

MODELLING and QUANTITATIVE METHODS in FISHERIES

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Fisheries, Population Dynamics, and Modelling

1.1 THE FORMULATION OF FISH POPULATION DYNAMICS

Fish populations can undergo many changes in response to being fished. These include changes to total numbers, total biomass, size-frequency distributions, age-structure, and spatial distributions. Fisheries science has naturally developed into using mathematical and statistical descriptions of these processes in attempts to understand the dynamics of exploited populations. The underlying assumption is that if we can understand how populations respond to different perturbations then we should be able to manage those fisheries according to our chosen objectives.

Unhappily, the astonishing local abundance of some fish species in the wild can lead fishers to believe they can have no impact on stocks. This unfortunate intuition is nicely illustrated by one of the more famous scientists from the 19th century. Thomas Huxley was impressed by the sheer abundance of some fish populations. In a paper published in 1881, he calculated the number of fish in a single school 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) [1 fathom = 1.83 m].

Huxley was explicit about his belief that human fishing could not have a negative 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).

Such arguments from astonishment are still met with today and have been referred to as the inexhaustibility paradigm (Mace, 1997). That some people 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 all commercial fishing in the North Sea during the years of the First World War demonstrated conclusively that catch levels were 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 experiment was repeated during the Second World War with the same 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 perception but it was at least three decades into the 20th 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 complete stocks so that emigration and immigration were irrelevant. 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 sum of the initial weights of all individuals recruiting to the stock each year, G is the sum of the growth in biomass of individuals already recruited to the stock, C is the sum of weights of all fish caught, and M is the sum of the weights of all fish which die of natural causes during the year. Nowadays we might use different letters [perhaps: $B_{i+1} = B_i + (R + G) - (F + M)$] to those used by Russell, but

that is a trivial difference (Krebs, 1985). We must be careful not to confuse the M used here, with the symbol generally 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 (Beverton and Holt, 1957; 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, and 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 it was published in Russian and only began to be recognized for its value much later (Ricker, 1944; 1975). Russell was almost dismissive of his own statements, but categorizing or estimating the factors identified by Russell (lately within age- or size- or spatially structured models) has been the main focus of fisheries scientists ever since. Methods of modelling the details of these processes have varied greatly but the underlying factors conveyed in Eq. 1.1 are standard.

The obvious factors missing from Russell’s formulation are the effects of other species (competitors, predators, etc.) and of the physical environment in which the species live, which can include everything from *el niño* effects to pollution stress (Pitcher and Hart, 1982). 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 currently movements towards encouraging management of ecosystems and multi-species management that are challenging that view (Pitcher, 2001; Pauly *et al*, 2001). Ecosystem management is becoming a trendy phrase in resource management and it may become a political reality before the technical ability is developed to understand ecosystem dynamics in any way useful to management. If resource management is to be guided by science rather than public opinion then ecosystem management may prove the greatest challenge yet for fisheries scientists.

The intuitions behind much of quantitative fisheries science are mostly the same now as earlier in the 20th century. The rising interest in

multi-species and ecosystem management, with the need for a precautionary principle and perhaps for marine protected areas, can be seen as a move to adopt a new set of intuitions about fished stocks and our interactions with them. These ideas are still under active development and are currently based upon extensions of methods used with single species (Garcia and Grainger, 1997; Walters and Bonfil, 1999). A completely different direction is being followed by users of simulation models such as EcoPath or EcoSim (introductions to EcoPath can be found on the WWW, for EcoSim see Walters *et al*, 1997). Despite all of this, in this present work we will be concentrating on single species systems, but some of the possible effects of environmental variability on such things as recruitment and growth (seasonal changes) will be included.

1.2 THE OBJECTIVES OF STOCK ASSESSMENT

Understanding the variations exhibited in the catches of different fisheries (Fig. 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. Care must be taken 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.

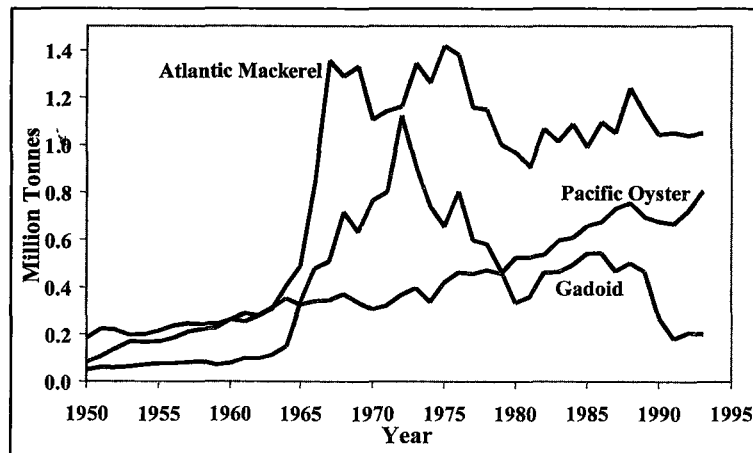


Figure 1.1. The yield of three different fisheries around the World from 1950 to 1993 (data from FAO, 1995). Pacific oyster refers to all oysters reported from the Pacific region and illustrates an increasing trend; Atlantic mackerel might include snoeks and cutlassfishes and exhibits a rise to a relatively stable fishery. Finally, Gadoids includes cods, hakes, and haddocks from the Arctic Atlantic and illustrates a fishery rising to a peak and then declining to a much lower level.

Fishing industries have the potential for fishing a stock too hard and bringing about a reduction in the potential sustainable harvest or even a stock 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 the primary task of a stock assessment. The fisheries illustrated in Fig. 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 be seen in particular species (Fig. 1.2).

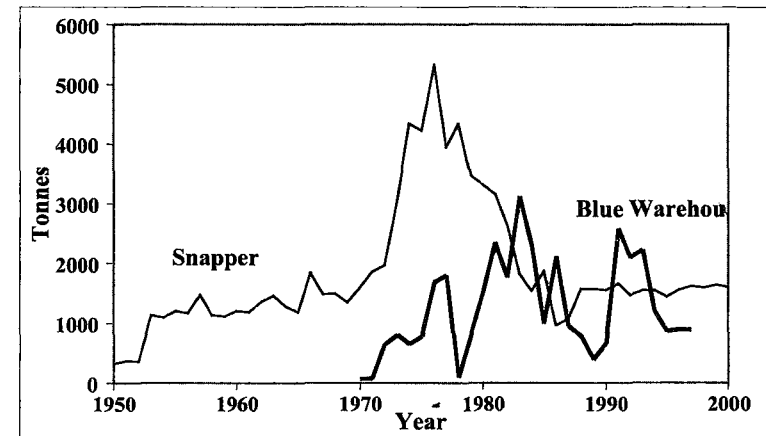


Figure 1.2. The yield of two New Zealand fisheries. The snapper (*Pagrus auratus*) is from the west of the North Island. It shows a fishery developing, the impact of pair-trawlers in the 1970s, and a subsequent serious decline to stability forced through a Total Allowable Catch. The blue warehouse (*Seriotelella brama*) is from the east and south of the South Island and shows a naturally variable fishery in which availability can vary between years (data from Annala *et al*, 2001).

The difficulty 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 by the major sources of productivity varying naturally through time. It is certainly the case that in many exploited species, recruitment is the most variable element of production. 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, probably as a consequence of the variability. 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 (Fig. 1.3) but that all are highly variable over varying time scales.

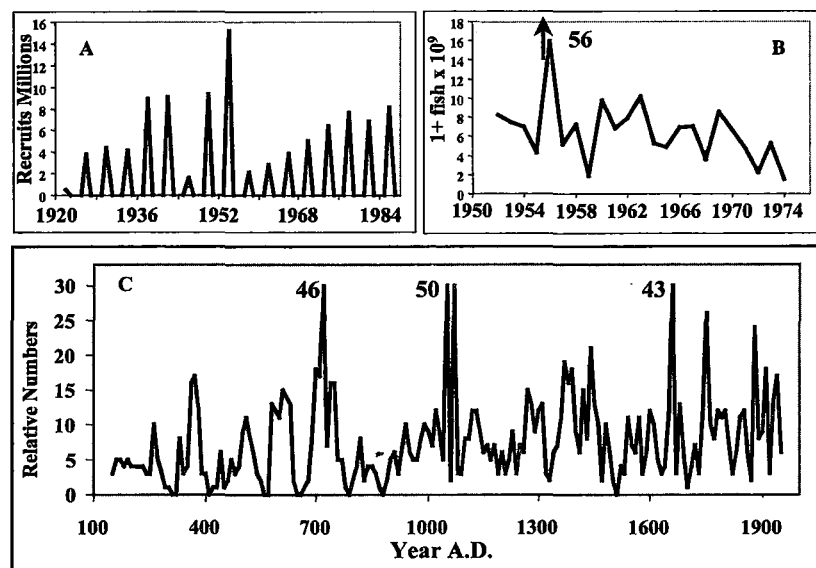


Figure 1.3 Recruitment variability in three species of fish across different time scales. Panel A relates to the dominant cohort of Fraser river sockeye salmon (data from Ricker, 1997). Panel B relates to North Sea herring the arrow refers to an exceptional recruitment in 1956 (data from Cushing, 1988). Finally, panel C relates to 1+ and older Pacific hake, note the exceptionally long time line extending back nearly 2000 years (data from Soutar and Isaacs, 1969). 1+ refers to fish that are between one and two years old. As with Panel B, the numbers next to the spikes in the diagram relate to exceptional time periods.

The biotic and abiotic factors affecting recruitment variation will thus strongly influence the resilience of those 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 pre-recruits, thereby affecting recruitment success). These effects could include predation, disease, parasitism, and availability of food and intra- and inter-specific competition. High recruitment success can appear to lead to reduced growth rates for the cohorts concerned, presumably due to competition (e.g. Punt *et al*, 2001).

If the natural mortality term (M) is taken to place a species in its

broader ecological context (not forgetting growth effects), 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. It is unfortunate that emphasis was focused upon equilibrium conditions because even if a stock appears to have reached equilibrium it will undoubtedly be, at most, a dynamic equilibrium. 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 non-equilibrium analyses.

Different exploited fish populations may express a wide range of dynamic behaviours (Figs. 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 clearly 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 really be managed separately for maximum efficiency and stock sustainability (Haddon and Willis, 1995). Stock determination 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; and references therein). While this cannot be denied 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 path is taken by natural resource managers in the future, a knowledge of the strengths and weaknesses of the kinds of mathematical models used will assist in using them more effectively.

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 we wish 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/phenomenon being modelled.

1.3.2 Limitations Due to the Modeller

As models are never perfect copies of the thing being modelled, there must be some degree of abstraction or selection of what the modeller considers to be essential properties of whatever is being modelled. A fundamental idea behind modelling is therefore to identify the properties that must be included in order that the behaviour of the model may be expected to exhibit a close approximation to the observable behaviour of the system being studied. This selection of what are considered to be the important properties of a system also permits the modeller to emphasize particular aspects of the system being modelled. A road map shows roads greatly magnified in true geographical scale because those are what are being emphasized. 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 tries to produce 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 appear to be 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 model. 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 and introduce the arguments used for and against application of the various approaches.

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 end 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 degree of impact 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 have to be estimated if a model is to be fitted to observed data. A model's variables must represent something definable or measurable in nature (at least in principle); ideally they must represent something that is real. 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 (Fig. 1.4).

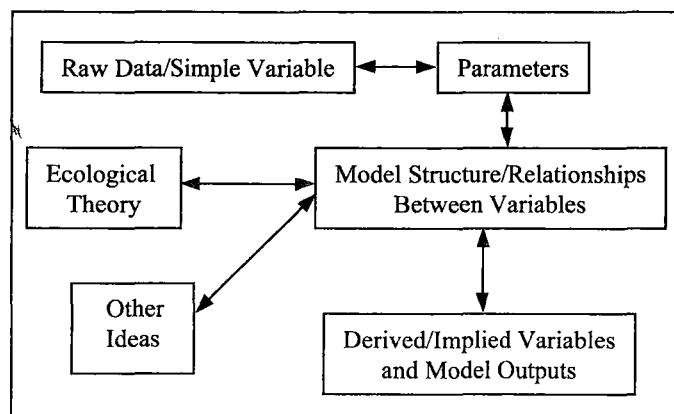


Figure 1.4 Schematic diagram of the relationships between raw data, fitted parameters, variables, ecological theory, and the model outputs, which make up a mathematical model. A model need not be fitted to data but it still requires parameter values.

In any model, such as Eq. 1.2, we must either estimate or provide values for the parameters. With the variables, one either provides observed values for them (e.g., a time series of catches) or they are an output from

the model. Thus, in Eq. 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”, then 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 as simple as represented (Fig. 1.4). Background knowledge and theory (“Other Ideas” in Fig. 1.4) 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 is available, or to be modulated by environmental variation*. Roughly speaking, models in which the parameters remain constant on the time scale of the model's application are referred to as **deterministic**. With a given set of inputs, because of its set of 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 time scale), 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 particular 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 – pdf, or 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

$$R_y = R_{\bar{y}} + N(0, \sigma^2) \quad (1.3)$$

where R_y is the recruitment in year y , $R_{\bar{y}}$ is the average recruitment, and $N(0, \sigma^2)$ 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 .

Given a set of input data, a deterministic model expresses all of its possible responses. However, there would be little point in running a stochastic model only once. Instead, 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 Eq. 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 non-linear aspects in the model, skew and other distortions may arise. We will be looking more closely at this phenomenon when discussing stock-recruitment relationships and Monte Carlo models.

Future projections, risk assessment, and the determination of the possible impact of uncertainty in one's data, all require the use of Monte Carlo modelling. 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 that will be of use when analyzing the stock dynamics of the fisheries for which they are responsible.

1.4.2 Continuous vs. Discrete Models

Early fishery modellers all used continuous differential equations to design their models, so the time steps in the models were all infinitesimal. This was because 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 towards difference equations, which attempt to model a system as it changes through discrete intervals (ranging from infinitesimal up 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 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. But when we consider the purpose for which a model is to be used, we should consider other properties relating to its design that also influence the potential scope and use of the model. For a model to be descriptive all it needs to do is mimic the empirical behaviour of the variables making up 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 look-up table which 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. We need not take notice of any assumptions or parameters used in their construction. Such purely descriptive models need not have elements of realism about them except for the variables being described (Fig. 1.5).

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, parameters, as well as the variables that make up the model (Fig. 1.5). By attempting to make the parameters, variables, and how the variables interact, reflect nature, explanatory models attempt to simulate events in nature. A model is explanatory if it contains theoretical constructs (assumptions, variables, and/or parameters), which purport to relate to the structure of nature and not just to how nature behaves.

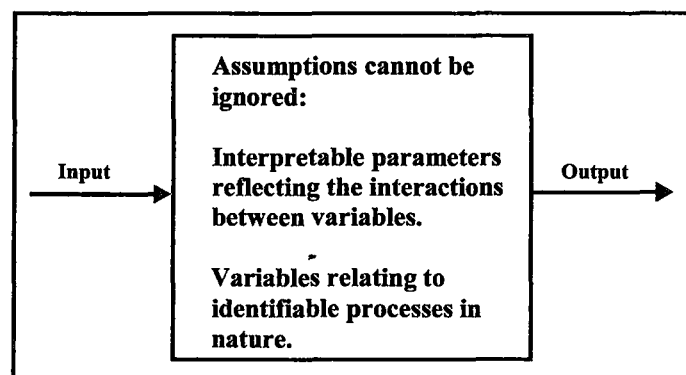


Figure 1.5 An explanatory model provides a description of the observable data but also reflects, mimics, or simulates the manner in which the modeller considers nature to be structured. It provides a reason for expecting the relationship between inputs and outputs to remain as the model predicts. In a purely descriptive model, the contents of the box are not particularly important.

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. The question arises: How do we test explanatory models? We can ask: Does fitting a model to data constitute a test of the model? Clearly, 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 also 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 refute 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 re-estimated. 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 that 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 very many parameters which provides an extremely good fit but this would not be considered a "better" model relative to a more realistic one (Fig. 1.6).

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 (Fig. 1.6). Clearly, in such cases, criteria other than just quality of numerical fit must be used to determine which model should be preferred.

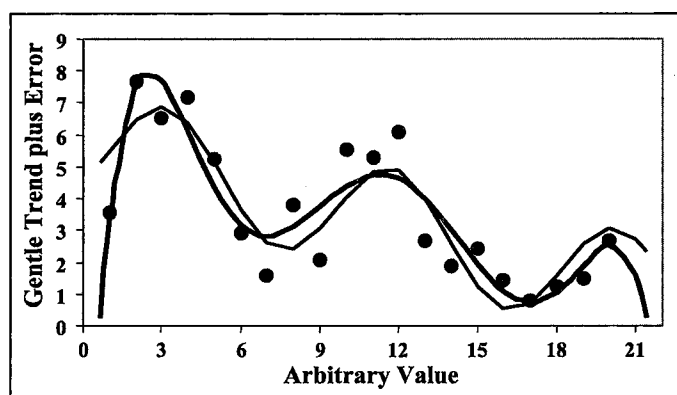


Figure 1.6 Artificial data generated from a straight-line decline ($Y = 6 - 0.25X$) plus normal random error [$N(0,2)$]. A straight line fitted to this data gives: $Y = 6.1583 - 0.2429x$, describing 44.1% of the variation in the data. The thick curved line that extrapolates severely downward beyond the data, is a sixth order polynomial equation with four more ($Y = -0.000045x^6 + 0.0031x^5 - 0.08357x^4 + 1.0714x^3 - 6.7133x^2 + 18.0600x - 8.9261$) parameters than the straight line. 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, however, we know the straight line to be the model that better represents the underlying process, the cyclicity is merely apparent. In Chapter 3 we consider methods for assessing whether increasing the number of parameters in a model is statistically justifiable, though with data such as this only further work could enlighten one as to the optimum model.

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 various parameters

(observation error) or in the system's responses, perhaps to environmental variation (process error). 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).

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 at all. 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 which lumped all age or size categories into one. But a model could be a combination of real and empirical.

For a model to be general would mean that it would have a very broad domain of applicability; it could be applied validly in very many circumstances. There have been many instances in the development of fisheries where a number of particular models describing a particular process (e.g., 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 the 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

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other words, the negative impact on population growth of increases in population size is linearly related to population size. 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 (non-linear 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 the assumptions in one's model.

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, relationships between variables, and error structures, independently from the quality of fit to observed outcomes. Of course, one way of determining whether there is something wrong with one's model is to compare expected outcomes with 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.