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# *Fisheries and Modelling*

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## 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

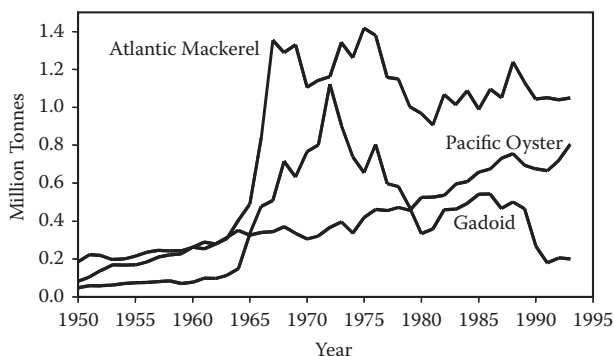
Understanding the variations exhibited in the catches of different fisheries (Figure 1.1) is a major objective for fisheries scientists. By referring to the yield from a fishery as its production there is a potential for confusion. Take care not to mix up a stock's production or yield with its productivity. 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:

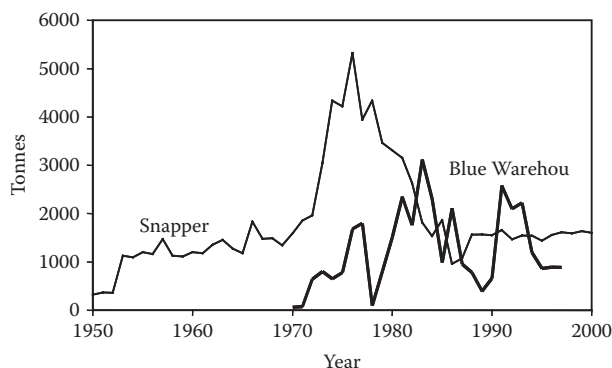
From year to year, recruitment varies between a factor of about three to more than two orders of magnitude. The response of recruitment to changes in spawning stock is obscure.... But this natural variation provides the mechanism by which the stock remains adapted to its environment. (Cushing, 1988,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

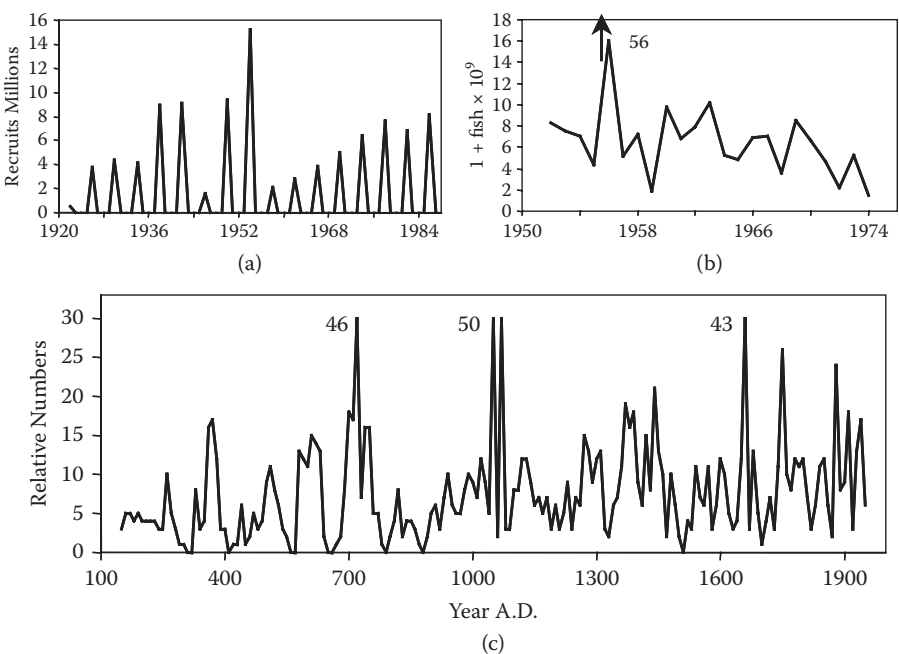
The yield of three different fisheries from 1950 to 1993 (data from FAO, 1995). Pacific oyster refers to all oysters reported from the Pacific region and illustrates an increasing trend; Atlantic mackerel might include snoeks and cutlassfishes and exhibits a rise to a relatively stable fishery. Finally, 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 (*Seriotele 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). LRPs 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,



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### 1.3.1 g eneral Properties

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.

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

### 1.3.3 Limitations Due to Model Type

### 1.3.4 The Structure of Mathematical Models

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

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

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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.

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## 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  $\sigma^2$ , 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.

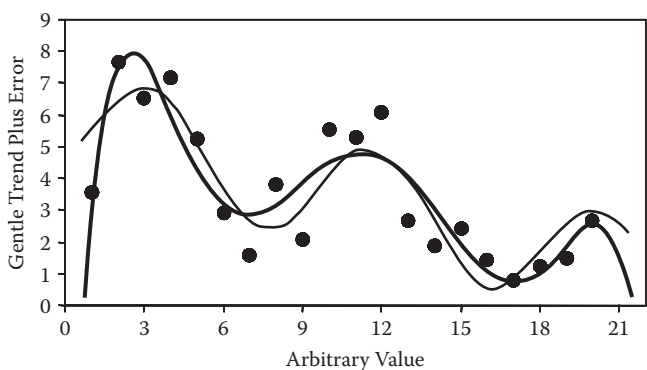
If novel observations are in accord with the model, then one has gained little. In practice, it is likely that the new data would then be included with the original and the parameters reestimated. But the same could be said about a purely empirical model. What are needed are independent tests that the 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

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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.

