C H A P T E R   1

Introduction

MUCH OF THIS BOOK is about the derivation, use, and abuse of various mathematical models used to make decisions about how to manage harvested aquatic ecosystems. There is a long tradition of such modeling, and many biologists still look upon that tradition with much puzzlement and even contempt. Anyone who has taken even a bit of time to look at any aquatic ecosystem cannot help having seen that such systems are incredibly complex in their spatial, temporal, and trophic organization. Further, the complexity is not just a matter of structural diversity (lots of kinds of creatures). It also involves dynamic complexity in the form of a rich variety of feedback effects. Changes in the abundance of any creature due to natural or human factors are likely to result in a cascade of changes in the vital statistics (birth, death, growth rates) of other creatures in the food web, which in turn can feed back to impact further changes in the abundance of that creature. In the face of this complexity, it often seems both arrogant and foolish to pretend that we can make any useful predictions about what will happen when people selectively harvest some species that are fun to catch or good to eat, or change ecosystem fertility through deliberate or inadvertent changes in nutrient loading, or alter the physical habitat of an ecosystem.

After much experience in the field, we would be the first to agree that it is indeed impossible to capture fully the rich behaviors of ecosystems in mathematical models, particularly when we try to include unregulated human activities (humans as dynamic predators) in the calculations. But in this chapter, we offer three main arguments about why it is important to keep trying to build useful models. The first, which we will not discuss any further because it is so obvious, is that modeling is a great and perhaps necessary way for scientists to force themselves to think clearly and to put their claims to understanding on the table in the form of specific predictions. The second, which we discuss in the following three sections, is that prediction in some form is *required* for management choice, i.e., the issue in management-policy design is not whether to model but rather how to go about it. The third, which we discuss in a closing section, is that there are some predictable regularities in the way natural populations and ecosystems respond to human disturbance, so that at least some kinds of useful predictions are not as likely to fail as they may initially appear.

1.1   THE ROLE OF PREDICTIVE MODELS

If the people in a fisheries management agency watch some fishery change while asserting that they are powerless to implement regulations that might

alter the path of change, then that agency is not really a management agency at all; at best, it is a monitoring agency. The very word "management" implies some capability for making choices among options that might make some difference. That is, management *is* making choices. But what is involved in making any choice among alternatives? If we can choose either option A or option B, then we must either toss a coin or consciously construct arguments in the form "we believe that the outcome of A will be X while the outcome of B will be Y, and we prefer X to Y." Such sentences contain two kinds of assertions: (1) about the outcome (or range of outcomes, or probabilities of various outcomes) for each choice, i.e., *predictions about what will happen in the future*, and (2) about management objectives, i.e., *which future outcomes would be preferred*.

So making choices necessarily involves some method for predicting the future. This means the issue in management decision-making is not whether to model the future somehow (that is inevitable) but, rather, what model to use in making the prediction(s). Here there are two basic choices: to predict using the sometimes wonderful intuitive (and largely subconscious) capabilities of the human mind, or to resort instead to some explicit model or "deductive engine" for piecing together known elements of the prediction in some conscious way.

It is worth noting in passing that scientific research also necessarily involves making predictions, whether or not these predictions are stated as explicit alternative hypotheses about the outcomes of alternative experimental treatments. Even purely "observational" or "natural history" research programs cannot be designed and implemented without making some very strong assumptions (predictions) about where, when, and what variables or factors are worth observing, i.e., are likely to carry useful information about causal relationships. The experimental scientist can escape some responsibility for making specific predictions by constructing treatments (choices) that give clear, qualitatively different predictions about directions of response under alternative hypotheses. And the scientist has another advantage in terms of being able to choose the questions (options) to be addressed without much regard for whether those questions are of general interest to anyone else. So it is perhaps not surprising that scientists are much more likely than managers to make misleading assertions, i.e., "prediction is impossible in complex systems" or "it is not necessary to construct quantitative models in order to make useful predictions." Scientists who make such claims are clearly not the people to provide guidance about policy choices, nor are they likely to have much experience with the agonies of having to make hard choices.

Given that natural ecosystems are very complex and will be "driven" to future change by unpredictable environmental changes as well as human activities, so that we cannot possibly produce good unconditional or "open loop" predictions of future change, how can we hope to manage ecosystems if management choices require prediction? Or how can we hope to compare

policy choices until we "understand" all the interactions and external forces that drive change? The answer to these questions is actually quite simple, if we look carefully at the character of the policy predictions required for decision-making: to choose between policy A and policy B, we do not, in fact, require unconditional predictions about the future, or even about most of the causes and patterns of variability that the future will bring. Rather, we need only to be able to predict whether policy A *will do better than* policy B for a sufficiently wide range of possible futures to make it a "better bet" than policy B. That is, policy predictions need not be about the future in general but, rather, only about those aspects of future change that could be directly impacted by the specific actions/interventions involved in the policy, and even in relation to these changes we generally require only predictions of *relative* performance. This means, e.g., that when someone asks, "How can you manage the fish when you do not even know how many there are?", we can answer by pointing out that we can compare policy choices for a wide range of possible actual numbers of fish, to find choices that are at least somewhat robust despite the uncertainty about the numbers. Further, we can generally specify policy choices as *rules for response to change* rather than absolute degree of impact. Consider the following example: suppose policy choice A is to allow a particular, fixed quota of fish to be harvested in perpetuity (i.e., a quota property right), and policy choice B is to allow some fixed proportion of the fish to be harvested each year (this proportion is called the exploitation rate). It is easy to show with practically any population or ecosystem accounting model that policy A is prone to catastrophic failure: under natural variation, the stock is bound to get low enough so that the quota looms larger and larger as a factor of change, driving the stock down faster and faster as the number of remaining fish (and hence the basis for future population growth) declines. On the other hand, policy B has built-in "feedback" to adjust harvests downward during stock declines (and hence help reverse the declines) and to take advantage of higher harvest opportunities when the stock is large. In this example, only a fool would advocate policy A, whether or not we can predict specifically what variation the future will bring.

1.2 The Distinction between Fish Science and Fisheries Science

We can provide useful predictions and advice about some kinds of management choices without resorting to precise, quantitative models that are bound to be incorrect to at least some degree. For example, it is easy to explain in qualitative terms why fixed-quota harvest policies are dangerous compared to feedback policies in which harvests are varied in response to unforeseen change. But most management decisions involve quantitative choices: *How many* fish should be harvested this year? *What sizes* of fish should be caught? *How large* should a protected area be? *How many*

licenses should be issued? *How much* unregulated fishing effort will occur this year if a given regulation is imposed on catch or size of fish or location of fishing? *How much* can we harvest without "impairing" the ability of the ecosystem to support other creatures that depend on the ones we harvest?

Somebody has to provide the answers to these difficult questions, i.e., somebody has to do some quantitative modeling and prediction, whether the work is done well and systematically or instead by some seat-of-the-pants calculation. In a way, it has been really unfortunate in the historical development of fisheries management that there has been a general assumption that the right people to answer such questions are fish biologists. There have been no real professional standards in fish or fisheries biology, and a high proportion of us got into the field in the first place because we could do so without a lot of distasteful quantitative training. We were taught to study biological process and pattern from a largely qualitative perspective, and we never expected to be "bean counters." Furthermore, most of us never imagined that many of the questions that we would be asked would not even be about fish at all but would, instead, be about the behavior of people (fishers). This state of affairs is changing rapidly, with recognition that there is a lot more to fisheries science than just studying biological processes and counting fish. But a new pathology is accompanying the change: the top levels of management agencies are dominated by people with the traditional training (and cunning as institutional players) who now have to turn to younger people for help when there is no way to sidestep the difficult quantitative questions. This means that as demands for improved, quantitative management prescriptions have grown in order to deal with more complex management options and trade-offs, key fisheries managers have had to rely more and more on people and methods (modeling) that they do not understand and certainly do not trust. Such specialization of capabilities and functions leads in turn to increased opportunities for misinterpretation and misunderstanding, among all stakeholders involved in management (fishers, managers, scientists, representatives of conservation interest groups, etc.).

1.3   Approaches to Prediction of Policy Impact

Given that predictions are an inevitable part of making management choices, what options does a fishery manager have for making these predictions? Surely there are alternatives to the rather complicated mathematical modeling described in this book; indeed, there are at least five alternative approaches that can be (and have been) used. These approaches are not mutually exclusive; each uses or is derived from at least some components or results of the others.

Appeal to Conventional Wisdom and Dogma

In a surprising variety of decision situations, fisheries managers have ignored empirical data and past experience in favor of essentially dogmatic assumptions about the responses to particular policy options and system disturbances. For example, it is routine to presume that habitat alterations to natural ecosystems always cause reduced productivity (because the organisms are "adapted to" the natural circumstances). Another common assumption is that harvesting always causes a reduction in the abundance of target species, even if/when the harvesting selectively removes individuals that differentially drive away or kill other conspecifics (e.g., cannibalism). When field evidence is found that contradicts such assumptions—e.g., evidence that coho salmon may actually be enhanced by forest harvesting in some watersheds of the Pacific northwest (Holtby 1988; Thedinga et al. 1989; see discussion in Walters 1993)—this evidence is either ignored entirely or is rejected as "nonrepresentative" or "atypical." When this happens, managers are essentially indicating their willingness to behave essentially as though some principles or assumptions were equivalent to religious dogma, i.e., were impervious to scientific invalidation.

Trend Extrapolation

A time-honored way of making fisheries management predictions has been by simple trend extrapolation: plot the historical data, and "eyeball" alternative projections forward in time while making some intuitive guess about the likely impact of policy change on the trend. We can, of course, formalize the eyeball part of this approach by using formal time-series analysis models, but that is unlikely to produce a better result (except perhaps in multivariate systems) than the remarkable integrative and pattern-finding abilities of the human eye.

This approach has failed in modern fisheries, for a variety of reasons. (1) It is really only valid for systems that exhibit *incremental*, slow change; modern fisheries can change very rapidly. (2) It is easy to confuse wishful thinking with good intuition in making predictions about the effects of policy change on trends, and to keep applying small Band-Aids to gaping wounds. (3) It is all too common to use misleading trend indicators, especially catches. In any fishery, catch results from three factors: the area "swept" by fishing, the size of the stock, and the area over which the stock is distributed. So an apparently "healthy" increase in catch can mean either that the stock is healthy, that the fishing effort (the area swept by gear) has increased, or that the range occupied by the stock has decreased. It does not help matters to use catch per effort, since this commonly used trend index can even increase during stock declines due to contractions in the range area used by the fish.

Empirical Models Based on Past Experience and/or Experience with Similar Systems

For many policy issues there is a rich range of historical and spatial comparative data upon which to base predictions about the responses to any particular new circumstances. Some fish stocks (e.g., Pacific herring off British Columbia) have been severely overfished, then allowed to recover, so that we have good information about likely stock response as a function of stock size. There are large data sets on how lakes and coastal areas respond to eutrophication, and strong regression relationships have been found between nutrient loading and performance measures such as chlorophyll concentration, so that the likely response in almost any new case can be "interpolated" from the regressions. For fish populations that are maintained through artificial stocking (hatcheries), there are large data sets on the effects of factors such as time and size of release and stocking density on performance measures such as survival rate and growth.

Unfortunately, most of the important policy issues in fisheries today involve options and performance measures for which there are no historical precedents. We have not yet tried to manage aquatic ecosystems in any holistic way, and in particular, we have not systematically gathered information on the abundances and spatial distributions of the wide variety of organisms (beyond harvested fish) in an expanded view of what would constitute a "healthy" managed ecosystem. Existing reviews of comparative data, e.g., May (1984) and Hall (1999), show mainly a confusing variety of fragmentary patterns.

Experimental Components Analysis (Reductionist) Modeling

This is the basic approach taken in most fisheries modeling. The idea is to try to break prediction problems into more manageable components, using some basic "tautologies" (statements that are true by virtue of how the words used in them are defined) to identify and synthesize the component predictions. For example, we typically model population change over time for a population defined over a large enough area to be closed to immigration and emigration (for a so-called "unit stock") by a simple balance relationship that we treat as a tautology: (population next year) = (survivors after harvesting this year) + (surviving new recruits). If there is no net migration (and no spontaneous creation of organisms), this balance relationship is a tautology because it re-expresses what we mean by (population next year) in terms of the component creatures that make up that population. In mathematical terms, the simplest way to express the balance relationship is

$$N_{t+1} = s_t(N_t - C_t) + R_{t+1},$$

where N_t = population size at the start of year t, s_t = survival rate, C_t = catch taken in year t, and R_{t+1} = surviving recruits. Note that "surviving recruits" generally refers to animals that graduate to an age or size class that are vulnerable to fishing gear. This statement tells us that to predict population change, (N_{t+1}), we need to have information on N_t and C_t, and we need to make some assumptions (called "functional relationships") about the survival and recruitment rates (s, R). That is, the balance relationship tells us that we can reduce the prediction problem to two "simpler" problems, predicting survival and recruitment rates, while accounting in the overall balance structure for two "known" temporal factors, N_t and C_t. In this approach, long-term predictions are constructed by applying the balance relationships recursively (repeatedly); by making a series of short-term, incremental predictions, we hope to be able to account for ecological feedback effects as expressed through possible changes in the s and R rates. For more complex situations, e.g., multiple stocks, we solve a list of such balance relationships in parallel, perhaps including terms that represent linkages among the variables (e.g., we might include predation effects as being either additions to the catch or effects on the survival rate s_t).

Several obvious things can, and regularly do, go wrong with this approach. We almost always leave out important variables, or equivalently fail to represent factors that cause change by treating some "parameters" such as the survival rate s_t as constant over time. We commonly use poor approximations for the forms of (and key variables that cause change in) functional relationships, particularly for the prediction of recruitment rates R_{t+1}. Solving the balance relationships recursively to obtain long-term predictions can lead to large, cumulative errors if the initial state and/or some key parameters are specified incorrectly. We will provide repeated examples and warnings of these and some other problems with mathematical modeling, and linking the models to data, throughout the book.

1.4 Experimental Management

The basic concept in this "actively adaptive" management approach (Walters and Hilborn 1976; Walters 1986) is not to pretend that a best policy option can be identified from experimental components modeling and analysis of historical data but, rather, to "embrace uncertainty" by using the modeling and analysis to identify a set of candidate policy options that are all defensible (and to screen out options that are likely inadequate to meet management objectives). Then these candidates are each given a "day in court" by applying them to the managed system as a set of experimental treatment options, either sequentially over time or on a set of hopefully similar experimental locations or units.

This approach has been successfully implemented in only a very few cases and has failed miserably in many, many others (Walters 1997). The failures have been caused by many factors. It has proven extremely difficult to obtain institutional support for programs that take a long time to produce results (sequential experiments may take decades to complete). There is a common management perception that experimentation is just too "risky" (see, e.g., Walters and Collie 1989; Parma and Deriso 1990b). Monitoring costs may be prohibitively large, especially for spatial experiments with a variety of experimental units and treatments. And perhaps worst of all, there is now quite a large community of scientists who are willing to sell modeling to managers as an alternative to hard, expensive experimentation, and this is too often an easy sell.

Theory versus Practice in Decision-Making under Uncertainty: Indecision as Rational Choice

For almost all important fisheries-management choices that have long-term ecological and economic consequences (e.g., the choice of target exploitation rate or stock size), we have to admit a wide range of uncertainty about those consequences. There are three basic reasons for uncertainty in long-term predictions, and only two of these can be reduced through an investment in measurement and modeling: (1) we do not know the current system state precisely (predictions must look forward from an uncertain starting point); (2) we do not know all of the "rules for change" (interactions, functional relationships) that will govern future dynamics; and (3) ecological dynamics are strongly influenced by environmental factors (physical and geochemical forcing, e.g., upwelling) that are not (as yet) predictable, especially in view of likely climate change. So even if we could measure ecosystem states (population sizes and such) much more accurately, and even if we knew and could model all of the ecological and economic interactions precisely, there would still be gross uncertainty about future change due to uncertainty about future environmental "forcing" patterns. This means that at best we can make only probabilistic statements about alternative futures, and much of the emphasis in stock-assessment research and modeling today is on how to do such probabilistic calculations more realistically (Patterson et al. 2001).

To objectively and quantitatively compare choices involving a range of possible outcomes, we need not only to place odds on those outcomes but also to combine the possible outcomes for each choice into some kind of overall utility measure for that choice (Raiffa 1982; Keeney and Raiffa 1976). There is no general standard or procedure for constructing utility functions to combine or weigh the possible outcomes in public decision-making that involves multiple stakeholders with varying interests and aversions to particular outcomes. The simplest or "expected value" utility measure would be to take an average of the outcomes, weighing each by its probability of occurrence. But this simple measure would not be acceptable to most fisheries

stakeholders: people concerned with long-term conservation want to see a differentially low utility placed on poor long-term outcomes, while people concerned with immediate income and employment want to see low utilities placed on outcomes that would involve short-term economic hardship.

A common reaction from fishing stakeholders to uncertainty has been to demand that governments "prove" that there will be a problem before introducing more restrictive harvest regulations. In decision theoretic terms, this amounts to demanding that the utility function for combining and weighing alternative outcomes place very low utility on outcomes that cause immediate economic hardship and/or demanding that utilities for long-term outcomes be discounted at high rates. Most fisheries-management agencies have now been given a mandate to resist such demands, through the widespread adoption of the "precautionary principle" (FAO 1995; UN 1996; Dayton 1998). According to this principle, the "burden of proof" should be reversed, i.e., it should be up to fishing interests to demonstrate that the odds of long-term harm are low. This amounts to demanding that the overall utility function be exactly the opposite to what fishing interests would advocate, placing a very low utility on undesirable long-term outcomes.

It will probably not be that difficult to apply the precautionary principle to new and developing fisheries, so as to ensure that development proceeds with a relatively low risk of overfishing and economic hardship. Unfortunately, most important fisheries management choices today involve the opposite end of the development spectrum, at which choices that might reverse historical declines (and improve the odds of long-term sustainability) are ones that would create immediate economic hardship (loss of income and employment, social displacement) for relatively large, dependent communities of fishers. In such situations, there are strong (and what conservationists might call "perverse") incentives for fisheries managers to avoid making hard choices, i.e., the rational personal choice for them is to be indecisive (fig. 1.1). To understand figure 1.1, try to put yourself in the position of a senior fishery administrator or politician faced with scientists who have come forward with dire predictions of ecological collapse unless a fishery is cut back severely. You know that if you do follow their advice, you will be vilified by people who depend on the fishery for their livelihoods, and you know from much experience with fisheries scientists that their predictions are not exactly reliable (to say the least). On the other hand, if you delay action and keep the support of fishing interests, your experience tells you that there is at least some chance the problem will correct itself (will turn out to have been caused not by fishing but by some environmental "regime shift" that will eventually reverse). Even if the scientists are right, there is a good chance that you can move along or retire before the situation becomes so poor that no rational person could ignore it. But even if you are somehow legally required to adopt a precautionary principle in making your decision, you have a variety of options for clouding the issue (and making the easy choice) by appealing to evidence (which some scientists are sure to have) that

(Choice Point)   (Possible outcomes)

-immediate outcry from stakeholders
-no guarantee of ecological recovery

Take decisive action
(reduce fishing)

Wait and see
(no reduction)

-maintain stakeholder support
-possible recovery due to favorable
 environmental conditions
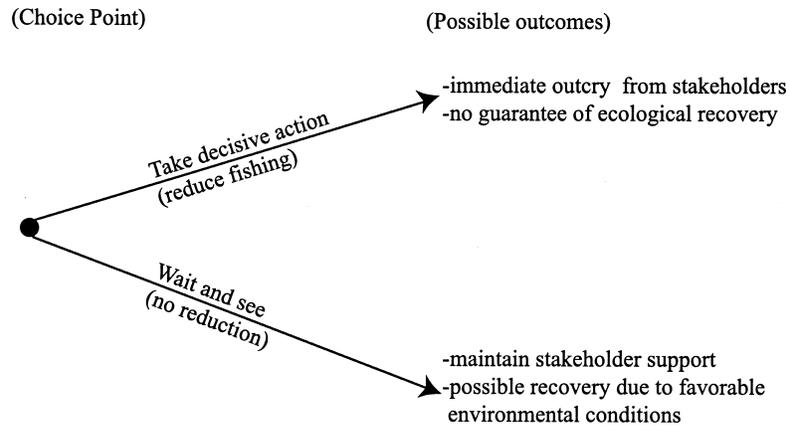
FIGURE 1.1: Indecision as a rational choice during a fishery decline. Viewed from a fishery manager's perspective in terms of a simple decision tree, it can be fully rational for the manager faced with either certain outcry from fishing stakeholders if decisive action is taken, or the possibility that nature will correct the situation without intervention even if no action is taken, to gamble on the situation's correcting itself (i.e., to be deliberately indecisive).

environmental factors have, indeed, been at least partly responsible for the "signals" that other scientists have interpreted as overfishing.

We warn readers of this book that there is no use pretending that the decision-making "pathology" (with respect to prudent, sustainable harvest management) shown in figure 1.1 can somehow be overcome through better scientific research and modeling. We cannot, even in principle, provide the certitude of predictions that would be required to demonstrate that gambling on inaction is wrong. Even more important, science cannot tell us what is right or wrong when there is a trade-off involving a hardship for people today versus a possible gain for people in the future.

1.5   The Ecological Basis of Sustainable Harvesting

However fisheries managers might behave when faced with a conflict between fishing and conservation interests, there is broad public support for moving toward fisheries that are sustainable in the long term and for implementing policy options that avoid the decision-making pathology (figure 1.1) that develops during fishery declines. There is also broad support for sustainable policies that recognize other ecosystem "values" or "services" besides harvesting, such as protecting the capability of ecosystems to support diverse assemblages of creatures that are valued in their own right (e.g., marine mammals, birds).

To people who pretend (or have been led to believe through popular ecology literature) that natural ecosystems are finely tuned machines that are

highly vulnerable to human disturbances, it might appear impossible to ever harvest various creatures on a "sustainable" basis without ultimately destroying the machinery. Never mind that people have been harvesting various creatures from most of the world's ecosystems for many thousands of years, so that we are hard put to even find a "natural" ecosystem. There is much fear that whatever early humans might have gotten away with, modern technology creates a destructive capability that is somehow unmanageable. It is easy to confuse two really different issues: what nature can produce, and what we can do to manage the activities of those who would capture that production. Presumably, we can do a better job with the management issue if we better understand the production issue.

Texts on fisheries science typically introduce the idea of sustainable harvesting in terms of "surplus production." A very simple logistic model, or any model with density-dependent rate processes, for population growth is used to argue that natural populations tend to "push back" against the impacts of harvesting by exhibiting positive population growth (surplus that can be harvested without further reducing the population) after being reduced in numbers by any harvest removal. Many ecologists are suspicious of this argument, not because of the ecological relationships behind it but because of the way the argument is built from a population model that we know is too simple to explain most of our field experience with how natural populations actually behave.

A more general way to understand the basic dynamics of, and basis for making predictions about, sustainable harvesting is to imagine going into a natural, unharvested ecosystem, picking a "target" population more or less at random, then starting to remove proportions N_t of that population over years t. If the ecosystem is not already undergoing some progressive development or recovery process (i.e., is not at an early successional stage), and if the study area is large enough so that numerical population changes are dominated by birth-death processes within the area (rather than dispersal to/from other areas), then we expect the chosen target population numbers N_t of animals at least one year old to satisfy the accounting balance relationship

$$N_{t+1} = s_{(a)t}N_t + s_{(j)t}f_tN_t = (s_{(a)t} + s_{(j)t}f_t)N_t = r_tN_t \qquad (1.1)$$

where $s_{(a)t}$ is the annual survival rate of animals more than one year old, $s_{(j)t}$ is the survival rate from egg/birth to age 1, f_t is the mean egg/birth production per animal present at time t, and $r_t = s_{(a)t} + s_{(j)t}f_t$ is the relative population growth rate from time t to time $t + 1$. If the target population is a naturally sustainable part of the ecosystem, i.e., is not on its way to natural extinction or on its way to becoming a much more dominant part of the ecosystem, then we expect to find the average value $\bar{r}$ of its r_t to be $\bar{r} = 1.0$, i.e., on average $N_{t+1} = N_t$. At this point, the reader needs to be really careful about equation 1.1; most biologists would automatically assume that since it is a very simple equation, it must be based on very simple biological assumptions, e.g., that every animal has the same survival rate and fecundity. That is not

BOX 1.1

REPRESENTATION OF RATE PROCESSES AND STATE CHANGE
IN FISHERIES MODELS

Quantitative models for fisheries-policy analysis generally involve predictions of change in numbers and/or biomass over time. Typically, the predictions are made in a series of time steps. For each time step, discrete "inputs" or gains due to processes like recruitment that typically occur over short periods or seasons are usually treated as occurring at the start of each step, then loss processes are treated as occurring continuously over the step. Two apparently distinct types of equations are used to represent the loss processes:

1. discrete-time survival equations that predict net, proportional change, like the term in equation 1.1 for surviving older fish: (surviving older fish) $= s_{(a)t}N_t$.
2. instantaneous rate equations of the form $dN/dt = -ZN$, where Z is called the "instantaneous rate"; if Z is constant from t to $t + 1$, the solution of such equations is $N_{t+1} = e^{-Z}N_t$, which is exactly the same as the discrete survival prediction if we set $s_{(a)t} = e^{-Z}$.

Note that instantaneous loss rates Z can take any positive value, while survival rates like $s_{(a)t}$ are bounded between zero and 1.0. For example, $Z = 3$ implies $s_{(a)t} = e^{-3} = 0.0498$. A word of warning for biologists who are trained to think about complexity in visual terms: it is common to confuse complexity created by mathematical notation with complexity created by realistic assumptions. Instantaneous-rate formulations typically look more complex and realistic to naïve biologists, even if they make simplistic assumptions. For example, the equation $N_{t+1} = N_t e^{-Z}$ appears more complex than $N_{t+1} = N_t s$ but, in fact, says exactly the same thing (makes exactly the same prediction when s is set to e^{-Z}).

The more cumbersome instantaneous-rate formulation is used in most fisheries-assessment literature for two reasons. First, it provides a convenient way to deal with risk factors, such as predation and seasonal fishing, which involve very high rates and can cause rapid change over short periods. For example, purse seine fisheries for Pacific salmon off the coast of British Columbia can generate fishing mortality rates on the order of 500/year, i.e., they knock down the fish abundance at rates that would remove 500 times the number of fish initially present if those fish kept being replaced over a whole year so as to prevent changes in the number of fish present at any moment during the year. Second, these formulations make it simple to partition losses among mortality agents. So, e.g., if we predict the total mortality rate Z to be $Z = M_o + M_p + F$, where the component rates are defined by $M_o =$ natural loss rate due to factors other than predation, $M_p =$ loss rate due to predation,

(*Continued*)

(*BOX 1.1 continued*)

and $F = $ loss rate due to fishing, then we can calculate the net loss of fish to each rate process as that rate over Z times the total deaths. Total deaths are predicted by $D_t = N_t(1 - e^{-Z})$ (numbers at t minus number of survivors to $t + 1$); e.g., loss to fishing (catch) is given by $D_t F/Z$, and total predator consumption by $D_t M_p/Z$. ∎

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correct: there is no such simplifying assumption at all in equation 1.1; the individuals making up N_t can, and generally do, consist of a complex mixture of ages, sizes, sexes, home-range locations, etc. To say that these creatures produce total eggs $f_t N_t$, or survivors $s_{(a)t} N_t$, is not to say that every animal is the same but, rather, just that there is some rate value f_t or $s_{(a)t}$ such that multiplying this value by N_t gives the numbers of eggs or survivors for year t. That is, the parameters f_t, $s_{(a)t}$, and $s_{(j)t}$ represent per-capita averages over N_t, and one of the reasons that we need to think of them as time-varying (t subscripts) is that they are likely to change with changes in the composition of N_t—e.g., f_t is likely to be larger in years when more of the N_t individuals are large, highly fecund females. We discuss methods for making more or less precise numerical predictions about changes in N_t using composition information in chapter 5 (single-species assessment).

Harvesting proportions u_t of the 1-year-old and older animals from the target population will obviously change the balance relationship, to $N_{t+1} = s_{(a)t}(1 - u_t)N_t + s_{(j)t}f_t N_t$, and this will result initially at least in $r_t < 1.0$, i.e., in population decline. Now suppose that variations in $s_{(a)t}$, $s_{(j)t}$, and f_t over t are due solely to what ecologists call "density-independent factors," i.e., the variations are (statistically) unrelated to N_t. In that case, the mean value of r_t will be less than 1.0 for any $u_t > 0$, and the expected long-term population trajectory is a decline toward extinction. That is, the only possible long-term ("sustainable") outcome of harvesting given only density-independent variation in the specific rates is extinction. Thankfully, this outcome is not what has been observed in virtually every case in which populations have been monitored during harvest development, and it is hard to imagine any viable natural population that would still be around if it exhibited such lack of response to variation in natural factors that have had an impact comparable to u_t. What we have seen, in fact, is at least some "density-dependent" or "compensatory" change in at least one of the specific rates, leading to improved survival and/or fecundity in response to a reduction in N_t. For modest u_t, such compensatory change tends to return r_t to a mean of 1.0, i.e., to stop the decline. *Hence, compensatory change in survival rates and/or fecundity is the fundamental ecological basis of sustainable harvesting.* So if someone argues that a given population exhibits no density-dependent or compensatory rate changes, i.e., if someone makes an oxymoron assertion like "the population is regulated purely by density-independent factors,"

then that person is, in fact, asserting that the population is incapable of producing a sustainable yield (and is incapable of exhibiting any sort of stable average population size under natural conditions either).

When we have been able to estimate changes in the rate factors $s_{(a)t}$, $s_{(j)t}$, and f_t over the history of fishery development, e.g., figure 1.2 from Martell (2002), a quite consistent response pattern has been observed that is largely independent of the type of creature being harvested (vertebrate or invertebrate, benthic or pelagic, lower trophic level or top predator, etc.). Methods for obtaining such estimates or historical "reconstructions" of population change are discussed in chapter 5. The typical response pattern has the following main features:

1. Mean fecundity f_t either remains relatively stable (in semelparous species like Pacific salmon that die immediately after first reproduction) or declines due to a reduction in the proportion of older, more fecund individuals in N_t; i.e., there is generally not a strong compensatory response in f_t.

2. Natural survival rate of older animals $s_{(a)t}$ also remains relatively stable, seldom showing any consistent compensatory improvement with reductions in N_t and often showing relatively little change even with large changes in presumed predation mortality.

3. "Juvenile" survival rate $s_{(j)t}$ shows compensatory improvement that is sometimes remarkably strong, typically leading to the total recruitment $R_t = s_{(j)t}f_t N_t$ being nearly independent of N_t over a wide range of N_t, even despite considerable decreases in f_t.

We discuss the ecological basis for observations (2) and (3) in chapters 6 and 10. Methods for predicting changes in $s_{(a)}$ and $s_{(j)}$ due to trophic relationships (predation, competition) are discussed in chapters 11 and 12, with particular emphasis on the observation by Hollowed et al. (2000) that useful predictive models for ecosystem management may need to involve a careful analysis of stage- and scale-dependent interaction impacts. Problems in measuring compensatory responses in $s_{(j)t}$ are discussed in chapter 7. In various chapters, we point out things that can go wrong with response (3), in particular factors that can cause a "depensatory" decrease in juvenile survival rates at low population sizes, so as to cause extinction or the failure of population recovery efforts. Chapter 13 discusses what happens when people get greedy and try to supplement or enhance natural recruitment through artificial propagation programs, since this has been one of the main suggestions for trying to beat the apparent natural limits to harvesting implied by compensatory changes in rate processes.

Just how well are the three assertions of the previous paragraph supported by empirical evidence, rather than by arm waving about how "viable" natural populations must exhibit some compensatory response(s)? There is no question about how most fisheries cause declines in average size (age) of fishes and, hence, declines in the mean fecundity f_t because of strong size-fecundity linkages. There are dozens of long-time series of age-composition
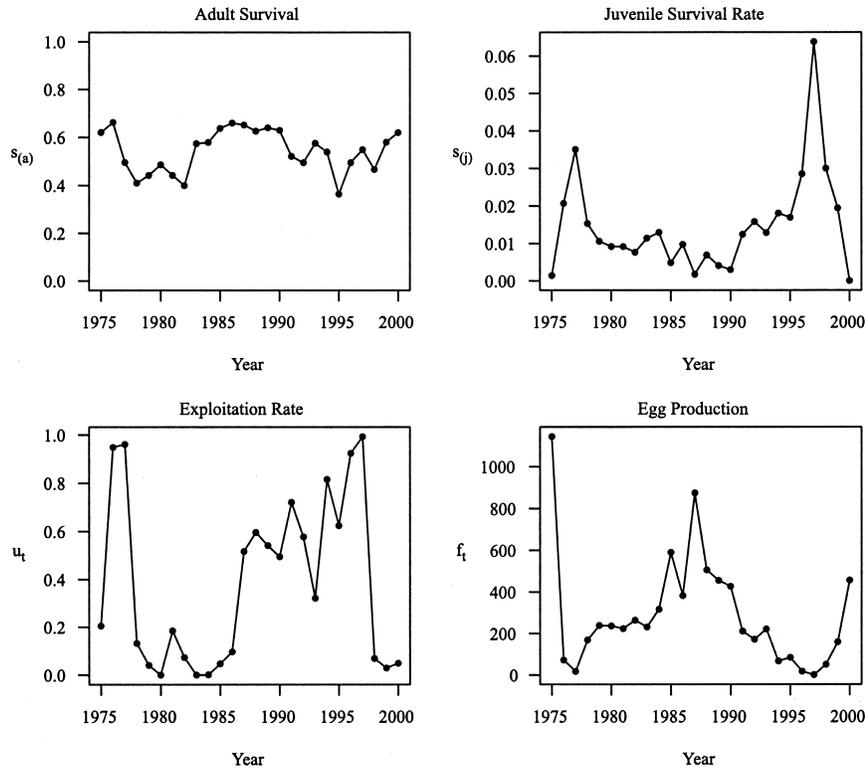
FIGURE 1.2: Variation in components of population change for pink shrimp on the west coast of Vancouver Island, B.C., from Martell (2002). These estimates were obtained by fitting an age-structured population-dynamics model to time-series data on relative-abundance, size-composition, and area-swept estimates of fishing mortality.

data that at least appear to support the assertion of stable adult survival $s_{(a)}$, though, in fact, what these data tell us is mainly about stability in the harvest-natural survival product $s_{(a)}(1-u_t)$. There are literally hundreds of data sets that demonstrate a lack of change in the recruitment rate with a change in spawner/egg abundance, i.e., density dependence in $s_{(j)}$. These recruitment data sets are readily available thanks to the painstaking efforts of Ransom Myers and his colleagues (*http://www.mscs.dal.ca/~myers/welcome.html*), and we strongly urge the reader to scan through them to see the variety of patterns that fish recruitments have exhibited.

It is not typical in fisheries texts to introduce the idea of surplus production in terms only of the numbers balance in equation 1.1. Most fisheries are measured and valued in terms of biomass (numbers x body weight), and growth in body weight is typically represented as an important component of biomass production. Equations such as production = growth + recruitment − mortality invite us to think of growth and recruitment as additive

and to imagine that growth might be more "important" than recruitment or might occur as an additive effect on production independent of what might happen to recruitment. Such equations are misleading. The biomass yield Y_t from a fishery can be represented as $Y_t = u_t N_t w_t$, where $u_t N_t$ is the numbers yield and w_t is the average body size of the harvested fish. Much of the classic "theory of fishing" (Beverton and Holt 1957) was concerned with how to adjust u_t and the size of fish harvested so as maximize the average Y_t, but subject to the assumption of a strong compensatory improvement in $s_{(j)}$. In fact, the average body size w_t typically decreases with increases in the harvest rate u_t, as does the average abundance N_t, even if there are (relatively uncommon) compensatory improvements in fish body-growth rates as abundance decreases. When predicting surplus production and average yield Y_t, it is not helpful to point out that biomass production due to body growth tends to increase on a per-capita (per N_t) basis due to shifting the composition of N_t toward younger, faster-growing individuals. Numbers sustainability, i.e., $s_{(a)t}(1 - u_t) + s_{(j)t} f_t = 1$ on average, remains a basic requirement no matter what might happen to per-capita body-growth rates, and no matter what units we might use to measure yield or value.

Unfortunately, the qualitative knowledge that a given species is likely to exhibit compensatory responses in $s_{(j)}$ is not a sufficient basis for designing sustainable harvest policies. Even if there is no concern about the impact of harvesting the species on other ecosystem functions and species, we must still deal with two difficult (and quantitative) issues: (1) how to vary the strategic harvest-rate goals u_t over the long term in response to uncontrolled natural changes in $s_{(a)}, s_{(j)}$, and f; and (2) how to limit u_t in the short term by using various harvest-regulation "tactics" such as closed areas. We discuss the first of these, the so-called "harvest strategy" problem, in chapter 3. We discuss the second in three chapters: chapter 4 discusses broad options for limiting u_t, while chapters 8 and 9 discuss spatial models that are needed for the evaluation of closed-area policies and models for the evaluation of the effects of unregulated fisher behavior (fishing-effort dynamics) on the efficacy of regulation schemes.

Further, modern fisheries management involves making predictions about far more complex trade-offs than those involved in single-species abundances, survival rates, and body sizes (chapter 2). In particular, it is no longer acceptable in many management settings to ignore the possible ecosystem effects of harvesting each species. The mortality losses $(1 - s_{(a)t})N_t$ and $(1 - s_{(j)t})f_t N_t$ are not just disappearances from ecosystems; rather, at least part of these losses represents "trophic support" provided by a species to higher trophic levels, i.e., part of the food supply of the species' predators. In single-species management, the historical tradition was either to treat such support functions as having no economic or social value, or to pretend that there is an ample supply of other food organisms to take up the slack when the production of any given species has been appropriated by fishing. Further, we have largely ignored the other side of the trophic coin, namely the

responses of other organisms when the "demand" on a given species's food supply (on "lower trophic levels") has been reduced through fishing on that species. For example, other organisms might use that food supply to prosper and become replacement food sources for predators, hence reducing the net effect on predators of taking away some of their usual prey. Chapters 10, 11, and 12 discuss our emerging ability to make useful management predictions about such food-web interaction effects.

There is a critical point for readers to keep in mind about the complex biology and modeling introduced in chapters 10–12 for making predictions about the effects of food-web interactions. We are not introducing this material as a substitute for single-species population-dynamics modeling or management, or on the pretense that including trophic interaction effects in predictions of $s_{(a)t}$, $s_{(j)t}$, and f_t will somehow lead to better, more precise predictions about how each species is likely to respond to harvesting. In fact, from a single-species management perspective, trying to model all of the interactions that lead to variation in survival rates, especially of juvenile fish, can easily result in an "overparameterized" calculation, subject to a larger average prediction error than could be achieved with more precise estimates for fewer parameters. Rather, our aim in introducing these models is to provide a capability for fisheries scientists to respond to a broader set of policy questions and predictive demands than can single-species analysis. These questions lead to a much broader set of options for future ecosystem management than might ever be imagined by thinking only of species populations one at a time (chapter 14).