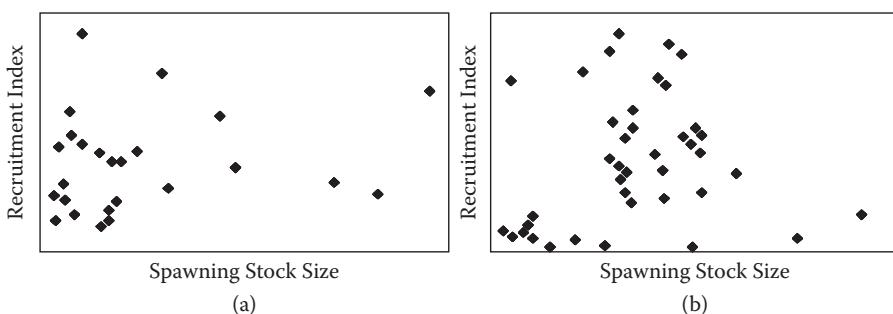
Growth overfishing is not difficult to detect. The data requirements for detection are a growth curve and an estimate of the age structure of the fishery. With this information, one could conduct a yield-per-recruit analysis and determine how close the fishery is to the theoretical optimum. There can 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 recruitment relationship

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).

**Figure 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 “good” Stock Recruitment Relationships

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

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 (dampening) 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 requirements—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

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 requirements—recruitment

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 intra-cohort competition for critical resources (Figure 10.2, Appendix 10.1):

$$R = \frac{S}{\alpha + \beta S} e^\epsilon \quad (10.1)$$

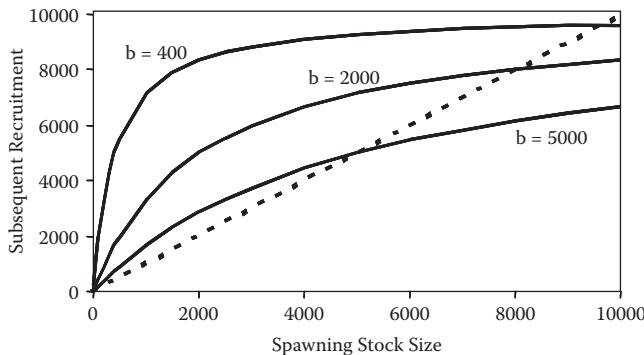


Figure 10.2

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

$$R = \frac{aS}{b+S} e^\varepsilon \quad (10.2)$$

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).

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	<i>a</i>	10000		10000
2	<i>b</i>	5000		2000
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
10	400	740.7		1666.7
11	500	909.1		2000.0
12	1000	1666.7		3333.3
13	1500	2307.7		4285.7
14	2000	2857.1		5000.0

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

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.

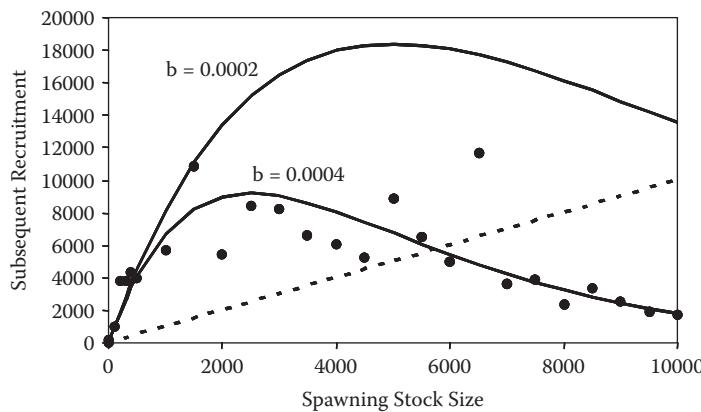
10.4 Ricker Model

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

$$R = aSe^{-bS}e^{\epsilon} \quad (10.3)$$

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.

**Figure 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
9	300		2419.6	2660.8
10	400		5203.6	3408.6
11	500		3240.6	4093.7

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:

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

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):

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

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).

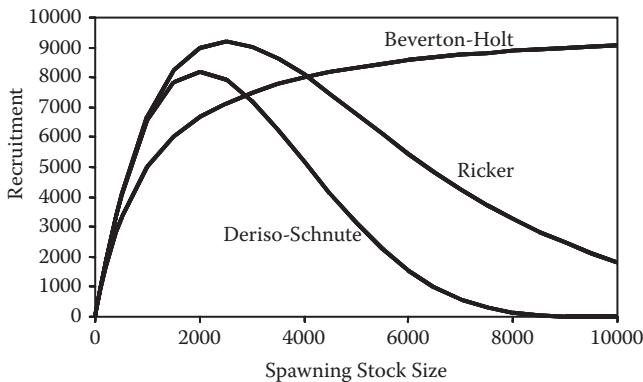
There are some mathematically unstable properties to the Deriso–Schnute model; consider the implication of $\gamma = 0$, which would lead to a mathematical singularity (divide by zero). The parameter limits should rather be $\gamma \rightarrow 0$, from either the negative or the positive direction.

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:

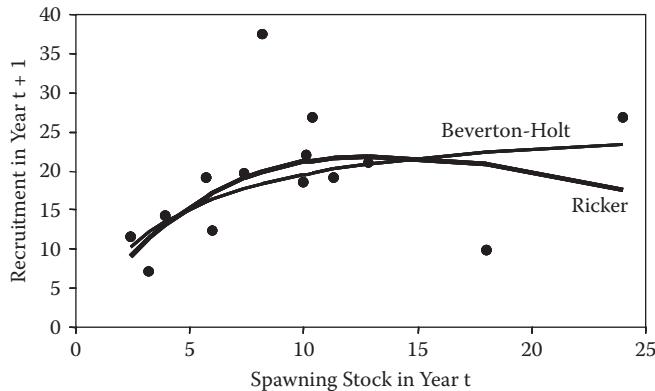
**Figure 10.4**

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		2307.69	4.883

**Figure 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).

$$S = S_1 S_2 S_3 \dots S_n \quad (10.6)$$

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:

$$\ln(S) = \sum \ln(S_i) \quad (10.7)$$

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

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

where the $N(0, \sigma_i^2)$ 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

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:

$$\ln\left(\frac{R}{S}\right) = \ln(a) - bS + \epsilon \quad (10.9)$$

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:

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.

$$\ln\left(\frac{R}{S}\right) = \ln(a) - \ln(b + S) + \epsilon \quad (10.10)$$

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 reality

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

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 relationships

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

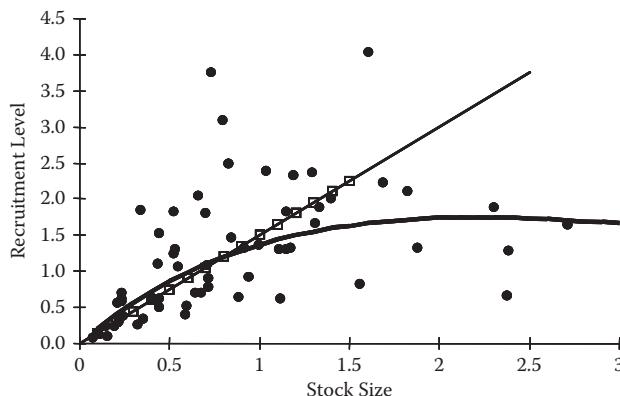
$$\hat{S} = Se^\epsilon \quad (10.11)$$

Similarly, for observing recruitment levels,

$$\hat{R} = Re^\epsilon \quad (10.12)$$

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.

**Figure 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_e 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:

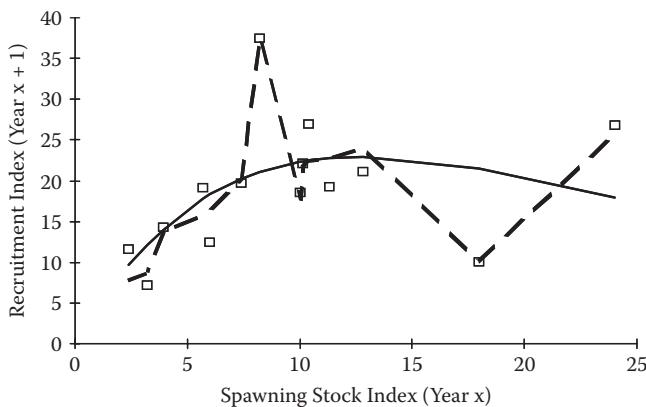
$$\ln(R_{t+1}) = \ln(a) + \ln(S_t) - (bS_t) + \varepsilon \quad (10.13)$$

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

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 ($R = 1.5 \times S$), 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*logninv(rand(),0,\$B\$1), and put =B5*logninv(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		0.400	0.803
9	0.2	0.3	0.200	0.473		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

**Figure 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)

$$R_{t+1} = aS_t e^{-bS_t} e^{cJ_t} e^{dF_t} e^{\epsilon} \quad (10.14)$$

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

$$\ln(R_{t+1}) = \ln(a) + \ln(S_t) - (bS_t) + (cJ_t) + (dF_t) + \epsilon \quad (10.15)$$

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.

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? ($AIC = n\ln(\sigma^2) + 2K$, where n is the number of observations =14, K is the number of parameters =2 or 4, and σ^2 is the sum of squared residuals (B5) divided by n , $=\sum\epsilon^2/n$.)

	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

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 recruitment relationships

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.

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 redefined

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,

$$R_0 = \frac{A_0}{\alpha + \beta A_0} \quad (10.16)$$

and, by definition,

$$hR_0 = \frac{0.2A_0}{\alpha + \beta 0.2A_0} \quad (10.17)$$

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):

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

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):

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

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 unfishered population given any constant recruitment level. The magnitude of A_0 will be scaled by the estimated virgin biomass, but its value, relative

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 R_0 is determined by a rearrangement of Equation 10.22. Notice that, by definition, A_0 should relate to mature biomass per recruit. However, unlike F7, the A_0 value in F6 is not divided by the number of recruits. If the constant recruitment level in B9 is altered from 1, A_0 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

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:

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

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

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

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 :

$$B_0 = R_0 \left(\sum_m n_{0,j} w_j \right) = R_0 A_0 \quad (10.22)$$

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,

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 B_0 , 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 B_0 value is altered. Clearly, given a B_0 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

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:

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

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 pre-recruit 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

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

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):

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

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.

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)

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

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 ,

$$N_t = N_0 e^{-pSt} e^{-qt} \quad (\text{A10.5})$$

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

$$R = fSe^{-pts} e^{-qt} \quad (\text{A10.6})$$

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

$$R = aSe^{-bs} \quad (\text{A10.7})$$

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

$$R_i = \frac{S_{i-1}}{\alpha + \beta S_{i-1}} \quad (\text{A10.8})$$

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

(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

$$R_0 = \frac{aB_0}{b + B_0} \quad (\text{A10.9})$$

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

$$hR_0 = \frac{0.2aB_0}{b + 0.2B_0} \quad (\text{A10.10})$$

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

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

Multiplying through and exchanging terms leads to

$$hb - 0.2b = 0.2B_0 - 0.2hB_0 \quad (\text{A10.12})$$

Multiplying both sides by 5 and simplifying leads to

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

and therefore

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

Reverting to Equation A10.9 we can see that

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

which multiplies through to become

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

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

$$a = \frac{R_0 - hR_0 + 5hR_0 - R_0}{5h - 1} = \frac{4hR_0}{5h - 1} \quad (\text{A10.17})$$

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

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

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 .

11

Surplus Production Models

11.1 Introduction

11.1.1 Stock Assessment Modelling Options

Surplus production models are the simplest analytical method available that provides for a full fish stock assessment. Described in the 1950s (Schaefer, 1954, 1957), they are relatively simple to apply, partly because they pool the overall effects of recruitment, growth, and mortality (all aspects of production) into a single production function. The stock is considered solely as undifferentiated biomass; that is, age and size structure, along with sexual and other differences, are ignored. The minimum data needed to estimate parameters for such models are time series of an index of relative abundance and of associated catch data. The index of stock abundance is most often catch-per-unit-effort, but could be some fishery-independent abundance index (e.g., from trawl surveys, acoustic surveys), or both could be used.

To conduct a formal stock assessment it is necessary, somehow, to model the dynamic behaviour of the exploited stock. One objective is to describe how the stock has responded to varied fishing pressure. By studying the impacts on a stock of different levels of fishing intensity it is possible to assess its productivity. If statistics are collected, the process of fishing a stock can provide information about how the stock responds to perturbations (the extra mortality, above natural mortality, imposed by fishing). If a reduction in the stock size cannot be detected reliably (i.e., catch rates or survey results are hyperstable relative to stock size), then stock assessment will be difficult, unreliable, or even impossible.

Given the necessary data, stock dynamics may be modelled using relatively simple surplus production models, also known as biomass dynamic models (Hilborn and Walters, 1992). These have already been briefly introduced in Chapter 2 and more in depth in Chapter 8. An alternative to surplus production models might be to use the more complex and data-demanding age-structured models (e.g., cohort analysis, virtual population analysis, or statistical catch-at-age; see Chapter 12; Quinn and Deriso, 1999). A less common alternative, which tends to be used with those species that are

difficult or impossible to age, would be to use a length- or size-based assessment model (see Chapter 13; Sullivan et al., 1990; Sullivan, 1992; Punt et al., 1997b). Because age-based models follow identifiable cohorts, they suffer from fewer problems than length-based models (given good data, which is not necessarily easy to obtain). Fisheries scientists usually try to collect the data required to produce an age-structured model in preference to the simpler data requirements of a surplus production model. However, Ludwig and Walters (1985, 1989) have shown that this is not always the best strategy, as surplus production models may produce answers just as useful and sometimes better for management than those produced by age-structured models, at a fraction of the cost. The usefulness of any model is directly related to how representative the available data are for a fished stock, and whether the index of relative abundance really does provide a clear index of relative stock size. If the index of relative abundance is informative but a set of ageing data are not necessarily representative, then we might expect a surplus production model to be more useful for the provision of management advice.

In a discussion of model selection, Hilborn and Walters (1992) suggest adopting a pragmatic approach. Assuming the data are available, they imply that one should apply both surplus production and age-structured methods, which, because they are fundamentally different, will provide a test of relative performance. They state: "If biomass dynamic methods provide a different answer than age-structured methods, then the scientist should try to understand why they are different and analyze the management implications of the different predictions, rather than concentrating on deciding which method is correct" (Hilborn and Walters, 1992, p. 329). Essentially, this is recommending that one examines whether the different available data streams (e.g., catch rates, age structure, length distributions, etc.) are internally consistent in their implications for the stock dynamics. Surplus production models, therefore, can be useful, and in this chapter we will be examining their use and properties in some detail.

Despite occasional recent use (Saila et al., 1979; Punt, 1994), the use of surplus production models went out of fashion in the 1980s. This was possibly because early on in their development it was necessary to assume the stocks being assessed were in equilibrium, and this often led to over optimistic conclusions that were not supportable in the longer term. Hilborn (1979) analyzed many such situations and demonstrated that the data used were often too homogeneous; they lacked contrast and hence were uninformative about the dynamics of the populations concerned. For the data to lack contrast means that fishing catch and effort information is only available for a limited range of stock abundance levels. However, a lack of contrast in this way can also lead to inconclusive results from age-structured models. There should also be concern that uncertainty (bias or lack of precision) in

the observed abundance estimates exacerbates this problem by reducing the information content of the data used in relation to the actual stock size.

11.1.2 Surplus Production

Surplus production, as the name implies, relates to the production from a stock beyond that required to replace losses due to natural mortality. Surplus production, in this case, is the sum of new recruitment and the growth of individuals already in the population minus those dying naturally. Early ideas on surplus production were discussed briefly in Chapter 2, when the logistic population model was introduced. Many of the intuitions regarding surplus production in fisheries derive from the logistic, and we will revisit them here in order that their strengths and weaknesses can be illustrated.

Schaefer (1954) first applied the logistic curve as a description of the production of Pacific halibut and later to eastern Pacific yellowfin tuna (Schaefer, 1957). Until then, no simple method of assessing a fished stock was available. Using the logistic as a foundation, Schaefer (1954, 1957) demonstrated a theoretical link between stock size and expected catch rates. This all related back to the expected level of surplus production produced by particular stock sizes. Thus, given a known stock biomass, the total production could be predicted thus:

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K} \right) \quad (11.1)$$

where B_t is the stock biomass at time t , r is the population growth rate, and K is the maximum population size for growth to be positive. Both r and K are

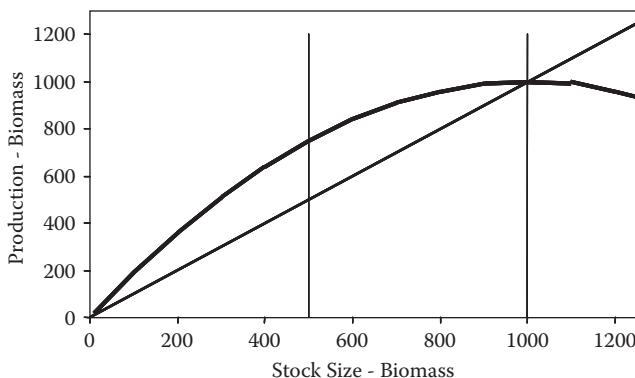


Figure 11.1

Production curve for the discrete logistic curve with $r = 1$ and $K = 1,000$. The right-hand vertical line indicates the carrying capacity, while the central line illustrates the point of maximum production at $K/2$. The diagonal line is the line of replacement (Example Box 11.1).

EXAMPLE BOX 11.1

Different production curves using an asymmetric production equation (Equation 11.2). Name cell B1 as r_i , cell B2 as K , and cell B3 as p . Extend the biomass levels in column A in steps of 100 down to 1,300 in row 20. Column B contains the equivalent of Equation 11.2, while column C indicates the production above replacement levels. Plot column B against A, adding a diagonal line as in Figure 11.1. Select D2:E3, copy, and paste special these data as a new series on the same graph to illustrate the stock size at maximum production. Using the solver, maximize C5 by modifying A5. This will automatically reposition the line of maximum production. Modify r and p to see their relative effects. When $p = 1$, the equation is equivalent to the simpler Schaefer equation. The effect of the asymmetry parameter is to make the effects of density-dependent regulation nonlinear (see Chapter 2).

	A	B	C	D	E
1	r_i		1		
2	K	1000		=A5	0
3	p	1		=D2	1200
4					
5	500	$=A5+(r_i/p)*A5*(1-(A5/K)^p)$	$=B5-A5$		
6	Biomass	Production	Surplus		
7	10	$=A7+(r_i/p)*A7*(1-(A7/K)^p)$	$=B7-A7$		
8	100	$=A8+(r_i/p)*A8*(1-(A8/K)^p)$	$=B8-A8$		
9	200	Copy down to row 20	Copy down		
10	300	510	210.0		
11	400	640	240.0		
12	500	750	250.0		

parameters of the logistic equation (see Chapter 2). A property of this equation is that the maximum production occurs at $K/2$ (Figure 11.1, Example Box 11.1).

Irrespective of the stock size, it should be possible to take the excess production, above the equilibrium line of replacement, and leave the stock in the condition it was in before production and harvesting (Figure 11.1). An obvious management strategy deriving from this theory would be to bring the stock to a size that would maximize the surplus production and hence the potential yield. This supports the intuition that it is necessary to fish a stock down in size so that it becomes more productive. There are, of course, many problems with this simplistic view of fisheries production. It assumes that the population is in equilibrium with all of its inputs and outputs (a poor assumption). It also implies that, while one may begin to fish inefficiently, one would not be able to crash a fish stock through overfishing (clearly a very poor assumption).

One problem that was easily solved was the fact that the logistic curve generated a symmetrical production curve, which was felt to be overly constraining. Pella and Tomlinson (1969) solved this by introducing an asymmetry term p , which modifies the logistic as follows:

$$B_{t+1} = B_t + \frac{r}{p} B_t \left(1 - \left(\frac{B_t}{K} \right)^p \right) \quad (11.2)$$

Equation 11.2 is from Polacheck et al. (1993) but is still referred to as the Pella–Tomlinson model because of the potential asymmetry in the production curve. This means that with this model, the stock size at which maximum production occurs is not necessarily at $K/2$ (Example Box 11.1).

11.2 Equilibrium Methods

Wherever possible, equilibrium methods should be avoided in fisheries assessments. With surplus production models, if a fish stock is in decline, then equilibrium methods consistently overestimate the sustainable yield. Their use in the past undoubtedly contributed to a number of major fishery collapses (Boerema and Gulland, 1973; Larkin, 1977). While equilibrium methods are no longer recommended, how they were used will be demonstrated so that the literature may be more easily understood.

Equilibrium methods are best described using the Schaefer or Pella–Tomlinson model of stock dynamics; this is just Equation 11.2 minus any catch:

$$B_{t+1} = B_t + \frac{r}{p} B_t \left(1 - \left(\frac{B_t}{K} \right)^p \right) - C_t \quad (11.3)$$

where C_t is the total catch in year t ; if $p = 1$, this is equivalent to the Schaefer model (Equation 11.1).

Equilibrium methods rely on the assumption that for each level of fishing effort there is an equilibrium sustainable yield. The stock is assumed to be at some equilibrium level of biomass producing a certain quantity of surplus production. If the fishing regime is changed, the stock is assumed to move immediately to a different stable biomass with its associated surplus production. This is patently wrong, as it ignores the difference in standing crop between the two different biomass levels and the time it takes the system to respond to changed conditions. At heart, the assumption is that the yield taken is always surplus production from a population in equilibrium. From this assumption it is possible to estimate the maximum sustainable yield (MSY) and the associated effort that will give rise to the MSY (E_{MSY}) given the

appropriate biomass (B_{MSY}). It is necessary to assume that the rate of change of biomass is zero for all years, i.e., $B_{t+1} = B_t = \text{constant}$, and that the relationship between the index of abundance and stock biomass (Equation 11.4) is exact. One requires a set of data to fit this model, and in the case of fisheries data, this is usually a time series of catch rates, I_t , from either fishery-independent surveys or commercial catch rates. In fact, because of the assumption of equilibrium, the time series nature of the data is ignored (another of the flaws in the methodology). Real contrast in the data is required (meaning that information on catch rates from widely different effort and stock size levels provide the best information for fitting fisheries models). To connect the population dynamics model (Equation 11.3) to reality, we connect the catch rates to the stock biomass, B , via q , the catchability coefficient (= proportion of the total stock taken by one unit of effort). Given that C is the catch and E is the associated effort, then

$$I = \frac{C}{E} = qB \quad (11.4)$$

Note the lack of any t subscripts. This is to emphasize that the time series nature of the data is ignored in this equilibrium method. At equilibrium, B_{t+1} will equal B_t , and so the year when each data point was generated becomes irrelevant. We can solve Equation 11.3 for C after assuming $B_{t+1} = B_t$, and after substituting

$$\frac{C}{(qE)} = B \quad (11.5)$$

for B in Equation 11.3 to give

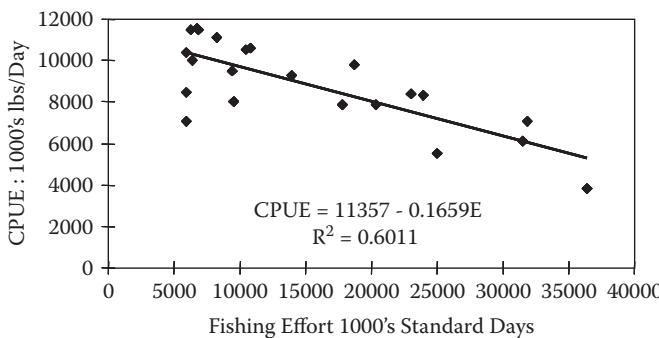
$$C = \frac{rC}{pqE} \left[1 - \left(\frac{C}{qEK} \right)^p \right] \quad (11.6)$$

which in turn can be solved for C/E or I (see Appendix 11.1), so that

$$I = \frac{C}{E} = \left(\left(qK \right)^p - \frac{pq^{p+1}K^p E}{r} \right)^{\frac{1}{p}} \quad (11.7)$$

If we reparameterize the constants, by defining $(qK)^p$ to be a new parameter a , and the second term, $(pq^{p+1}K^p)/r$, to be a new parameter b , this would lead to the form (Polacheck et al., 1993)

$$C/E = (a - bE)^{1/p} \quad (11.8)$$

**Figure 11.2**

Relationship between CPUE and effort for eastern tropical Pacific ocean yellowfin tuna. (Data from Schaefer, 1957; see Table 11.1.) Given $p = 1$ and the parameters a (11,357) and b (0.1659) permits the calculation of an equilibrium MY and E_{MSY} (194,366,258 lb and 34,228 class 4 clipper days, respectively).

and therefore, the equilibrium catch is

$$C = E(a - bE)^{1/p} \quad (11.9)$$

The sum of squares estimates of the parameters a , b , and p can then be obtained by minimizing the quantity

$$\sum (I - \hat{I})^2 \quad (11.10)$$

where $(C/E) = I$ is the observed catch rate from which we subtract the predicted or expected catch-per-unit-effort from the model (denoted by the \hat{I} symbol). If we assume $p = 1$, the model simplifies to the original Schaefer stock production model. Estimates for the two parameters a and b can then be obtained using standard linear regression techniques (Figure 11.2, Example Box 11.2).

Referring to Equation 11.8 makes it clear why plotting CPUE against effort was such a popular analytical tool in the past (Figure 11.2). When $p = 1$, $a = qK$, and $b = (q^2K)/r$, differentiating Equation 11.9 with respect to E gives

$$E_{MSY} = \frac{a}{-2b} = \frac{r}{2q}, \text{ if } p < 1 \quad E_{MSY} = \frac{a}{b(p+1)} = \frac{r}{q(p+1)} \quad (11.11)$$

Substituting Equation 11.11 into Equation 11.6 gives

$$MSY = \frac{(a/2)^2}{b} = \frac{rK}{4} \quad (11.12)$$

and if $p > 1$, then $a = (qK)^p$ and $b = (pq^{p+1}K^p)/r$, so that

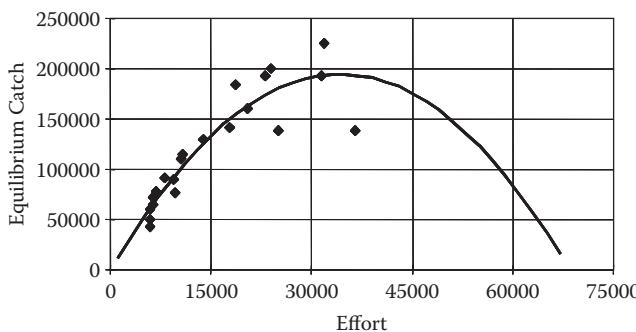
EXAMPLE BOX 11.2

An equilibrium surplus production model fitted to peruvian anchovy data (after Pitcher and Hart, 1982). The equations used in B4 and B5 are Equations 11.11 and 11.13. Select B1:C1, type =linest(D7:D15,C7:C15, true, true), then press <Ctrl><Shift><Enter> to enter the array function for linear regression (see Excel help). The gradient is in B1 and the intercept in C1. Column F is Equation 11.9, but for the Schaefer model (i.e., p = 1). Plot the regression data (columns D against C) and add a linear trend line, showing the equation (cf. Figure 11.2). In a separate graph, plot column F against E as a line. Add columns C vs. B as a scatter of points to mimic the type of graph shown in Figure 11.3 (select and copy them, select the graph, paste special as a new series, edit the series so that column C is on the x axis and column B on the y axis). Replace the data in columns A to C with the eastern Pacific yellowfin tuna data from Schaefer (1957), found in Table 11.1. Alter the Linest function in B1:C1, and the effort values in column E appropriately. Do the calculated values for a, b, MSY, and E_{MSY} match those given in Figure 11.2?

	A	B	C	D	E	F
1	Linest	-0.01409	0.782203			
2	a	=C1				
3	b	=B1				
4	MSY	=((B2/2)^2)/-B3				
5	Emsy	=B2/(-2*B3)				
6	Year	Catch	Effort	CPUE	E	Equil C
7	60	6.00	10.1	0.594	2	=(\$B\$2+\$B\$3*E7)*E7
8	61	8.40	12.0	0.700	6	=(\$B\$2+\$B\$3*E8)*E8
9	62	10.10	21.0	0.481	10	6.413
10	63	10.60	24.0	0.442	14	8.188
11	64	11.00	28.0	0.393	18	9.513
12	65	9.00	25.0	0.360	22	10.387
13	66	9.20	22.0	0.418	26	10.809
14	67	10.75	21.5	0.500	30	10.781
15	70	12.70	30.0	0.423	34	10.301

$$MSY = \frac{p}{b} \left(\frac{a}{p+1} \right)^{\frac{p+1}{p}} = \frac{rK}{\left(p+1 \right)^{\frac{(p+1)}{p}}} \quad (11.13)$$

The best way to visualize these analyses is to plot the expected equilibrium catches and the observed catches (as in Figure 11.3) against the imposed effort. The outcome of this equilibrium analysis can appear dangerously

**Figure 11.3**

Equilibrium analysis of eastern tropical Pacific ocean yellowfin tuna. (Data from Schaefer, 1957.) The expected equilibrium catches for particular effort levels (thousands of class 4 clipper days) are represented by the curve's solid line. The observed catch levels (thousands of pounds) are the scattered points. The maximum sustainable yield (MSY) is the top of the curve, and the optimum effort (E_{MSY}) is directly below the MSY peak of equilibrium catch ($C = (a - bE)E$; see Example Box 11.2).

TABLE 11.1

Total Eastern Pacific Catch of Yellowfin Tuna, Catch per Standard Day Fishing, and Calculated Relative Fishing Effort

Year	Catch	Effort	CPUE	Year	Catch	Effort	CPUE
1934	60,913	5,879	10,361	1945	89,194	9,377	9,512
1935	72,294	6,295	11,484	1946	129,701	13,958	9,292
1936	78,353	6,771	11,572	1947	160,134	20,381	7,857
1937	91,522	8,233	11,116	1948	200,340	23,984	8,353
1938	78,288	6,830	11,462	1949	192,458	23,013	8,363
1939	110,417	10,488	10,528	1950	224,810	31,856	7,057
1940	114,590	10,801	10,609	1951	183,685	18,726	9,809
1941	76,841	9,584	80,18	1952	192,234	31,529	6,097
1942	41,965	5,961	7,040	1953	138,918	36,423	3,814
1943	50,058	5,930	8,441	1954	138,623	24,995	5,546
1944	64,094	6,397	10,019	1955	140,581	17,806	7,895

Source: Data from Schaefer, M. B., *Bulletin, Inter-American Tropical Tuna Commission*, 2, 247–85, 1957.

Note: Catch is in thousands of pounds, effort is in standardized class 4 clipper days, and catch rates are in pounds per class 4 clipper day. These data are used in Example Boxes 11.2 and 11.3 and are illustrated in Figures 11.3 and 11.5.

convincing, but this is to be resisted, as it usually overestimates the safe catch levels (Example Box 11.2). Such analyses can be conducted with remarkable speed, but these should be considered examples where the approximations and assumptions used (especially the assumption of equilibrium) mean the analyses cannot be used validly.

Surplus production models no longer need the assumption of equilibrium to enable them to be fitted to fisheries data. The nonequilibrium approach to fitting the models means they are better able to represent the dynamics of fished populations. Nevertheless, the inherent simplicity of surplus production models means there are limits to how far their development may be taken. We will investigate some recent developments after a discussion of the different methods that can be used to fit nonequilibrium surplus production models.

11.3 Surplus Production Models

11.3.1 Russell's Formulation

Surplus production models relate directly to Russell's (1931) verbal formulation of stock dynamics and, in difference equation or discrete form, have the general structure

$$B_{t+1} = B_t + f(B_t) - C_t \quad (11.14)$$

with

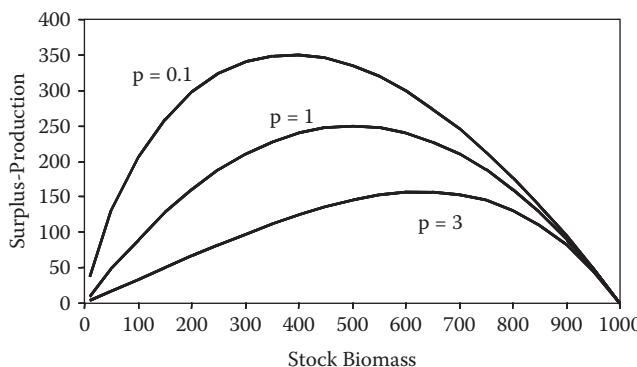
$$\hat{I}_t = \frac{C_t}{E_t} = qB_t \quad (11.15)$$

where B_{t+1} is the exploitable biomass at the end of year t or the beginning of year $t+1$, B_t is the exploitable biomass at the start of year t , $f(B_t)$ is the production of biomass, as a function of biomass at the start of year t , C_t is the biomass caught during year t , I_t is the an index of relative abundance for year t , and q is the catchability coefficient. The $\hat{\cdot}$ symbol above a parameter denotes a value estimated from the model. The function describing the production of biomass in any year can take many forms; here are three that all derive from a form of the logistic equation. This is especially clear in the Schaefer model:

$$f(B_t) = rB_t \left(1 - \frac{B_t}{K}\right) \quad \text{classic Schaefer (1954) form} \quad (11.16)$$

$$f(B_t) = Ln(K)rB_t \left[1 - \left(\frac{Ln(B_t)}{Ln(K)}\right)\right] \quad \text{modified Fox (1970) form} \quad (11.17)$$

$$f(B_t) = \frac{r}{p} B_t \left[1 - \left(\frac{B_t}{K}\right)^p\right] \quad \text{modified Pella and Tomlinson (1969)} \quad (11.18)$$

**Figure 11.4**

Influence of the parameter p (with values 0.1, 1, and 3) on the discrete Pella–Tomlinson version of the biomass dynamic model. When $p = 1$, the equation is equivalent to the Schaefer model, and thus has a symmetrical production curve around the midpoint in biomass. Values of $p < 1$ skew the curve to the left and values >1 skew it to the right.

where r is a growth rate parameter (derived from the intrinsic rate of natural increase), and K is the virgin biomass (B_0) or the average biomass level prior to exploitation (derived from the idea of carrying capacity). If $p = 1$, then Equation 11.18 is equivalent to Equation 11.16. As p tends to zero, Equation 11.18 becomes equal to Equation 11.17. The usual manner of writing the Fox model is without the $\ln(K)$ at the front of the production equation (Equation 11.17). However, without its inclusion, while the two equations take on an equivalent form as p tends to zero, they do not produce exactly the same value for production. The particular form of Equation 11.18 was given by Polacheck et al. (1993), and alternative forms for the Pella–Tomlinson model exist (the most common alternative using an asymmetry parameter $m - 1$ instead of the p parameter). The key property of the Pella–Tomlinson model is its ability to express an asymmetric production curve with potentially many shapes.

The linear density-dependent effects built into the logistic Schaefer model become nonlinear with the addition of the p parameter, leading to the asymmetry of the production curve (Figure 11.4). Note that by modifying p the absolute level of production alters (Figure 11.4, Example Box 11.1), which implies that adding the asymmetry term has altered the interpretation that can be placed upon the other parameters. For example, as p decreases below a value of 1, and all other parameters do not change, the absolute production increases. This increase could be offset during the model fitting process by a decrease in the value of r . The point is that it is not possible to directly compare the parameter values of the three different models (although if the $\ln(K)$ term is included in the Fox model, then Equations 11.17 and 11.18 are directly comparable if p is very close to zero).

Equation 11.15 captures how the expectations from the model are compared against reality. The equation constitutes a very strong assumption, which is that catch rates are linearly related to stock biomass. The catchability coefficient, q , is often referred to as a nuisance parameter whose job is simply one of scaling the modelled stock biomass to match the trends in catch rates. Assessment becomes very difficult without some time series of relative abundance estimates. Surplus production methods tend to be used when large amounts of good quality data are not available. The assumption that catch rates relate to the stock biomass must be considered carefully when such analyses are conducted.

11.3.2 Alternative Fitting Methodology

In the development of fisheries methods a number of contrasting algorithms or strategies have been used for fitting stock production models to observed data on catches and catch rates. These methods differ with regard to whether or not they assume the population to be in equilibrium with the exploitation rate. They also differ with regard to where the residual errors are attributed between the model and the data.

The earliest method used two estimated equilibrium management targets, the MSY and E_{MSY} . For this method to be valid, the fishery was assumed to be in equilibrium. It was recognized, however, that fish stocks are rarely in equilibrium. An early solution to this problem was to use a weighted average of a number of years' fishing effort for each year instead of just observed effort for that year. Unfortunately, if this is done, the interpretation of the relationship between catch and effort becomes problematical. While effort averaging certainly improved the analyses in a limited way, it is an *ad hoc* solution that can be thought of as spreading an invalid assumption of equilibrium across a number of years. Here, it will not be pursued further.

Process error estimators were then developed, which assumed all observations, such as catch rates, were made without error (Equation 11.15 was exact or without error), and that all error was in the equation describing changes in population size (Equation 11.14 was imprecise). Thus, in any one year, to obtain a close match between the predictions of the model and the data, residual errors would need to be added to some or all of the parameters (Polacheck et al., 1993).

Alternatively, observation error estimators have been developed that assume all residual errors are in the catch rate or biomass observations (Equation 11.15), and that the equation describing the time series of biomass values (Equation 11.14) is deterministic and without error. In this chapter we will focus our efforts on this method of fitting surplus production models.

More recently, attempts have been made to create estimators that use both forms of error, most notably using a technique borrowed from control engineering termed the Kalman filter (Meinhold and Singpurwalla, 1983). However, currently, there are no generally available methods that can make

estimates where both types of error are being modelled without constraints (Quinn and Deriso, 1999).

Process errors assume that the observations used to fit the model are made without error; thus, all error occurs in the predicted change in population size (i.e., observations are made without error, but the model does not exactly mimic reality). Observation error is the inverse of process error, i.e., $B_{t+1} = \hat{B}_{t+1}$, with no error term (once again, the $\hat{\cdot}$, or caret symbol, denotes the expected or estimated parameter value), so that observations are made with error but the model exactly describes the population dynamics. Observation errors imply

$$C_t/E_t = qB_t e^{\varepsilon_t}$$

where C_t is catch and E_t is the fishing effort in year t . The term e^{ε} represents log-normal residual errors. Alternatively, in this model process errors would imply

$$r = \hat{r} + \varepsilon_r \quad \text{or} \quad K = \hat{K} + \varepsilon_K$$

However, the form of the residual errors here could be other than normally distributed.

The approach of observation error estimation is the method now most commonly recommended because simulations have demonstrated that it can more closely reflect the circumstances underlying the observations (Hilborn and Walters, 1992; Polacheck et al., 1993; Punt, 1990, 1995). Generally, if both types of error are present (seems generally likely), then so far it has been found to be more efficient to assume only the presence of observation error (Ludwig and Walters, 1989). There has been some work attempting to model some restricted types of fisheries data using both kinds of residual error via the Kalman filter (Sullivan, 1992; Reed and Simons, 1996). But this remains generally intractable. One way in which both types of error could be modelled would arise if there were an estimate of the ratio of the respective variances of the two processes (Ludwig et al., 1988). In practice, it is extremely difficult to work with both forms of error in an estimation model.

11.4 Observation Error Estimates

11.4.1 Outline of Method

If we assume that the equation describing the stock dynamics is deterministic (i.e., zero process residual error), then all residual errors are assumed to occur in the relationship between stock biomass and the index of relative abundance. The stock biomass time series can therefore be estimated

by projecting forward the initial biomass, B_0 , at the start of the catch series, using the selected biomass dynamic model and the historic annual catches (Example Box 11.3, Equation 11.19):

$$B_{t+1} = B_t + \frac{r}{p} B_t \left(1 - \left(\frac{B_t}{K} \right)^p \right) - C_t \quad (11.19)$$

Using Equation 11.19, and given the observed C_t s, the parameters r , K , and p , and an initial starting biomass B_0 , a series of expected B_t s, can be produced. In the following example, the asymmetry parameter p is set to 1, so the model simplifies to the Schaefer model. The discrete version of the surplus production model is used to produce the predicted series of B_t s, and these, given a q value, are used to produce a predicted series of CPUE values ($C/E = qB$; see Equation 11.20) that can be compared with those observed, using either maximum likelihood or least squares.

In summary, one makes predictions about the deterministic trajectory of the system from a hypothesized set of parameters and initial starting conditions, and then compares the observed values with the predictions (Figure 11.5). Connecting the deterministic series of biomass levels to observed catch rates is implemented using

$$\hat{I}_t = \frac{\hat{C}_t}{E_t} = qB_t e^\varepsilon \quad \text{or} \quad \hat{I}_t = q \frac{(B_{t+1} + B_t)}{2} e^\varepsilon \quad (11.20)$$

where the e^ε indicates that the residual errors are assumed to be lognormally distributed (a standard assumption with catch rate data). Taking the average of two biomass levels relates to using the average biomass at the start and end of year t so that the catches relate to the biomass more realistically. In effect, the expected catch rates are related to midyear biomass. In the process of fitting the observed data to the model, it will be necessary to log-transform both the observed and the predicted catch rates to normalize the residual errors.

11.4.2 in Theory and Practice

Assuming that the error in Equation 11.20 is multiplicative and lognormal with a constant variance (i.e., $I_t = qB_t e^\varepsilon$, where $\varepsilon = N(0; \sigma^2)$), the estimates of the model parameters (B_0 , r , q , and K) are obtained by maximizing the appropriate likelihood function:

$$L(\text{data} | B_0, r, K, q) = \prod_t \frac{1}{I_t \sqrt{2\pi\hat{\sigma}}} e^{-\frac{(\ln I_t - \ln \hat{I}_t)^2}{2\hat{\sigma}^2}} \quad (11.21)$$

EXAMPLE BOX 11.3

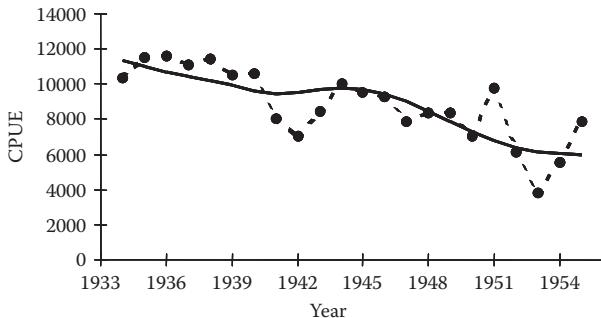
A nonequilibrium Schaefer surplus production model fitted to Schaefer's (1957) original eastern Pacific yellowfin tuna data (Table 11.1). Copy the data into columns A to C, down to row 31. In D11 put Equation 11.19 as =max(D10+\$B\$1*D10*(1-(D10/\$B\$2))-B11,100). The max function ensures that the stock biomass cannot go extinct when using the solver. In E10 put =((D10+D11)/2)*\$B\$4, the midyear biomass in a given year multiplied by the estimate of q (in E31 put =D31*\$B\$4). Put =(C10-E10)^2 into F10 to obtain the squared normal residual errors. In G10 put =Ln(C10/D10), to generate the contributions to the q estimate. In H10 put =(Ln(C10)-Ln(E10))^2 to generate the residuals for lognormal random errors. Select D11:H11 and copy down to row 31. Complete the worksheet by putting =exp(average(\$G\$10:\$G\$31)) into B4 to calculate the closed form of q (see Equation 11.23). Count the number of observations by putting =count(C10:C31) into B6, and finally, to estimate the standard deviation of the residuals, put =sqrt(sum(H10:H31)/B6) into B7 (see Equation 11.22). Plot columns C and E against column A (use different colours). The parameters shown are close to the initial optimum. Use the solver to maximize the log-likelihood in E7 by changing B1:B3. Compare the results obtained by minimizing the sum of squared residuals in E8. They should be the same. How different are the answers when you minimize E6, which contains normal random residual errors instead of lognormal? How stable is the answer? Start the model from different starting points (e.g., r_i , K_i , $B_0 = 0.05, 1,500,000, 1,500,000$; or $0.5, 3,500,000, 1,000,000$). In the solver options, turn on automatic scaling and increase the required precision and decrease the convergence limits. Try removing the max function from column D. Try estimating q directly (just vary the values of B1:B4 when using the solver). Put the p parameter into B5. Alter column D to match Equation 11.19 and E3 and E4 to match Equations 11.11 and 11.12. How does permitting an asymmetric production curve affect the results? Are the results biologically sensible?

	A	B	C	D	E	F	G	H
1	r_i	0.17830		Bcurr	=D31			
2	K_i	2525547		Bcurr/K	=E1/B2			
3	B_0	2748326		MSY	=B1*B2/4			
4	q_i	0.00436		Emsy	=B1/(2*B4)			
5	p	1		FFinal	=B31/E31			
6	n	22		SSQ_I	=sum(F10:F31)			
7	Sigma	0.1726		LogLik	=-(B6/2)*(Ln(2*pi())+2*Ln(B7)+1)			

continued

EXAMPLE BOX 11.3 (continued)

	A	B	C	D	E	F	G	H
8				SSQ_Ln(I) =sum(H11:H32)				
9	Year	Catch	O(I)	ExpectB	E(I)	SSQ_I	Expt_q	Ln(I-I)
10	1934	60913	10361	=\$B\$3	11763.4	1966371.8	-5.542	0.0161
11	1935	72294	11484	2549745	11330.2	23763.4	-5.403	0.0002
12	1936	78353	11572	2467036	10943.8	394501.1	-5.362	0.0031
13	1937	91522	11116	2385705	10585.9	281500.8	-5.369	0.0024


Figure 11.5

Observed index of relative abundance (dotted line) vs. year, with best fit initial predicted index of relative abundance superimposed (smooth line) for the eastern tropical Pacific ocean yellowfin tuna. (Data from Schaefer, 1957; Table 11.1). The model fitted is the Schaefer surplus production model (Equation 11.19 with $p = 1$). Because the index of relative abundance (CPUE) is only qB_t , where q is a constant, the thick line is also a representation of the time series of predicted stock biomass levels (Example Box 11.3).

where $L(\text{data} | B_0, r, K, q)$ is the likelihood of the data given the parameters, the product is overall years (t) for which CPUE data are available, and (Neter et al., 1996, p. 34)

$$\hat{\sigma}^2 = \sum_t \frac{(\ln I_t - \ln \hat{I}_t)^2}{n} \quad (11.22)$$

and n is the number of observations (maximum likelihood estimate of the variance uses n rather than $n - 1$). An estimate of q , which maximizes Equation 11.21, is given by the geometric average of the time series of individual q estimates (see Appendix 11.2 for the derivation); thus,

$$\hat{q} = e^{\frac{1}{n} \sum \ln \left(\frac{I_t}{\hat{B}_t} \right)} \quad (11.23)$$

Alternatively, one could estimate the q value directly using the solver, but the value thus determined should differ from that derived from Equation 11.23 by only a small fraction. Such closed-form estimates, as in Equation 11.23, are valuable because, on average, the model tends to be quicker to fit and more robust when it has fewer directly estimated parameters.

With a model as indicated in Equations 11.19, 11.20, and 11.23 (with $p = 1$), the actual fitting process would be as follows: given a time series of catches (C_t), and guesses at r , K , and B_0 , the model produces a series of expected biomass values, \hat{B}_t . Then, given a catchability coefficient q (see Equation 11.23), the \hat{B}_t are used to produce a series of expected catch rates $\hat{C}/E = \hat{I} = q\hat{B}_t$ (Equation 11.20), and these are compared with the observed catch rates (Equation 11.21; in fact, Equation 11.25).

There is more than one method available for determining B_0 . It can be set equal to K (i.e., $B_0/K = 1$), or it can be estimated by $\hat{B}_0 = \hat{I}_0/q$ (forces the first point of the fitted curve to coincide with the first point of abundance index, one degree of freedom is lost), or B_0 can be estimated directly as a separate parameter. These alternatives can give very different results, and which method is used might depend upon whether fishing had occurred before records of catch were available. Punt (1990) found, using simulations, that even with situations where B_0/K was substantially different from unity, estimation performance was better when B_0/K was set at unity than when attempts were made to estimate B_0 separately. However, there are situations, especially in fisheries for shorter-lived, more recruitment-driven species, where a direct estimation of B_0 tends to be more efficient (Haddon, 1998).

In a similar example to the one illustrated here, Hilborn and Walters (1992) used a least squares criterion of fit using normal random residual errors between the observed CPUE, I_t , and the expected CPUE, \hat{I}_t .

$$\sum \left(\frac{C_t}{E_t} - \frac{\hat{C}_t}{E_t} \right)^2 = \sum (I_t - \hat{I}_t)^2 \quad (11.24)$$

An obvious alternative is to use a log-likelihood approach (Polacheck et al., 1993). In addition, instead of using normal random errors (implied in Equation 11.24), one generally uses lognormal residuals because we are dealing with catch rate data. Equation 11.21 can be converted to a log-likelihood and greatly simplified (see Appendix 11.3 and Example Box 11.3) so that

$$LL = -\frac{n}{2} \left(\ln(2\pi) + 2\ln(\hat{\sigma}) + 1 \right) \quad (11.25)$$

where LL refers to log-likelihood, n is the number of observed catch rates, and σ is the square root of Equation 11.22.

11.4.3 Model Outputs

A general objective of fisheries modelling is to generate outputs in terms useful to fisheries management. There are many outputs possible from most fishery models, but focus tends to be placed on those that can act as fishery performance measures or that inform about selected limit thresholds. The two classical performance measures that derive from surplus production modelling are the maximum sustainable yield (MSY) and the effort, E_{MSY} , that, given $B_{MSY} = K/2$ (for the logistic), should lead to the MSY (as in Equations 11.11 and 11.13):

$$E_{MSY} = \frac{r}{2q} \quad MSY = \frac{rK}{4} \quad (11.26)$$

In addition, we could consider such outputs as the current estimated biomass, the ratio of the current biomass with K or B_0 , and possibly include an estimate of fishing mortality rate, F (see Example Box 11.3). A number of alternative methods exist for calculating various model parameters and outputs.

The instantaneous fishing mortality rate can be estimated in two ways. The first is as a conversion of the annual exploitation rate (catch/biomass) to an instantaneous fishing mortality rate:

$$F_t = -Ln\left(1 - \frac{C_t}{(B_t + B_{t+1})/2}\right) \quad (11.27)$$

where F_t is the instantaneous fishing mortality rate in year t , C_t is the catch in year t , and $(B_t + B_{t+1})/2$ is the midyear biomass for year t (as in Equation 11.20 and Example Box 11.3). Alternatively, we could use the standard catch equation so that instantaneous fishing mortality relates to expected effort and the catchability coefficient, q :

$$F_t = qE_t = q \frac{C_t}{C_t/E_t} = q \frac{C_t}{\hat{I}_t} \quad (11.28)$$

But in this case the F_t is an annual harvest rate rather than an instantaneous rate (this relates to when the standard catch equation was a differential equation rather than a difference equation). Given Equation 11.28, and that $E_{MSY} = r/2q$ (from Equation 11.26), we can see that the harvest rate at MSY, F_{MSY} , would be

$$F_{MSY} = qE_{MSY} = q \frac{r}{2q} = \frac{r}{2} \quad (11.29)$$

Prager (1994) described many extensions to standard surplus production models, and one of these was to point out that $F_{0.1}$ (see Chapter 2) is

approximately 90% of F_{MSY} . Thus, it would be simple to include both of these potential management targets in the outputs from the model.

The real-world interpretation of management targets is not always straightforward. An equilibrium is now assumed to be unlikely in a fished population, so the interpretation of MSY is more like an average, long-term expected potential yield if the stock is fished optimally. The E_{MSY} is only the effort that should give rise to the MSY if the stock biomass is at B_{MSY} , the biomass needed to generate the maximum surplus production. Clearly, a fishery could be managed by limiting effort to E_{MSY} , but if the stock biomass is depleted, then the average long-term yield will not result. In fact, the E_{MSY} effort level may be too high to permit stock rebuilding.

Few of these potential management outputs are of value without some idea of the uncertainty around their values. It would also be very useful to be able to project the models into the future to provide a risk assessment of alternative management strategies.

11.5 Beyond Simple Models

11.5.1 introduction

Prager (1994) described and reviewed a range of extensions to simple surplus production models. He gave detailed descriptions of some of the fundamental equations relating to the population dynamics and to some of the management targets ($F_{0,1}$ has already been mentioned). He also discussed the handling of multiple data series and missing data, along with suggestions for dealing with changing catchability through time. He briefly described how to estimate the uncertainty around parameters using bootstrap procedures, and an algorithm, that was an extension of the bootstrap, for using surplus production models in projections. Projections are necessary for conducting risk assessments of different proposed management options.

Prager's (1994) paper is recommended reading, but we will still consider some of these subjects here so as to give more detail and make further extensions. We will focus on the more general surplus production model suggested first by Pella-Tomlinson but developed by Polacheck et al. (1993) (Equation 11.19 and following equations, but with p constrained to =0.00000001 instead of =1; Sections 11.3.1 and 11.4.1).

When $p = 1$ the Pella-Tomlinson model is algebraically identical to the Schaefer model. This fact, and its symmetrical production curve, has even led to suggestions that the simpler Schaefer model no longer be used (Maunder, 2003). However, as Prager (2003) argues well, it is often difficult to generate an acceptable estimate of the asymmetry parameter, p , and when data are limited or of marginal quality, the well-known and simpler model has

advantages (the Schaefer model is simpler because it implies linear density dependence). One of Prager's (2003, p. 154) conclusions was: "For any stock analyzed with a production model, it will be useful to conduct sensitivity analyses of management recommendations to assumptions on model shape." This is eminently sensible advice and reflects the fact that any model is likely to have assumptions that may not be met by a natural population. Irrespective of how well a model fits to available data, it remains only an abstraction of reality and it is best to be suspicious of its behaviour. Such suspicions may be alleviated through well-chosen sensitivity tests.

11.5.2 Changes in Catchability

One major assumption in the use of surplus production models is that the relationship between catch rates and stock biomass is constant ($C/E = qB$). This relationship implies that the catchability coefficient, q , remains constant through time. In fact, because fishers tend to be good at what they do, there tend to be continual improvements to fishing gear and fishing practices such that the effectiveness of each unit of effort increases through time. This effort creep is often considered in terms of changes in fishing power brought about, for example, by introducing new gear such as radar, coloured echo sounders, and Global Positioning System (GPS) receivers and plotters (Brown et al., 1995). By using general linear models to compare the catch rates of vessels that had adopted GPS and related plotters in different years, Robins et al. (1998) found that vessels in the Australian Northern Prawn Fishery obtained a 4% advantage with the introduction of GPS, and this figure grew to 7% if a plotter was also installed. Over the subsequent two years there were further improvements of between 2 and 3% per year (i.e., learning was a factor). Overall, once the complete fleet had adopted the technology (a matter of three to four years), the increase in fishing power accorded to this alteration alone was 12%. Multiplying the units of effort by 1.12 is a possibility, but such an approach would make the units of effort confusing. For example, if effort were in hours fished, then it would become necessary to refer to effort as hours standardized relative to some reference year (100 hours in 1998 might be 112 hours in 1994). Instead, perhaps the simplest interpretation to place on increases in fishing power is to consider them as changes to the catchability coefficient. In numerical terms, because $C = qEB$, it does not matter whether the E or the q changes.

Clearly, the assumption that q is a constant is rather an oversimplification. Prager (1994) pointed out that if it were suspected that the catchability coefficient had changed rather suddenly, then the nonequilibrium model could be applied as if there were two time series of catches and catch rates. The same parameters (r , K , B_0 , and perhaps p) would apply to each time series and would be fitted together. However, there would need to be as many q parameters as there were separate time series, and these would need to be fitted separately. Alternatively, two or more sets of closed-form calculations could be produced, but if the number of observations in each time series becomes very

low, then the closed-form calculations may become suboptimal and direct estimation might be more robust. Each suspected major change in catchability would entail the addition of a further parameter. Naturally, as the number of parameters increases, one would expect the quality of model fit to improve. Prager (1994) suggests using an *F* ratio test to compare the simple models with the more complex. This would be equivalent to using a likelihood ratio test.

Prager (1994) also considers a linear increase in catchability through time. This would be equivalent to a constant absolute improvement each year:

$$q_t = q_0 + q_{\text{add}} \times t \quad (11.30)$$

where the *t* subscript denotes the particular year, 0 to $n - 1$, q_0 is the catchability in the first year, and q_{add} is the constant increase added to the catchability each year. Prager (1994) suggested this could be parameterized by estimating the first and last year's *q* and interpolating for the intervening years. Perhaps this would be most easily implemented by using Equation 11.30, directly estimating the q_0 for the first year and then the q_{add} that provides the best fit. Alternatively, a closed-form estimate of q_0 and q_{add} can be generated by implementing the appropriate regression analysis (see Appendix 11.2 for the derivation).

In some fisheries it has been suggested that there is a constant proportional increase in catchability each year. For example, in the Australian northern tiger prawn fishery the annual proportional increase in the effectiveness of effort previously accepted by managers and industry (for purposes of discussing effort reduction targets) was 5% per annum (Pownall, 1994). Thus, instead of Equation 11.30, we would need

$$q_t = q_0 \times q_{\text{inc}}^t \quad (11.31)$$

where q_t is the catchability in year *t* and q_0 is the catchability in the first year. In year 0, the q_{inc} would be raised to the power zero and hence equal 1. For a 5% per annum increase, $q_{\text{inc}} = 1.05$. As with the additive form of catchability increase, closed-form estimates of q_0 and q_{inc} can be obtained if we log-transform Equation 11.31 to give it the form of a linear regression (see Appendix 11.2 for the derivation):

$$\ln(q_t) = \ln(q_0) + t \times \ln(q_{\text{inc}}) \quad (11.32)$$

11.5.3 The Limits of Production Modelling

We will consider the Australian northern tiger prawn fishery and illustrate some of the variations possible when implementing nonequilibrium surplus production models. This fishery extends across the top of Australia from the Gulf of Carpentaria to the west of Joseph Bonaparte Gulf (Pownall, 1994). The fishery has been operating for over thirty-eight years with significant tiger prawn catches since 1970 (Table 11.2, Figure 11.6). Management is via

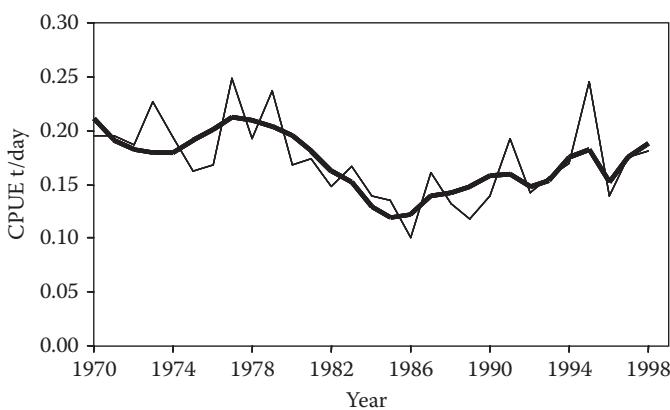
TABLe 11.2

Published Catch, in Tonnes, and Effort, in Fishing Days, for the Northern Australian Tiger Prawn Fishery

Year	Catch	Effort	Year	Catch	Effort	Year	Catch	Effort
1970	1,138	5,818	1980	5,124	30,594	1990	3,550	25,525
1971	1,183	6,057	1981	5,559	31,895	1991	3,987	20,744
1972	1,380	7,380	1982	4,891	32,956	1992	3,084	21,789
1973	1,672	7,362	1983	5,751	34,551	1993	2,515	16,019
1974	666	3,439	1984	4,525	32,447	1994	3,162	18,592
1975	973	6,010	1985	3,592	26,516	1995	4,125	16,834
1976	1,118	6,660	1986	2,682	26,669	1996	2,311	16,635
1977	2,900	11,673	1987	3,617	22,478	1997	2,694	15,385
1978	3,599	18,749	1988	3,458	26,264	1998	3,250	18,003
1979	4,218	17,791	1989	3,173	27,036			

Source: From Pownall, 1994; AFMA, 1999.

Note: Data are for both the brown (*Penaeus esculentus*) and grooved tiger prawns (*P. semisulcatus*) combined. Catch rates for each year can be determined by dividing the catch by the effort for each year.

**Fig ur e 11.6**

Observed catch-per-unit-effort data from the northern Australian tiger prawn fishery (see Table 11.2) as the fine irregular line, with an optimal model fit as the thicker smoother line (Example Box 11.4). The optimal model was constrained to be equivalent to the modified Fox model ($p = 0.0000001$; Equation 11.17; Fox, 1975).

input controls (being a mixture of limited entry, closed seasons, closed areas, and gear controls), and stock assessment uses a relatively complex model (Wang and Die, 1996). Nevertheless, because effort creep has been identified as a major issue in this fishery, it provides an opportunity to apply the techniques described earlier involving the estimation of effort creep levels.

EXAMPLE BOX 11.4

Nonequilibrium surplus production model of the northern Australian tiger prawn fishery (Table 11.2, Figure 11.6). The row numbers are omitted to save space, but they start in row 1. The manipulations in C1:C4 assist the solver by keeping the values to vary similar in value; alternatively, logs could be used. Name C1 as *re*, C2 as *K*, and C4 as *p*. Select B5:C5 and put =linest(F9:F37,I9:I37,true,false) using <Ctrl><Shift><Enter> to enter the array function (cf. Equation 11.32). The closed-form estimates of *q* and *qinc* are in B6:C6. Column I contains numbers 0 to 28 representing *t*-1 in the closed-form calculations. In B7 put =-(F6/2)*(Ln(2*pi())+2*Ln(F7)+1), which is Equation 11.25. Enter the data into columns A to C from Table 11.2 (CE_Obs is Catch/Effort). D9 is B0 (=C3). D10 is =max(D9+D9*(*re*/*p*)*(1-(D9/*K*)^{*p*})-B9,100), which is Equation 11.33 with the max function preventing the possibility of negative biomass (which would halt the solver). G9 is =(Ln(C9)-Ln(E9))², which represents the lognormal squared residuals. Select E9:G9 and copy down to row 10. Select D10:H10.

Plot columns C and E against A to mimic Figure 11.6. Optimize the model fit by maximizing B7 by varying B1:B3, leaving the *p* value as it is. Save the parameter and model output values somewhere else on the sheet. Now solve by varying B1:B4 to see the impact on the *p* value when it is free to vary. Are the values for *qinc*, *p*, and *B0/K* reasonable? Would the shape of the production curve make biological sense (cf. Figure 11.1)? Alter the structure of the sheet to estimate a constant *q* (put =exp(average(F9:F37)) into C6, and copy H9 down to row 37). Re-solve, for either B1:B3 or B1:B4. How big an impact would this have on the model outputs? Because the multiplicative effects of *qinc* lead to an exponential impact on catchability, the results are very sensitive to the model of *q* used. Try implementing the additive model of *q* and *qadd*. When solving this model, it may be necessary to search carefully for the optimal solution. Try solving for individual parameters and moving toward the correct solution if you lose the optimum. Try varying the parameters to see how sensitive the solution is to the starting position. Can you find any false minima? If you do, does altering the options in the solver alter the solution? Is adding a constraint that *p* be greater than zero a good idea? Try the different possibilities listed for generating B0 (independent fit, =K, =CE/q). How much do they affect the results? Plot the predicted biomass history for the stock. Are things looking good for the northern Australian tiger prawn fishery according to this model? Compare the solution obtained for the maximum likelihood with that obtained from the summed squared residuals. Implement normally distributed residuals (put =(C9-E9)² into G9 and copy down), and solve by minimizing these. How big a difference does the residual error structure make?

continued

EXAMPLE BOX 11.4 (continued)

A	B	C	D	E	F	G	H	I
r	32.965	=B1/100		B98	=D37			
K	27.3301	=B2*1000		B98/K	=F1/C2			
B0	42.1005	=B3*1000		MSY	=C1*C2)/((C4+1)^(C4+1)/C4))			
p	1	=B4/1E9		B0/K	=C3/B2			
q	0.0763	-12.2195	Ln(q0)	Ssq	=sum(G9:G37)			
qinc	=exp(B5)	=exp(C5)	q0	n	=count(G9:G37)			
LL	17.2676			Sigma	=sqrt(average(G9:G37))			
Year	Catch	CE_Obs	PredB	Pred_I	Pred_q	SSQ	q	Yr
1970	1138	0.1956	=C3	=D9*H9	=Ln(C9/D9)	0.0072	=\$C\$6	0
1971	1183	0.1953	35774	0.1905	-12.118	0.0006	=H9*\$B\$6	1
1972	1380	0.1870	31593	0.1816	-12.037	0.0009	0.0000058	2
1973	1672	0.2271	28840	0.1789	-11.752	0.0569	0.0000062	3
1974	666	0.1937	26767	0.1792	-11.837	0.0060	0.0000067	4
1975	973	0.1619	26377	0.1906	-12.001	0.0267	0.0000072	5

The dynamics of the model are described by the same nonequilibrium model as used with the Schaefer data (Equation 11.19), along with the relationship between catch rates and biomass illustrated by Equation 11.20. The estimation of q will involve either the constant catchability (Equation 11.23) or the additive or the multiplicative incremental increases in q , as in Equations 11.31 and 11.32. The precise relationship between catch rates and stock biomass is

$$\hat{I}_t = \frac{\hat{C}_t}{E_t} = qB_t e^\epsilon \quad (11.33)$$

In this case the biomass is not averaged across two years, as the prawns are almost annual in their life cycle, with very few animals surviving from one year to the next.

When fitting such an array of options it is obviously best to start simple and progress to the more complex.

11.6 Uncertainty of Parameter Estimates

11.6.1 Likelihood Profiles

Polacheck et al. (1993) used the log-likelihood criterion, even though it provides the same estimates as the least squares estimates (as long as the

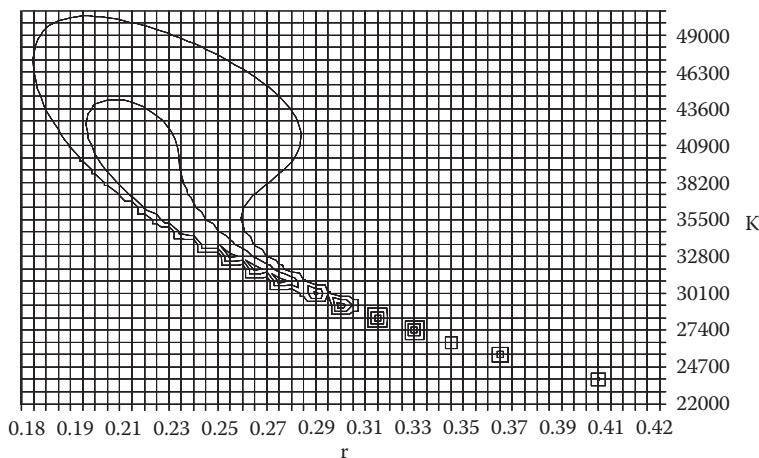


Figure 11.7

Approximate 95% confidence intervals from the two-dimensional likelihood profile, for the r and K parameters in the nonequilibrium surplus production model for the northern Australian tiger prawn fishery (as in Example Box 11.4). The optimum solution was at $r = 0.32965$ and $K = 27,330$. The target log-likelihood was 14.273, which is the outer curve (Example Box 11.5). The gaps in the tail are unreal, and the resolution of the graph is insufficient to show the detail of connected contours.

I values are log-transformed first so as to keep the same error structures). They did this because they also suggested using Venzon and Moolgavkar's (1988) approximate likelihood profile method to produce confidence intervals around the parameter estimates. The methodology behind this was discussed in Chapter 3 on parameter estimation (Section 3.4.14) and in Chapter 8 (Section 8.4). For single parameters the results are essentially the same as standardizing the log-likelihoods so they all add to 1, and then finding the confidence intervals by using the parameter limits that contain 95 or 99% (or whatever confidence interval chosen) of the likelihood curve. Polacheck et al. (1993) found that the likelihood profiles obtained when using observation error estimators were much smaller than those deriving from process error estimators.

A maximum of two parameters can be visualized at one time. To determine the likelihood profile confidence intervals, as shown in Chapters 3 and 8, involves subtracting $5.9915/2$ ($= \chi^2/2$, for 2 degrees of freedom) from the maximum likelihood and searching for the parameter combinations that generate this likelihood (Figure 11.7, Example Box 11.5).

11.6.2 Bootstrap Confidence intervals and estimates of Bias

There are disadvantages to using likelihood profiles. These include the complexity of implementing the method when there are many parameters

EXAMPLE BOX 11.5

The generation of confidence intervals using likelihood profiles. First construct the table of likelihoods from the array of values for the two parameters of interest, in this case, r and K . The sixth row relates to the K value, and column U7 downwards, to the r parameter. Copy W6 across to column BB, then copy U8 down to row 59. Cell U6 points to the likelihood value in B7. Select U6:BB59 (or however big you have made the table), then choose the Data/Table menu item. In the dialog box the row input cell is \$B\$2 and the column input cell is \$B\$1. This should complete the Excel table. To plot this as a contour surface plot it is best to convert the borders to text so that the axes are automatically labeled. In V66 put =text(V6*1000,"#0") and copy across to column BB. In U67 put =text(U7/100,"#0.000") and copy down to row 119 to match the table above. In V67 put =V7 and copy down, and then copy the column across to regenerate the table. Select the whole table, including the borders (U66:BB119), and generate the contour surface plot by selecting the appropriate menu item (Insert/Chart/Surface). The target log-likelihood for the approximate 95% confidence intervals for two parameters would be the optimum $\pm 5.99/2$ (=B7-chiinv(0.05,2)), which in this case = 14.273. Double-click on the legend and alter the scale to a minimum of 13.273 and a major unit (tick value) of 1.0, which will lead to a graph similar to Figure 11.7. Drag the graph up near to U1:U4 and experiment with the table ranges and the scale shown. Be wary of selecting a major unit that is too small, else the poor hardworking hardware can reach its limits and you will need to crash out of the program. Do *not* run the solver if a table is active unless you have a great deal of time to spare (deleting the core of the table—V7:BB59—will fix that problem).

	T	U	V	W	X
1	K	22			
2		0.9			
3	r	17.5			
4		0.48			
5					
6		=B7	=U1	=V6+\$U\$2	26.2
7		=U3	=table(B2,B1)	=table(B2,B1)	=table(B2,B1)
8		=U7+\$U\$4	=table(B2,B1)	=table(B2,B1)	=table(B2,B1)

involved (parameter correlation usually increases the width of confidence intervals), and likelihood profiles give no indication of any bias in the parameter estimates and bias can be an important aspect of uncertainty. Fortunately, alternative methods exist for fitting confidence intervals around parameter estimates. A common approach is to use a bootstrap strategy as introduced in Chapter 6. This approach resamples the residuals from the optimum fit to generate new bootstrap samples of the observed time series. The model is fitted to many replicate bootstrap samples and the outputs stored so that percentile confidence intervals can be determined, as is usual with bootstrap methods. The confidence intervals generated can be asymmetric and synthesize the effects of all the parameters varying at once. A further advantage of the bootstrap strategy is that one can estimate whether or not the parameter estimates are biased.

Surplus production models are fitted to time series of relative abundance indices (CPUE). To obtain confidence intervals and bias estimates using bootstrap procedures, it is important that the time series nature of the data not be disrupted. So that the time series nature of the CPUE data is retained, one should not bootstrap the raw data but instead bootstrap the residuals between the observed and expected values, i.e., randomly sample from the original best fit residuals, with replacement, to generate a new vector of bootstrapped residuals. This vector of bootstrapped residuals is combined with the optimum vector of expected CPUE data to obtain each new bootstrap sample of CPUE data (Prager, 1994; Haddon, 1998).

If we had been using normal, additive errors, then the residuals would simply be (observed CPUE – expected CPUE), and after bootstrapping, these would each have been added to the sequence of original expected CPUE value (Equation 11.34):

$$I_t^* = \hat{I}_t + (I_t - \hat{I}_t)^* \equiv \hat{I}_t + \varepsilon^* \quad (11.34)$$

where I_t^* is the bootstrapped CPUE value that equals the expected CPUE value, \hat{I}_t , plus a bootstrapped normal residual $(I_t - \hat{I}_t)^*$, which is equivalent to combining each expected catch/effort value with a bootstrapped error or residual term. In this way a new time series of bootstrapped “observed” CPUE data is generated to which the model may be refitted and the parameters may be reestimated. However, with lognormal, multiplicative errors (see Equation 11.33), we must use the ratio of the CPUE values (observed/expected) to calculate the residuals that are to be bootstrap sampled. To obtain the bootstrapped CPUE values the residuals are multiplied with their respective original expected CPUE values (Equation 11.35):

$$I_t^* = \hat{I}_t \times \left(\frac{I_t}{\hat{I}_t} \right)^* \quad (11.35)$$

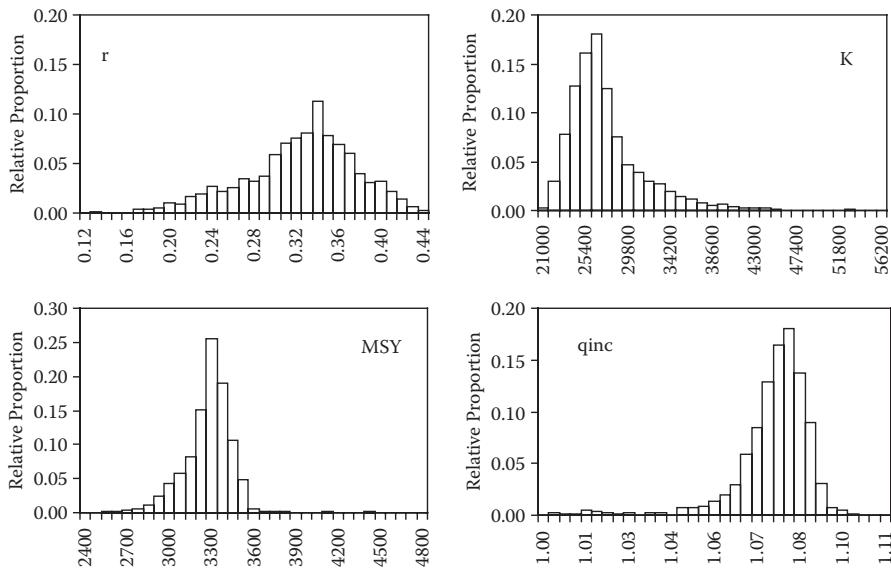


Figure 11.8

Bootstrap distributions for four of the parameters and model outputs from Example Box 11.6, for tiger prawns until 1998. By comparing the panels for the r and K parameters and Table 11.3, the first-order bias correction can be seen to shift the confidence intervals in the direction of the skew of the distribution of bootstrap values (Example Box 11.7). The lower two panels represent values of interest to management. The MSY can be interpreted as the long-term average yield expected from the stock when it is at its optimum size. The value of q_{inc} suggests the level of effort creep, and this indicates the urgency of any measures to limit effort in the fishery.

Confidence intervals can be estimated by generating thousands of bootstrap samples, refitting the model, and generating an equal number of parameter estimates (these could include outcomes such as MSY). The central 95% of these (the 0.025 and 0.975 percentile values of the sorted estimates) would represent the bootstrap percentile confidence intervals (Figure 11.8, Example Box 11.6).

If we wished to take into account any bias in the parameter estimates, we would do best to calculate bias-corrected percentile confidence intervals (Efron and Tibshirani, 1993). Percentile confidence intervals are determined by using the 25th and 975th ordinal values (out of one thousand replicates for 95% intervals). Bias correction leads one to use different percentile values, depending on whether the parameter estimates are positively or negatively biased. The procedure begins by determining what proportion (LT) of the bootstrap replicates are less than the original optimal fit estimate of the parameter or output of interest, and this value is transformed via the inverse cumulative standard normal distribution (Φ^{-1}):

$$z = \Phi^{-1}(LT) \quad (11.36)$$

EXAMPLE BOX 11.6

Bootstrap implementation for the surplus production model from Example Box 11.4. The procedure replaces the observed catch rates with a bootstrap sample; it is therefore prudent to store a copy of the original catch rate data into column J. Select E9:E37, copy as values into K9 (Paste Special/Values). Given the optimum fit put =C9/E9 into L9 and copy down L37. These are the residuals around the catch rates calculated as (observed/expected). An easy error is to forget to convert these to values. Select L9:L37, copy, and paste as values onto themselves so they are ready for bootstrap sampling. The resampling is conducted in column M using the offset function. The $\text{trunc}(\text{rand()}\times 29)+1$ will provide a random integer between 1 and 29. Copy M9 down to row 37. The bootstrap sample is generated in column N by multiplying the selected residual with the expected catch rate in that year. To conduct the bootstrap select N9:N37 and copy as values into C9 and re-solve for an optimum to provide a single set of bootstrap estimates, which will need to be stored as values somewhere else on the worksheet. The cells in column P have been arranged to make this copying and storage a simpler process. Of course, to do the bootstrapping in a sensible way, one needs to write a macro to do the necessary copying, solving, and storing of results. Cells L1:L3 and M1:M3 all relate to a suitable macro to do the bootstrapping. Before constructing the macro, carry out the bootstrap a few times manually. Under the solver options be sure to provide generous time and iteration limits, and refine the precision and convergence criteria. For this problem the other options that seem to provide stable answers are Estimate: Tangent, Derivatives: Forward, and Search: Conjugate, but do try the alternatives. Do you think it is a good idea to always start the search from the original optimum? To provide a convenient source of the optimum value is why they were copied into L1:L3 before bootstrapping started. Do you ever have to run the solver twice to find a stable optimum? It would be a good idea to run it twice for each bootstrap sample, giving the solution a slight shift before the second solve (the reason for M1:M3). Add a few of the bootstrap samples to the plot of the observed and expected catch rates (retaining the original observed values). How closely do they compare? Create a macro to do the bootstrapping. Start with only a few bootstraps to see how long it takes and whether there are problems. Then set it going for one thousand bootstraps. See the following macro for details that cannot be recorded.

continued

EXAMPLE BOX 11.6 (continued)

	K	L	M	N	O	P
1	r	32.969	=B1+B1/100		r	=C1
2	K	27.328	=B2+B2/100		K	=C2
3	B0Est	42.106	=B3+B3/100		B0Est	=C3
4					p	=C4
5					q0	=C6
6					qinc	=B6
7					Bcurr	=F1
8	ExpIy	Resid	Resample Residuals	Bootstrap	Bcurr/K	=F2
9	0.2117	0.9242	=offset(\$L\$8,trunc(rand()*29)+1,0)	=K9*M9	MSY	=F3
10	0.1897	1.0295	=offset(\$L\$8,trunc(rand()*29)+1,0)	=K10*M10	B0/K	=F4
11	0.1812	1.0320		0.83075	LogLike	=B7

Note the solver is used twice and that the predicted biomass time series and the bootstrap sample are all stored along with the results. The times will only be indicative but will determine the approximate time taken for one thousand replicates. You may wish to place labels across the columns starting at S13 with r. All bootstrap analyses should include the original optimum solution (put it in S14:AC14). The bootstrap estimates may be tabulated and percentile intervals calculated (Example Box 11.7, Figure 11.8).

```

Option Explicit
Sub Do_Bootstrap()
Dim i As Integer
Application.ScreenUpdating = False
For i = 1 To 10          ' Set the number of bootstraps
    Range("N9:N37").Select
    Selection.Copy
    Range("C9").Select
    Selection.PasteSpecial Paste:=xlValues
    Range("L1:L3").Select      ' Paste original optimum
        solution
    Selection.Copy
    Range("B1").Select
    Selection.PasteSpecial Paste:=xlValues
    SolverOk SetCell:="$B$7", MaxMinVal:=1, ValueOf:="0",
        ByChange:="$B$1:$B$3"
    SolverSolve (True)

```

continued

EXAMPLE BOX 11.6 (continued)

```

Range("M1:M3").Select      ' optimum + 1%
Selection.Copy
Range("B1").Select
Selection.PasteSpecial Paste:=xlValues
SolverOk SetCell:="$B$7", MaxMinVal:=1, ValueOf:="0",
ByChange:="$B$1:$B$3"
SolverSolve (True)
Range("P1:P11").Select    ' Save the answers
Selection.Copy
ActiveCell.Offset(13 + i, 3).Range("A1").Select
Selection.PasteSpecial Paste:=xlValues, Transpose:=True
Range("D9:D37").Select    ' Save the biomass values
Selection.Copy
ActiveCell.Offset(5 + i, 26).Range("A1").Select
Selection.PasteSpecial Paste:=xlValues, Transpose:=True
Range("C9:C37").Select    ' Save the bootstrap data
Selection.Copy
ActiveCell.Offset(5 + i, 56).Range("A1").Select
Selection.PasteSpecial Paste:=xlValues, Transpose:=True
Application.CutCopyMode = False
Next i
Application.ScreenUpdating = True
End Sub

```

A convenient way to do this would be to use the $z=NORMINV(LT,0,1)$ in Excel, where the mean of 0 and the standard deviation of 1 imply the standard normal distribution. This z value is used in the cumulative standard normal distribution (Φ) to calculate the appropriate percentile to use instead of the standard 25th and 975th:

$$\begin{aligned} P_{lower} &= \Phi(2z - 1.96) \\ P_{upper} &= \Phi(2z + 1.96) \end{aligned} \quad (11.37)$$

where Φ is the cumulative standard normal distribution function, conveniently provided by $NORMDIST(P_{index}, 0, 1, 0.05)$, where the 0 and 1 define the normal distribution to be standard, and the 0.05 and 1.96 reflect the normal values required for 95% intervals. With first-order bias-corrected confidence intervals, if LT were 0.5, then z would be zero and we would, of course, obtain the 25th and 975th percentiles (Haddon, 1998). However, if, for example, LT were 0.459, then z would be -0.10295 , which would lead us to

TABLe 11.3

Comparison of Different Approximate Confidence Intervals for the Two Parameters r and K , from the Nonequilibrium Surplus Production Model for the Northern Australian Tiger Prawn Fishery (Example Boxes 11.4 to 11.7)

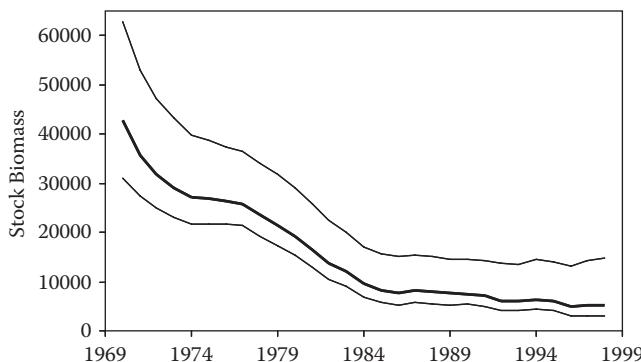
Interval type	r	r	r	K	K	K
	Lower95	Average	Upper95	Lower95	Average	Upper95
Likelihood profile	0.1825	0.32965	0.4050	23,800	27,330	50,400
Bootstrap percentile	0.2303	0.32965	0.4194	23,475	27,330	38,820
BC_1 percentile	0.1954	0.32965	0.4098	24,095	27,330	44,905

Note: The first-order bias-corrected bootstrap percentile intervals are closer to the likelihood profile intervals than the straight percentile intervals. These intervals are only approximate and are likely to be underestimates; it is therefore tempting to adopt the widest as providing the best estimates, or having the greatest chance of covering the true value.

use the 16th and 960th percentiles (note they are no longer necessarily symmetrical around the median).

The percentile confidence intervals around the parameter estimates for the northern Australian tiger prawn fishery tend to be narrower than the likelihood profile intervals (Table 11.3). However, all of these confidence intervals are only approximate and only capture the variability inherent in the data, ignoring other sources of variability. These would include the simplicity of the model failing to capture the full dynamics of the population (for example, there are two species of tiger prawns that are lumped in the catch and catch rate information) and the short time series of fisheries data not capturing the full range of environmental variation possible.

The confidence intervals produced by both likelihood profile and bootstrap methods will often be asymmetric and will vary greatly between parameters (Figure 11.8). The predicted biomass estimates can be treated in exactly the same way as the parameter estimates, so that the estimated history of the stock biomass can be illustrated (Figure 11.9). The confidence intervals are relatively wide around B_0 , which would be typical of the uncertainty surrounding this parameter (Figure 11.9). In this fishery, the situation is even more complicated in that the fishery was only developing over the years 1970 to 1975, so it is difficult to be certain as to how meaningful the early catch rates are in terms of stock biomass. Note the asymmetry of the confidence intervals. The lower bound is much closer to the average than the upper. This makes sense, as there must be a certain minimum present to sustain the history of the catches that have been taken from the fishery. In this case, bias correction makes only a slight difference (from Example Box 11.7, try plotting the two data series for comparison). Clearly, the model outputs are consistent with the stock being in

**Figure 11.9**

The predicted time series of stock biomass for the northern Australian tiger prawn fishery (Example Boxes 11.6 and 11.7). Most of the severe decline is driven by the continually increasing catchability coefficient. If q is increasing and catch rates stay stable, then this actually implies that the stock biomass must be declining. This is one reason why unstandardized catch rates are dangerous as a basis for managing a fish stock.

a relatively depressed state. Over the last ten to twelve years the stock has been in a relatively low level, below the size at which we might expect it to be maximally productive.

None of the parameter estimates and model outputs in the tiger prawn fishery are especially certain. It would almost always be a good strategy to obtain further information from the fishery rather than attempting to estimate peripheral parameters within the model. Systematic changes in catchability can have a huge effect, and using such a model form should not be adopted routinely. In the case of the tiger prawns, if changes to catchability could be determined empirically by determining the timing of novel gear changes and introductions, and their relative effect, this would have the potential for providing greater certainty. Of greatest value would be to obtain a direct and relatively precise estimate of abundance in more than one year. This could be used to anchor the model to reality along with the catch rates. More than one data series can be included in the likelihood equation. Each series might best be weighted in accord with its relative precision (standard error or coefficient of variation for each estimate, or some other estimate of its relative precision).

11.7 Risk Assessment Projections

11.7.1 introduction

Invariably, there will be many sources of error and uncertainty that are not accounted for in the model. Determining the uncertainty in an analysis only

EXAMPLE BOX 11.7

Calculation of the bootstrap percentile confidence intervals and the first-order bias-corrected percentile intervals from the results of the bootstrapping from Example Box 11.6. The macro shown in Example Box 11.6 will deposit the bootstrap estimates in cells S14:CI1013 (assuming one thousand replicates). If more than one thousand are calculated, then the ranges in the various functions listed here will need to be extended. This assumes that the optimum answers were all selected and pasted into row 14 (hence S4 and T4). S1:S3 are just the standard bootstrap percentile intervals and the bootstrap estimate of the parameter. Generally the median in S5 (could be =median(S14:S1014)) will be closer to the optimum model fit when there is any bias. S6 is the count of bootstrap estimates that were less than the optimum value in S4, which must be converted to text for the countif function to work. The many decimal places are to obtain robust answers across the range of values experienced by the different parameters. S7 is Equation 11.36 and S8:S9 is Equation 11.37, which are used in the percentile estimates of S10:S11. S12 is an estimate of the bias shown in the bootstrap estimates. Select S1:S12 and copy across to column BF. The formatting (number of decimal places) will need adjustment in each column. Store these equations in a separate worksheet and delete the originals if you wish to do more bootstrapping (otherwise they slow the calculations a great deal). Your row 15 will differ from that shown here because the bootstrap replicates will differ. Construct a bootstrap for the eastern Pacific yellowfin tuna (Example Box 11.3). How certain is the nonequilibrium estimate of the average long-term yield, MSY? The bias correction is converting the confidence intervals from being centered on the average to being centered more on the median of the distribution.

	R	S	T	U	~	X
1	U95%	=percentile(S14:S1014,0.975)		64250.4		1.09289
2	Average	=average(S14:S1014)		43169.6		1.07631
3	L95%	=percentile(S14:S1014,0.025)		31376.5		1.05388
4	Optimum	=S14	=T14	42105.6		1.07931
5	Median	=percentile(S14:S1014,0.5)		42512.1		1.07902
6	LT_mean	=countif(S14:S1014,"<" & text(S4,"#0.0000000"))				359
7	Z	=norminv(S6/1000,0,1)		-0.60828		-0.91727
8	Pupper	=normdist(2*S7+1.96,0,1,0.05)		0.77139		0.54992
9	Plower	=normdist(2*S7-1.96,0,1,0.05)		0.00075		0.00007
10	U95%	=percentile(S14:S1014,S8)		48094.6		1.07992

continued

EXAMPLE BOX 11.7 (continued)

	R	S	T	U	~	X
11	L95%	=percentile(S14:S1014,S9)		22299.0		0.99272
12	%Bias	=100*(S2-S4)/S4				
13		r	K	B0Est		Qinc
14		0.32969	27327.694	42105.588		1.079306
15		0.210056	40102.191	45006.252		1.039695

tells us that we need to be careful when attempting to interpret the model outcomes; it cannot inform resource managers about the risk level associated with a particular management option. To answer such questions a risk assessment is required.

Risk assessment implies projecting the population dynamics model into the future under the constraint of different management options (for example, a particular catch or effort regime, or different open and closed areas, etc.). Given the selected catch or effort, we need to be able to model the projected recruitment levels in a stochastic manner, with the variability of that recruitment reflecting the stock dynamics observed in the available time series of data. The projected recruitments would be offset against the catches, and the trajectory of the stock biomass through time could thus be generated. The problem, when using surplus production models, is to generate these stochastic recruitments.

11.7.2 Bootstrap Projections

Prager (1994) suggested that because surplus production models imply a recruitment function, they could be used to make projections based upon hypothetical catch or effort allocations. In the standard operation of surplus production models the stock biomass is projected forward under the constraint of the time series of catches and catch rates (e.g., Equation 11.19). To do this for a risk assessment would be simply to extend this stock biomass projection beyond the years for which data are available. The projected catches or efforts (which, given the catchability and stock biomass, would imply catches) would be dictated by proposed management options. The stock biomass projections are deterministic, so a mechanism for introducing the required stochastic element is still required. Prager's (1994) suggestion for varying the population projections was to conduct a bootstrap analysis and project each bootstrap forward to obtain a risk assessment at the same time as a determination of the level of uncertainty in the analysis. This mechanism uses the variation inherent in each bootstrap sample to represent the variation likely to occur in the stock dynamics of the species

concerned. The variation is represented by the residuals between the observed and predicted catch rates, which are assumed to relate back to stock biomass via the catchability coefficient ($C/E = qB$).

11.7.3 Projections with Set Catches

Many fisheries are now managed through output controls in the form of a total allowable catch (TAC). In such fisheries, a vital management control is to set the TAC at a level consistent with stock sustainability and, often, with optimizing production. Investigation of the implications of setting different catch levels is relatively simple with the surplus production models described in this chapter. If the stock dynamics are assumed to be described by the deterministic equation

$$B_{t+1} = B_t + \frac{r}{p} B_t \left(1 - \left(\frac{B_t}{K} \right)^p \right) - C_t \quad (11.38)$$

or any production function from which a catch is subtracted, then forward projection only requires those catches to be defined and the projections can be implemented (Example Box 11.8).

Exactly what characteristic of the population to consider in the projections can vary, depending on circumstances and what would be most informative. For example, a common performance indicator would be to determine whether the predicted stock biomass in any given projection year is greater than a selected reference year. If many replicate projections are generated, then in any year the proportion in which the stock biomass is greater than that in the reference year can represent the probability that the modelled stock will have increased in size in that year (cf. Figures 11.10 and 11.11). Alternatively, if there is a risk of stock collapse, then the number of replicates under a given set of management constraints that led to collapse (defined as some low biomass level) can also be collated and graphed.

11.7.4 Projections with Set effort

The northern Australian tiger prawn is an input-controlled fishery, so the management controls used to constrain the projections will involve considering the impact of different effort levels. There is also the problem of effort creep to attend to in the risk assessment. In theory, it should be possible to constrain the annual proportional increase in the effectiveness of effort. The presently accepted level is 5% per annum, but it is recognized that this level cannot continue, so alternative, lower levels will also need consideration. The best strategy is to conduct a grid analysis, running the projections for each selected effort level and all the levels of the annual increment in catchability ($qinc$) that are to be considered (Figures 11.10 and 11.11, Example Box 11.8).

EXAMPLE BOX 11.8

Additions to the bootstrapping procedure, implemented in Example Boxes 11.6 and 11.7, to permit risk assessment projections based upon setting the future catch or effort levels. Save the workbook from Example Box 11.6 under a new name and make the following changes. The worksheet below reflects the original data and optimal fit, before any bootstrapping has occurred. In this fishery we do not assume the catchability will stay constant, but will need to trial different catch or effort levels against different levels of q_{inc} (hence H1:H2). To use allocated catch levels put =H\$1 into B38 and copy down to row 44. To use allocated effort levels put =D38*H38*\$H\$1 into B38 and copy down to row 44 (this is just $C = qEB$; Equation 11.39). Select D37:E37 and copy down to row 44. Copy H37 down to row 44. These simple extensions will generate the population projection for a single instance of the combination of catch or effort level and q_{inc} . To generate replicates we need to modify the macro controlling the bootstrap to save only the data we are interested in during the projections (see below). The bootstrap percentile limits can be used to describe the projections as with the usual analysis, but the projections permit many other questions to be answered. Beside the columns of projected stock biomass, we can add columns determining whether, for example, the biomass in the given year is greater than in some reference year. Thus, if only years 1985–2005 are stored according to the following macro, then in AN14 we could put =if(AG14>AF14,1,0), where AG14 is the predicted biomass in 1999 and AF14 is that in 1998, the selected reference year. If AN14 is copied across to column AT and down to however many replicates were run, we can sum the columns relating to each of the projected years and ask about the probability of the stock being larger than the reference year under the catch or effort and q_{inc} regime adopted (Figures 11.10 and 11.11). Any reference year can be chosen. In this way, risk-averse management strategies can be developed.

	A	B	C	D	E	F	G	H
1						Future catch or effort		14500
2						Managed q_{inc}		1.02
~								
8	Year	Catch	Obs_CE	Biomass	Pred_CE	Pred_q	Ln(I-I)	q
~								
36	1997	2694	0.1686	4431.5	0.1749	-10.139	0.0000	0.00002167
37	1998	3250	0.2142	4395.4	0.1872	-10.100	0.0013	0.00002287

continued

EXAMPLE BOX 11.8 (continued)

	A	B	C	D	E	F	G	H
38	1999	=D38*H38*\$H\$1		3793.4	0.1648		=H37*\$H\$2	
39	2000	=D39*H39*\$H\$1		3873.3	0.1716		=H38*\$H\$2	
40	2001	=D40*H40*\$H\$1		3879.6	0.1754		=H39*\$H\$2	
41	2002	2563		3833.9	0.1768			0.00004610
42	2003	2559		3753.4	0.1765			0.00004703
43	2004	2539		3650.8	0.1751			0.00004797
44	2005	2507		3534.5	0.1729			0.00004893

```

Option Explicit                               ' set values in H1 and H2
Sub Projection()
Dim i As Integer
Calculate
Application.ScreenUpdating = False
For i = 1 to 100                            ' Number of projections
    Range("N9:N37").Select                  ' Copy the bootstrap
    Selection.Copy
    Range("C9").Select
    Selection.PasteSpecial Paste:=xlValues
    Range("L1:L3").Select                  ' Save optimum solution
    Selection.Copy
    Range("B1").Select
    Selection.PasteSpecial Paste:=xlValues
    SolverOk SetCell:="$B$7", MaxMinVal:=1, ValueOf:="0",
        ByChange:="$B$1:$B$3"
    SolverSolve (True)
    Range("M1:M3").Select                ' optimum + 1%
    Selection.Copy
    Range("B1").Select
    Selection.PasteSpecial Paste:=xlValues
    SolverOk SetCell:="$B$7", MaxMinVal:=1, ValueOf:="0",
        ByChange:="$B$1:$B$3"
    SolverSolve (True)
    Range("D24:D44").Select              ' Save biomass values
    Selection.Copy
    ActiveCell.Offset(-10 + i, 15).Range("A1").Select
    Selection.PasteSpecial Paste:=xlValues, Transpose:=True
Application.CutCopyMode = False

```

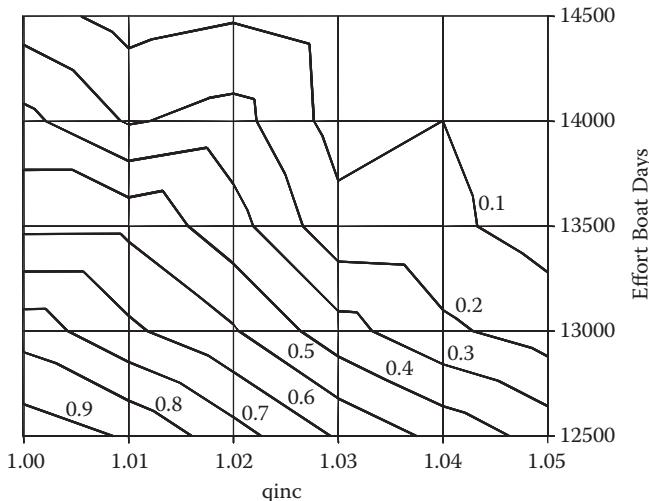
continued

EXAMPLE BOX 11.8 (continued)

```

If (i Mod 10) = 0 Then      ' Keep a check on progress.
    Range("L6").Value = i
    Application.ScreenUpdating = True
    Application.ScreenUpdating = False
End If
Next i
Application.ScreenUpdating = True
Beep ' Announce completion
End Sub

```

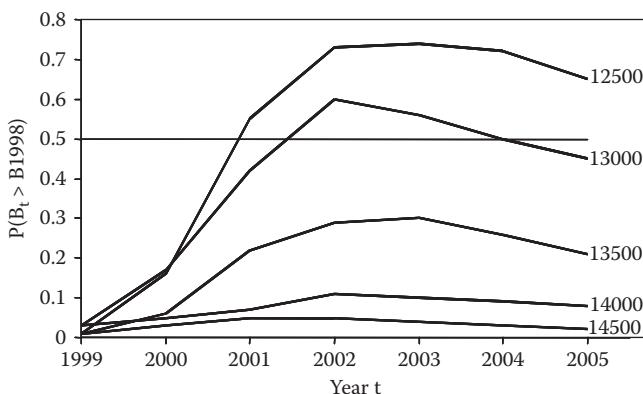
**Figure 11.10**

The contours are the probability of stock biomass being greater in the year 2002 than it was in 1998. The contours are not particularly smooth because each intersection is only represented by one hundred bootstrap projections, using a fixed effort strategy in the northern Australian tiger prawn fishery. It is clear that positive stock growth, relative to 1998, will only have a greater than 50% chance of occurring if effort creep (q_{inc}) is kept below 3.5% per annum, and effort is less than 13,500 fishing days.

Given a recommended effort level, the model can still be projected into the future by calculating the catch implied by the stock biomass, the catchability in that year, and the effort imposed:

$$C_t = q_t E_t B_t \quad (11.39)$$

Of course, the catches in each projected year are likely to vary from year to year. It is harder to make the stock crash with a constant effort management

**Figure 11.11**

An alternative view of risk assessment output for the northern Australian tiger prawn fishery. The vertical axis is the probability of the stock biomass in a projected year being greater than the stock biomass in 1998. Each curve relates to a given effort level depicted at the end of each line. The annual increase in catchability was set at 2% ($q_{inc} = 1.02$) for all series. The fine horizontal line is at 50%, indicating the desirability of fixing effort at less than thirteen thousand fishing days to encourage stock rebuilding if $q_{inc} = 1.02$.

scenario than with a constant catch level. This is because as stock biomass declines, so does the catch from a certain effort. But a constant catch can be taken until there is no biomass left to take (until an infinite effort is implied).

11.8 Practical Considerations

11.8.1 introduction

Despite only having minimal data requirements, surplus production models purport to provide an assessment of the state of a given fishery at a particular time. The assumption that the stock and its dynamics can be described purely in terms of its biomass exposes this class of models to some problems peculiar to themselves. Because stock biomass can be either recruitment or standing crop, these possibilities can be confounded in the model outputs.

If the available data exhibit a steady decline in catch rate through time, with no contrast in the ranges of effort imposed over the different stock biomass levels, then the data have little information with respect to the trajectory taken by the stock biomass. The model can have trouble distinguishing between a stock with a high population growth rate and low standing crop and a stock with almost no production but an enormous standing crop from which all the catches have been taken. All the model can do is present outputs that are consistent with the input data, and both of these interpretations

can provide an internally consistent description of events. As long as one is aware of the possibility of the catch rate data having little useful information about the stock biomass, care can be taken in the interpretation of the results from surplus production models.

Equilibrium surplus production models will almost always provide apparently workable management advice, whereas nonequilibrium models can lead to the conclusion that the data provide no information. This latter situation may not appear to be useful, but it is far better to know that the information one has is noninformative than to follow model results blindly.

11.8.2 Fitting the Models

Many options for the implementation of surplus production models have been described in this chapter, and it is unlikely that only a single set of options will suit a particular problem. If the results of the modelling are similar irrespective of the options selected, then at least there is a consistent story to tell. If different options lead to different results, then how they differ should inform us about the value of the data and the relative sensitivity to the different parameters. The point is that, wherever possible, multiple options should be used.

In the case of the northern Australian tiger prawns, the constant proportional increase in the catchability coefficient (q_{inc}) has an overwhelming impact on the assessment provided by the surplus production model. This parameter has important management implications. If it is assumed equal to 1 (i.e., constant catchability), then the stock does not appear to be as depleted. These simple assessment models can emphasize where research effort should be focused to improve an assessment.

Where there are sufficient years of data available, it is worthwhile to conduct hind-casting trials to compare the assessment results for different series of years. Thus, if data are available from 1970 to 1998, then tabulating any changes derived from comparing years 1970–1995, with 1970–1996, with 1970–1997, and so on, can provide insight into the stability of the model and its outputs.

11.9 Concluding Remarks

Now that surplus production models have moved away from their equilibrium-based origins they provide a useful tool in the assessment of stocks for which there is only limited information available. Their simplifying assumption implies that any conclusions drawn from their outputs should be treated with caution. Nevertheless, given the constraints of only considering the

total stock biomass, they can provide insights as to the relative performance of the stock through time.

Surplus production models now have surprising flexibility and can be used in risk assessments and to produce management advice that goes well beyond the old traditional performance measure notions of MSY and E_{MSY} .

Surplus production models have now been developed to a point where even if more information is available and more complex and realistic models can be implemented, it would be sensible to implement a simpler model if only to act as a contrast.

Appendix 11.1: Derivation of Equilibrium-Based Stock Production

The steps between Equation 11.3 and Equation 11.9 are as follows:

$$B^* = B^* + \frac{r}{p} B^* \left(1 - \left(\frac{B^*}{K} \right)^p \right) - C^* \quad (\text{A11.1})$$

where the $*$ superscript denotes an equilibrium level. The left-hand B^* and first B^* on the right-hand side can be cancelled, and the C^* can be moved across:

$$C^* = \frac{r}{p} B^* \left(1 - \left(\frac{B^*}{K} \right)^p \right) \quad (\text{A11.2})$$

Substituting $B^* = C^*/qE^*$ (Equation 11.5), by assuming equilibrium at all times, we obtain

$$C^* = \frac{rC^*}{pqE^*} \left[1 - \left(\frac{C^*}{qE^* K} \right)^p \right] \quad (\text{A11.3})$$

$$pqE^* = \frac{rC^*}{C^*} \left(1 - \left(\frac{C^*}{qKE^*} \right)^p \right) \quad (\text{A11.4})$$

$$\frac{pqE^*}{r} = 1 - \left(\frac{C^*}{qKE^*} \right)^p \quad (\text{A11.5})$$

$$\left(\frac{C^*}{qKE^*} \right)^p = 1 - \frac{pqE^*}{r} \quad (\text{A11.6})$$

$$\frac{(C^*)^p}{(qK)^p (E^*)^p} = 1 - \frac{pqE^*}{r} \quad (\text{A11.7})$$

$$\frac{(C^*)^p}{(E^*)^p} = (qK)^p - \frac{pqq^p K^p E^*}{r} \quad (\text{A11.8})$$

$$\left(\frac{C^*}{E^*}\right)^p = (qK)^p - \frac{pq^{p+1} K^p E^*}{r} \quad (\text{A11.9})$$

and finally

$$\frac{C^*}{E^*} = \left[(qK)^p - \frac{pq^{p+1} K^p E^*}{r} \right]^{\frac{1}{p}} \quad (\text{A11.10})$$

If we reparameterize by defining $(qK)^p$ to be a new parameter a , and the second term, $(pq^{p+1} K^p)/r$ to be the new parameter b , this would lead to the form

$$\frac{C^*}{E^*} = (a - bE^*)^{\frac{1}{p}} \quad (\text{A11.11})$$

If $p = 1$, Equation A11.11 collapses to $C/E = (a - bE)$.

Appendix 11.2: The Closed Form of the Estimate of the Catchability Coefficient

Version 1: Constant q

Derivation of the statement that we can directly estimate the value of q , which relates to the maximum likelihood fit of the model, by using the geometric average of the time series of q estimates I_t/\hat{B}_t :

$$\hat{q} = e^{\frac{1}{n} \sum \ln\left(\frac{I_t}{\hat{B}_t}\right)} \quad (\text{A11.12})$$

By definition we have

$$\hat{I}_t = \hat{q}_t \hat{B}_t \quad (\text{A11.13})$$

where \hat{I}_t is the expected CPUE in a given year t , \hat{q}_t is the expected catchability coefficient in year t , and \hat{B}_t is the predicted biomass in year t . However, the assumption is that the catchability coefficient is a constant and each \hat{q}_t is only an estimate of the overall \hat{q} . We can either directly estimate this expected

catchability coefficient by using nonlinear estimation, or we can modify Equation A11.13 to include observed data instead of purely expected values. In this way we can generate the expected catchability coefficient; this is known as a closed form of the equation.

Using observation errors that are lognormal, multiplicative, and with a constant variance, we could fit the model using the sum of squared residuals criterion. The model residuals are related to the observed data in the usual way for lognormal errors:

$$I_t = \hat{I}_t e^\varepsilon \quad \text{or} \quad \frac{I_t}{e^\varepsilon} = \hat{I}_t \quad (\text{A11.14})$$

where I_t is the observed CPUE in a given year t . In order to obtain the closed form of Equation A11.13, we can substitute the right-hand version of Equation A11.14 into Equation A11.13 to include the observed CPUE values instead of the expected values:

$$\frac{I_t}{e^\varepsilon} = \hat{q}_t \hat{B}_t \quad (\text{A11.15})$$

which is equivalent to

$$I_t = \hat{q}_t \hat{B}_t e^\varepsilon \quad \text{or} \quad \frac{I_t}{\hat{B}_t} = \hat{q}_t e^\varepsilon \quad (\text{A11.16})$$

and log-transforming this gives

$$\ln\left(\frac{I_t}{\hat{B}_t}\right) = \ln(\hat{q}_t) + \varepsilon \quad (\text{A11.17})$$

The value of \hat{q} that minimizes the residuals, ε , in Equation A11.17 (remember because of the normalized error term this would be the same as maximizing the likelihood) would be the value that minimized the residuals of Equation A11.17 for all the observed values of catch effort (I_t) and biomass B_t . If there are n observations, then the best estimate of the log of the constant, \hat{q} , is simply the mean of the t estimates from the set of observed catch effort values with associated expected biomass values:

$$\ln(\hat{q}) = \frac{\sum_{t=1}^n \ln(\hat{q}_t)}{n} = \frac{\sum \ln\left(\frac{I_t}{\hat{B}_t}\right)}{n} \quad (\text{A11.18})$$

To obtain the expected value of q we clearly need to antilog the outcome of Equation A11.18, which is, in fact, the geometric mean of the original estimates of q_t :

$$\hat{q} = e^{\frac{1}{n} \sum \ln(\hat{q}_t)} = e^{\frac{1}{n} \sum \ln\left(\frac{I_t}{\hat{B}_t}\right)} \quad (\text{A11.19})$$

Version 2: Additive increment to Catchability

In the case where the catchability is assumed to increase by a constant absolute amount each year, the q value for each year, q_t , can be determined using a simple linear equation:

$$q_t = q_0 + t \times q_{add} \quad (\text{A11.20})$$

where q_t is the catchability in year t , q_0 is the catchability in the first year for which data are available (time zero), and q_{add} is the constant absolute amount by which the catchability is incremented each year. Estimation of the two parameters involves finding the gradient, q_{add} , and intercept, q_1 , of a linear regression between q_t and time t , where t ranges from 0 to $n - 1$ years (a total of n years).

In the model, for each year, the implied estimate of q_t is obtained by dividing each observed catch rate (I_t) by the estimated biomass for that year:

$$\hat{q}_t = \frac{I_t}{\hat{B}_t} \quad (\text{A11.21})$$

In the maximum likelihood fit one would have a time series of expected catchability coefficients, which would be described in the model by Equation A11.20 or A11.21. Equation A11.20 has the form of a linear regression, so the equations to find the closed-form parameter estimates are thus

$$q_{add} = \frac{\sum_0^{n-1} \left((t - \bar{t}) \left[\left(\frac{I_t}{B_t} \right) - \left(\sum \left(\frac{I_t}{B_t} \right) \right) / n \right] \right)}{\sum (t - \bar{t})^2} \quad (\text{A11.22})$$

and

$$q_0 = \frac{\sum \left(\frac{I_t}{B_t} \right)}{n} - (q_{add}) \bar{t} \quad (\text{A11.23})$$

where n is the number of years of data and \bar{t} bar is the mean of the t values representing the 0 to $n - 1$ years of data (i.e., with none years of data \bar{t} bar would equal 4.0, i.e., the mean of 0 ... 8).

By estimating these parameters using the closed form, the number of parameters directly estimated by the fitting procedure is reduced, which simplifies the procedure and speeds the process.

Version 3: Constant Proportional increase— $qinc$

In the case where the catchability is assumed to increase annually by a fixed proportion, the q value for each year q_t is determined as in exponential growth or compound interest:

$$q_t = q_0 \times q_{inc}^t \quad (\text{A11.24})$$

which, when log-transformed, takes the form

$$\ln(q_t) = \ln(q_0) + t \times \ln(q_{inc}) \quad (\text{A11.25})$$

where t ranges from 0 to $n - 1$ years. In the final maximum likelihood fit one would have a time series of expected catchability coefficients that would be described in the model by Equation A11.24 or A11.25 (cf. Figure A11.1). Thus, the estimation of the two parameters involves finding the gradient ($\ln(q_{inc})$) and intercept ($\ln(q_0)$) of a linear regression between $\ln(q_t)$ and time t , where time t ranges from 0 to $n - 1$ years.

The closed-form equations are thus

$$\ln(q_{inc}) = \frac{\sum_{t=0}^{n-1} \left((t - \bar{t}) \left[\ln\left(\frac{I_t}{B_t}\right) - \left(\sum \ln\left(\frac{I_t}{B_t}\right) \right) / n \right] \right)}{\sum (t - \bar{t})^2} \quad (\text{A11.26})$$

and

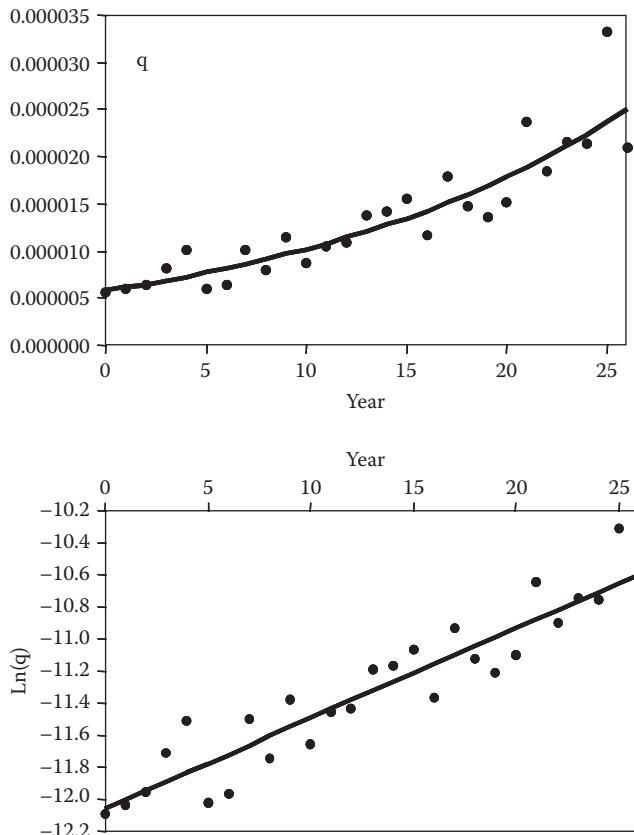
$$\ln(q_0) = \frac{\sum_{t=0}^{n-1} \ln\left(\frac{I_t}{B_t}\right)}{n} - \ln(q_{inc}) \bar{t} \quad (\text{A11.27})$$

where n is the number of years of data and \bar{t} bar is the mean number of years of data. The final parameter estimates are determined by antilogging the values from Equations A11.26 and A11.27.

Appendix 11.3: Simplification of the Maximum Likelihood Estimator

Showing the simplification of the maximum likelihood estimator for lognormal random errors. Given Equation 11.21,

$$L(\text{data} | B_0, r, K, q) = \prod_t \frac{1}{I_t \sqrt{2\pi\hat{\sigma}^2}} e^{-\frac{(\ln I_t - \ln \hat{I}_t)^2}{2\hat{\sigma}^2}} \quad (\text{A11.28})$$

**Figure A11.1**

The top panel is the final distribution of expected catchability coefficients with the fitted curve of form Equation A11.24. In order to estimate the two parameters q_0 and q_{inc} , instead of a simple geometric average of the expected q values, we have to fit the curve. By log-transforming each q_t value and plotting these against the number of times the q_{inc} is applied to the starting value a straight line is obtained, as in the lower panel. The straight line is defined by Equation A11.25, so the two parameters may be determined by antilogging the two parameters from the linear regression. Data are a bootstrap sample from the northern Australian tiger prawn fishery (see Example Box 11.6).

we can convert this to a log-likelihood:

$$LL = \sum \ln \left[\frac{1}{I_t \sqrt{2\pi} \hat{\sigma}} e^{-\frac{[(\ln(I_t) - \ln(\hat{I}_t))^2]}{2\hat{\sigma}^2}} \right] \quad (\text{A11.29})$$

Simplifying this by removing constants from the summation and cancelling the \ln and e , we obtain

$$LL = n \ln\left(\frac{1}{\sqrt{2\pi}\hat{\sigma}}\right) + \sum \ln\left(\frac{1}{I_t}\right) + \dots \\ \frac{1}{2\hat{\sigma}^2} \sum \left[-\left[(\ln(I_t) - \ln(\hat{I}_t))^2 \right] \right] \quad (A11.30)$$

where the maximum likelihood estimator of the standard deviation σ is given by

$$\hat{\sigma} = \sqrt{\frac{\sum \left[(\ln(I_t) - \ln(\hat{I}_t))^2 \right]}{n}} \quad (A11.31)$$

Note the division by n instead of $n-1$ to give the maximum likelihood estimate (Neter et al., 1996). Given Equation A11.31, we can simplify Equation A11.30 much further by substituting one into the other:

$$LL = n \ln\left(\frac{1}{\sqrt{2\pi}\hat{\sigma}}\right) + \frac{-\sum \left(\ln(I_t) - \ln(\hat{I}_t) \right)^2}{2 \sum \left(\ln(I_t) - \ln(\hat{I}_t) \right)^2} + \sum \ln\left(\frac{1}{I_t}\right) \quad (A11.32)$$

All terms can be further simplified:

$$LL = n \ln\left(\left[\sqrt{2\pi}\hat{\sigma}\right]^{-1}\right) + \left(\frac{-1}{2/n}\right) + \sum \ln(I_t^{-1}) \quad (A11.33)$$

which simplifies again to become

$$LL = -n \ln(\sqrt{2\pi}\hat{\sigma}) - \frac{n}{2} - \sum \ln(I_t) \quad (A11.34)$$

A little algebra leads to an alternative final version in A11.38:

$$LL = -n \left[\ln\left([2\pi]^{\frac{1}{2}}\right) + \ln(\hat{\sigma}) \right] - \frac{n}{2} - \sum \ln(I_t) \quad (A11.35)$$

$$LL = -n \left[\frac{1}{2} \ln(2\pi) + \ln(\hat{\sigma}) \right] - \frac{n}{2} - \sum \ln(I_t) \quad (A11.36)$$

$$LL = -\frac{n}{2} \left(\ln(2\pi) + 2\ln(\hat{\sigma}) \right) - \frac{n}{2} - \sum \ln(I_t) \quad (\text{A11.37})$$

$$LL = -\frac{n}{2} \left(\ln(2\pi) + 2\ln(\hat{\sigma}) + 1 \right) - \sum \ln(I_t) \quad (\text{A11.38})$$

The final summation is a constant and is usually omitted. If the initial negation is omitted, this would provide the negative log-likelihood.

12

Age-Structured Models

12.1 Types of Models

12.1.1 introduction

Surplus production models (Chapter 11) ignore sexual, size-, and age-based differences by treating a stock as undifferentiated biomass. Even a superficial consideration of the ecological differences to be found within and between the members of a population suggest that this assumption may be leaving out important influences on the population dynamics. An obvious example would be the time delays present in the dynamics of populations that have a number of years between biological recruitment as juveniles and sexual maturity. In a favourable year, leading to a strong year class, there will be a major increase in stock biomass, but it may take a few years before that biomass starts to contribute to reproduction. By lumping growth, reproduction, and mortality into one production function, dynamic interactions between these processes are ignored.

The obvious solution is to differentiate a stock's biomass into component parts. To describe the dynamics of the population, we will still need to account for recruitment, growth, and mortality, but these processes will either have to be dealt with separately or be included in however the stock biomass is subdivided. Thus, we could generate production models of a stock in which the two sexes are differentiated. Similarly, one could generate a length-structured model of stock dynamics, as briefly discussed in Chapter 8 on growth (Section 8.3.5; Sullivan et al., 1990). The most commonly used option, however, is to subdivide the population into age classes or cohorts and follow the dynamics of each cohort separately, combining them when inputs to the dynamics, such as recruitment, and outputs, such as yield, are being considered. Of course, to utilize age-structured methods, it must be possible to age a species accurately, or at least with a known error rate. There are methods for accounting for ageing error, but ideally the ageing should be highly accurate and with low bias.

The age-structured models to be discussed in this chapter are relatively complex and have more parts than the models presented in earlier chapters.

Indeed, the example boxes will need to be generated in sections to account for the model complexity. In fact, rather than using Excel to work with these models, it will usually be more efficient to adopt a programming language and write custom programs to conduct the model fitting. If a modeller wishes to utilize such complex models, then eventually the need for expertise in a programming language becomes essential. Which language is used is not an issue, as there are active modellers using Pascal, Fortran, C, C++, Visual Basic, APL, and others. Fortran used to be the language of choice among fishery modellers (the new Visual Fortran 90 and 95 is a nicely versatile and very fast language), but C++ is now gaining headway. Personally, I find C++ to be more of a computer programmer's language requiring a higher level of programming skill than that needed in, say, Pascal or Fortran. However, as with all software, the choice is up to particular users, and generally all languages permit the necessary speed and complexity.

Despite this need for custom programs we will continue to use Excel in the examples in this chapter. We will only be considering relatively simple age-structured models, but even so in one of the models we will attempt to estimate twenty-nine parameters. This chapter only aims to introduce some of the more important ideas behind age-structured models. It does not investigate all of their intricacies and will only attempt to describe a fraction of the range of possibilities. Detailed reviews of age-structured models, such as those by Megrey (1989) and Quinn and Deriso (1999), provide a great deal more information and detail about the complexities and other developments possible with this class of models. To treat these models with the same detail as that given to the simpler models in this book would require a much larger book.

In this chapter we will first generalize the standard catch curve (Beverton and Holt, 1957) into a dynamic system of equations simulating the dynamics of an age-structured population. We will then provide a very brief introduction to cohort analysis (Gulland, 1965, cited in Megrey, 1989; Pope, 1972), followed by an introduction to statistical catch-at-age methods (Doubleday, 1976; Methot, 1989, 1990). In this latter section we will also consider the algorithms necessary to conduct bootstrap estimates of uncertainty around parameter estimates and model outputs. There have been developments in the public provision of generalized catch-at-age software (SS3; originating from Methot, 1990, now based in AD-Model Builder), and any serious user should consider this option (Methot, 2009).

We have already considered some of the fundamentals of the dynamics of cohorts in the coverage of yield-per-recruit in Chapter 2 and in the Monte Carlo simulation of catch curves in Chapter 7. Following the dynamics of each cohort has the advantage that after each cohort has recruited, assuming there is no immigration or emigration, the numbers present in the population can only decline. Age-structured models are founded on the basis that a careful examination of this decline can provide information on the total mortality being experienced. If there is an estimate of the natural mortality

TABLE 12.1

Number of North Sea Plaice in Each of Nine Age Classes, Landed at Lowestoft per 100 Hours Fishing by British First-Class Steam Trawlers from 1929 to 1938

Year/Age	2+	3+	4+	5+	6+	7+	8+	9+	10+	Effort
29/30	328	2,120	2,783	1,128	370	768	237	112	48	5.81
30/31	223	2,246	1,938	1,620	302	106	181	58	18	5.84
31/32	95	2,898	3,017	1,150	591	116	100	82	33	4.97
32/33	77	606	4,385	1,186	231	138	42	21	51	4.91
33/34	50	489	1,121	4,738	456	106	80	27	18	5.19
34/35	44	475	1,666	1,538	2510	160	50	43	14	4.94
35/36	131	1,373	1,595	1,587	1,326	883	144	30	28	4.63
36/37	38	691	2,862	1,094	864	382	436	27	15	4.44
37/38	138	1,293	1,804	1,810	426	390	163	228	26	4.39

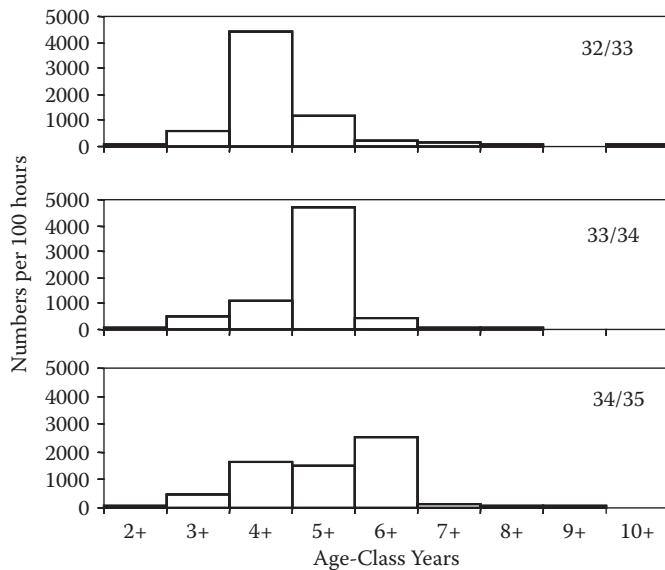
Source: Data from Table 13.1 in Beverton, R. J. H., and Holt, S. J., *U.K. Ministry of Agriculture and Fisheries, Fisheries Investigations* (Series 2), 19, 1–533, 1957.

Note: The fishing year is April 1 to March 31. The + symbol after the age indicates that a fish of $t+$ years is in its $t + 1^{\text{th}}$ year, somewhere between t and $t + 1$ years old. Note there are relatively strong year classes, such as the one highlighted, which would have arisen in 1928–1929. Despite being standardized to the same levels of effort the 5+ group in 33/34 is larger than the 4+ group in 32/33. This suggests that the early ages are not fully selected (Figure 12.1). Effort is in millions of steam trawler hours fishing (from Table 14.15 in Beverton and Holt, 1957).

then, clearly, deductions can be made concerning the exploitation rates of each cohort.

As with surplus production models, we need to have data on the total catch (fishing mortality can include discarding mortality) as weight, but we also need data on the numbers-at-age in the catch. Ideally, for each year of the fishery, there will be an estimate of the relative numbers caught in each age class (e.g., Table 12.1). Effort information or some index of relative abundance is also required to obtain an optimum fit in all of the models. Beyond this minimum there are many other forms of information that can be included in such stock assessment models. Such information might include estimates of annual recruitment, stock biomass estimates, catch rates, and the mean length and weight of animals in the catch.

A commonly observed phenomenon in age-structured data is the progression of year classes (Table 12.1, Figure 12.1). This also provides evidence that the ageing of the animals concerned is at least consistent through time, and also that the ring counts used to age the animals actually relate to yearly increments. Note also that the absolute numbers and proportions caught in each year do not necessarily decline through time as one might expect. If the availability of each age class changes from year to year, for example, for reasons of selectivity, or through different fishing gear being used, or different people doing the fishing, then a simple progression of the cohorts will not be observed. The North Sea plaice data (Table 12.1) are standardized to a constant amount of the same kind of effort so, after the species is fully selected

**Figure 12.1**

Progression of a relatively strong year class (recruited into the population as 0+ in 1928–1929) through the population of North Sea plaice over the three years from 1932–1933 to 1934–1935 (Table 12.1). The fishery is primarily imposed upon three- to seven-year-old fish. (Data from Beverton, 1957.)

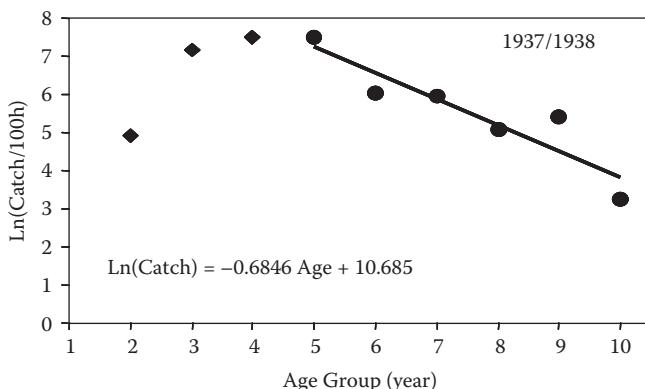
by the gear (age 5+ and older), the numbers always decline from one year and age to the next (Figure 12.1).

Data on catch and catch-at-age will provide information regarding the population dynamics. However, for stock assessment purposes, some index of relative abundance through time is required to strengthen the attachment of the model to changes in stock size through time or to provide robust estimates of fishing mortality. A suitable index could use catch rates or the effort imposed to obtain the standardized catches, or even fishery-independent survey estimates. In summary, the minimum data requirements are the commercial catches, the catch-at-age as numbers, and effort or some index of relative abundance through time.

12.1.2 Age-Structured Population Dynamics

As demonstrated in Chapters 2 and 7, if there is no emigration or immigration, then, after recruitment, the numbers in any cohort will decline exponentially through time with a rate of decline equal to the instantaneous total mortality rate:

$$N_y = N_0 e^{-Zy} \quad (12.1)$$

**Figure 12.2**

Natural logarithm of the average number of North Sea plaice in each age group caught per one hundred hours fishing by a first-class steam trawler in 1937–1938. (Data from Beverton and Holt, 1957.) The negative gradient of the slope estimates the total mortality $Z = 0.685$. Age groups 2 to 4 are omitted from the regression because they are not fully selected by the fishing gear. The elevated value in the ninth age group derives from the strong year class that arose in 1928–1929 (Table 12.1).

where N_y is the numbers in year y , N_0 is the initial recruitment into the cohort, and Z is the instantaneous rate of total mortality (M is natural mortality and F is fishing mortality; $Z = M + F$). A log transformation leads to the familiar

$$\ln(N_y) = \ln(N_0) - Zy \quad (12.2)$$

which has the form of a linear relationship and is the basis of the classical catch curve (Figure 12.2; Beverton and Holt, 1957). There are two kinds of catch curves possible. The first samples all age classes present in a particular year, assumes the system is in equilibrium, and treats the proportions of the different age classes as if they were the product of a single cohort (Figure 12.2). The major assumptions here are that there has been a constant recruitment level in all years, that all ages have been exposed to the same history of fishing mortality (fishing mortality is constant across years), and that after age 4+ all animals are fully selected and have the same catchability. One problem with using this snapshot approach is that standardizing the data collected to a constant amount of effort using a particular gear does not necessarily remove all occasions where an age class is more numerous than the previous age class (e.g., age groups 8 and 9 in Figure 12.2). This is a combination of a failure of all or some of the assumptions of this approach to catch curves and also may reflect the impact of sampling error. The assumption of constant recruitment is particularly unlikely, as demonstrated by the strong year classes evident in Table 12.1.

The second kind of catch curve follows the fate of single cohorts (Figure 12.3). This approach is more difficult because it relies on standardizing the catch

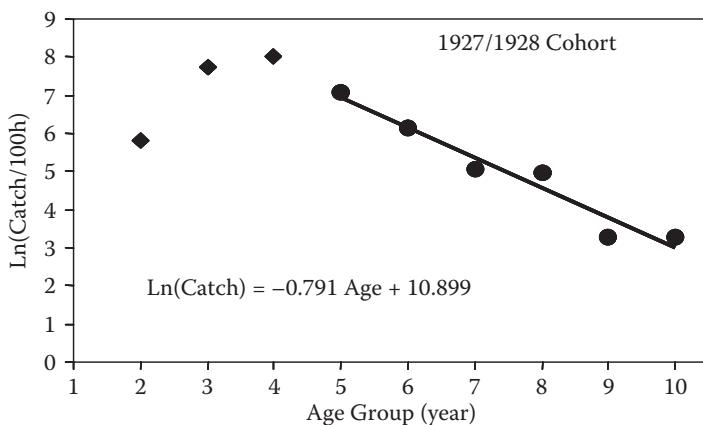


Figure 12.3

A catch curve following the average number of North Sea plaice from a single cohort caught per one hundred hours fishing by a first-class steam trawler over the years 1929 to 1938 (Table 12.1). (Data from Beverton and Holt, 1957) The negative gradient of the slope estimates the total mortality $Z = 0.791$. Age groups 2 to 4 are omitted from the regression because they are not fully selected by the fishing gear (despite, in this instance, age 4 appearing to be selected as well as later ages).

of the cohort being followed to a given amount of effort with a particular type of fishing gear. This is necessary because if catchability varied between years, then cohort numbers would not always decline in the steady fashion required by the catch curve methodology. Also, of course, many more years of comparable sampling are required to generate a single catch curve.

In Chapter 7, a Monte Carlo simulation of an age-structured population was produced that included variable recruitment and sampling error (Section 7.4.3; Example Boxes 7.6 and 7.7). This used the approach of sampling the whole population in any one year and treating the combination of many cohorts as a single pseudocohort to be analyzed.

The next step would be to extend Equation 12.1, which deals solely with ages within a given year, to add sequential years to the system. Obviously, the system has to start somewhere, and there are two alternatives commonly used when conducting stock assessments of age-structured populations.

The first is to assume the modelling starts at the beginning of exploitation and to ascribe an equilibrium age structure to the starting population. The second is to directly estimate the starting numbers-at-age in the model (this has the obvious disadvantage of adding the same number of parameters as there are age classes to the estimation problem). At equilibrium, in an unexploited population, the age structure would be the result of natural mortality acting alone upon the average virgin levels of recruitment. Thus, the relative numbers in each age class in the initial year would be equivalent to the single-year catch curve where all of the assumptions have been met:

$$N_{a,1} = \begin{cases} R_{0,1} & a = 0 \\ N_{a-1,1}e^{-M} & 1 \leq a \leq a_{\max} - 1 \\ N_{a_{\max}-1,1}e^{-M}/(1-e^{-M}) & a = a_{\max} \end{cases} \quad (12.3)$$

where $N_{a,1}$ is the numbers of age a , in year 1, a_{\max} is the maximum age modelled (the plus group), and M is, as usual, the instantaneous rate of natural mortality. Recruitment variability has been omitted from Equation 12.3, but this will be addressed later. In a preexploitation population there is no fishing mortality. The final component of Equation 12.3, where $a = a_{\max}$, is referred to as the plus group because it combines ages a_{\max} and all older ages that are not modelled explicitly. The inclusion of the $(1 - e^{-M})$ divisor forces the equation to be the sum of an exponential series (Example Box 12.1).

After initial conditions are defined (e.g., Example Box 12.1), the population will grow approximately in accord with some stock recruitment relationship and the mortality imposed naturally and via fishing pressure. In yearly steps, the numbers in each age class in each year will depend on the numbers surviving from the preceding age class from the preceding year:

$$N_{a+1,y+1} = N_{a,y}e^{-(M+s_a F_y)} \quad (12.4)$$

which is the numbers at age a in year y , multiplied by the survivorship (e^{-Z}) after natural mortality M , and $s_a F_y$ the selectivity for each age a times the fully selected fishing mortality in year y . This is equivalent to the catch curve equation and could be transformed into a linear format. Not all age classes are necessarily fully selected; thus, the fishing mortality term must be multiplied by the selectivity associated with the fishing gear for age a , s_a . We use a lowercase s for selectivity to leave the uppercase S for the survivorship term. We also need a term for the recruitment in each new year, and this is assumed to be a function of the spawning biomass of the stock in the previous year y , B_y^s (Example Box 12.2); thus,

$$N_{a,y+1} = \begin{cases} f(B_y^s) = R_{0,y+1} & a = 0 \\ N_{a-1,y}e^{-(M+s_{a-1} F_y)} & 1 \leq a \leq a_{\max} - 1 \\ N_{a_{\max}-1,y}e^{-(M+s_{a-1} F_y)} + N_{a_{\max},y}e^{-(M+s_a F_y)} & a = a_{\max} \end{cases} \quad (12.5)$$

where the plus group is modelled by applying the total mortality to the preceding age class and the maximum age class in the preceding year. These two cannot be combined prior to multiplication by the survivorship term if the selectivities of the two age classes are different (Example Box 12.3).

EXAMPLE BOX 12.1

An equilibrium age-structured simulation model illustrating the initial age structure (using Equation 12.3). The selectivities in row 11 are constants, but an equation could be used. In B9 put =\$E\$1*(1-exp(-\$E\$2*(B12-\$E\$3))) and in B10 put =\$E\$4*B9*\$E\$5. Select B9:B10 and copy across to column K. Copy C13 across to column J, and in K13 put =J13*exp(-M)/(1-exp(-M)) to obtain the plus group. Copy C7 across to column K and modify K7 to be =J7*exp(-M)/(1-exp(-M)) to obtain the per-recruit numbers at age. Copy C8 into B8 and into D8:K8 to obtain the biomass per recruit, needed for the estimation of the stock recruitment relationship. To test the plus-group calculation, record the value in K13 (133) and extend the ages across to age 25 in column AA; then copy J13 across to column AA and in K6 put =sum(K13:AA13). This summation should also equal 133. B13 is the first term, C13:J13 is the second, and K13 is the third term from Equation 12.3 (see Example Boxes 12.2 and 12.3 to fill column O).

	A	B	C	D	E	~	J	K
1	Steepness	0.75		Linf	200			
2	Nat Mort	0.4		K	0.45			
3	Bzero	1000		t0	-0.02			
4	a Recruit	=1/O2		a_Wt	0.0002			
5	b Recruit	=O1/O2		b_Wt	3			
6	R0	=O3		q	0.0005			
7	Rec_Nage	1	=B7*exp(-\$B\$2)	0.4493	0.3012	~	0.0408	0.0829
8	Rec_Biom	1E-06	=C7*C10/1000	0.153	0.1977	~	0.0601	0.1259
9	Length	1.8	73.6	119.4	148.6	~	194.6	196.5
10	Weight	0.0012	79.793	340.57	656.49	~	1473.5	1518.5
11	Selectivity	0	1	1	1	~	1	1
12	Year/Age	0	1	2	3	~	8	9
13	1967	=B6	=B13*exp(-\$B\$2)	720	482	~	65	133

Compare Equation 12.5 with Equation 12.3 to see the impact of including fishing mortality.

The spawning biomass is defined as

$$B_y^s = \sum_{a=c}^{a_{\max}} w_a N_{a,y} \quad (12.6)$$

where w_a is the average weight of an animal of age a , c is the age of sexual maturity, and a_{\max} is the maximum age class. The weight can be determined

EXAMPLE BOX 12.2

The derivation of the recruitment parameters from the growth and mortality rates. This section of the worksheet should be added to that given in Example Box 12.1. The explanations behind these equations and their relationships are given in Section 10.9.3 and Example Boxes 10.7 and 10.8. The alpha and beta in column O are used to calculate the Beverton and Holt stock recruitment parameters in B4:B6.

	M	N	O
1	Alpha	=N4*(1-B1)/(4*B1*N3)	=O4*(1-B1)/(4*B1*O3)
2	Beta	=(5*B1-1)/(4*B1*N3)	=(5*B1-1)/(4*B1*O3)
3	R0	=N4/N5	=O4/O5
4	B0	=N5	=B3
5	A0	=sum(E8:K8)*exp(-B2)	=N6
6	A0/Rec	=N5/B7	

empirically by market measuring or from a growth curve derived independently of any model fitting (Example Box 12.1)

$$w_a = a \left[L_\infty \left(1 - e^{-K(a-a_0)} \right) \right]^b \quad (12.7)$$

where the constants a and b alter the von Bertalanffy growth curve into a curve relating to mass (see Chapter 9). The fully selected fishing mortality rate can be determined if there is an estimate of the catchability coefficient and measures of the relative effort imposed each year:

$$\hat{F}_y = \hat{q} E_y e^e \quad (12.8)$$

These estimated fishing mortality rates could be used when fitting the model.

One way of defining the recruitment terms was described in Chapter 10 on recruitment (Section 10.9.3 and Example Boxes 10.7 and 10.8; Example Box 12.2).

12.1.3 Fitting Age-Structured Models

The series of equations represented in Example Boxes 12.1 to 12.3 provide for a relatively simple simulation of an age structure population starting from equilibrium. The end product is a matrix of numbers-at-age for the population after it has been exposed to natural and fishing mortality. Many of the features used to illustrate the simulation of an age-structured population are also used when the objective is to fit an age-structured model to observations

EXAMPLE BOX 12.3

Extension of Example Boxes 12.1 and 12.2. The years extend down to 1979 in row 25. Effort is arbitrary values between 50 and 1,200. Row 13 is explained in Example Box 12.1. To generate the spawning biomass from each year, put =sumproduct(C13:K13,\$C\$10:\$K\$10)/1000 into L13 and copy down to row 25. Put =E\$6*O14 into N14 and copy down to row 25. To reflect Equation 12.5, generate the expected recruitment from the spawning biomass and put =B\$4*\$L13/(\$B\$5+\$L13)*loginv(rand(), 0,M14) into B14. Into C14, put =B13*exp(-(\$B\$2+B\$11*N14)) and copy across to J14. Finally, into K14 put =J13*exp(-(\$B\$2+J\$11*N14))+K13*exp(-(\$B\$2+K\$11*N14)) to generate the plus group. Select B14:K14 and copy down to row 25 to complete the matrix of numbers at age. The sig_r introduces random variation into the stock recruitment relationship. To remove its effects make the values in column M very small; this, approximately, enables the deterministic behaviour to be exhibited. If you set all the effort values to zero, only natural mortality will occur and the population will stay in equilibrium except for the effects of recruitment variability on the lower half of the matrix. If you set sig_r to 0.000001 and have a constant effort, then the whole population will attain an equilibrium. By plotting each year's numbers as a series of histograms vertically above each other (as in Figure 12.1), relatively strong year classes should be visible through time (press F9).

	A	B	C	D	~	J	K	L	M	N	O
12	Yr\Age	0	1	2	~	8	9	Bs	sig_r	F	Effort
13	1967	=B6	1074	720	~	65	133	1822.6			
14	1968	2118	1074	720	~	40	81	1235.6	0.5	0.5	1000
15	1969	1914	1420	720	~	25	51	1014.7	0.5	0.45	900
16	1970	2380	1283	952	~	13	25	847.0	0.5	0.7	1400
17	1971	2078	1595	860	~	11	22	1080.8	0.5	0.15	300
18	1972	2516	1393	1069	~	10	19	1315.8	0.5	0.125	250

made on a fishery. As stated before, the minimum data required comprise the relative catch-at-age for a number of years of the fishery, plus some estimate of effort imposed upon the fishery through time or some index of relative abundance. The aim, when fitting the model, will be to attempt to back-calculate a matrix of numbers-at-age that would have given rise to the observed catches, given the imposed fishing effort (or catch rate) and estimates of the catchability coefficient and the selectivity coefficients. We will introduce the two main strategies used for conducting such analyses.

Virtual population analysis (VPA) was the analytical strategy developed first, and this relies on the idea that if one has records of the catch-at-age

of a set of cohorts until the cohorts all die off, then one should be able to literally back-calculate what the numbers-at-age must have been. In this way the numbers in the population can be projected backwards until estimates are obtained of the original recruitments. This requires an estimate of the natural mortality and estimates of the fishing mortality by age and year.

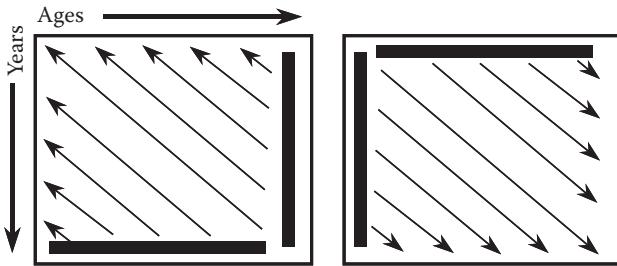
The data requirements for a VPA are fairly stringent in that there can be no years of missing information if the calculations are to continue uninterrupted. VPA models are sometimes referred to as cohort analysis, although Megrey (1989) indicates some differences. The number of parameters estimated equals the number of data points available, so neither approach is fitted to fisheries data using an objective function, such as by minimizing a sum of squared residuals or a negative log-likelihood. Instead, solutions to the model equations are determined through iterative, analytical methods. There are many alternative VPA fisheries models (Megrey, 1989), but we will only consider one of the simplest.

The second analytical strategy appears to be the reverse of the first and goes under a number of names. Methot (1989) termed this approach the synthetic analysis, but others have referred to this analytical strategy as integrated analysis (Punt et al., 2001). Given equations describing the population dynamics, such that if we know $S_{a,y}$ the survivorship of age a to age $a + 1$ from year y to $y + 1$, and that $N_{a+1,y+1} = S_{a,y}N_{a,y}$, then, given knowledge of the initial population in year 1 and of the recruitments in each subsequent year, the numbers-at-age for the full population can be calculated. This approach requires the model to be fitted to data using some form of minimization routine. The parameter estimates include the initial population age structure, the recruitment levels in each year, the selectivity by age class, and often other parameters as well. It is common to estimate tens of parameters, and models exist that estimate hundreds of parameters. Of course, the number of parameters that can be estimated efficiently in any model will be at least partly determined by the number of independent data points available. The point is, however, that although integrated analyses share some equations with cohort analysis, the methods differ fundamentally from each other (Figure 12.4). A knowledge of both methodologies is helpful in fisheries stock assessment.

12.2 Cohort Analysis

12.2.1 introduction

Given that we are dealing with cohorts, the change in the numbers in each cohort can be derived each year from the numbers at age a at the start of year y , $N_{a,y}$, and the survivorship during that year, as in Equation 12.4 (where

**Figure 12.4**

Alternative analytical strategies adopted in efforts to model commercial fisheries using age-structured information. The general objective is to estimate a vector of numbers-at-age or fishing mortalities-at-age for each year of the fishery. The left-hand panel relates to cohort analysis/VPA, while the right-hand panel reflects integrated analysis or statistical catch-at-age. In cohort analysis, the calculations proceed given knowledge of all ages in the last year and the last age class in all years, and projecting backwards through time and ages. In statistical catch-at-age, knowledge is assumed of all ages in the first year and the first age class in all years (recruitment), projecting the cohorts forward through time and ages.

M and F are the instantaneous rates of natural and fishing mortality, and s_a is the age-specific selectivity of the fishing gear used):

$$N_{a+1,y+1} = N_{a,y} e^{-(M+s_a F_y)} = N_{a,y} e^{-M} e^{-s_a F_y} \quad (12.9)$$

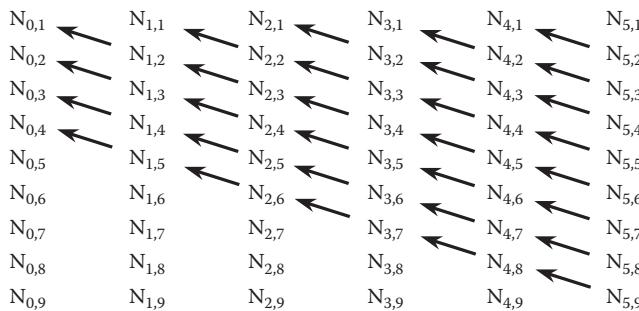
Unfortunately, the number of fish present in early years is unknown, so forward projections cannot be made. However, there will be an age at which the number of fish remaining in the cohort is effectively zero. We can rearrange Equation 12.9 to start at a known number of fish in the oldest age class and back-project the population until we reach the age of recruitment (which need not be age 0). Thus, if we have an estimate of natural mortality and an age class in which the number of survivors is trivially small, then the fishing mortality for each age in each year can be estimated by back-calculating from the catches, $C_{a,y}$, and the natural mortality; this implies that there are as many parameter estimates as there are data points. Given

$$N_{a,y} - C_{a,y} = N_{a,y} e^{-s_a F_y} \quad (12.10)$$

rearrange Equation 12.9 to give

$$N_{a,y} = \frac{N_{a+1,y+1}}{e^{-M}} + C_{a,y} \quad (12.11)$$

While Equation 12.11 provides a mechanism for calculating the relative numbers at age in each year, it is limited to complete cohorts (those that reach the maximum age class considered; Figure 12.5).

**Figure 12.5**

A table of numbers-at-age in each year showing the backward progression of cohorts from their last age class. The columns represent age classes (first subscript), while the rows represent nine years of data (second subscript). The arrows represent the direction of calculation using Equation 12.11. Only completed cohorts, which have attained an age at which negligible animals remain, can be back-projected validly. This means that we are most uncertain about the most recent cohorts, the ones of most current interest.

One of the ways in which the many variants of VPA/cohort analysis differ is in how they address this problem of incomplete cohorts (Megrey, 1989; in Edwards and Megrey, 1989). Given a_{MAX} age classes, in the last year of data there will be $a_{\text{MAX}} - 1$ incomplete year classes; these will be along the bottom of the numbers at age matrix but will not have reached the maximum age. Some way of estimating the fishing mortality rate in these age classes in the final year of data is required to complete the table of estimates of numbers-at-age in each year. These fishing mortality rates are referred to descriptively as terminal F estimates.

The data available include the catch-at-age and effort data. There is more than one way to fit a cohort analysis model (referred to by Megrey, 1989, as sequential population analysis (SPA)) to these data. We can either generate a fit directly to the fishing mortality rates for each age in each year, or fit to the numbers-at-age in each year. It is an odd fact that some of the seminal papers in fisheries modelling are published in obscure places (e.g., Gulland, 1965, cited in Megrey, 1989). Fortunately, alternative listings of these developments are available (Gulland, 1983; Megrey, 1989; Hilborn and Walters, 1992).

12.2.2 The equations

The basic equation relating the numbers in a cohort in one year to those in the previous year is

$$N_{y+1} = N_y e^{-(M+F_y)} \quad (12.12)$$

where N_y is the population size in year y , and M and F are the instantaneous rates of natural and fishing mortality, respectively. This implies that $e^{-(M+F)}$ is the survivorship, the proportion of a population that survives from year to

year. The survivorship itself can be determined simply as the ratio of numbers from one year to those in the year previous (starting from the last age class whose numbers are known from the catch data):

$$\frac{N_{y+1}}{N_y} = e^{-(M+F_y)} = e^{-M} e^{-F_y} \quad (12.13)$$

The complement of survivorship would be the total loss from year to year, and this can be represented a number of ways:

$$N_y - N_{y+1} = N_y - N_y e^{-(M+F_y)} = N_y (1 - e^{-(M+F_y)}) \quad (12.14)$$

The catch each year would be the proportion of this total loss due to fishing:

$$C_y = \frac{F_y}{M + F_y} N_y (1 - e^{-Z_y}) = \frac{F_y}{M + F_y} [N_y - N_{y+1}] \quad (12.15)$$

which is the total loss by the proportion of mortality due to fishing. It would be possible to remove explicit mention of F_y from Equation 12.15 if we solved Equation 12.13 for F_y :

$$\frac{1}{e^{-F_y}} = \frac{N_y}{N_{y+1}} e^{-M} \quad (12.16)$$

remembering that $1/e^{-F_y} = e^F_y$, we can log-transform Equation 12.16 to give F_y :

$$F_y = \ln\left(\frac{N_y}{N_{y+1}}\right) - M \quad (12.17)$$

This puts us into a position of being able to estimate the catch-at-age from knowledge of the catches, the final N_{y+1} , and a given value for M , and these estimates can be used to fit the model to the data:

$$C_y = \frac{\ln(N_y/N_{y+1}) - M}{\ln(N_y/N_{y+1}) - M + M} [N_y - N_{y+1}] \quad (12.18)$$

Equation 12.18 simplifies to

$$C_y = \left(1 - \frac{M}{\ln(N_y/N_{y+1})}\right) [N_y - N_{y+1}] \quad (12.19)$$

or

$$0 = \left(1 - \frac{M}{\ln(N_y/N_{y+1})}\right) [N_y - N_{y+1}] - C_y \quad (12.20)$$

There is no direct analytical solution to Equation 12.20, but there are two ways in which the equation may be solved to produce a matrix of numbers-at-age that would balance Equation 12.20.

12.2.3 Pope's and MacCall's Approximate Solutions

An approximate solution to Equation 12.20 can be used to give the required matrix of numbers-at-age. Pope (1972) produced the following approximation (note that the exponents are positive):

$$N_y = N_{y+1}e^M + C_y e^{M/2} \quad (12.21)$$

which derives from Equation 12.12:

$$\frac{N_{y+1}}{e^{-F}e^{-M}} = N_y = N_{y+1}e^M e^F \quad (12.22)$$

Pope's (1972) advance was to introduce the discrete approximation of using the addition of $C_y e^{M/2}$ to be equivalent in effect to the multiplication by e^F . Being discrete changes the multiplication in Equation 12.22 into an addition but assumes that all fishing occurs instantaneously in the middle of the year (hence the $e^{M/2}$ to account for natural mortality acting before the fishery operated). Pope (1972) showed that his approximation was usable with values of M up to 0.3 and F of 1.2 over the time periods used in the model. Thus, if M or F is greater than these limits, cohort analysis can still be used if the catch-at-age data can be divided into shorter intervals than one year. MacCall (1986) provided an alternative approximate solution that was an improvement over Pope's (1972) equation:

$$N_y = N_{y+1}e^M + C_y \left(\frac{M}{1 - e^{-M}} \right) \quad (12.23)$$

MacCall's equation behaves rather better at higher values of M and is also less sensitive to the assumption that all the catch is taken halfway through the fishing year (Example Box 12.4).

It is no longer necessary to use the approximations by Pope (1972) and MacCall (1986), but they can still be used as the starting point for the second approach that can be used to solve Equation 12.20.

12.2.4 Newton's Method

Classical analytical methods can be used to find values of N_y and N_{y+1} for each cohort that will solve Equation 12.20 so that it approximates to zero. Newton's method provides a simple and powerful method for finding the roots of a function of the form $f(N_y) = 0$ (Jeffrey, 1969). This is an iterative

EXAMPLE BOX 12.4

Two alternative approximate calculations of the matrix of numbers-at-age (Equations 12.21 and 12.23) by Pope (1972) and MacCall (1986). This worksheet will become much larger, so care is needed in its construction. Extend the column labels in row 5 across to column J with 4+, 5+, ..., 10+. Fill in the catch-at-age data from Table 12.1. Copy the column and row labels across into L5:U5 and L6:L14, respectively. Name cell J17 as M , the natural mortality rate, or use $\$J\17 wherever we need M . In U6 put $=V7*\exp(M)+J6*\exp(M/2)$ and copy it down to U14 to obtain Pope's approximation (column V is deliberately empty). Copy U6:U14 back across to column M to create the matrix of values. Select L5:U14 and copy the contents, select A19 and paste as values (edit/paste special/values; <Alt>ESV). Fishing mortalities and other statistics may be calculated from this matrix. This new matrix, denoting an approximation to the numbers-at-age, in B20:J28, will contribute to the extension of this worksheet in Example Box 12.5, as will I15:J16. In A18 put the text "Numbers-at-Age." To compare the results with those obtained from MacCall's (1986) approximation, create another table with row labels in W5:W14 and column labels in X5:AF5. Column V must be left clear or else the calculations in column U will receive interference (trace the precedents of U6). In AF6 put $=AG7*\exp(M)+J6*(M/(1-\exp(-M)))$ and copy down to AF14. Copy AF6:AF14 across to column X to generate the matrix. Compare this with the results from Pope's (1972) approximation. Notice that the values from MacCall's method tend to be slightly smaller than those from Pope's method. The absolute values are of less interest than the relative proportions by age, and while these still differ the differences are less marked. Consider the values in row 14 from column M to T. They also have no preceding data (no N_{y+1}) and yet are not the end of a cohort. Is this important?

	A	B	C	~	J	~	L	M	~	R	S	T	U
4	Catch-at-Age		Approximation to Numbers-at-Age										
5	Year\Age	2+	3+	~	10+	~	Y/A	2+	~	7+	8+	9+	10+
6	29/30	328	2120	~	48	~	29/30	15283.6	~	1409.2	414.6	153.1	54.4
7	30/31	223	2246	~	18	~	30/31	38952.0	~	348.0	419.7	113.7	20.4
8	31/32	95	2898	~	33	~	31/32	13196.1	~	276.6	177.5	167.1	37.4
9	32/33	77	606	~	51	~	32/33	11922.0	~	420.3	113.0	50.0	57.8
10	33/34	50	489	~	18	~	33/34	7664.2	~	284.9	205.5	51.0	20.4
11	34/35	44	475	~	14	~	34/35	11736.4	~	503.6	128.3	89.5	15.9

continued

EXAMPLE BOX 12.4 (continued)

	A	B	C	\sim	J	\sim	L	M	\sim	R	S	T	U
12	35/36	131	1373	\sim	28	\sim	35/36	4524.2	\sim	2060.9	251.0	55.8	31.7
13	36/37	38	691	\sim	15	\sim	36/37	1924.4	\sim	670.0	825.8	68.4	17.0
14	37/38	138	1293	\sim	26	\sim	37/38	156.4	\sim	441.9	184.7	258.4	29.5
15	Use Terminal F												
16			Limit										
17			M	0.25									

method in which the solution is modified by the ratio of the function and the first differential of the function:

$$N_y^{Updated} = N_y^{Orig} - \frac{f(N_y^{Orig})}{f'(N_y^{Orig})} \quad (12.24)$$

Starting from the first iteration, N_y^{Orig} would be the individual elements of the numbers-at-age matrix derived from one of the approximations listed earlier. The modifier is made up of $f(N_y^{Orig})$, which would be Equation 12.20 for each particular age and year being considered. This means that $f'(N_y^{Orig})$ is the differential of Equation 12.20 with respect to N_y :

$$f'(N_y^{Orig}) = 1 - \frac{M}{\ln(N_y/N_{y+1})} + \frac{(1 - N_{y+1}/N_y)M}{(\ln(N_y/N_{y+1}))^2} \quad (12.25)$$

There are no N_{y+1} when the N_y in the last age class are being considered (e.g., in the North Sea plaice example there is no 11+ age class), so Equation 12.25 would fail if applied without modification. Thus, when N_{y+1} is zero one can use

$$f(N_y^{Orig}) = \left(1 - \frac{M}{\ln(N_y)}\right)N_y - C_y = 0 \quad (12.26)$$

and

$$f'(N_y^{Orig}) = 1 - \frac{M}{\ln(N_y)} + \frac{M}{(\ln(N_y))^2} \quad (12.27)$$

Obviously, if N_y is zero, there can be no older animals in that cohort, so one should return a zero.

When Equation 12.24 is completed to include both Equations 12.20 and 12.25, along with the option of Equations 12.26 and 12.27, the result looks

dauntingly long and complex. Fortunately, the elements are simple, and with care they are easily implemented, even in Excel (see Example Box 12.5).

In operation, the initial guess at the numbers-at-age matrix (from one of the approximations) is updated using the function to be solved and its differential, as in Equation 12.24. Then the original values are replaced by the updated, which leads to a new set of updated values. This iterative process is repeated until no perceptible difference between the original and the updated values is observed. Usually, a stopping rule needs to be defined that stops the iterations once some threshold similarity has been reached (see Example Box 12.5, Figure 12.6).

12.2.5 Terminal F estimates

In the last age class the assumption is that the cohort will all die out. It is this termination of the cohort in the fishery that permits the backwards calculation of the numbers-at-age from the catch data and the natural mortality estimate. However, in the last year of data not all age classes will represent completed cohorts. If there are A year classes, then there will always be an $A - 1 \times A - 1$ triangle of incomplete cohorts arrayed along the bottom left of the numbers-at-age matrix. If we are to calculate their relative abundance in a valid manner, we must find a way to estimate the numbers-at-age in the unknown lower-left triangle of incomplete cohorts. Unfortunately, these incomplete cohorts are of most interest because they will affect future stock numbers; i.e., we know least about the year classes we need to know the most about.

Direct survey estimates of numbers- or fishing mortality-at-age, perhaps using tagging, are possible but rarely made. The most common approach is to produce independent estimates of the fishing mortality experienced by the cohorts being fished. Given a value of F_y and the catch-at-age in the final year, the numbers-at-age for the incomplete cohorts may be estimated using a rearrangement of Equation 12.15:

$$N_y = \frac{C_y}{1 - e^{-Z_y}} \frac{F_y + M}{F_y} \quad (12.28)$$

The independent estimates of F_y are known as terminal F estimates and, used with Equation 12.28, can give rise to improved estimates of the numbers-at-age in the bottom row of the numbers-at-age matrix.

The terminal F estimates may be obtained through some survey method or from the standard equation $F_y = q_a E_y$. The catchability coefficients for each age class a are commonly obtained by calculating the fishing mortality rate for complete cohorts, and then, using effort data in the years in which they were fished, the catchability by age can be determined from $q_a = F_y / E_y$. Given q_a and effort in the final year, the terminal numbers-at-age may be determined from Equation 12.28 (Example Box 12.6).

EXAMPLE BOX 12.5

Gulland's cohort analysis focused on numbers-at-age. This is an extension to the worksheet generated in Example Box 12.4. It assumes that the catch-at-age data are in B6:J14 and that Pope's approximation to the numbers-at-age, as values, is in B20:J28. The matrix described below describes the modifier in Equation 12.24, i.e., it is the $f(N_y)/f'(N_y)$. The Excel equation looks terrific and great care is needed to put in the correct number of brackets. In U20 put =IF(J20>0,IF(K21>0, (((1-(M/Ln(J20/K21)))*(J20-K21))-J6)/(1-(M/Ln(J20/K21)) + (((1-K21/J20)*M)/(Ln(J20/K21)^2))), (((1-(M/Ln(J20)))*(J20)-J6)/(1-(M/Ln(J20)) + (M/(Ln(J20)^2)))),0). If you have the data entered correctly and the Pope's approximation is correct, the value in U20 should be 3.14. If this is the case, then copy U20 down to U28 and copy U20:U28 across to column M. Remember that cell J17 is named M. The equation inside the if statement has two options: first is Equation 12.20 divided by Equation 12.25, second is Equation 12.26 divided by Equation 12.27. The first option is for when both N_y and N_{y+1} are available, while the second option is for when no N_{y+1} are available. Thus, option 2 will be used in column U and in row 28. Copy the column labels down into L31:U31 and the row labels from L20:L28 into L32:L40. In U32 put =J20-U20 and copy down to U40 and copy U23:U40 across to column M. This completes Equation 12.24 and provides an updated version of the numbers-at-age. Notice that if the modifier matrix is negative in any cell this will increase the corresponding cell of the numbers-at-age matrix. Copy M32:U40 and paste as values over the top of the original numbers-at-age matrix in B20:J28. This updates the modifier, which updates the derived numbers-at-age. If this copying as values onto the original numbers-at-age matrix is repeated enough times the cells in the modifier matrix will tend to zero. In J16, put =sum(M20:U28) to enable a watch on the sum of the modifier matrix. Repeat the copying of the updated M32:U40 onto the original B20:J28 until the J16 limit is very small. At this point the numbers-at-age matrix should have stabilized to a solution. Does it appear to be closer to Pope or MacCall's approximation?

Once the spreadsheet is constructed and working it can be improved by automating the copying and pasting required in the Newton's method iterations. Buttons can be added that set up the original numbers-at-age matrix as a set of values from either Pope's or MacCall's approximations. A final button can be added that automates the copying of the updated numbers-at-age matrix as values onto the original numbers-at-age. A map of the worksheet developed in Example Box 12.5 should appear to be very similar to Figure 12.6.

continued

EXAMPLE BOX 12.5 (continued)

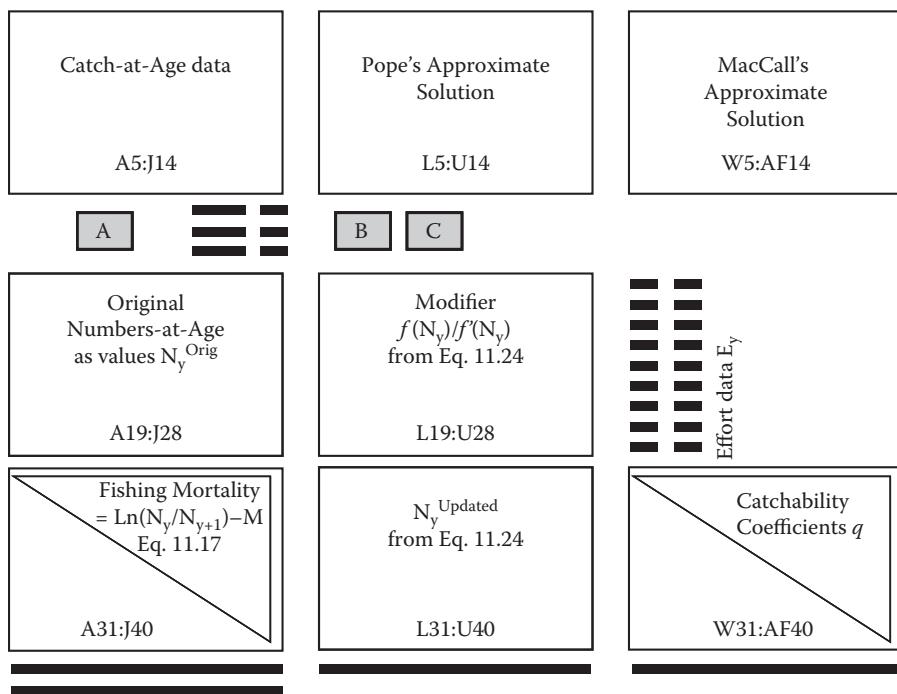
	L	M	N	O	P	Q	R	S	T	U
19	Y\Age	2+	3+	4+	5+	6+	7+	8+	9+	10+
20	29/30	1.16	22.12	43.02	25.91	6.68	18.87	6.24	4.57	3.14
21	30/31	0.69	19.53	32.07	33.47	5.54	1.35	3.30	1.30	0.75
22	31/32	0.30	16.35	54.47	28.28	12.55	2.05	2.58	1.75	1.91
23	32/33	0.24	2.77	40.53	20.89	3.54	1.89	0.65	0.37	3.39
24	33/34	0.16	2.15	8.22	75.47	7.48	1.64	1.30	0.64	0.75
25	34/35	0.13	2.46	17.58	20.62	49.09	2.12	0.81	0.89	0.46
26	35/36	0.49	10.04	25.31	28.06	33.97	16.00	3.81	0.72	1.51
27	36/37	0.13	6.23	60.53	30.06	21.99	10.01	10.25	0.45	0.53
28	37/38	11.08	125.6	178.2	178.9	38.50	34.99	13.37	19.45	1.36
~										
31	Y\Age	2+	3+	4+	5+	6+	7+	8+	9+	10+
32	29/30	15282	8677	7461	2148	859	1390	408	=I20-T20	=J20-U20
33	30/31	38951	11594	4872	3355	692	347	416	=I21-T21	=J21-U21
34	31/32	13196	30123	7008	2081	1197	275	175	I22-T22	=J22-U22
35	32/33	11922	10191	20874	2817	624	418	112	50	54

12.2.6 Potential Problems with Cohort Analysis

The name *virtual population analysis* or *cohort analysis* refers to a class of models each of which relies upon knowledge of final fishing mortality rates and the back-calculation of numbers-at-age in the fished population. The method is clearly sensitive to the estimates of the terminal F values that permit the analysis to be extended to the incomplete cohorts. If these estimates are flawed, the analysis will be biased. Other sources of potential bias include the presence of ageing error in the determination of the catch-at-age. This is especially a problem if recruitment is highly variable. A 10% ageing error will not affect a small year class too badly, but a large year class could inflate the apparent numbers of smaller year classes around it. Thus, ageing errors will tend to obscure recruitment variability (Richards et al., 1992). A further problem relates to the idea of following particular cohorts. If there is significant immigration to a region, then the numbers in a cohort may increase through time, and thus lead to an overestimate of the cohort size. This effect would be greatest if older fish are the ones that migrate the most. Finally, errors in the natural mortality estimate can have relatively complex impacts on the estimation of fishing mortality (Mertz and Myers, 1997).

12.2.7 Concluding Remarks on Cohort Analysis

Only a very introductory treatment of cohort analysis is presented here. Virtual population analysis remains the preferred method of stock

**Figure 12.6**

A schematic map of the worksheet developed in Example Boxes 12.4 and 12.5. Each block contains a matrix and its column and row labels. The contents are identified along with the cell positions on the sheet. The three grey objects are buttons attached to macros. The three sets of lines are text labels and numbers, including natural mortality, M . The rectangles with unbolted text will be added later. The triangles imply that these are only upper-triangular matrices. The lines below MacCall's solution represent the effort data. The lines below the lower boxes are summary data, such as average age-specific fishing mortality (see later). The effort data are used to calculate the terminal F values.

assessment in the European Community and other parts of the Atlantic. Not surprisingly, there is an enormous literature, both grey and formal, dealing with the various techniques, ways to improve their performance, and how to "tune" the VPA to information from the fishery. The aim of this chapter was only to introduce the reader to the methodology so that a more detailed investigation of the primary literature would be more understandable. Megrey (1989) and Quinn and Deriso (1999) provide excellent reviews of the recent developments in the techniques used.

Without using an optimization technique (such as minimizing the sum of squared residuals), model selection and determination of uncertainty levels along with model projections for risk assessments present their own challenges. The alternative analytical strategy of statistical catch-at-age or catch-at-age with ancillary information, or integrated analysis, permits these options in a very straightforward manner.

EXAMPLE BOX 12.6

Calculation of the instantaneous fishing mortality rates for complete cohorts. This extends Example Boxes 12.4 and 12.5. Using Equation 12.17, and checking for zeros, put =if(T32>0,if(U33>0,Ln(T32/U33)-M,"—"),"—") into I32. Copy this down to row 39, then copy I32:I39 across to column B. Delete the subdiagonal elements. In B41 put =average(B32:B39) and copy across to column I to provide the estimates of average fishing mortality rate on each age class. One might be tempted to use the average fishing mortality in Equation 12.28, but this would ignore variations in fishing effort in each year. Put the effort data into X20:X28 (from Table 12.1; it is best to label the column as effort in X19 and put year labels in W20:W28). Then, in B42 put =X41*\$X\$28 to estimate F_a as $q_y E_y$ and copy across to column I. Note that these only go across to where the incomplete cohorts apply. The effort data in the final year (X28) and average catchability for each age class are described below as estimates of the catchability coefficient by age class and year. The column labels, below, extend across to AF31, but that column does not produce numbers and is suppressed here for brevity.

	A	B	C	D	E	F	G	H	I	J
31	Year\Age	2+	3+	4+	5+	6+	7+	8+	9+	10+
32	29/30	0.025	0.325	0.547	0.885	0.664	0.964	1.050	1.766	—
33	30/31		0.249	0.596	0.781	0.676	0.428	0.681	0.881	—
34	31/32			0.662	0.958	0.807	0.647	1.020	0.835	—
35	32/33				0.643	0.541	0.470	0.551	0.657	—
36	33/34					0.590	0.550	0.590	0.922	—
37	34/35						0.452	0.587	0.803	—
38	35/36							1.055	0.945	—
39	36/37								0.607	—
40	37/38	—	—	—	—	—	—	—	—	—
41	Average F	0.025	0.287	0.602	0.817	0.656	0.585	0.791	0.927	
42	Terminal F	0.019	0.217	0.482	0.669	0.541	0.485	0.674	0.789	

In AE32 put =if(isnumber(I32),I32/\$X20,"—") and copy down to row 40. Copy AE32:AE40 across to column X (and into AF for completeness). In X41 put =average(X32:X40) and copy across to column AE to generate the average catchability coefficient for each age class. These get used, along with the last year's effort in X28, to generate the age-specific fishing mortalities for the incomplete cohorts (across in B42:I42). In X42 put =(B14/(1-exp(-(M+B42))))*((B42+M)/B42), which is Equation 12.28, and

continued

EXAMPLE BOX 12.6 (continued)

copy across to column AE to generate the terminal N_y values. These are then ready for pasting into the left-hand side of the bottom row of the original numbers-at-age matrix. The algorithm is now to paste as values the approximation of the terminal Ns onto the estimated numbers-at-age matrix. Therefore, copy X42:AE42 and paste as values into B28:I28. This will produce a new updated numbers-at-age matrix along with a new estimate of the terminal F_y and N_y . This row copying procedure is iterated until the limit of precision selected has been reached. When using the terminal F estimates the limit is found by summing the modifier matrix except the bottom row (i.e., =sum(M20:U27) instead of =sum(M20:U28) in J16). To ensure no errors it is best to write a few short macros to do the copying and pasting of values. As in Figure 12.6, create two buttons with attached macros, one of which copies and pastes Pope's approximation and the other MacCall's approximation into B20:J28. The third button should conduct the copy/pasting relating to the Newton's method iterations. If J15 is given an integer value greater than zero, it would be possible to turn the use of the terminal F values on and off using a macro similar to that printed next. In this way it would be possible to easily compare the results obtained from the different starting points. How different are the answers if the terminal F values are used? Do the years with complete cohorts change or is it just the numbers-at-age for the incomplete cohorts?

	W	X	Y	Z	AA	AB	AC	AD	AE
30	Catchability Coefficient								
31	Y\Age	2+	3+	4+	5+	6+	7+	8+	9+
32	29/30	0.0043	0.0560	0.0942	0.1523	0.1142	0.1660	0.1807	0.3039
33	30/31	—	0.0427	0.1021	0.1337	0.1157	0.0733	0.1166	0.1508
34	31/32	—	—	0.1333	0.1928	0.1625	0.1301	0.2052	0.1680
35	32/33	—	—	—	0.1309	0.1103	0.0957	0.1122	0.1337
36	33/34	—	—	—	—	0.1137	0.1060	0.1136	0.1776
37	34/35	—	—	—	—	—	0.0914	0.1189	0.1625
38	35/36	—	—	—	—	—	—	0.2280	0.2041
39	36/37	—	—	—	—	—	—	—	0.1367
40	37/38	—	—	—	—	—	—	—	—
41	Av_q	0.0043	0.0494	0.1098	0.1524	0.1233	0.1104	0.1536	0.1797
42	Term N	8363	7468	5277	4135	1139	1136	370	465
43	Min N	370.4							

VBA macro to perform the Newton's method iterations with or without terminal F_y estimates leading to terminal N_y estimates for the incomplete cohorts. By placing 1 in J15 the terminal F estimates are made. If J15 is zero, then the original approximations are used.

continued

EXAMPLE BOX 12.6 (continued)

```

Sub do_vpa()
Dim termf As Integer
termf = Range("J15").Value
If termf > 0 Then
    Range("J16").Select      ' Alter the limit summation
    ActiveCell.FormulaR1C1 = "=SUM(R[4]C[3]:R[11]C[11])"
Else
    Range("J16").Select
    ActiveCell.FormulaR1C1 = "=SUM(R[4]C[3]:R[12]C[11])"
End If
Range("M32:U40").Select      ' copy and paste the updated
Selection.Copy                ' numbers-at-age
Range("B20").Select
Selection.PasteSpecial Paste:=xlValues
Range("B19").Select
If termf > 0 Then           ' If the terminal F option
    Range("X42:AE42").Select  ' Copy and paste terminal N
    Selection.Copy
    Range("B28").Select
    Selection.PasteSpecial Paste:=xlValues
    Range("B12").Select
End If
Application.CutCopyMode = False
End Sub

```

12.3 Statistical Catch-at-Age**12.3.1 introduction**

Statistical catch-at-age will be referred to here as integrated analysis (Punt et al., 2001). Unlike VPA, integrated analysis estimates fewer parameters than the available number of data points, although one can still be estimating tens of parameters. An objective function (least squares or maximum likelihood) is used to optimize the fit of the model to the available data. It requires catch-at-age data along with some information to tie the model to the stock size (either catch rates, or effort, or independent population estimates). The numbers-at-age at the start of the first year in the population being modelled are model parameters along with recruitment levels in each year of the fishery. With further parameters describing age-specific selectivity, it is possible to project each cohort forward to generate a matrix of numbers-at-age. From this it is possible to generate a matrix of predicted catch-at-age that can

be compared with the observed data and the fit optimized. Catch-at-age data alone are usually insufficient to tie the model to reality, so a further connection, either through effort or catch rates, is necessary.

12.3.2 The equations

The equations behind integrated analysis are remarkably simple; the complex part is organizing the information and calculations. The fully selected fishing mortality rate in year y , F_y , is one of the foundations of the analysis, and values for each year are treated as model parameters in the fitting process. The fishing mortality rate for each age, a , in each year y , $F_{a,y}$, is

$$F_{a,y} = s_a \hat{F}_y \quad (12.29)$$

where \hat{F}_y is the fitted fishing mortality rate in year y and s_a is the selectivity of age a (Figure 12.7). The fishing mortalities are combined with the natural mortality, M , to generate the age- and year-specific survivorships, which are used to complete the matrix of numbers-at-age:

$$N_{a+1,y+1} = N_{a,y} e^{-(M+s_a \hat{F}_y)} = N_{a,y} e^{-M} e^{-s_a \hat{F}_y} \quad (12.30)$$

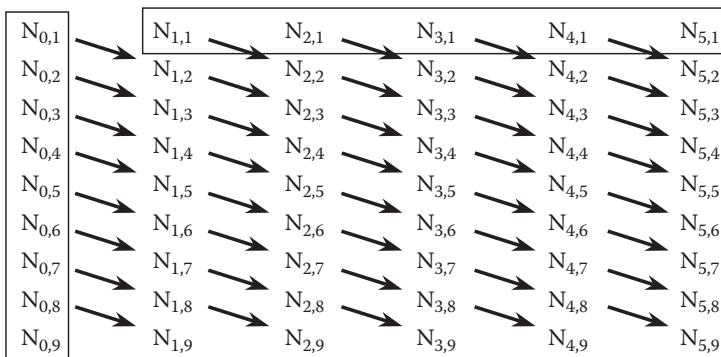
where, as before, $N_{a,y}$ is the numbers of age a in year y (Figure 12.8).

Selectivity can be estimated either directly for each age or the parameters of an equation describing the shape of the selectivity curve can be estimated. A logistic equation is often used to describe selectivity. Given a as age, a_{50} as



Figure 12.7

Selectivity curve generated by Equation 12.31. It is not smooth because the different ages have been treated as integers. By varying the parameters a_{50} and a_{95} the steepness of the curve and its location along the age axis can be altered.

**Figure 12.8**

In integrated analysis the initial population age structure and each year's recruitment (boxed off in the diagram) are estimated parameters. The survivorship of each age class in each year is calculated ($e^{-(M+sF)}$), and these survivorships are used to complete the numbers-at-age matrix using Equation 12.30.

the age at which selectivity is 50%, a_{95} as the age at which selectivity is 95%, and s_a as the selectivity at age a (Figure 12.7), age-specific selectivity is

$$s_a = \frac{1}{1 + e^{-\frac{\ln(19)}{(a_{95}-a_{50})}} \frac{(a-a_{50})}{(a_{95}-a_{50})}} \quad (12.31)$$

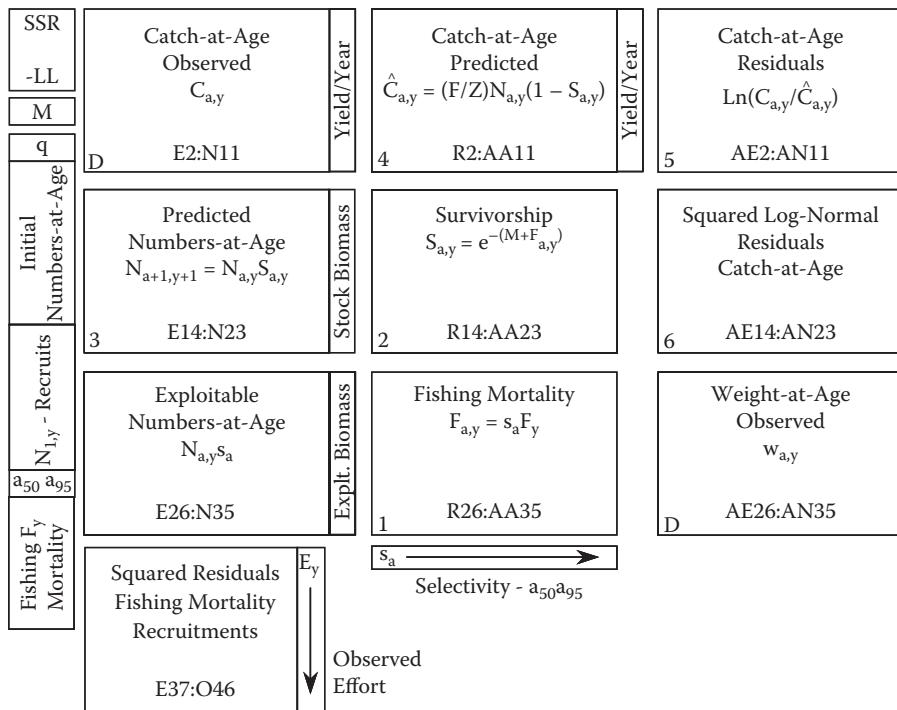
Fitting the model involves estimating the N_{ay} for all ages in year 1, and for the first age class in all subsequent years (Figure 12.8).

Despite estimating a large number of parameters, the calculations for an integrated analysis can still be conducted successfully on an Excel worksheet. We will construct an example of an integrated analysis using the data from Beverton and Holt (1957) that was used in the cohort analysis. Once again, this will be a complex worksheet and care is needed in its construction. The map in Figure 12.9 indicates the broad structure.

The algorithm begins by calculating the age-specific fishing mortality for each year from the selectivity equation parameters and the fishing mortality parameters (Equation 12.29, Figure 12.9). These are combined with the natural mortality rate to generate the age-specific survivorships, which are used, in turn, to complete the numbers-at-age matrix (Equation 12.30).

12.3.3 Fitting to Catch-at-Age Data

Once the predicted numbers-at-age are calculated, the predicted catch-at-age can be generated, which provides the first opportunity to generate an objective function for use when fitting the model by comparing the observed catch-at-age with the predicted. Predicted catch-at-age is

**Figure 12.9**

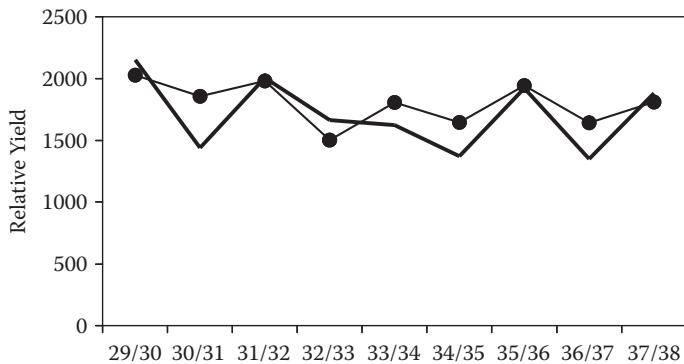
Schematic map of an Excel worksheet illustrating a possible layout for an integrated analysis. Each of the nine main boxes would have its upper edges labeled with ages and left-hand edges labeled with years. The small, upper, left-most box is where the minimizations occur. The model parameters are listed down the left-hand side of the worksheet below the natural mortality M . Each of the estimated parameters is natural log transformed, which scales all parameters to similar sizes and makes all parameter changes proportional changes. In the worksheet they are back-transformed as appropriate. The catch-at-age residuals in the top right are there for ease of plotting as a diagnostic relating to the quality of fit (Figure 12.11). The heavy numerals in the lower left of some of the boxes relate to the order of calculation in the algorithm. The capital D, in the same place, implies these are data matrices. See Example Boxes 12.7 and 12.8.

$$\hat{C}_{a,y} = \frac{F_{a,y}}{M + F_{a,y}} N_{a,y} (1 - e^{-(M+F_{a,y})}) \quad (12.32)$$

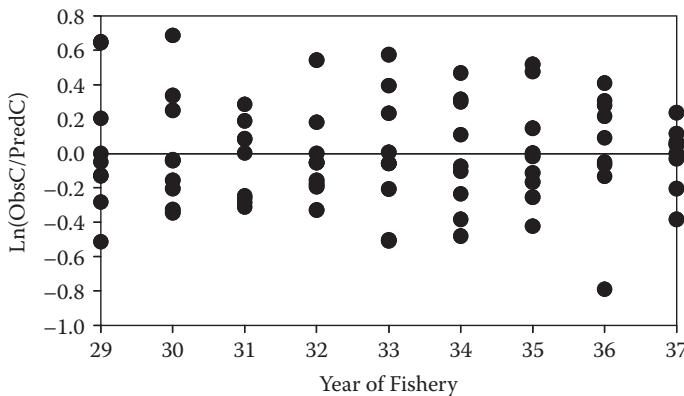
Doubleday (1976) suggested using lognormal residual errors:

$$SSR_C = \sum_a \sum_y \left(\ln \left(C_{a,y} / \hat{C}_{a,y} \right) \right)^2 = \sum_a \sum_y \left(\ln C_{a,y} - \ln \hat{C}_{a,y} \right)^2 \quad (12.33)$$

With the Beverton and Holt (1957) North Sea plaice data, an optimum fit gives rise to a relatively even spread of residuals (according to Equation 12.33, Figures 12.10 and 12.11, Example Box 12.7).

**Figure 12.10**

A plot of observed yield (fine line with dots) and predicted yield (thick line) against fishing year (April to March) deriving from a fit on catch-at-age alone (see Example Box 12.7). The pattern matches well but is exaggerated in 30/31, and is less pronounced in 33/34.

**Figure 12.11**

Catch-at-age residuals against fishing year when fitting the model only to catch-at-age data (see Example Box 12.7). The overall fit is good; a regression through these residuals is essentially flat (residual = 0.0156 – 0.00047 year).

Doubleday (1976) was able to show that if one only fits the stock assessment model using catch-at-age data, as with Equation 12.33, then correlations between some of the parameter estimates could be so extreme that some of the parameter estimates can be effectively linear combinations of others. While this may be acceptable for estimating changes in the relative abundance, at least over short periods, catch-at-age data alone are insufficient to estimate absolute abundance. It is for this reason that integrated analysis is sometimes referred to as catch-at-age analysis with auxiliary data (Deriso et al., 1985, 1989). A common addition is to include observed effort into the model, combined with an extra parameter, the catchability coefficient.

EXAMPLE BOX 12.7

An integrated analysis of the North Sea plaice data (Beverton and Holt, 1957; see Table 12.1 and earlier example boxes). In preparation for later developments put =sum(AF15:AN23) in B2 and =sum(K38:K46) into B3. In B5 put =C2*B2+C3*B3 to get the total weighted sum of squared residuals. The log of the initial numbers-at-age estimates are given in B9:B16 (e.g., Ln_N_29_10 is the log of numbers-at-age 10 in 1929), and the log recruitments in each of the nine years are given in B17:B25 (e.g., Ln_R_30_2 is the log recruitment into age 2+ in year 1930). The logged parameters of the selectivity equation are given in B26:B27. Finally, the log fishing mortality rates are given in rows 28 down to 36. Initiate all parameters (the logs of the first row and column of Pope's approximation will fill B9:B25; you can get the values from Example Box 12.6; see Appendix 12.1), and then enter the catch-at-age data (from Table 12.1) in F3:N11 along with appropriate column and row labels (as in E3:E11 and E2:N2). Equivalent weight-at-age data should be entered into AF27:AN35 (with labels in row 26 and column AE); the weight data are in Appendix 12.1. In R37 put the label "Age," in S37:AA37 put the numbers 2 to 10, and in S38 put =1/(1+exp(-Ln(19)*(S37-exp(\$B\$26)))/(exp(\$B\$27)-exp(\$B\$26)))), which is Equation 12.31. Copy S38 across to column AA to calculate selectivity (label as "Selectivity" in R38). In R25 put the label "Fishing Mortality by Age by Year" and label ages in S26:AA26 and years in R27:R35 as before. To calculate these fishing mortalities put =S\$38*exp(\$B28) into S27, being sure to get the single \$ signs in the correct places. Copy S27 down to row 35, then copy S27:S35 across to column AA to generate the required matrix. Put =exp(-(S27+\$B\$6)) in S15 and copy down to row 23, then copy S15:S23 across to column AA to generate the survivorships by age and year. Again label for rows and columns appropriately.

	A	B	C	D	E	F	G	H
1	Source	Value	Wt		Catch-at-Age—Observed			
2	SSRC	7.6363	1		Year\Age	2+	3+	4+
3	SSRE	0.3789	1		29/30	328	2120	2783
4					30/31	223	2246	1938
5	SSRT	8.0152			31/32	95	2898	3017
6	Natural M	0.2			32/33	77	606	4385
7	Parameter	Ln(value)			33/34	50	489	1121
8	Ln_q	-2.0981			34/35	44	475	1666
9	Ln_N_29_10	4.4570			35/36	131	1373	1595

continued

EXAMPLE BOX 12.7 (continued)

	A	B	C	D	E	F	G	H
10	Ln_N_29_9	5.0806			36/37	38	691	2862
~	~	~			~	~	~	~
17	Ln_R_29_2	9.3607			31/32	10807	25748	6614
18	Ln_R_30_2	10.3659			32/33	10684	8747	17685
19	Ln_R_31_2	9.2879			33/34	7478	8680	6359
~	~	~			~	~	~	~
25	Ln_R_37_2	9.5997			Exploitable Numbers-at-Age			
26	Ln_Sel50	1.2232			Year\Age	2+	3+	4+
27	Ln_Sel95	1.4784			29/30	177.6	1468.7	6398.4
28	Ln_F_29	-0.0739			30/31	485.2	2195.2	3545.5
29	Ln_F_30	-0.4475			31/32	165.1	6024.9	5671.0

From the worksheet map (Figure 12.9), you should now have in place the parameters, both D (data) matrices and the fishing mortality (1) and survivorship (2) matrices. The predicted numbers-at-age matrix is constructed in two parts. In F15 put =exp(B17) and copy down to F23 to obtain the estimated recruitments. In G15 put =exp(B16), in H15 put =exp(B15), and similarly across to N15 with =exp(B9), to list the initial numbers-at-age. The matrix can then be completed by putting =M15*Z15 into N16 and copying down to N23, and then copying N16:N23 across to column G. Finally, to obtain the total biomass estimates the numbers in each age class must be multiplied by their respective average weight and summed. Put =sumproduct(F15:N15,AF27:AN27)/1000 into O15 and copy down to O23. The division by 1,000 is to keep the numbers manageable. The variation in recruitment from year to year is obvious, as are the strong year classes passing through the fishery. The stock biomass can be used as a diagnostic to indicate annual trends in relative abundance. By putting =sumproduct(F3:N3,\$AF27:\$AN27)/1000 into O3 and copying down to O11, an equivalent column can be added to the observed catch-at-age matrix; these values would be observed annual yield. From the matrix of numbers-at-age we calculate the predicted catch-at-age by putting =(S27/(S27+\$B\$6))*F15*(1-S15) into S3 and copying down to S11 and across to column AA. This is Equation 12.32, with S15 being the survivorship calculated previously. You should label the rows and columns appropriately. Copy O3:O11 and paste into AB3:AB11 to obtain the predicted annual yield. The final two matrices are made by putting =Ln(F3/S3) into AF3, copying down to AF11 and

continued

EXAMPLE BOX 12.7 (continued)

across to column AN. These are just the residuals and can be plotted against the year of the fishery to act as a diagnostic relating to how well the fitting process is proceeding (cf. Figure 12.11). To obtain the squared residuals put =AF3^2 into AF15 and copy across to AN15 and down to row 23. This has the effect of completing the sum of squared residuals for the catch-at-age held in B2. With 8 in B9:B25, 1.25 in B26, 1.75 in B27, 0 in B28, and -0.4 in B29:B36 the SSR_C is about 176.938. Use the solver to minimize B2 by changing B9:B36 (twenty-eight parameters). If it does not converge to about 7.265 try a different starting point (cf. Figures 12.10 and 12.11). The values below are close to those obtained once Example Box 12.8 is implemented and completed.

	E	F	G	H	I	J	K	L	M	N	O
14	Yr\Age	2+	3+	4+	5+	6+	7+	8+	9+	10+	Biomass
15	29/30	11623	6277	7462	2274	1087	1539	441	161	86	6721
16	30/31	31755	9382	4136	2755	741	352	498	143	52	9048
17	31/32	10805	25746	6614	1957	1197	320	152	215	62	8404
18	32/33	10685	8746	17684	2845	761	463	124	59	83	7483
19	33/34	7478	8680	6359	9370	1408	375	228	61	29	7034
20	34/35	11660	6076	6336	3419	4717	706	188	114	31	6967
21	35/36	9599	9480	4469	3501	1776	2442	366	97	59	6957
22	36/37	7889	7780	6648	2075	1488	751	1032	154	41	5777
23	37/38	14765	6407	5629	3460	1006	718	362	498	75	7093

12.3.4 Fitting to Fully Selected Fishing Mortality

Including the observed fishing effort (E_y) adds a further nine data points, which offsets the fact that an estimate of the catchability coefficient (\hat{q}) must be made. The two are combined to generate a semiobserved fishing mortality (F_y), which is compared with the fully selected fishing mortality parameters (Example Box 12.8, Figures 12.12 and 12.13). Take note that this fishing mortality is not the instantaneous fishing mortality rate but is rather the annual harvest rate:

$$F_y = \hat{q}E_y \quad (12.34)$$

and thus:

$$SSR_E = \sum_y \left[\ln(\hat{F}_y) - (\ln(\hat{q}) + \ln(E_y)) \right]^2 \quad (12.35)$$

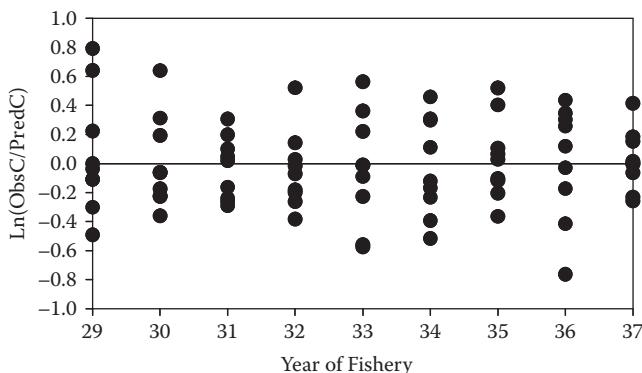
EXAMPLE BOX 12.8

Include observed effort data into O38:O46 in the worksheet developed in Example Box 12.7 (the data are in Table 12.1). Copy J38:N38, as below, down to row 46. Column N is Equation 12.34, column J is the inner part of Equation 12.35, deriving from the parameter estimate of F_y and the semiobserved in column M. Column K is the residual squared, which generates the sum of squared residuals in B3. Columns L and N are for plotting as a visual diagnostic of the quality of fit (Figure 12.13), though one could equally well plot column J. If the worksheet has been solved for an optimum fit to catch-at-age and $\ln_q = -2$, then B3, the sum of squared residuals against effort, should be about 4.55. If both contributions to the total sum of squared residuals in B5 are given equal weight (i.e., 1 in C2:C3), then one can minimize B5 using the solver to modify cells B8:B36 (twenty-nine parameters). Given equal weight, the optimum balance between the two sources of squared residuals appears to be where $SSR_C = 7.636$ and $SSR_E = 0.378$. The parameters that give rise to this result are given in Appendix 12.1. It may be necessary to run the solver more than once, or from different starting points (the results from a VPA, or one of the approximations, would be a reasonable starting point—try the values obtained from Example Box 12.6). How robust are the answers when each SSR is given equal weighting? How sensitive are the results to the relative weighting of the two sets of squared residuals? The values below are for the optimum fit with equal weights.

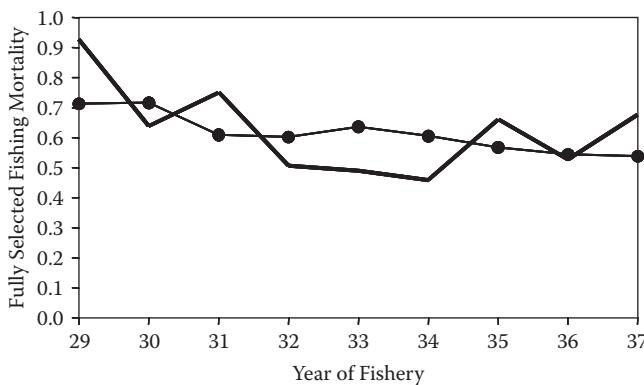
	I	J	K	L	M	N	O
37	Yr	F_res	SSq	Pred_F	ObsLnF	ObsF	Effort
38	29	=B28-M38	=J38^2	=exp(B28)	=Ln(N38)	=exp(\$B\$8)*O38	5.81
39	30	=B29-M39	=J39^2	=exp(B29)	=Ln(N39)	=exp(\$B\$8)*O39	5.84
40	31	0.2080	0.0432	0.7506	-0.4949	0.6096	4.97
41	32	-0.1712	0.0293	0.5075	-0.5070	0.6023	4.91
42	33	-0.2610	0.0681	0.4904	-0.4516	0.6366	5.19
43	34	-0.2787	0.0777	0.4586	-0.5009	0.6060	4.94
44	35	0.1522	0.0232	0.6613	-0.5658	0.5679	4.63
45	36	-0.0304	0.0009	0.5283	-0.6077	0.5446	4.44
46	37	0.2305	0.0531	0.6781	-0.6190	0.5385	4.39

12.3.5 Adding a Stock recruitment relationship

There is very little information relating to the last few cohorts, with the extreme being the single catch data point for the very latest recruits. Fitting the model to the catch-at-age and estimates of fully selected fishing mortality could generate relatively uncertain estimates of the status of the affected years and age classes. One suggested solution (Fournier and Archibald, 1982)

**Figure 12.12**

A plot of the residuals between the log of the observed catch-at-age and the log of the expected catch-at-age, from the North Sea plaice data (Beverton and Holt, 1957), fitted to catch-at-age and fishing mortality (Example Boxes 12.7 and 12.8). A regression line fitted to these data, as shown by the fine line, is essentially flat along the zero line (residual = 0.00389–0.00012 year). Note the differences between this residual plot and that shown in Figure 12.11.

**Figure 12.13**

Estimated fully selected fishing mortality (thick line) vs. observed fishing mortality rates (as in Equation 12.35).

is to impose a stock recruitment relationship (see Chapter 10) to add extra constraints to the last few years of recruitment. This will also be necessary if risk assessment projections are to be made. Spawning stock size may be defined as the mature biomass, or the stock size times the relative fecundity at age, or some other available measure. In addition, one can use a variety of stock recruitment relationships (e.g., Beverton and Holt or Ricker). In general, as discussed in Chapter 10, the residual errors used would tend to be lognormal. Of course, if the age at recruitment is not 0+, then the implied time lag between spawning stock size and subsequent recruitment must be accounted for:

$$\hat{N}_{r,y+r} = \frac{\alpha B_y^S}{\beta + B_y^S} e^\varepsilon \quad (12.36)$$

where r is the age at recruitment, B_y^S is the spawning stock size in year y , and $y + r$ is the year plus the time lag before the recruits join the fishery. The parameters α and β are from the Beverton and Holt stock recruitment relationship. Whether the predicted number of recruits in year $y + r$ are derived from a Beverton and Holt, a Ricker, or any other stock recruitment relationship does not affect the form of the squared residuals:

$$SSR_R = (\ln N_{r,y+r} - \ln \hat{N}_{r,y+r})^2 \quad (12.37)$$

which compares the observed model parameters for recruitment in the r th year onwards (i.e., the fitted recruitments in B17:B25) with those expected from the stock recruitment relationship (Example Box 12.9, Figure 12.14).

12.3.6 Other Auxiliary Data and Different Criteria of Fit

We have considered fitting the catch-at-age stock assessment model through using catch-at-age data, using relative effort (fishing mortality) data, and adding a stock recruitment relationship. Other possible sources that could be added include fishery-independent surveys of stock size and fishery-dependent catch/effort rates. If a series of fishery-independent surveys is available, then either they should derive from a standardized design or some measure of the relative efficiency of each survey (a relative catchability coefficient) would be required. If commercial catch rates are to be used, then, ideally, these should be standardized to remove noise unrelated to changes in stock size (Kimura, 1981, 1988; Klaer, 1994).

With catch rates, lognormal residuals tend to be used. The expected catch rates derive from the simple relation

$$\hat{I}_y = q B_y^E = q \sum_a w_a s_a N_{a,y} \quad (12.38)$$

where q is the catchability coefficient, B_y^E is the exploitable biomass in year y , w_a is the average weight of fish of age a , s_a is the age-specific selectivity, and $N_{a,y}$ is the numbers-at-age a in year y . The sum of squared residuals for this potential component of the total would be (Example Box 12.10)

$$SSR_I = \sum_y (\ln(I_y) - \ln(\hat{I}_y))^2 \quad (12.39)$$

A similar arrangement can be used for fishery-independent surveys, although a separate q estimate would be required for the survey estimates of exploitable biomass.

EXAMPLE BOX 12.9

Implementation of a stock recruitment relationship into the worksheet developed in Example Boxes 12.7 and 12.8. Copy F40:G40 down to row 46. In A37 put “Alpha” and A38 “Beta,” adding the logged initial value ready for fitting the model ($\alpha = 9$ and $\beta = -5$, are reasonable beginnings for the Beverton and Holt relationship, in B37:B38). If a Ricker relationship is preferred then put $=\exp(\$B\$37)*O15*\exp(-\exp(\$B\$38)*O15)$ into F40 and copy down to row 46. In this case starting values would need to be something like ($\ln(\alpha) = 1.6$ and $\ln(\beta) = -8.6$). Plot the recruitment parameters against those predicted from the stock recruitment relationship. Which appears best, the Beverton and Holt or the Ricker? F38:F39 are empty because of the lag of r years. There are now thirty-one parameters for the solver, B8:B38.

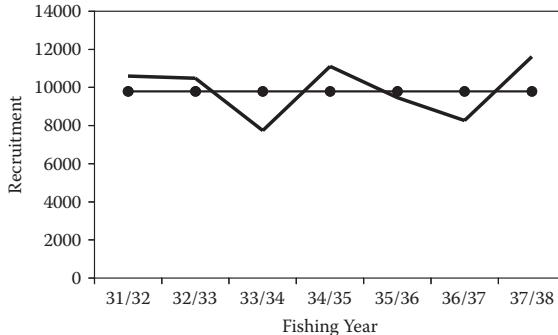
	E	F	G
37	Year\Age	Beverton and Holt	Sum Squared Residual
38	29/30		
39	30/31		
40	31/32	$=\exp(\$B\$37)*O15/(\exp(\$B\$38)+O15)$	$=(B19-\ln(F40))^2$
41	32/33	$=\exp(\$B\$37)*O16/(\exp(\$B\$38)+O16)$	$=(B20-\ln(F41))^2$
42	33/34	9625	0.059
43	34/35	9625	0.027
44	35/36	9625	0.002
45	36/37	9625	0.003
46	37/38	9625	0.038

The sum of squared residuals for all the additions to the integrated analysis. SSR_C relates to fitting the model to the catch-at-age data, SSR_E relates to fitting the model to the fully selected fishing mortality estimates, and SSR_R relates to the inclusion of the stock recruitment relationship to the model fitting. The total sum of squared residuals, SSR_T , is the sum of each of the separate contributions after each is weighted according to the predefined weightings. As with all weighted least squares methods, ideally the weighting should relate to the variability in the estimates of the statistics involved; unfortunately, this is often unknown. Experiment with different relative weightings to see the impact upon the final model fit. If it is desired to turn off a particular component, simply give it a weighting of zero. Does the impact of adding the stock recruitment relationship differ depending upon whether a Beverton and Holt or a Ricker relationship is used?

continued

EXAMPLE BOX 12.9 (continued)

	A	B	C
1	Source	Value	Weighting
2	SSRC	=sum(AF15:AN23)	1
3	SSRE	=sum(K38:K46)	1
4	SSRR	=sum(G40:G46)	1
5	SSRT	=C2*B2+C3*B3+C4*B4	
6	Natural M		0.2


Figure 12.14

Fitted recruitment levels (thick line) vs. expected recruitment levels from a Beverton-Holt stock recruitment relationship ($\text{Ln_Alpha} = 9.1920$ and $\text{Ln_Beta} = -5.000$). The stock recruitment relationship predicts effectively constant recruitment.

While we have consistently been using the sum of squared residuals as the criterion of model fit, we could equally well have used maximum likelihood methods and their extensions into Bayesian methods. Using the same weightings and the lognormal residuals, we would expect to obtain essentially the same answers, but if any of the contributions fit very closely, the log-likelihoods for that component could go negative, which will distort the impact of that component and a different result may occur. If the model is fitted to only one component, then the same parameters will be found as with the least squares method.

The multinomial distribution has been suggested as an alternative likelihood function for fitting the catch-at-age data (Deriso et al., 1985, 1989), especially where measurement errors are primarily due to ageing errors and sampling error in the catch sampling:

$$\text{LL} = \sum_y \sum_a n_{a,y} \ln(\hat{p}_{a,y}) \quad (12.40)$$

EXAMPLE BOX 12.10

Exploitable biomass and expected catch rates. In E25 put the label “Exploitable Numbers-at-Age” and then label the columns as age classes in F26:N26 and the rows as years in E27:E35. Put =F15*\$S\$38 into F27 and copy down to row 35 and across to column N to generate the required matrix. Label O26 as “Biomass.” Put =sumproduct(F27:N27,AF27:AN27)/1000 into O27 and copy down to row 35 to generate the exploitable biomass in each year of the fishery. Put =O27*exp(\$B\$8)/1000 into P27, and copy down to row 35 to generate the expected catch rates (as per Equation 12.38). Label P37 Obs(CE) and in P38 put AB3/(O38*1000), which divides the expected yield by the scaled effort. Then a column of the squared residuals (as per Equation 12.39) can be placed somewhere convenient on the worksheet and the weighted sum can be added to the total sum of squared residuals in B5.

where LL is the multinomial log-likelihood, n_{ay} is the number of fish of age a , aged in year y , and \hat{p}_{ay} is the expected proportion of animals age a in year y . Equation 12.40 does not actually involve the amount of catch, so it has been suggested that it might be more stable to add a penalty term along the lines of $\sum (C'_y - C_y)^2$, weighted so that the expected catches (C'_y) are close to the observed (Quinn and Deriso, 1999). An alternative approach has been suggested by Schnute and Richards (1995) that does not require this extra term. If the use of multinomial likelihoods is relatively unstable, it is also an option to solve the model initially using lognormal likelihoods, and then, when near the optimum fit, begin using multinomial likelihoods.

12.3.7 relative Weight to Different Contributions

Irrespective of whether maximum likelihood methods, Bayesian methods, or sum of squared residuals are used as the criterion of optimum fit, when there are a number of categorically different sources contributing to the overall likelihood or sum of squares, then each contribution will receive a relative weighting. Providing no explicit weighting implies an equal weighting of 1 for each component of the total. With weighted least squares, and maximum penalized likelihood, it is usual to weight each component in relation to the degree of uncertainty associated with the data or statistic used. Thus, if some estimate of the variance or coefficient of variation for each data source is available, then the inverse of these would be used to ascribe relative weights to each component; the greater the variability, the less the relative weight.

If each of the sources of information is consistent with the others, then fitting the model should not prove difficult. For example, in Example Box 12.8, where a stock recruitment relationship was added to the model, the impact

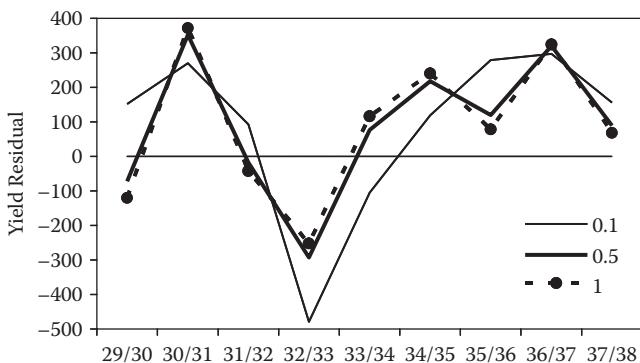


Figure 12.15

The impact of different relative weights (1.0, 0.5, and 0.1) being ascribed to the sum of squares contribution from the catch-at-age (SSR_C) when the model is fitted only to catch-at-age and effort data (i.e., only the optimum stock recruitment relationship included). The fine dotted line reflects the weights of observed catches, the fine solid line is where a weighting of 0.1 is used, the thicker line is where a weighting of 0.5 is used, and the dashed line with dots has a weighting of 1.0. The heavier weighting improves the fit in the first, third, fifth, seventh, and ninth years, but the relative improvements in fit decline past a weighting of 0.5.

of the Beverton and Holt relationship was minimal. At least it could be said not to be contradictory to the other data sources.

Problems can arise when the separate contributions to the overall criterion of fit are inconsistent or contradictory (Richards, 1991; Schnute and Hilborn, 1993). Under the schema described earlier, if one had contradictory data sets, then the final outcome of the analyses would be largely influenced by the relative weights ascribed to the various components of the fit. The result will reflect the weighted average of the different conclusions deriving from the different components. As a minimum, it is a good idea to conduct a series of sensitivity trials with different sets of weightings to determine the implications of whether one source of data is more reliable than the others (Figure 12.15; Richards, 1991).

Schnute and Hilborn (1993) go somewhat further and suggest that, as with robust statistics (Huber, 1981), where individual data points that are really noninformative outliers may still have a nonzero likelihood, whole data sets may be noninformative in an analogous fashion. In effect, they recommend a more formal, structured investigation of the impacts on the quality of the overall fit of giving different emphases to the different contradictory data sets.

The issue of what weightings to use is one that will not go away and must be treated explicitly in any formal assessment. If a definite selection of relative weights is made instead of conducting a sensitivity analysis, then these weights require a formal justification. Further examples of the impacts of these weightings should be published. Further work along the lines suggested by Schnute and Hilborn (1993) may also prove helpful.

12.3.8 Characterization of uncertainty

As with all other stock assessment analyses, one obtains a specific optimum model fit that will have a variety of management implications. From the integrated analysis one can obtain estimates of stock biomass, fully selected fishing mortality, and average fishing mortality, along with other, possibly related, performance indicators. Although the analyses generate specific values for all of these parameters and outputs, a further step is required to obtain an indication of the level of uncertainty associated with each estimate. Depending upon how the minimization is conducted, some software will provide asymptotic standard errors around each parameter estimate. However, these standard errors rely on linear statistical theory, and in all cases will be symmetrical (unless results are transformed). Confidence intervals derived from such standard errors are recognized as being only approximate.

A better way of obtaining approximate confidence intervals or of generating likelihood profiles around model estimates would be to use either Bayesian methods or bootstrapping. As described in Chapter 3 on parameter estimation and Chapter 8 on characterizing uncertainty, Bayesian methods retain the original data and describe uncertainty by determining how well different combinations of parameters fit the available data. Bootstrapping techniques recognize that the available data are only a sample of what was possible. By generating bootstrap samples from the data, refitting the model, and collating the resulting sets of parameter estimates, it is possible to generate percentile confidence intervals. In this chapter we will only be considering bootstrap methods. See Punt and Hilborn (1997) for a description of Bayesian methods as applied to integrated analysis stock assessment models. The methods described in Chapter 8 for generating posterior distributions using the Gibbs sampler are very general, but applying such methods to a twenty-nine-parameter model in Excel would be remarkably inefficient. Even bootstrapping will be slow, but it is at least manageable (Example Box 12.11, Figure 12.16).

With catch-at-age data there are many serial correlations between age classes and years. When generating the required bootstrap samples it is best to resample the residuals from the optimum model fit and combine them with the expected catch-at-age data to form the bootstrap catch-at-age sample. Thus, the bootstrap samples (C^b) would be

$$C_{a,y}^b = \hat{C}_{a,y} \left(\frac{C_{a,y}}{\hat{C}_{a,y}} \right)^{boot} \quad (12.41)$$

where \hat{C} is the expected catch-at-age and the residual, $(C_{a,y}/\hat{C}_{a,y})^{boot}$, is a randomly selected residual from those available (Figure 12.16).

The bootstrapping highlights the level of uncertainty in the various parts of the analysis and permits the investigator to make stronger statements

EXAMPLE BOX 12.11

A macro for conducting bootstraps on the catch-at-age worksheet (see Example Boxes 12.7 to 12.10 and Figure 12.16). Once you have an optimum model fit, put =F3/S3 into AR15, copy down and across to AZ23. Select AR15:AZ23, copy and save as values onto itself; these are the residuals to be bootstrapped. Copy the original data (F3:N11) into AR27:AZ35, and copy the optimum predicted catch-at-age from S3:AA11 into AR3:AZ11. Put =AR3*offset(\$AQ\$14,trunc(rand()*9)+1,trunc(rand()*9)+1) into AR39 and copy down to row 47 and across to column AZ to create bootstrap samples (see Figure 12.16). Put =O15 into B39 and copy down to row 47, to make storing model results slightly easier. Copy the optimum parameter values and outputs B8:B47, and paste special/transpose into BE7:CR7. This will be used as the starting point for fitting each bootstrap sample to the model. The results will be pasted underneath these optimum values by the macro. It took just under two hours to conduct one thousand bootstraps on a 2.5 Ghz dual-core computer (Figures 12.17 and 12.18), when solving for twenty-nine parameters. Time how long it takes to conduct ten bootstraps on your own machine before setting it off on a marathon.

```

Sub Do_Boot()
Dim i As Integer
Application.ScreenUpdating = False
For i = 1 To 1000
    Range("AR39:AZ47").Select      ' Replace original data
    Selection.Copy
    Range("F3").Select
    Selection.PasteSpecial Paste:=xlValues,
        Transpose:=False
    Range("BE7:CG7").Select      ' Paste in Optimal
    Selection.Copy
    Range("B8").Select
    Selection.PasteSpecial Paste:=xlValues,
        Transpose:=True
    Application.CutCopyMode = False
    SolverOk SetCell:="$B$5", MaxMinVal:=2, ValueOf:="0",
        ByChange:="$B$8:$B$36"
    SolverSolve (True)           ' Run the solver twice to
    SolverOk SetCell:="$B$5", MaxMinVal:=2, ValueOf:="0",
        ByChange:="$B$8:$B$36"
    SolverSolve (True)           ' in the solution

```

continued

EXAMPLE BOX 12.11 (continued)

```

Range("B8:B47").Select
Selection.Copy
Range("BE8").Select
ActiveCell.Offset(i, 0).Range("A1").Select
Selection.PasteSpecial Paste:=xlValues,
Transpose:=True
Next i
ActiveWorkbook.Save           ' just in case
Application.ScreenUpdating = True
End Sub

```

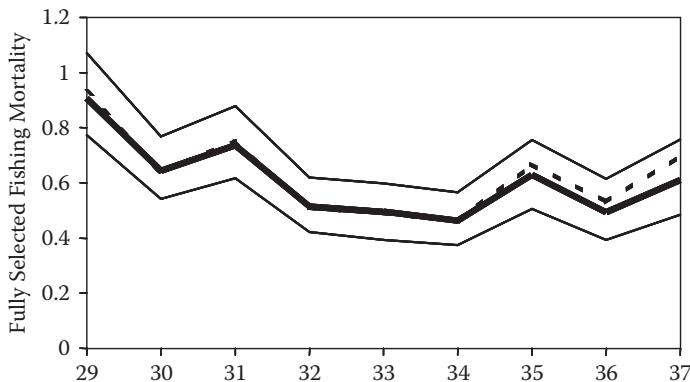
Optimum Predicted Catch-at-Age values $\hat{C}_{a,y}$ AR3:AZ11
Catch-at-Age Residuals $(C_{a,y} / \hat{C}_{a,y})$ as values AR15:AZ23
Original Catch-at-Age Data $C_{a,y}$ AR27:AZ35
Bootstrap sample $\hat{C}_{a,y} (C_{a,y} / \hat{C}_{a,y})^{\text{boot}}$ AR39:AZ47

Figure 12.16

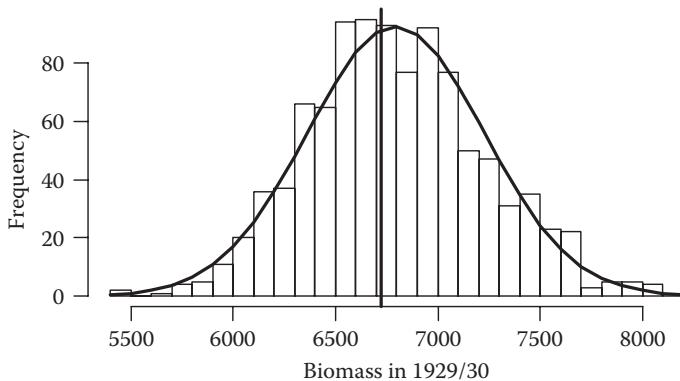
Schematic map of a worksheet arrangement for conducting bootstraps on the catch-at-age data and model. The cell ranges depict where the actual values go; it is assumed that the rows and columns will be labeled appropriately. The top three matrices are filled with values; only the bottom matrix contains equations. A macro is used to run the bootstrap (Example Box 12.11).

about the management implications of the results. In this instance it also confirms the suspicions (Figure 12.14) that the estimate of the fully selected fishing mortality in the fishing year 1929–1930 is biased (Figure 12.16). The ability of the bootstrapping procedure to identify bias in the parameter estimates is a real advantage, although, as discussed in Chapter 6, once bias is detected, it is difficult to know specifically what to do about it.

In this case, it is only the first year that is exhibiting bias, and this suggests a closer consideration of the first year's data. Perhaps the effort data used are

**Figure 12.17**

Bootstrap 95% confidence intervals around the fully selected fishing mortality through the years of the fishery. The heavy line is the bootstrap average while the dotted line is the optimum fit. There is little evidence of bias except in the last three years, where the optimum fit appears to be biased high (5.9% in 35, 6.9% in 36, and 12.8% in 37). That the most bias occurs in the final year is not surprising because that year has the least information available.

**Figure 12.18**

Bootstrap 95 percentile confidence intervals around the stock biomass estimate for the 1929–1930 fishing year. The optimum index, using fixed optimum Beverton and Holt recruitment parameters, was $67,721t$ and the fitted normal curve has a mean of $6,794t$. The small amount of bias early becomes greater as the years advance. Possibly, using the Ricker would be less biased; alternatively, one could solve for the recruitment parameters in each bootstrap, which would increase the variation but may reduce the bias.

more error prone than imagined. However the case may be, awareness of the problem is the first step to a better understanding of our perception of the fishery. Once again, the stock assessment model synthesizes a wide range of information and provides a more convenient and defensible statement about the status of the stock. Standard diagnostic tests, such as plotting residuals

and other visual indicators (Richards et al., 1997) should always be made on the analysis results.

12.3.9 Model Projections and Risk Assessment

As with surplus production models, characterization of the uncertainty in an assessment model is only the first step. Ideally, it should be possible to decide on a management strategy (be it a certain catch level or fishing mortality level), impose that on the model fishery, and project the population forward in time to determine the consequences of different strategies. This would be the basis behind a formal risk assessment (Francis, 1992). With the integrated analysis model this can be implemented relatively easily.

If a particular fully selected fishing mortality rate has been selected as the management strategy, this might also entail imposing a particular selectivity curve. However, in the following discussion we will only consider imposing a particular fishing mortality rate. Assuming the model has been optimally fitted to catch-at-age, effort, and the stock recruitment relationship has been included, the algorithm would be the following:

1. Calculate age-specific fishing mortality rates—from $s_a F_y$.
2. Calculate age-specific survivorship rates—from $S_{a,y} = \exp(-(M + s_a F_y))$.
3. Calculate the predicted numbers-at-age for age classes above the age of recruitment—from $N_{a+1,y+1} = N_{a,y} S_{a,y}$, Equation 12.30.
4. Calculate predicted numbers-at-age for recruits from the stock recruitment relationship and the biomass from r years previous using Equation 12.36, including a stochastic residual term.
5. Calculate the predicted catch-at-age as per Equation 12.32.
6. Calculate the fishery performance measures.
7. Repeat for the next year of projection.
8. Repeat a sufficient number of times to obtain summary information from the stochastic nature of the projections.

The predicted recruitment should have some intrinsic variation away from the deterministic recruitment value predicted from the spawning stock biomass from the requisite number of years prior to the recruitment year. This stochasticity could either be selected at random from the residuals available (analogous to a bootstrap sample) or, if the time series of residuals is short, should be selected at random from under a probability density function used to describe the recruitment residuals (usually a lognormal pdf would be used). What this implies is that the projections would be in the nature of a Monte Carlo simulation requiring numerous replicates to obtain the necessary summary information.

12.4 Concluding Remarks

In this chapter we have considered both of the main analytical strategies adopted for assessing age-structured fishery data. Which approach best suits a particular situation will depend upon circumstances. The fact that integrated analyses are less stringent in their data requirements means that they are a more useful method for many fisheries in countries that do not have long traditions of collected detailed age-structured information.

Both VPA (in all its forms) and integrated analyses are large fields of endeavour with many examples in the literature and many developments not covered in this chapter. Each of the analysis strategies would form the basis of a significant book by themselves. This introduction covers a number of the important issues, but these models continue to be developed and articulated (Myers and Cadigan, 1995; Schnute and Richards, 1995; Methot, 2009).

In real-life situations there are likely to be different stocks present within a single fishery, and possibly there will be more than one fishing fleet exploiting the various stocks (e.g., trawl and nontrawl), each with their own selectivity characteristics. These would require separate treatments, which implies parallel analyses for each fleet (the fleets are separated by their relative effort, their selectivity curves, and the particular stocked fished) and for each stock (recruitment being kept separate). These multiple analyses would imply the necessity for more extensive data sets relating to catch-at-age and related effort (Punt et al., 2001).

The analyses in this chapter were conducted inside Excel. The fact that it took under two hours to conduct one thousand bootstraps in the integrated analysis means that the need for custom computer programs seems to have lessened. However, implementing a more sophisticated multifleet, multi-stock, catch-at-age model in Excel would be stretching the abilities of the Excel solver, although a stepped approach to solving subsets of the model would be possible. In the end, custom computer programs to conduct these stock assessments are still the optimum approach (Richards et al., 1997). The ability to mimic such models in Excel is, however, a handy double-check on the defensibility and reality of the results obtained from more sophisticated programs. Excel is remarkably good, but its limits must be recognized, and when dealing with significantly complex problems, the analyst's life is made easier by using some other software platform.

Once the basics have been absorbed, the best teacher relating to these methods is experience with different fisheries and problems. There are large numbers of options available when implementing one of these models. A good strategy is not to restrict oneself to a single model but to implement different versions of an assessment to investigate the implications of the different data sets and the different model structures.

Appendix 12.1: Weight-at-Age Data and Optimum Fit to Catch-at-Age Model

TABLe A12.1

Average Weight in Grams of North Sea Plaice in Each Age Class Measured from Market Samples Taken in Lowestoft and Grimsby during 1929–1938

Year\Age	2+	3+	4+	5+	6+	7+	8+	9+	10+
29/30	167	190	218	270	289	392	574	665	802
30/31	136	190	257	340	441	498	582	740	961
31/32	127	152	221	349	440	503	593	675	809
32/33	132	143	182	297	421	535	641	721	827
33/34	146	165	189	251	383	528	645	787	818
34/35	157	189	202	229	277	521	711	798	819
35/36	154	178	214	280	313	383	643	789	876
36/37	149	171	198	255	338	377	467	781	885
37/38	160	173	222	310	383	490	519	624	845

Source: Data from Table 16.2 in Beverton and Holt, 1957.

Note: In the original table the weights went up to age 20, but are truncated here at age 10 to match the ageing data. In addition, the weights were given for calendar years while the ageing was for fishing years (April 1 to March 31); weights from 1929 were assumed to hold for the 1929–1930 fishing year, and equivalently for later years. Data used in Example Box 12.7.

TABLe A12.2

Parameter Values and Sum of Squared Residuals for the Optimum Fit from Example Boxes 12.7 and 12.8

Source	Value	Weight			
SSQC	7.6366	1	SSQT	8.0152115	
SSQE	0.3786	1	Natural M	0.2	
Parameter	Ln(value)				
Ln_q	-2.09828				
N_29_10	4.4570	N_30_2	10.3658	LnF_29	-0.0740
N_29_9	5.0807	N_31_2	9.2878	LnF_30	-0.4475
N_29_8	6.0900	N_32_2	9.2766	LnF_31	-0.2869
N_29_7	7.3389	N_33_2	8.9197	LnF_32	-0.6782
N_29_6	6.9909	N_34_2	9.3640	LnF_33	-0.7126
N_29_5	7.7294	N_35_2	9.1696	LnF_34	-0.7796
N_29_4	8.9176	N_36_2	8.9735	LnF_35	-0.4135
N_29_3	8.7447	N_37_2	9.6004	LnF_36	-0.6380
N_29_2	9.3607	Sel50	1.2232	LnF_37	-0.3885
		Sel95	1.4785		

Note: SSQC is the sum of squared residuals from the catch-at-age data, SSQE is from the fully selected fishing mortality rate comparison, and SSQT is simply the sum of both sources weighted by their respective weights. Natural mortality is assumed to be constant.

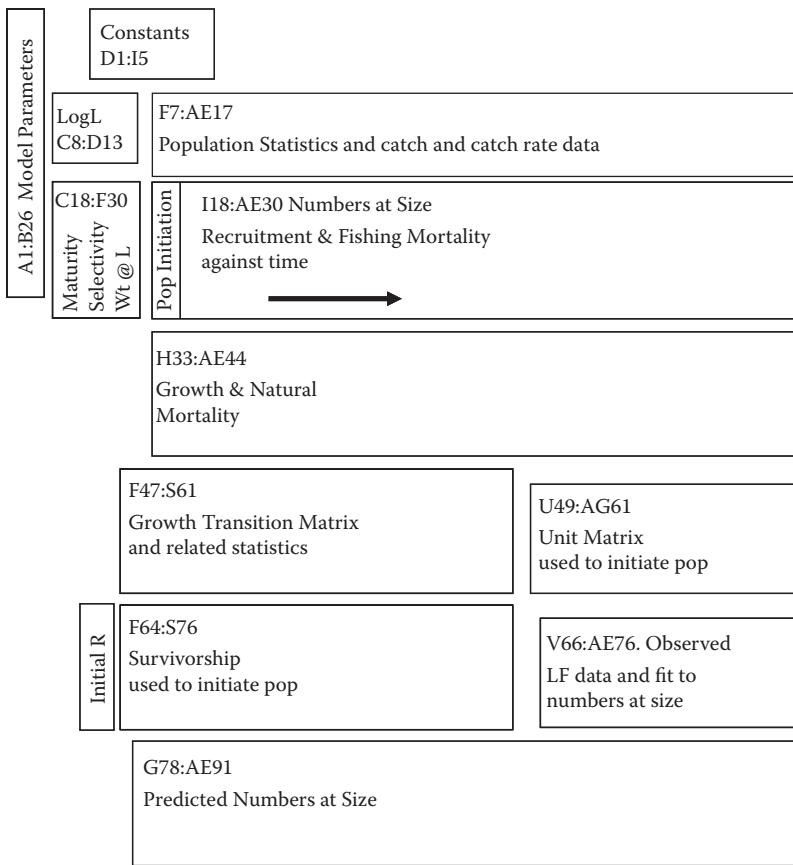
13

Size-Based Models

13.1 Introduction

13.1.1 Stock Assessment Modelling Options

Commercial fisheries for abalone and rock lobster (and many other invertebrates) often suffer from the fact that the species concerned are difficult or impossible to age using readily available technology. Nevertheless, many of these species are the basis of valuable fisheries, and thus require an assessment of some kind to assist with the adequate management of each stock. The use of age-structured models for assessing these species is compromised, so alternatives must be considered. It would be possible to use a surplus production model, which does not require age-structured information (see Example Boxes 8.4 and 8.5 for an example with abalone). However, an alternative that permits the use of more than just catch and catch rate data would be to use a size- or stage-structured model, with the basic form of these models described by Sullivan et al. (1990) and Sullivan (1992); also see Caswell (2001), and a fully developed model for abalone is described by Breen et al. (2003). Such models follow the fate of the numbers in a set of size classes, which contrasts with age-structured models that follow numbers in each age class or cohort through time. A major difference is that the size classes are not related to specific cohorts, and so the growth of individuals passing from one size class into another is not automatic as the years pass. The transition of animals from size class to size class requires an adequate description of the growth of the species concerned. In particular, this would need to be in terms of the expected growth increment of given sizes of animals, which preadapts the method to use growth estimates derived from tagging studies. In addition, one requires data on catches and catch rates, but one can also include data describing the size distribution of the commercial catch (commonly collected and known as shed or market sampling), as well as fishery-independent surveys of abundance and field surveys of the size distribution of abalone after fishing. As with the age-structured integrated analysis, it is possible to include different forms of ancillary data once the basic size-based stock assessment model is developed. Size-structured models are relatively complex, and the examples in this chapter will need to be developed in stages (Figure 13.1); we will use

**Figure 13.1**

Worksheet map for the size-based model to be developed in this chapter; it will be developed in five stages. There are two selectivity curves to reflect a change of legal minimum length from 132 mm to 140 mm in 1990.

the same western zone abalone data from Tasmania, Australia, as was used in Chapter 8 (Table 8.1). The examples in this chapter use only twelve 10 mm size classes, which is a major simplification. With Tasmanian blacklip abalone (Haddon, 2009), seventy-six 2 mm size classes are used to describe the populations being assessed.

13.2 The Model Structure

The population being modelled is described by a vector, \mathbf{N}_t , of the numbers in a defined set of size classes at time t :

$$\mathbf{N}_t = \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ \vdots \\ N_{n,t} \end{bmatrix} \quad (13.1)$$

where \mathbf{N}_t is a vector of n size classes indicating the numbers in length class i at time t . At each time step, the individuals in the population in \mathbf{N}_t either grow or not, which implies that they either stay in their original size class or move into a larger one (negative growth is usually disregarded, though in principle it could be included). Mathematically, this growth is described by using a transition or projection matrix containing the probabilities of shifting from one size class into others in whatever time step the model is designed around. The population vector is repeatedly multiplied by the growth transition matrix to describe the changing population size structure brought about by growth through time. The transition matrix contains the probability that the individuals in length class j (matrix columns) at time t have grown into length classes i^* (matrix rows) during a single time increment. The growth transition matrix can be combined with survivorship probabilities and recruitment relationships (Caswell, 2001); however, it is often simpler and more flexible to keep them separate. The proportions of animals growing from length class j into length classes i^* are estimated using a probability density function whose parameters are the average expected growth increment (from each initial length class j) surrounded by some measure of variation. Any probability density function of a suitable shape could be used to describe the growth increments, although, naturally, the distribution used should reflect the observed distribution of growth increments; the normal distribution has been used (Punt et al., 1997; Breen et al., 2003; Haddon et al., 2008), as has the gamma distribution (Sullivan, 1992). In matrix notation the growth transition matrix would be represented thus:

$$\mathbf{G} = \begin{bmatrix} G_{1,1} & 0 & . & 0 \\ G_{1,2} & G_{2,2} & & \\ . & . & . & 0 \\ G_{1,n} & . & G_{n-1,n} & G_{n,n} \end{bmatrix} \quad (13.2)$$

where \mathbf{G} is the square transition or projection matrix in which the $G_{i,j}$ are the probabilities that an animal in size class j (along the columns) will grow into size class i (along the rows). The upper triangle of zeros indicates that negative growth is not being modelled (if it were, then some of these matrix cells would be nonzero). The generation of the individual $G_{i,j}$ entails using a probability distribution to describe the different likelihood of growing from one size to another, rather than using some deterministic growth trajectory.

Generally, a growth curve, such as the von Bertalanffy curve, is used to estimate the average length increment for a given size class, and then the probability distribution chosen is used to describe how individuals would be distributed around the average expected increments. Using a normal distribution to describe the transition probabilities, we need to estimate the proportion of the expected distribution of growth increments to be found between the limits of each size class. With the focus on the bottom of each size class (L_i) of width CW, the expected probabilities of growing from size class j into size class i ($G_{i,j}$) would be defined as

$$\begin{aligned}
 G_{i,j} &= \int_{-\infty}^{L_i + CW} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left[\frac{(L_i - \bar{L}_j)^2}{2(\sigma_j)^2}\right]} dL \quad L_i = L_{Min} \\
 G_{i,j} &= \int_{L_i}^{L_i + CW} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left[\frac{(L_i - \bar{L}_j)^2}{2(\sigma_j)^2}\right]} dL \quad L_{Min} < L_i < L_{Max} \\
 G_{i,j} &= \int_{L_i}^{+\infty} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left[\frac{(L_i - \bar{L}_j)^2}{2(\sigma_j)^2}\right]} dL \quad L_i = L_{Max}
 \end{aligned} \tag{13.3}$$

where σ_j is the standard deviation of the normal distribution of growth increments for size class j . \bar{L}_j is the expected average size for size class j after the growth expected in one time interval, that is, $L_j + \Delta\hat{L}_j$, where $\Delta\hat{L}_j$ is the average expected growth increment for size class j . Summing the smallest size class to $-\infty$ and the largest size class to $+\infty$ effectively makes both these size classes plus groups that ensure that the transition probabilities for all n size classes sum to 1. Using the Fabens version of the von Bertalanffy growth equation means that

$$\Delta\hat{L}_j = (L_\infty - L_j)(1 - e^{-K}) \tag{13.4}$$

where L_∞ is the length at which growth increments are zero and K is the rate at which the maximum length, L_∞ , is approached. However, any other growth curve that can predict growth increments for a given initial length could be used. For example, in Tasmania, the growth of blacklip abalone (*Haliotis rubra*) appears to be best described with a growth trajectory that reflects an inverse logistic curve (Haddon et al., 2008).

Multiplying the numbers-at-size vector, \mathbf{N}_t , by the transition matrix leads to

$$\mathbf{N}_{t+1} = \mathbf{G}\mathbf{N}_t \quad (13.5)$$

which describes growth in the population size structure without recruitment or mortality (Example Box 13.1).

The full stage-structured model uses the transition matrix along with descriptions of the processes of mortality and recruitment to describe the calculation of \mathbf{N}_{t+1} . The population dynamics can be described by repeated application of these processes. Natural mortality can be represented in this model by the annual survivorship in year t in each length class i , $S_{i,t}$, and is easily included in the model either as a vector of individual terms or as a zero square matrix with only the diagonal elements filled:

$$\mathbf{S}_t = \begin{bmatrix} S_{1,t} & 0 & 0 \\ 0 & S_{2,t} & \\ & . & 0 \\ 0 & 0 & S_{n,t} \end{bmatrix} \quad (13.6)$$

Annual survivorship, accounting for natural mortality only, would be

$$S_{i,t} = e^{-M_{i,t}} \quad (13.7)$$

where $M_{i,t}$ refers to the instantaneous rate of natural mortality for size class i during period t ; generally this is held constant across size classes and through time. If there is also some size-selective fishing mortality, then the annual survivorship would include

$$S_{i,t} = e^{-(M_{i,t} + s_i F_t)} \quad (13.8)$$

where s_i is the selectivity that applies to length class i and F_t is the fully selected instantaneous fishing mortality in year t . Using matrix notation, the model now becomes

$$\mathbf{N}_{t+1} = \mathbf{G}\mathbf{S}\mathbf{N}_t \quad (13.9)$$

Finally, the expected recruitment in each time step can be literally added as a vector of the numbers of recruits into each size class (Example Box 13.2):

$$\mathbf{N}_{t+1} = \mathbf{G}\mathbf{S}\mathbf{N}_t + \mathbf{R}_t \quad (13.10)$$

Care must be taken concerning the order of multiplication of the growth and survivorship matrices with the numbers-at-size vector. It is the case that

EXAMPLE BOX 13.1

The generation of the size transition matrix, using abalone as an example. The placement allows space for later developments. Cells H1:I4 are constants. SigmaG is the standard deviation of the growth residuals, and SigmaR will be used in the penalty that limits the variation of the recruitment residuals. Note the jump from 170 to 200 in G61; this group acts as a plus group so each column sums to 1.0. Into H47 put =If((H49+H48)<H49,H49,H49+H48), which precludes negative growth. Put =(\$I\$1-H49)*(1-EXP(-\$I\$2)) into H48. Select H47:H48 and copy over to column S. Now the complicated bit: put =if(H\$49>\$F50 ,0,if(H\$49=\$F50,normdist(\$G50,H\$47,\$I\$3,true),normdist(\$G50,H\$47,\$I\$3,true)-normdist(\$F50,H\$47,\$I\$3,true))) into H50. Check all brackets and \$ signs. Copy down to H61 and across to column S; this is the transition matrix. Select H50:S61 and name it "Grow" in the name box just above the "A" column to simplify later use. To illustrate the use of the transition matrix, in G19:G30 put the size classes 60 to 170, and in H18 to AE18 put the years 1985 to 2008. Put zeros into H20:H30 and 1e6 into H19. Select I19:I30 and type =mmult(Grow,H19: H30), then press <Ctrl><Shift><Enter> all at once to enter the matrix multiplication array function. Select I19:I30 and copy across to column AE. The effect of growth without mortality or recruitment should be clear. Vary K and Linf to see the effect.

	F	G	H	I	J	R	S
1			Linf	172			
2			K	0.36			
3			SigmaG	5.714			
4			SigmaR	0.6			
47		PredL	93.860	100.837	107.814	163.628	170.605
48		ExptDL	33.860	30.837	27.814	3.628	0.605
49		Grow	60	70	80	160	170
50	60	70	0.0000	0.0000	0.0000	0.0000	0.0000
51	70	80	0.0076	0.0001	0.0000	0.0000	0.0000
52	80	90	0.2420	0.0288	0.0009	0.0000	0.0000
53	90	100	0.6090	0.4128	0.0848	0.0000	0.0000
54	100	110	0.1389	0.5038	0.5633	0.0000	0.0000
60	160	170	0.0000	0.0000	0.0000	0.8676	0.0000
61	170	200	0.0000	0.0000	0.0000	0.1324	1.0000

EXAMPLE BOX 13.2

Simple size-based model dynamics. To include natural and fishing mortality plus recruitment add the constants as indicated in D1:I5, and copy I17 to AE17. Maturity and weight-at-length will be used later, but selectivity will be used now. In C19 put Equation 13.21 = $1/(1+(\exp(\$E\$3+\$E\$4*G19))^{-1})$, and put Equation 13.20 into D19: = $1/(1+\exp(-\ln(19)*(G19-\$G\$1)/(\$G\$2-\$G\$1)))$. The legal minimum length changed in 1990, so put = $1/(1+\exp(-\ln(19)*(G19-\$G\$3)/(\$G\$4-\$G\$3)))$ into E19, and put Equation 13.19 into F19 = $(\$E\$1*G19^{\$E\$2})/1000$. Select C19:F19 and copy down to row 30. Fill H20:H30 with zeros and put 1e6 in H19. Select H33:H44 and type =mmult(Grow,H19:H30)*\$G\$5, and then press <Ctrl><Shift><Enter> all at once to enter the matrix multiplication array function; this is growth and natural mortality (Equation 13.9). Select H33:H44 and copy over to column AE. To include fishing mortality and recruitment, put =(1000000)+H33 into I19 (i.e., constant recruitment of 1e6), and in I20 put =H34*(1-H\$17*\$D20) and copy down to I30. Select I19:I33 and copy across to column M. Because the selectivity changed in 1990, alter M20 to become =L34*(1-L\$17*\$E20), then copy down to M30 across to column AE. Compare the size distribution in column AE if the harvest rate in H17:AE17 is set at 0.2 or at 0.0 (Figure 13.2).

	C	D	E	F	G	H	I
1		Wta	5.62E-05	Sell50_85	127	Linf	172
2		Wtb	3.1792	Sell95_85	132	K	0.36
3		SaMa	-16.8	Sell50_90	139	Sigma	5.714
4		SaMb	0.14	Sell95_90	146	SigmaR	0.6
5		M	0.2	NatSurv	=exp(-E5)	TAC	900
17				Harvest		0.2	=H17
18	Maturity	Sel to 89	Sel 90 on	Weight at L	SizeClass	1985	1986
19	0.0002	0.0000	0.0000	0.0253	60	1000000	1000012
20	0.0009	0.0000	0.0000	0.0413	70	0	6243
30							
	0.9991	1.0000	1.0000	0.6931	170	0	0
33					60	12	12
34					70	6243	6244
35					80	198144	198442
44					170	0	0

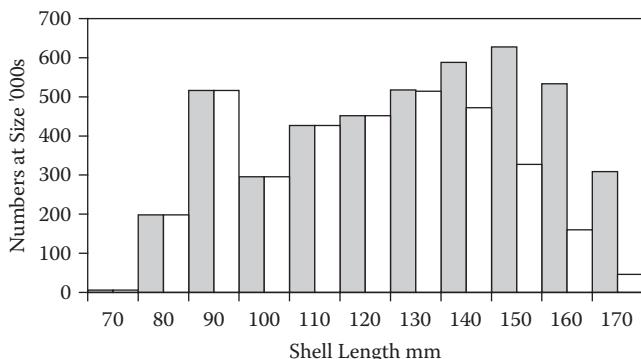


Figure 13.2

The size structure obtained in a hypothetical abalone population with a constant recruitment of 1 million individuals into the 60 mm size class each year and a constant harvest rate of either 0.2 (20%; the open columns) or 0.0 (the grey columns), as in Example Boxes 13.1 and 13.2. The difference shows the effect of fishing on a virgin stock.

G(SNt) (survive first, then grow) is only the same as **S(GNt)** (growth first, then survive) if the survivorship is constant across all sizes, which will not be the case if there is size-selective fishing. Which order is chosen in practice will depend on when in the year the fishery concerned tends to operate. One way of reducing the impact of when mortality is applied, relative to when growth is applied, is to break each year up into a number of seasons and generate a transition matrix for each season. This is the strategy used when generating transition matrices to describe the growth of the southern rock lobster, *Jasus edwardsii*, around Tasmania, Australia; Punt et al. (1997) used twelve monthly periods, while Haddon and Gardner (2009) used eight periods (six monthly and two three-monthly). Combining such partial year matrices in the appropriate order means the recruitment and mortality processes that occur in a particular fishery may be represented more realistically; however, here in our examples we will restrict ourselves to an annual model.

The dynamics of a population can thus be described if one has details of growth, an estimate of natural and fishing mortality, and an average annual recruitment. The recruitment can be represented by a vector of zeros except for the first size class, though in reality we might expect new recruits to be spread across a few size classes, especially if the size classes were small enough. By repeatedly applying Equation 13.10, that is, multiplying the vector of numbers-at-size by the survivorship matrix, the growth transition matrix, and then adding the recruitment vector, with or without a constant fishing mortality, eventually a stable size structure and population size becomes established (Sullivan, 1992; Example Box 13.2, Figure 13.2). Such asymptotic behaviour is also useful for determining the expected size structure (and hence the biomass, given weight-at-length) in the absence of fishing. This unfished or virgin biomass is part of various

biological reference points often used as targets and limits when managing a resource.

A complete history of each fishery from its start to the current day is often not known, and so instead of starting the modelling from an unfished state, it would be useful if we could initiate the model by estimating the size structure and state of depletion in the first year when data of sufficient quality and completeness are available. It would be possible to do this in the same way as estimating the unfished state by using an average recruitment and an initial harvest rate and repeatedly applying these until an equilibrium arises (see Example Box 13.2). However, in an assessment context using asymptotic behaviour is inefficient, as it can take many iterations to achieve equilibrium. Instead, it is possible to use relatively simple matrix algebra to derive the initial equilibrium size structure in an analytical fashion. At equilibrium, \mathbf{N}_{t+1} is the same as \mathbf{N}_t (represented by \mathbf{N}^*):

$$\mathbf{N}^* = \mathbf{GS}\mathbf{N}^* + \mathbf{R} \quad (13.11)$$

$$\mathbf{N}^* - \mathbf{GS}\mathbf{N}^* = \mathbf{N}^* (\mathbf{I} - \mathbf{GS}) = \mathbf{R} \quad (13.12)$$

and thus

$$\mathbf{N}^* = (\mathbf{I} - \mathbf{GS})^{-1} \mathbf{R} \quad (13.13)$$

where \mathbf{I} is the identity or unit matrix (see Figure 13.1), \mathbf{S} is a square survivorship matrix describing the combination of both natural mortality and size-selective fishing mortality, and \mathbf{R} is a vector of recruitment values in each size class (Example Box 13.3). Explicitly this is denoted

$$\begin{bmatrix} N_1 \\ N_2 \\ \vdots \\ N_n \end{bmatrix} = \left(\begin{bmatrix} 1 & 0 & & 0 \\ 0 & 1 & & 0 \\ & & \ddots & 0 \\ 0 & 0 & 1 & \end{bmatrix} - \begin{bmatrix} G_{1,1} & 0 & & 0 \\ G_{1,2} & G_{2,2} & & \\ \vdots & \vdots & \ddots & 0 \\ G_{1,n} & \vdots & \vdots & G_{n,n} \end{bmatrix} \cdot \begin{bmatrix} S_1 & 0 & & 0 \\ 0 & S_2 & & \\ & & \ddots & 0 \\ 0 & 0 & \ddots & S_n \end{bmatrix} \right)^{-1} \begin{bmatrix} \bar{R} \\ 0 \\ \vdots \\ 0 \end{bmatrix} \quad (13.14)$$

In practice, instead of generating matrices for the survivorship terms, to speed the computations, the survivorship following fishing mortality may be added to the noninitiation dynamics independently of the survivorship from natural mortality. Equation 13.10 thus becomes

$$\mathbf{N}_{t+1} = ((\mathbf{G}\mathbf{N}_t)e^{-M}) \otimes \mathbf{e}^{-sF} + \mathbf{R}_t \quad (13.15)$$

where the numbers-at-size is matrix multiplied by the growth transition matrix, and then the elements of the resulting numbers-at-size are multiplied by the scalar describing the survivorship following natural mortality,

EXAMPLE BOX 13.3

The survivorship and unit matrices. Extend the recruitment deviates as model parameters from B6:B26 as rdev88 to rdev08; set these at 1.0. Put =exp(average (H15:AE15)) into B1 to estimate the closed form of q for later (Equation 13.25). Fill E66:E76 with zeros and copy F67 down to F76. Extend the size classes from G65 to 170 in G76, and from H64:S64. Fill H65:S76 with zeros and then put =(\$G\$5–(\$D19*\$F65)) into H65, making sure the \$ are put in correctly. Copy H65 and paste it diagonally to fill I66, J67, and so on to S76; this makes a square survivorship matrix used in the initiation. Select H65:S76 and name it “Surv” in the name box. Copy G64:S76 and paste as values in U49. Replace the diagonal values with 1s to form a unit matrix. Select V50:AG61 and name it “Unit.” To generate the initial vector of numbers-at-size select H19:H30 and type =mmult(minverse(Unit–mmult (Grow, Surv)), E65:E76), then press <Ctrl><Shift><Enter> all at the same time to enter the array functions used. Replace I19 with =(\$B\$2*\$B4)+H33 and copy across to column AE. Then in J19 replace the reference to \$B4 with a =(\$B\$2*\$B5)+I33 so that it references the recruitment deviate for 1987. In K19 have it point to B6. This change needs to be made right across to AE19, which should read =(\$B\$2*\$B26)+AD33. These will be used when we fit the model to data. If you change B2:B3 the initial size distribution will also change.

	A	B	E	F	G	H	I
1	q	#DIV/0!	5.62E-05	Sell50_85	127	Linf	172
2	AvRec	11112562	3.1792	Sell95_85	132	K	0.36
3	InitH	0.26632	-16.8	Sell50_90	139	Sigma	5.714
4	rdev86	1	0.14	Sell95_90	146	SigmaR	0.6
5	rdev87	1	0.2	NatSurv	0.8187	TAC	900
64			InitR	Harvest	Survival	60	70
65			=\$B\$2	=\$B\$3	60	0.8187	0
66			0	=F65	70	0	0.8187
67			0	=F66	80	0	0
68			0	0.2663	90	0	0

e^{-M} , which is constant across size classes and time, to form a new intermediary numbers-at-size, which is then multiplied element by element by the vector representing survivorship following fishing mortality, e^{-s^F} , which represents nonconstant survivorship across size classes due to the selectivity vector s (the symbol \otimes represents element-by-element multiplication). Finally, the vector of recruitments for the given year (the average recruitment multiplied by the lognormal recruitment deviate; $\bar{R} \times e_t^{N(0, \sigma_R^2)}$) is added to the

numbers-at-size to generate the final numbers-at-size for time $t + 1$. Given that the harvest rate, H_t , can easily be estimated,

$$H_t = C_t / B_t^E \quad (13.16)$$

where C_t is the catch taken in year t and B_t^E is the exploitable biomass in year t . Equation 13.22, the complement of this, adjusted for selectivity, would be the survivorship following fishing mortality; thus, Equation 13.15 can be represented as

$$\mathbf{N}_{t+1} = \left(((\mathbf{G}\mathbf{N}_t)e^{-M}) \otimes (1 - \mathbf{s}_t H_t) \right) + \mathbf{R}_t \quad (13.17)$$

which is what is used in Example Boxes 13.2 and 13.3. In addition, the predicted vector of numbers-at-size in the commercial catch, \mathbf{N}_t^C , which can be compared with the observed catch at size, can then be described by

$$\mathbf{N}_t^C = \left(((\mathbf{G}\mathbf{N}_t)e^{-M}) \otimes (\mathbf{s}_t H_t) \right) \quad (13.18)$$

where the vector of numbers-at-size after natural mortality and growth is multiplied element by element by the vector of selectivity, \mathbf{s}_t , for that year, t , after it has been multiplied by the scalar representing the harvest rate, H_t , in year t .

There are various other simple relationships that are required to connect the population dynamics model to a real fishery. Just as with the age-structured models described in Chapter 12, we require a formal description of any selectivity that applies to the fishing (determined by the legal minimum length and diver behaviour); in addition, a length-to-weight relationship is also required. A simple power relationship can be used between length and weight:

$$w_i = aL_i^b \quad (13.19)$$

where w_i is the expected weight of an animal in length class i , a and b are curve parameters, and L_i is the length of abalone in length class i . Selectivity is described using a logistic curve:

$$s_i = \frac{1}{1 + \exp\left(-Ln(19)\frac{L_i - L_{50}}{L_{95} - L_{50}}\right)} \quad (13.20)$$

where L_i is the length of length class i , L_{50} is the length at which 50% of abalone are selected, and L_{95} is the length at 95% selection. Size-at-maturity is described using an alternative version of the logistic:

$$m_i = \frac{1}{1 + (\exp(a + bL_i))^{-1}} \quad (13.21)$$

where m_i is the proportion mature at length L_i of length class i , and a and b are the logistic parameters ($-b/a$ is the size at 50% maturity). To generate predicted catch rates and harvest rates we need to be able to estimate the exploitable biomass:

$$B_t^E = \sum_{i=1}^n N_{t,i} w_i s_i \quad (13.22)$$

where B_t^E is the exploitable biomass at time t , n is the number of size classes, $N_{t,i}$ is the numbers in size class i at time t , w_i is the weight of size class i , and s_i is the selectivity of the size class i (if s_i were omitted, this would generate the total biomass). To estimate the degree of depletion of the spawning stock, we need to be able to estimate the spawning biomass:

$$B_t^S = \sum_{i=1}^n N_{t,i} w_i m_i \quad (13.23)$$

where B_t^S is the spawning or mature biomass at time t , n is the number of size classes, $N_{t,i}$ is the numbers in size class i at time t , w_i is the weight of size class i , and m_i is the proportion mature within size class i .

Just as with surplus production and age-structured models, we use the concept of catchability to make predictions of the expected catch rates, \hat{I}_t , given a particular exploitable biomass in a given year t :

$$\hat{I}_t = q B_t^E \quad (13.24)$$

where q is the catchability (defined as the proportion of the exploitable biomass taken with one unit of effort). As with surplus production and age-structured models, a closed-form estimate of catchability can be obtained using the observed catch rates and the estimates of exploitable biomass:

$$\hat{q} = e^{\frac{1}{n} \sum \ln\left(\frac{I_t}{\hat{B}_t^E}\right)} \quad (13.25)$$

Finally, when fitting the model to observations from a fishery, we need some objective function to optimize the model fit. We could use the least sum of squared residuals for the catch rates (using lognormal errors), but for

ease of expansion later, we will use maximum likelihood methods, as was done with the surplus production modelling in Chapter 8:

$$L(\text{data} | \bar{R}, H^I, q) = \prod_t \frac{1}{I_t \sqrt{2\pi\hat{\sigma}}} e^{-\frac{(\ln I_t - \ln \hat{I}_t)^2}{2\hat{\sigma}^2}} \quad (13.26)$$

where $L(\text{data} | \bar{R}, H^I, q)$ is the likelihood of the data given the parameters (for example, as here: average recruitment, initial harvest rate, and catchability), the product is overall years (t) for which CPUE data are available, and

$$\hat{\sigma}^2 = \sum_t \frac{(\ln I_t - \ln \hat{I}_t)^2}{n} \quad (13.27)$$

where n is the number of observations (maximum likelihood estimate of the variance uses n rather than $n - 1$; Neter et al., 1996, p. 34). A simplified version of the same maximum likelihood equation is

$$LL^{CE} = -\frac{n}{2} (\ln(2\pi) + 2\ln(\hat{\sigma}) + 1) \quad (13.28)$$

(see Appendix 11.3 for its derivation). If only the three parameters shown in Equation 13.26 are used, this equation can stand as it is; however, instead of using only an average recruitment level for each year, it is possible to estimate recruitment residuals that modify the level of recruitment in each year:

$$R_t = \bar{R} \cdot e_t^{N(0, \sigma^2)} \quad (13.29)$$

The model can estimate the lognormal recruitment residuals $e^{\epsilon_R} = e^{N(0, \sigma^2)}$ for each year t . However, to prevent a perfect fit from overparameterization and to avoid the model generating biologically meaningless estimates, a penalty term is required as well as additional data where available. The penalty term on the recruitment residuals, P_R , includes an estimate of the expected variation of the recruitment residuals:

$$P_R = \sum_{t=1}^n \ln(e^{\epsilon_R})^2 / 2\sigma_R^2 \quad (13.30)$$

where σ_R^2 is the expected variance of the recruitment residuals (Example Box 13.5). The smaller the value attributed to σ_R^2 (SigmaR), the less variable the recruitment deviates can be, and as a consequence, the fit to the catch rate time series declines (Figures 13.3 to 13.5).

With only two parameters directly estimated, the fit of the model to the observed catch rates is not as good as was obtained with the surplus production model (compare Figure 13.3 with Figure 8.5). Obviously, by estimating the recruitment deviates (Figure 13.4), the fit of the model increased substantially, but we have also increased the number of parameters. While we haven't included any further direct data, we have included information in the form of the selectivity, maturity, and weight-at-length relationships, as well as the information in the growth transition matrix. The last recruitment deviate (for 2008) does not differ from 1.0, and that for 2007 is close to 1.0. This is because there is little information about the recruitment strengths in 2007 and 2008 in the catch rate data. It will take at least two to three years for animals to grow through the Legal Minimum Length (LML) from recruitment in sufficient numbers to influence catch rates, and so these parameters stay near 1.0. They need not be fitted, which would reduce the number of fitted parameters by two. However, to improve the balance between fitted parameters and number of observations, we could include data that the surplus production model could not include. If we had the size distributions of commercial catches, these could be compared to the predicted proportions in the different size classes that can be derived from the model (see Equation 13.18). The comparison of the relative proportional distribution of numbers across a set of size classes is best made using multinomial likelihoods:

$$LL^{LF} = \sum_{i=140}^{170} N_{t,i}^C \ln \left(\frac{\hat{N}_{t,i}^C}{\sum \hat{N}_{t,i}^C} \right) \quad (13.31)$$

where LL^{LF} is the negative log-likelihood for the length frequency data, $N_{t,i}^C$ is the observed numbers in the commercial catch in size class i at time t , and $\hat{N}_{t,i}^C$ is the predicted numbers in the commercial catch in size class i at time t . This is combined with the negative log-likelihood for the catch rate data, and its penalty term, using a weighting term, λ , that scales the two values to become approximately the same order of magnitude (in the example λ was about 0.001; we divided the sum in D9 of Example Box 13.4 by 1,000).

$$LL = LL^{CE} + \lambda LL^{LF} - PenR \quad (13.32)$$

The penalty is subtracted from the negative log-likelihood, as the aim is to maximize Equation 13.32 in order to optimize the model fit (Example Box 13.5). Observed length frequencies from the commercial catch need to be summarized into the same size classes as in the model (Table 13.1). Unfortunately, the 10 mm size classes used in the examples are rather too coarse for these data to have much effect on the model fit. This is the case because the wide size classes tend to smooth over the effects of size-selective

EXAMPLE BOX 13.4

Initial fit of the size-structured model. Extend the years from H7 to 2008 in AE7. The catch and catch rate data in H12:AE13 are from Table 8.1 in Chapter 8. Alter the harvest rates in H17:AE17 as shown. Put =100*H10/\$G\$7 into H8. In H9 put =sumproduct(H33:H44,\$F\$19:\$F\$30)/1000, in H10 put =sumproduct(H33:H44,\$F\$19:\$F\$30,\$C\$19:\$C\$30)/1000 for the mature biomass, and in H11 put =sumproduct(\$F\$19:\$F\$30,H33:H44,\$D\$19:\$D\$30)/1000. Select H8:H11 and copy across to column AE. In H15 put =LN(H13/H11); the lognormal catch rate residuals are in H16:AE16. Select H14:H17 and copy across to column AE. That summarizes the dynamics of the model. In D8 put =count(H13: AE13) to get the number of years of data. In D9, for later, put =SUM(W66:AE69)/1000, while in D10 put Equation 13.28 =-(D8/2)*(Ln(2*pi()) +2*Ln (D11) +1). To calculate the sigma in D11 put =sqrt(sumxmy2(Ln(H13:AE13), Ln (H14:AE14))/D8) (look up the function help if needed). The recruitment deviate penalty is =10*sumproduct(Ln(B4:B26)* Ln(B4:B26))/(2*\$I\$4 *\$I\$4) in D12 (Equation 13.32). Finally, in D13 put =D10+D9-\$D\$12. The model can now be fitted by using the solver. First, maximize D13 by changing B2:B3. Plot the years against the catch rates and predicted catch rates, as well as against the residuals to obtain something similar to Figure 13.3. Plot the recruitment residuals against the years 1986–2008 to get something like Figure 13.4. Now try using the solver maximizing D13 by changing B2:B26. The plots should now look more like Figure 13.5. Once the optimum fit has been obtained set the InitialH to 0.0 and copy the mature biomass in H10 as a value into G7, then put 0.28624 back into B3. Vary the value in SigmaR; the smaller this value, the smoother the recruitment deviates become, and so the fit to the catch rates declines (Figure 13.6).

	C	D	E	F	G	H	I
7				BzeroSp	12898	1985	1986
8	n	24		Depletion SpawnB		43.42	44.90
9	LF_LL	0.0000		Total biomass	8185.390	8206.561	
10	CE_LL	70.2138		Mature biomass	5600.913	5790.924	
11	sigma	0.0130		Exploitable Biomass	5098.539	5289.981	
12	PenaltyR	11.2365		Catch		1018.884	742.347
13	LL	58.9773		Catch Rates		1	1.0957
14				Predicted Catch Rates	=\$B\$1*H11		1.0586
15				q_contrib		-8.5367	-8.4822
16				ResidualCE		=H13/H14	1.0351
17				Harvest		=H12/H11	0.1403

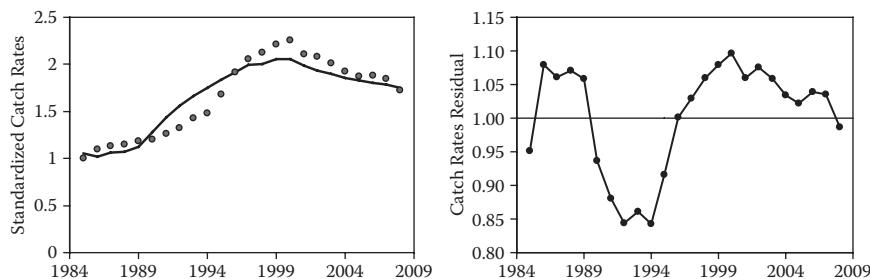
EXAMPLE BOX 13.5

Inclusion of predicted catch at size. Extend the years from W71 to 2008 in AE71. Enter the observed length frequency data and totals from Table 13.1 into W72:AE76. In W79 put =W33*W\$17*\$D19 (Equation [13.18]) and copy down to W90. In W91 put =sum(W87:W90), which sums the total count in size classes 140:170. Select W79:W91 and copy across to column AE. For completeness, select W79:W90 and copy across to column H (=1985, alter the selectivity from \$E19 to \$D19 from 1989 to 1985). Finally, in W66 put =(W72)*LN(W87/W\$91), and copy down to W69. Select W66:W69 and copy across to column AE. This should fill the log-likelihood component for length frequency data in D9. Solving for the maximum of D13 by changing B2:B25 should generate a log-likelihood of about -2.39, with a weight of 0.001 given to the length frequency log-likelihood. In this case the addition of the length frequency data only makes a minor difference (a slight improvement in the fit; Table 13.2).

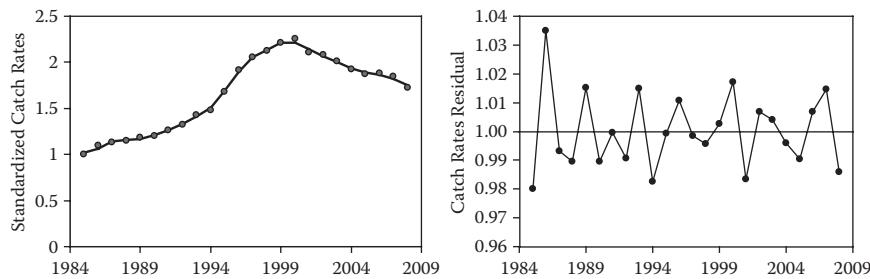
	V	W	X	Y	Z	AA	AB
71		2000	2001	2002	2003	2004	2005
72	140	567	1870	1029	1431	590	1198
73	150	959	2941	1478	2164	1027	1448
74	160	815	2115	1259	1748	948	1053
75	170	566	832	620	715	467	489
76		2907	7758	4386	6058	3032	4188
77							
78	1999	2000	2001	2002	2003	2004	2005
79	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0
88	408965	609693	591705	559054	567949	543900	533408
89	243686	387614	398092	396101	417293	404826	395641
90	86254	140751	150633	157440	174779	177995	180887
91	Totals ~>	1751891	1714120	1645940	1713613	1670758	1662564

fishery; nevertheless, the principles remain the same. In an operational model many more size classes would be used, and these increase the sensitivity of the dynamics to the available data.

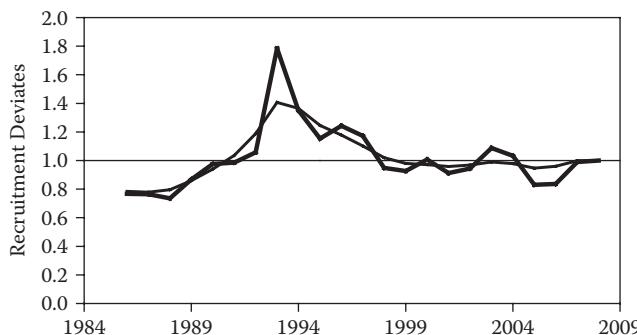
In 1985 the Tasmanian western zone stock was in a relatively depleted state, which led to large catch reductions. We can compare the size distribution of the stock in 1985 with that expected in an unfished population to see the effect of fishing. As might be expected, once depleted away from the unfished state, many of the larger animals are selectively removed from the stock and the size structure is greatly modified (Figure 13.6).

**Figure 13.3**

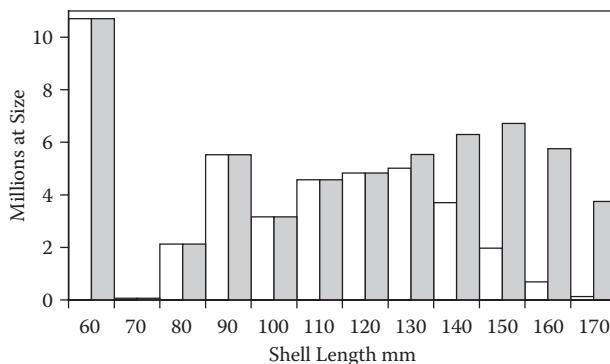
The fit to observed standardized catch rates as expressed by the values themselves (left panel) and by the lognormal residuals (right panel) when only using the average recruitment and initial harvest rate parameters. This is not as good a fit as that obtained with the surplus production model in Chapter 8.

**Figure 13.4**

The fit to observed standardized catch rates as expressed by the values themselves (left panel) and by the lognormal residuals (right panel). Not surprisingly, because of the increased number of parameters, this is rather a better fit than obtained with the surplus production model in Chapter 8.

**Figure 13.5**

The recruitment deviates from the initial fit to catch rate data in Example Box 13.4. The thick spiky line relates to a $\Sigma\mu$ value of 0.6, while the finer, smoother line relates to a $\Sigma\mu$ of 0.3. With less variation in the recruitment deviates, the ability to fit the catch rate data is reduced.

**Figure 13.6**

The equilibrium initial size structure of the population from Example Box 13.5. The shaded bars relate to an average recruitment set at 10,405,973 with a zero initial harvest, while the open bars relate to an initial harvest rate of 0.28738. The legal minimum length in 1985 was 132 mm; the depletion of the larger size classes away from the unfished exploitable biomass is clear.

TABLE 13.1

Observed Frequencies of Different 10 mm Length Classes in the Commercial Blacklip Abalone (*Haliotis rubra*) Catch Taken in the Western Zone of Tasmania from 2000 to 2008

Year	140	150	160	170	Total
2000	567	959	815	566	2,907
2001	1,870	2,941	2,115	832	7,758
2002	1,029	1,478	1,259	620	4,386
2003	1,431	2,164	1,748	715	6,058
2004	590	1,027	948	467	3,032
2005	1,198	1,448	1,053	489	4,188
2006	1,483	1,844	1,392	631	5,350
2007	646	882	599	214	2,341
2008	3,073	3,790	2,415	1,008	10,286

The data suggest that the Tasmanian western zone stock exhibited lower than average recruitment prior to about 1992, but then was fortunate enough to receive well above average recruitment between 1993 and 1997 (Figure 13.5), which, along with the reduced catches at that time, significantly rebuilt the stock. Fishing on the eastern coast of Tasmania is much simpler than the more exposed western coast, and from about 1989 to 2000 a large proportion of the available total allowable catch (TAC) was being taken from the east. In an attempt to distribute the effort more evenly across the resource, zonation was introduced in 2000, which significantly increased the catches expected to be taken from the western zone each year. The immediate effect of this was for catch rates to begin to decline from very high levels in the west (Figure 13.4). These changes to the fishery and management led

TABLe 13.2

The Main Parameters and Likelihood Components of the Two Models

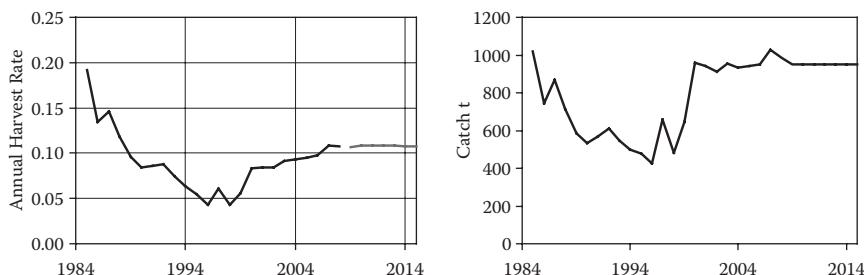
	Example Box 13.4	Example Box 13.5
q	0.000200	0.0002011
AvRecruit	10436714	10405978
Initial H	0.286243	0.287383
LF_LL	0	-61.3695
CE_LL	70.2138	70.17077
Sigma	0.012978	0.01300
PenaltyRec	11.23654	11.19408
Log likelihood	58.97725	-2.39281

Note: Example Box 13.4 is without the length frequency data and Example Box 13.5 includes that data. The fit to the catch rates is slightly reduced, the average recruitment is slightly decreased, and the initial harvest rate is slightly increased. The weighting given to the length frequency data was 0.001, which scales it closer to the log-likelihood for the catch rates.

to the fishery data having remarkable contrast. Initially, in the 1980s, large catches were taken out and the stock was depleted, but then the TAC was greatly reduced and most fishing moved to the east coast so that catches in the west declined markedly and the stock rebuilt, then catches in the west were again increased. Such treatment, heavy fishing followed by reduced fishing followed again by heavy fishing, can provide excellent information about how the resource responds to fishing pressure. Such high contrast is one of the reasons why the model fit is remarkably good (even the surplus production model in Chapter 8 provides an excellent fit). Of course, in a real fishery assessment, more size classes would be used and more specific details from the fishery included so that one would have more confidence in the outcomes of the modelling.

There is naturally a close relationship between the catches removed and the annual harvest rate. In 1997 the catches increased from about 450 t to about 650 t and then back down to about 450 t, and this is apparent in the resulting harvest rate (Figure 13.7). The impact of zonation and the forcing of catch back onto the west coast is also apparent.

The assessment model as it stands provides an adequate summary of what has happened in this fishery. But to make it useful for management, we need to be able to project its dynamics forward to see the expected effects of different levels of catch and the influence of any other management changes. Besides projecting the effects of different catch levels, which is simple to do (Example Box 13.6), as with the surplus production models in Chapter 11 and the age-structured models in Chapter 12, it would be possible to bootstrap the residuals to the catch rate fit and to the length frequency fit and characterize some of the uncertainty around any projections. However, capturing all of the uncertainty in these assessments would be difficult. Abalone are notoriously

**Figure 13.7**

The annual catch in the western zone (right panel) and the resulting harvest rate (left panel). Note the effect of the increase in catches in 1997 on the harvest rates. The right-hand extension of both graphs is where the model is being used for projecting given catch levels forward.

variable (and seemingly those around Tasmania especially so). There is variation in the weight-at-length relationships, the selectivity relationships, the size-at-maturity relationships, and especially in the description of growth. This is one occasion where it might be better to sample vectors of parameters from the posterior distribution of a Markov chain Monte Carlo (MCMC) and use them as the basis of projections rather than use simple bootstrapping.

13.3 Concluding Remarks

Integrated size or length-based assessment models offer the possibility of producing detailed stock assessments for difficult to age species that could be used in formal management systems. The most valuable fisheries in Tasmania include rock lobster (*Jasus edwardsii*) and abalone (*Haliotis rubra*), and the management of rock lobster is very dependent on length-based models (Haddon and Gardner, 2009), and the abalone fishery is beginning to use them (Haddon, 2009), though characterizing the variation around the coast is slowing their implementation. They are also used in other abalone and rock lobster fisheries elsewhere (Breen et al., 2003). Not surprisingly, size-based models are very sensitive to having an adequate description of the growth process; the growth transition matrix is a vital component. Using abalone in the example may not have been optimal, as these species tend to be highly variable in their biology. The new western zone is the bottom half of the west coast of Tasmania, and this extensive area contains many populations of abalone producing about 1,000 tonnes a year. An assessment model that attempts to capture the dynamics of this large area averages over much of the variation present between populations within the zone. Nevertheless, the potential value of size-based models should be apparent, as important management questions can be answered. The expected population trajectory

EXAMPLE BOX 13.6

Projecting the size-based model. Extend the years from AE7 to 2015 in AL7 and from AF18 to AL18 (you could go further if wished). Select AE8:AE11 and copy across to column AL. Copy AH12 across to AL12. Select AE14:AE17 and copy across to column AL (delete AF15:AL16). Finally, select AE19:AE44 and copy across to column AL, and that is all that is needed to conduct deterministic projections. Plot the spawning biomass or the catch rates or harvest rates, treating the data from 1985:2008 as one data series and the projection data as another, akin to Figure 13.7. Then try altering the TAC in I5 and consider the impact; do not expect rapid effects. You could copy the row labels from F7:F17 into AM7:AM17 to make things more clear.

	AF	AG	AH	AI	AJ	AK	AL
7	2009	2010	2011	2012	2013	2014	2015
8	69.2	69	69	69.3	69.6	69.9	70.2
9	11498	11494	11521	11561	11606	11648	11687
10	8930	8893	8905	8939	8980	9021	9058
11	8475	8427	8441	8479	8522	8564	8603
12	=I5	=AF12	=AG12	900	900	900	900
13							
14	1.7045	1.6948	1.6977	1.7053	1.714	1.7225	1.7302
15							
16							
17	0.1062	0.1068	0.1066	0.1061	0.1056	0.1051	0.1046
18	2009	2010	2011	2012	2013	2014	2015
19	10406099	10406099	10406099	10406099	10406099	10406099	10406099
20	64973	64973	64973	64973	64973	64973	64973

under different catch regimes can be determined, or the effect of a change in legal minimum length can be identified, along with other, more site-specific questions. Age-structured models naturally follow the fate of cohorts, and the annual incrementing of ages is an automatic clock in such models. Size-based models are not so constrained by their internal dynamics, and the growth of organisms can be highly variable. The intuition is that such models are going to be less certain in their predictions. Age-based models now have a long history and their behaviour is well known. Size-based models are relatively new, and until more experience with using them in real situations has been accrued and reported, especially where the biology of the modelled species is highly variable, it would be well to be cautious with their use.

Appendix A: The Use of Excel in Fisheries

A.1 Introduction

Excel has three main uses for fisheries scientists:

1. Entry and editing of data—Formal tabulation of one's data.
2. The display and illustration of a data set's properties—Data can be graphed or compared visually, which can be useful for detecting anomalous data. Tends to be preliminary to any detailed analysis.
3. Determination of a data set's properties—This can include simple analyses such as summary statistics and fitting linear regression lines, but can extend to estimating the parameters of nonlinear equations and models, of varying complexity, to available data.

There always appears to be more than one way of doing things inside Excel. This may seem redundant, but by allowing greater flexibility, more people should be able to find ways of working with Excel. The simple trick is to find which way works best for you and stick with it.

In this appendix, aspects of the functionality of Excel that the author has found useful will be introduced. This will not be an exhaustive list, and functions or practices that others find indispensable may be omitted; however, this is only meant to be an introduction. There are many excellent texts on the use of Excel and programming in the Visual Basic for Applications (VBA) language built in to the program. We will introduce ideas relating to the basic use of the program, a set of the most useful functions, with their strengths and weaknesses, and a short introduction to VBA, sufficient for the needs of this book.

A.1.1 Getting Started

The first edition of this book was written using Excel 1997 and 2000. Since then there have been three more versions of Excel (Excel 2003, Excel 2007, and Excel 2010). There were few differences between Excel 2000 and Excel 2003, so most of this appendix is directly applicable. If you are using Excel 2003, make sure you have the Windows Service Pack 3 installed; otherwise, the random number generators will not work correctly, leading to some very strange

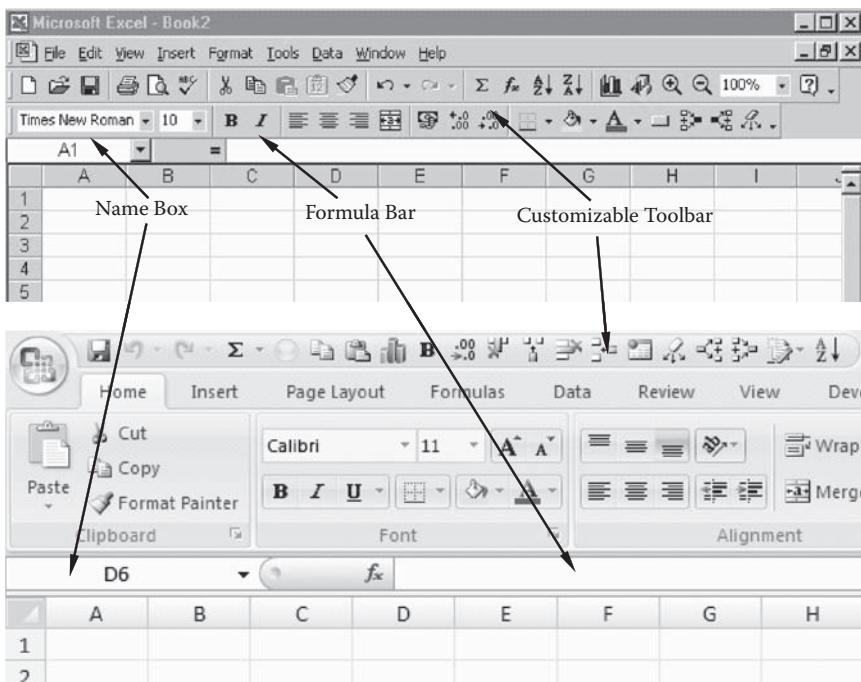
results. If you are using E2007, then all the commands are still there, but they may have been moved. If you know the E2003 keyboard shortcuts they can still be used. For example, after using <Ctrl>C to copy a set of data it is possible to paste the values of those cells and transpose them by typing <Alt> e s v e (for Edit/Special/Value/Transpose) and E2007 will recognize that.

All of the example boxes in this book assume that Excel worksheet rows are numbered and the columns are titled with letters. If your copy has numbered columns you can fix that under Tools/Options/General by unticking the R1C1 reference style box. In E2007, click the Office icon in the top left, and under Excel Options/Formulas untick the R1C1 reference style. While I appreciate the larger worksheets in E2007 (it is very convenient for managing large data sets), I still fail to appreciate the new ribbon style for presenting options. It is not so bad on a large screen, but on a laptop the ribbon takes up a good deal of screen and seems to me to be a slower way of doing things. I feel like a luddite, but I have populated the customizable toolbar on the top to speed many operations. However, it remains a remarkable program of terrific flexibility and power. Fortunately, the new Excel 2010 is reported by Microsoft to have customizable ribbon tabs, which should improve things.

A.2 Workbook Skills

A.2.1 Tools/Options, Auditing, and Customization

It is assumed the reader knows the Excel interface and has some knowledge of the functions of the bits on the Excel window (Figure A1.1). Perhaps the first thing to do is to set up Excel with more of your preferences. Try pressing the Tools/Options menu item (Options is near the bottom of the list of menu items under the Tools menu). In the resulting dialog box you can set many properties inside Excel. Under the General tab, you can set a default directory in which Excel should begin searching for files, plus the default font. Other than that, it is useful to go to the Edit tab and change at least two items. Excel often comes with the options “Edit directly in cell” and “Move Selection after enter” ticked as a default. The moving selection after pressing <Enter> is a matter of personal preference. I find it a nuisance, preferring to press the down arrow when entering data rather than relying on the software to move the cursor down a cell with each data record. But the “Edit directly in cell” option can be more troublesome. Apart from often being in a tiny font, when one enters a formula, one’s typing can obscure the contents of the cell(s) immediately to the right. This can be a nuisance if one wants to refer to that cell by pointing with the mouse. Try turning these options off and seeing which setup you prefer. You can return to the Tools/Options dialog box at any time and alter the settings. It is worth experimenting with the various

**Figure A1.1**

A typical view of a newly opened Excel spreadsheet in E2003 (top) and E2007 (bottom). It is currently named Book2. The usual menu items are listed across the top. Note the toolbars, which contain many shortcuts to actions, such as saving the file or chart, and function wizards. These toolbars can be customized to include the shortcuts of most use to individual users. Also highlighted is the “Name” box, which can be used to name cells for added convenience when creating equations, and the “Formula” area, where most of the editing of equations takes place. The ribbon in E2007 is obvious; unfortunately, it cannot be customized.

options just to see what is possible. Customization is not just playing about. Having a comfortable working environment can aid productivity. In E2007, the customization menus can be accessed under the Office icon and pressing the Excel Options button. The editing options discussed above are under the Advanced menu. Explore the various options and settle on those that suit your own way of operating.

It is valuable to familiarize oneself with the toolbars and ribbon (Figure A1.1) and what they can do for you. By placing your mouse cursor over a button (and *not* clicking), the button’s name will appear, which generally describes its function. You can also customize the toolbars as they appear on your computer so that its functionality reflects your individual needs.

Some of the most useful buttons available include the auditing buttons  (under the Formulas tab in E2007); these are useful for tracking down which cells are related to which. They can be added to the toolbars already available by clicking anywhere in the toolbar region using the

right-hand mouse button, and selecting the Customize option at the bottom of the resulting menu (alternatively, View/Toolbars/Customize). This will give rise to a dialog box with three tabbed options. Select the middle Commands tab and then the Tools options under Categories. There are many useful tools listed, but if you scroll down you will find the ones figured above. They are the Trace Precedents, Trace Dependents, and Remove All Arrows buttons. If a cell has an equation that refers to a number of other cells, pressing the Trace Precedents button will generate fine blue arrows to the cells involved. Similarly, pressing the Trace Dependents will identify any cells influenced by the active cell. To include a tool on a Toolbar, click and drag it from the Dialog box onto the selected Toolbar (if it just disappears you have probably missed placing it onto the Toolbar). To remove a button, just click and drag it off the Toolbar into anywhere else. I also find the Zoom In and Zoom Out buttons  to be very useful. These can be found under the View category. Further buttons to add would include the Paste Values button  (under Edit) and the Button button  (for generating active buttons for use with macros on the worksheet), which is found in the Forms category (not the control toolbox), and plus many others that may suit your own style of working. In E2007, right mouse clicking the customizable toolbar enables the selection of the "Customize the Quick access toolbar" option.

There are many other ways that a worker can customize his or her version of Excel, and it is recommended that you search for the setup that suits your own uses and needs. If you are relatively new to Excel, then do try experimenting with the different setup arrangements to see which you like the best. Personally, the author tries not to have more than two rows of toolbars visible, so as to have a good balance between having numerous useful buttons and an extensive view of the active worksheet.

A.2.2 Data entry

Data entry is straightforward. Get to know the number keypad and use it wherever you can for greater speed (laptop users will just have to suffer). If you enter data in columns, get used to typing a number and entering it by pressing the down arrow. There is no need to type a zero when entering a fractional number (e.g., 0.234 can be typed as .234).

If you need to copy a number down a column, enter the number, then place the cursor over the small dot , the copy handle, at the lower right hand corner of the selected cell. The cursor should convert to a thick cross or addition sign. You can drag this down to copy the cell automatically into the selected area. If you require a series, such as 1, 1.5, 2, 2.5, ..., begin the series (e.g., 1, 1.5), then select the two cells containing the two numbers, grab the copy handle, and drag in the direction (up, down, or across) you require. You should see the count of the extent of the series to help you know when to stop. If the increment

TABLE A1.1

Keyboard Commands for Moving Rapidly around the Worksheet and Workbook

<Home>	Moves the active cell to the first column of the ActiveRow.
<Ctrl><Home>	Makes cell A1 the ActiveCell.
<Ctrl><PageUp>	Makes the WorkSheet to the left of the ActiveWorkSheet the ActiveWorkSheet.
<Ctrl><PageDown>	Makes the WorkSheet to the right of the ActiveWorkSheet the ActiveWorkSheet.
<Ctrl><End>	Makes the Cell at the bottom right of the ActiveArea the ActiveCell.
<Ctrl><-->	If the ActiveCell is empty, these key combinations move the ActiveCell in the direction of the arrow until it meets the first filled cell or a spreadsheet boundary. If the ActiveCell is full it moves until it meets an empty cell or a sheet boundary. Very useful for moving around large worksheets.
<Ctrl><↑>	
<Ctrl><-->	
<Ctrl><↓>	
<F5>	Opens the “Goto” Dialog box into which you could type a cell reference and thereby move the ActiveCell.
DropList button on the NameBox	This provides a list of Named cells and ranges in the WorkBook. By selecting a Name from the list, the cell or range referred to becomes the ActiveCell or ActiveRange, even if it is on a different Worksheet to the ActiveWorkSheet.

Note: If more than one key is involved, they must both be pressed together; i.e., press the <Ctrl> key, hold it down, and then press the other key.

you want is one, then just enter the starting number, grab the copy handle, and drag while holding the <Ctrl> key; this will extend a series from a single value in steps of one. If you enter text followed by a number, such as Year88, grab the copy handle and drag in the desired direction; the number following the text will increment by one in each cell dragged across. It should be emphasized that none of these shortcuts are necessary; they simply increase the speed with which data and worksheets can be worked with.

A.2.3 Movement around Worksheets

There is a suite of keyboard commands for moving rapidly around a worksheet, and these are generally some key combined with the <Ctrl> key (Table A1.1).

A.2.4 Range Selection

There are a number of options for selecting a range of cells:

1. If the range is small (completely visible on the screen), then one drags the mouse over the required range to make it the ActiveRange.

2. Alternatively, one could first press $<F8>$, which turns “extension” or “selection mode” on, and then proceed with one of the keyboard controls for moving the ActiveCell (Table A1.1). The use of $<F8>$ is advantageous for one-handed keyboard work, but if you are using two hands, it is often simpler to hold down the $<\text{Shift}>$ key when operating the keyboard movement commands. Thus, at the top of a column of ten thousand filled cells, pressing $<\text{Shift}><\text{Ctrl}><\downarrow>$ selects the entire column of ten thousand cells (assuming there are no missing data points).
3. Finally, if it desired to select noncontiguous ranges (e.g., when selecting data to be graphed), one can proceed as in step 2 to select the first range. Then one has to hold down the $<\text{Ctrl}>$ key when clicking the cursor at the start of the next selection, after which one can proceed as before as many times as required.

When creating formulas in cells, one very often refers to other cells (e.g., $=A5*B6$). Instead of typing these addresses, it is most simple to start typing the formula and when an address is required, use the mouse pointer to select the required cell. This puts the correct address into the formula. Very often one wants some degree of absolute reference. Thus, $\$A\5 refers to the cell A5, and even if this is copied somewhere else, it will still refer to A5. Similarly, \$A5 will always refer to column A when copied elsewhere, although the row number may change appropriate to the move. Instead of typing the dollar signs, once the cell reference or range has been input (either by typing or pointing), then assuming A5 has been entered, pressing the $<\text{F4}>$ button will cycle through $\$A\5 , A\$5, \$A5, A5.

A.2.5 Formatting and Naming Cells and ranges

A range can be either a single cell or a block of cells. It is often convenient to give a cell a particular name (such as Gradient or M), which then makes referring to that cell in equations very simple. It is far more readable to type “ $=\text{exp}(-M)$ ” than it would be to type “ $=\text{exp}(-\$A\$2)$,” assuming that cell A2 has been named M. This facility is especially useful when working with matrices or arrays.

Naming a cell or range is most simply done by selecting the cell(s) required, typing the desired name into the NameBox, and pressing $<\text{Return}>$ or $<\text{Enter}>$. If one omits the last step, for example, by completing the action through clicking elsewhere with the mouse, the name will not be accepted. To see the name of a cell or range, make the cells the ActiveCell or range, and their name will be seen in the NameBox. If the name is selected in the DropDownList associated with the NameBox, the named cells become the ActiveCell/Range.

A range can be formatted by selecting the cells, clicking the right mouse button, and selecting the Format Cells option. Alternatively, the Format/Cells

menu item can be selected and the required options selected. If it is desired to have multiple fonts in one cell, then enter the text, select the particular letters, and use the menu commands to alter the font. When the <Enter> key is pressed, the text is entered into the cell and the multiple fonts are visible.

Under the Format/Conditional Formatting menu item it is possible to make the formatting of a cell dependent upon the value in the cell. This possibility can be surprisingly useful when manipulating data or model outputs.

A.2.6 Formulas

To use any data entered into an Excel Workbook some form of manipulation of the data will be necessary. This is where Excel really starts to show its power. To enter an equation, start by selecting the cell into which the equation is to be placed. Start all equations with an “=” symbol. This is always the case unless there is a function or equation within an equation, e.g., =if(isnumber(A2),1,0). If the equals sign is omitted, Excel will react as if you entered text and nothing interesting will happen. If on entering a formula the formula remains visible and its value fails to appear, check in Tools/Options, under the View tab, that the Formulas option is not ticked. If you want to enter text but Excel keeps treating your entry as a formula or a number, then start the text with an ‘ symbol, which will not remain visible.

If you wish to concatenate text and numbers, which can be useful with functions such as =countif(), then, assuming cell A5 contained a value of 0.53, we could type =countif(A6:A1005,”<=” & A5), which would be equivalent to =countif(A6:A1005,”<=0.53”). The active agent in that is the “&” symbol. This can be very useful when manipulating cell references or creating text out of multiple nontext cells. If transferring your equations to a program like Word, take care that it doesn’t correct your &s into “and”s, which will obviously fail to work if pasted back into Excel.

A.2.7 Functions

Two very useful buttons are the summation button, which generates an =SUM() function, and the generalized Paste Function button . This latter can lead you to any one of the more than two hundred worksheet functions that are available in Excel. It is strongly recommended that you explore what is available by looking through the contents of this dialog box. In the example boxes throughout the text of this book there are many functions used whose entry can be simplified by using this shortcut button. Using this shortcut, you can obtain help in relation to any function as well as prompts for the parameters required by the various functions. We will consider some of the more useful ones to illustrate some of what is available. In general, if there is a function you want, it is likely to be already available. If it isn’t, Excel has the flexibility to enable you to write your own custom functions (see, for example, Walkenback, 1999). Thus, typical things

such as =EXP(), =LN(), which is log to base e , =AVERAGE(), =STDEV(), =PI() are all available. There has been some criticism of Excel's use for statistical calculations. Some of these are correctly pointing out that some of the algorithms used are not necessarily the optimum available. However, in reality, this usually only influences the eighth or ninth significant digit in just a few functions, and while this may not be acceptable for high-energy physics, it is not a problem for most ecological data (especially in fisheries). So there are functions available for most of the obvious needs, but some of the most valuable are not so obvious.

A.2.7.1 =SumProduct()

A very common thing to want to do is to take two columns of numbers, multiply the elements together, and sum the results. When we do a least squared residual analysis in the example boxes, we typically subtract one column's values from another, square the result, and then in a cell above the column we sum to the total. Assuming we have one thousand observed values in column C and the predicted values in column D, if we fill column E with =(C2-D2) (it's always a good idea to plot residuals), we could just put =SUMPRODUCT(E2:E1000,E2:E1000) into any cell in which we wished to obtain the sum of the squared residuals. In the examples given we generally calculated the squared residuals explicitly and summed those in an effort to be clear. As an alternative, it would also be possible to use the =sumxmy2 function. You may wish to modify some of the example boxes to implement the simpler approach of the =sumproduct() function. In Chapter 11, we used columns of numbers-at-age and combined them with the average weight at age inside a =sumproduct() function to obtain total biomass.

A.2.7.2 =Frequency() and Countif()

Very commonly it is desired to convert a column of data into frequency counts relative to different categories. Thus, in the example box testing the Excel random number generator function, =RAND(), after generating a column of one thousand random numbers, it is desired to count how many lie between 0.0 and 0.1, then between 0.1 and 0.2, and so on. One of the best ways of doing this is with the =frequency() function. Given one thousand random numbers in A5:A1004 and the numbers 0.0, 0.1, 0.2, ..., 1.0 in cells C3:C13, to construct the frequency counts, one selects D3:D13, types =frequency(A5:A1004,C3:C13), and then presses $\langle\text{Ctrl}\rangle\langle\text{Shift}\rangle\langle\text{Enter}\rangle$ all at once. This latter combination is required to enter an array function. This will generate the required numbers, which will approximate one hundred in the cells opposite 0.1, 0.2, ..., 1.0, and should be zero opposite 0. This may appear odd to biologists because they are usually trained to consider such frequency counts from the lowest category up. This means that the class 0.0, followed by 0.1, is often taken to mean everything greater than and equal to 0.0 but

less than 0.1. However, for unknown reasons, in Excel, the frequency counts start from the top and work down. Thus, in the example, the category 1.0 refers to all values ≤ 1.0 but > 0.9 . Similarly, the 0.9 category refers to all values ≤ 0.9 but > 0.8 , and so on down. It is important to realize that the 0.1 category refers to everything ≤ 0.1 and greater than 0.0. Thus, the 0.0 category refers to the number of zeros present and anything less than 0.0. This may all seem messy, but it works well with integer data, and as long as one is aware of how this function works, it can be used successfully with real numbers as well.

People may be more comfortable with an alternative approach that produces frequencies more in line with the usual way of counting frequencies. Given our random number example, if the data are in column A, it would be possible to generate a set of bins from 0 to 1.0 in steps of 0.1 in column C. Frequency counts can be produced by putting in column D: =countif(\$A\$5:\$A\$1004,">=" & C3) - countif(\$A\$5:\$A\$1004,">=" & C4) and copying this down to calculate the required frequencies.

A.2.7.3 =Linest()

This is another array function, which can be used to fit a linear regression in real time on the worksheet. It can be used to provide just the parameters or the parameters along with an array of related statistics. Its format is =LINEST(Y-Values, X-Values, Boolean for Constant, Boolean for Statistics). If one enters TRUE for the first Boolean (true/false), then the regression includes a constant; if one enters a FALSE value, then it is fitted through the origin. Given a true for the second Boolean will generate the related statistics (e.g., sum of squared residuals, number of observations, correlation coefficient). To use this function, one selects a five-row-by-two-column range, types in the function, and then presses $\langle \text{Ctrl} \rangle \langle \text{Shift} \rangle \langle \text{Enter} \rangle$, as usual with an array function. Check the function help for all details.

A.2.7.4 =Vlookup()

The =vlookup() function, along with the other reference functions (e.g., =offset()), enables the user to implement lookup tables within Excel. This is used in many of the computer-intensive statistical routines. There is a slight quirk to the =vlookup() function that is worth knowing about.

If one is using the =vlookup() function to select from a series of real numbers, then it is essential to use the full syntax. The =vlookup() function requires (1) the Lookup_Value, which is the value to be found in the first column of the lookup table; (2) the Lookup-Table address, which is the range where the information columns are found; (3) the column_index_number, which is the column within the lookup_table from which to obtain the data; and (4) the so-called range_lookup, which is an optional argument that defaults to true if omitted. This latter parameter has a significant quirk such that if this is set as true, the action will be to find the closest match; if it is

false, it must find an exact match (or give an error message). If you require an exact match but put or leave true by default in this last, optional function argument, then even if the lookup_value is not present, the closest match will be returned. Generally, in fisheries work, one would always wish to place "false" in the range_lookup argument.

A.2.7.5 *Other Functions*

There are too many useful functions to detail here, but it may help to know that there are matrix algebra functions, text handling functions, statistical distribution functions, logical functions, lookup and reference functions, data and time functions, and others besides. Do not assume you understand how a function behaves. Just because it sounds just like something you do all the time does not imply that it does what you want in exactly the same way. Read through the help file relating to each function you use.

A.3 Visual Basic for Applications

A.3.1 **introduction**

There are many places in which it is necessary to use a computer program to control or manipulate data beyond that which can be performed on the worksheets. Excel has Visual Basic built in to it in a version that can interact with the objects and functions that make up the Excel program. Thus, it is possible to refer to cells on the worksheets, and interact with Visual Basic programs in real time.

Fortunately, it is possible to record large amounts of the code required by the language using the Tools/Macro/Record New Macro menu item. Record as much of each macro as possible to save typing and ensure accuracy of syntax. In order to modify or articulate a program, I often record small snippets of extra code and cut and paste them into my main subroutine. Get used to the development environment and once again learn what setup and operational procedure best suits you.

A quick way into the VBA editor is to press <Alt><F11>. A quick way to record a macro is to place a macro button on the sheet (from the Forms toolbar; in E2007 use the Developer tab, select "Insert a control," and click the Forms button), name the macro, and select the Record button on the dialog box.

I find it is best to type any VBA code in lowercase (except names if you wish to use capitals) and without spaces because if the syntax is correct, the code lines will be properly spaced out and recognized commands will be capitalized when the line is entered.

Always have Option Explicit at the top of your code, as this requires one to declare all variables, which helps prevent errors introduced through spelling a variable incorrectly somewhere in your code. When in the VBA editor window ($<\text{Alt}><\text{F11}>$) the Tools/Options menu brings up a dialog box, and when you first begin creating programs, it is reasonable to tick all of the options under the Editor tab.

One good way to learn is to have both the Excel sheet in which one is recording and the VBA editor window visible on the sheet at the same time. By using the worksheet you will be able to see commands being generated inside the VBA window. Not everything recorded is required in the final program; any extraneous code can be deleted.

A note of warning is necessary. Macros are very powerful and can overwrite data on a worksheet without warning. You are in control, but as should always be the case, you should take responsibility for that control.

A.3.2 An example Macro

An example of a subroutine is provided along with explanations for each line and each component. All the following subroutine does is copy one number from cell N7 down into a sequence of cells starting five cells ($4 + i = 5$ when $i = 1$) below it. The macro works because the action of pasting anything on the active sheet causes the cell to recalculate (assuming calculation is set to Automatic). This resets all the calls to `=Rand()`, which generates random numbers on the sheet. The sheet must be designed to automatically change the numbers used in a calculation whose final outcome is in N7, so the net effect is to calculate this statistic one thousand times and store the results in column N. First we give the macro and then describe every line in the macro.

```
' Macro1 Macro Operates the Bootstrap Routine
' Macro recorded by Malcolm Haddon
Sub Macro1()    ' You would normally give it a recognizable name
    Randomize
    Calculate
    Application.ScreenUpdating = False
    For i = 1 To 1000
        Range("N7").Select
        Selection.Copy
        ActiveCell.Offset(4 + i, 0).Range("A1").Select
        Selection.PasteSpecial Paste:=xlValues,
            Operation:=xlNone, _
            SkipBlanks:=False, Transpose:=False
        Application.CutCopyMode = False
    Next i
    ' sort the bootstrap replicates
    Range("N12:N1011").Select
```

```

Selection.Sort Key1:=Range("N12"), Order1:=xlAscending,
    Header:= _
        xlGuess, OrderCustom:=1, MatchCase:=False, Orientation:= _
        xlTopToBottom
    Application.ScreenUpdating = True
End Sub

```

Comments in VBA are signified by a single apostrophe, '. When you create a VBA subroutine in a module by recording keystrokes (Tools/Macro/Record New Macro), the program is always prefaced by a five-line comment. On the author's machine any text following on the same line turns green. Comments can start anywhere on a line:

```

' this is a comment
for i = 1 to 1000      ' this is also a comment

```

would both work. Annotations are useful in understanding the program months after they were written; try to keep them brief but informative.

Randomize resets the computer's random number generator. The format Randomize 12345 can also be used, where the number would be an initiator or seed to the pseudorandom number sequence. It cannot be recorded.

Calculate is the same as pressing F9 on a worksheet. It causes the worksheet to calculate all its equations. If you have many random numbers on a sheet, it is a good idea to start the program in this way so as to randomize the data before any calculations are carried out. It can be recorded by pressing F9.

Application.ScreenUpdating = False is a very handy command that stops the screen updating until the next **Application.ScreenUpdating = True**. This is valuable because if the macro moves around the screen a good deal, it can waste a huge amount of computer time rewriting the screen. It cannot be recorded.

For i = 1 to 1000 is a standard For loop in Basic that can enclose a block of code and thereby bring about a set of iterations (one thousand in this case). The **i** is the counter variable, which can be used in equations inside the block of code (any valid name can be used). The block of code is defined by the **For** loop and by a **Next i** found below in the code. This command cannot be recorded.

Range("N7").Select moves the cursor on the active spreadsheet to cell 'N7' so that "N7" becomes the ActiveCell.

Selection.Copy copies the value in the selection ready for pasting somewhere else.

ActiveCell.Offset(4 + i, 0).Range("A1").Select contrasts with Range("N7").Select, which is the way of selecting a particular cell. ActiveCell.Offset.etc is the way to reference cells relative to the current ActiveCell. You will not need to type this; instead, it is best to record it. The cell referenced is in

position ActiveCell.Offset(4 + i, 0), where the 4 + i refers to how many rows down, away from the current active cell, to move, and the zero is how many columns across to move. You will need to edit the recorded text to include the counter variable *i* into the command. To use this command one first has to use “relative references,” which means instead of absolute references (as in Range(“N7”).Select), you can record the offsets from the current active cell.

```
Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, _
SkipBlanks:=False, Transpose:=False
```

is a two-line command, which again is best recorded. It is simply telling Excel to Paste/Special/Values whatever was previously copied somewhere else in the program into the current active or selected cell. The default values for Operation, SkipBlanks, and Transpose can be deleted for clarity.

Application.CutCopyMode = False (again recorded by pressing the <Esc> key) simply turns off the highlighting around a copied cell and prevents the accidental pasting of the clipboard into a cell by pressing return after a macro has finished running. This is handy at the end of a macro but can be deleted from most places within the body of a macro.

Next i is just the end of the For loop that started a few lines before (see earlier). This command needs to be typed, as it cannot be recorded.

‘sort the bootstrap replicates’ is just another comment inside the program that describes the following lines of code.

Range(“N12:N1011”).Select Range(“”).Select can be used to select single or multiple contiguous cells. For a group of cells the syntax is to separate their addresses with a colon. In this case the program has generated one thousand bootstraps of some statistic, and those one thousand numbers are to be sorted in order. First, they must be selected. This command was recorded.

```
Selection.SortKey1:=Range(“N12”), Order1:=xlAscending, Header:= _
xlGuess, OrderCustom:=1, MatchCase:=False, Orientation:= _
xlTopToBottom
```

is a three-line command that is recorded, and it simply sorts the selection into ascending order.

Application.ScreenUpdating = True turns screenupdating back on. If there was no initial turning off, then this does nothing. Screenupdating automatically turns back on at the end of a macro.

End Sub complements the **Sub Macro1()**, which the recorder places at the front of the macro. The two together define the body of the macro, and it is this name, Macro1, which is used to identify the subroutine when it is called. You can change this name at any time (e.g., to Fred, or RandomRegress, or whatever you wish), but it is perhaps best to name the macro when it is first written or recorded.

A.3.3 Using the Solver inside a Macro

When using computer-intensive methods it is common to want to apply the solver inside a macro. This is simple to do, but there are a couple of tricks that may cause problems unless care is taken. The solver can be recorded inside a macro like most other actions. In Excel 97 and 2000, one obtains something like

```
SolverOk SetCell:="$B$12",MaxMinVal:=1,ValueOf:="0", ByChange:=$B$2:$B$5"  
SolverSolve (true)
```

In order for this to proceed without calling up the “Solver has converged to a solution” dialog box, one needs to add the text in *italics* (*true*). Of course, in that case you will need to ensure that an accepted solution really is acceptable without individual inspection.

Sometimes, after recording a macro that includes the solver, the macro fails to run when called and the program opens up the Visual Basic editor and complains that there is a “Compile Error, Cannot find Project or Library.” You need to reset the program (the small blue square in the Visual Basic editor toolbar) and then go to the menu item Tools/References and tick the Solver box. If it says the Solver.xla is missing, then you will need to browse for its location. This should fix the problem. One way of preventing this is to call the solver from the worksheet before running the macro.

A.4 Concluding Remarks

This very brief introduction to the use of Excel is only designed to encourage those people who are relative beginners and those others who feel that one should not use such a program for serious fisheries work. In the body of the book the example boxes range from very simple to highly complex. The ability to conduct a length frequency decomposition or a statistical catch-at-age analysis on a modern spreadsheet illustrates how powerful such software has now become. While I am not recommending that this is a suitable vehicle for conducting large-scale serious assessments, Excel has huge advantages as a medium for teaching the details of different analyses. It is a very common, highly flexible program, it hides almost nothing, and a workbook can be audited by anyone. The addition of the built-in programming language means that almost anything is possible, although the speed may not be great. As an aid to teaching I have found it invaluable. On the other hand, programs written in some computer language, especially the more object-oriented languages such as C++ and Delphi, would make an appalling teaching medium. Hopefully, readers will find that the worked

examples help them understand the algorithms and equations that make up the variety of quantitative methods illustrated in this book.

Excel is so easy to use that it is possible to fall into the trap of typing in a model before writing out the full set of equations. It is always best to know the full model structure before starting. In this way the most efficient layout can be selected. As implied in the preface, the best way of learning a method is to use it, so I encourage you to implement your own problems using your own data.

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