

AN ASSESSMENT OF SEVERAL OF THE HISTORICALLY MOST INFLUENTIAL THEORETICAL MODELS USED IN ECOLOGY AND OF THE DATA PROVIDED IN THEIR SUPPORT

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ABSTRACT

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Certain theoretical models (the logistic, Lotka–Volterra and density-dependent stock recruitment models in fisheries) and their mathematical representations are used pervasively in the teaching of ecology and in the application of ecology to various applied problems. Although few claim that these models will or should give accurate predictions of populations in nature, it nevertheless is claimed routinely that they have great heuristic value and are ‘a good place to start’ when making more complex and, presumably, more accurate formulations. Yet if these equations are a good place to start, there should be some data to show that they are good predictors of populations in nature under at least some conditions. Considerable data do exist in the literature that have been used to support the use of these equations. I examine these data and find that in fact none of it supports the predictions of the equations for which they are offered as support. Some implications of the transfer of these unvalidated models to management are discussed with particular reference to Pacific salmon.

INTRODUCTION

It is the purpose of this paper to review some of the most commonly used, and – at least in some quarters – commonly accepted, simple models that have been most influential historically in ecology to determine whether they are appropriate for the situations in which they are used. In addition, I will examine some of the data that have been offered in their support to see whether they do in fact support the validity of the basic equations. My concern is that I believe that many ecologists have not looked very carefully at the models that they have used routinely for teaching, for theoretical

exercises, and for certain applied problems, and have been too willing to accept data that superficially seemed to be in agreement with popular models but which in fact were not. While I have no desire to throw out the many excellent existing theoretical babies in the bathwater of my discontent, I do believe that some intellectual housecleaning is in order. I emphasize that I am focusing on historical, not present-day events, for there are signs (including some in other papers in this volume) that many of my concerns are being addressed by theoretical modelers. I want to state explicitly that my argument is not necessarily with either the concept of theoretical modeling or the use of analytic techniques per se, but rather with the particular mechanisms that have dominated the models that we have used most commonly in the past and with the procedures we have used to 'verify' models. It is my hope that we will all learn how to model better in the future from this effort.

This paper should be viewed as purposely 'on the other end of the seesaw' from the following paper by Hal Caswell, for each of us is deliberately staking out a rather extreme position for the purpose of this discussion. But even with such a proviso such an exposition is fraught with political difficulties. The first is that if my fundamental premise is correct then a large body of teaching and research in ecology is quite unfounded. Second, I know, like and respect many people who do such theoretical modeling and have no desire to antagonize them (further!). On the other hand I would like to see their work, and mine, be as useful as possible, and to me, at least, utility means that theoretical exercises must be connected fairly closely with reality at least eventually, and that models should at some point meet minimum standards of both mechanism and predictability vis-a-vis nature. Others argue that it is irrelevant whether theoretical models are immediately applicable to specific situations in nature or even whether theoretical models are ever connected with empiricism or not. Their argument is that we can learn a great deal even from completely unrealistic models through the use of 'what if...' scenarios. I do not argue with that approach as long as we call it mathematics, or mathematical theory. But it seems to me that we should not use the words 'theoretical ecology' unless the model has either passed some degree of validation vis-a-vis nature or at least it is made very clear how such validation might be attempted. (See also the article by Onstad, this issue). In all fairness it can be argued that other branches of ecology are rarely sufficiently validated either, and that there is no particular reason to pick on those who call themselves 'theoretical ecologists'. I agree that good validation is generally needed throughout our discipline, and support that effort wherever it is needed (see e.g. James and McCulloch, 1985). The issue here, however, is very specifically oriented towards theoretical mathematical models purporting to be general.

The question of the reliability of theory is far from merely academic. I believe, and I will attempt to demonstrate here, that a number of widely accepted but quite untested and almost certainly incorrect theoretical formulations are taught widely as truth, and, in addition, are used routinely by many managers who may be unaware of the problems that may be associated with their use. The application of such formulations occasionally have had enormous and often adverse impacts on resource management and the resources themselves, and that impact has itself rarely been examined. Finally the routine use of incorrect theoretical formulations in management has diverted a large amount of scientific effort by management agencies that might have been more profitably directed.

My perspective is that of a card-carrying modeler and occasional theorist with a long history of fieldwork. My wish is not to destroy general confidence in models or their use and potential but rather to use models with greater scientific rigor. Debates like that in this volume are hardly a novel perspective, and in ecology they go back at least to the 1920's and 30's (e.g. Kingsland, 1985; McIntosh, 1985) and much further in other disciplines. Elements of this debate are also extant in ecology today in various quarters (see, for example, Peters, 1980 a, b; Romesburg, 1981; Simberloff, 1982, Sharp and Csirke, 1983; Hall and DeAngelis, 1985; James and McCulloch, 1985; Hairston, 1986). I have found a great deal of support for my perspective from many colleagues and more than a little animosity as well. These varying responses can be seen in the reviews of this paper, two of which were very negative ("frustrating and annoying...mean spirited and narrow minded, hiding behind a mask of noble-sounding respect for 'reality'...") and two were very positive ("I find myself in close agreement...", "someone needs to jump on them (invalidated theoretical models)", and "... (theoretical) modelers (need to be) placed in perspective, primarily by getting them out of the main stream of decision making in resource sciences..."). Interestingly I find myself agreeing in part with both sets of reviewers, and know of no way to resolve the issue except to simply set out my original arguments and let the reader conclude what he or she wishes to.

SOME CHARACTERISTICS OF THEORETICAL MODELING IN ECOLOGY

I believe that there are three rarely stated but fundamental questions residing in debates such as are found in the above list of publications and in the issues addressed in this volume. The first is 'to what degree is it possible to extract the essence of a problem in few rather than many (or even very many) equations', the second is 'to what degree do the solution of those equations by mathematical means give you additional insights into the

TABLE 1

Classification of mathematical problems and their ease of solution by analytical methods

Equation	Linear equations			Nonlinear equations		
	One equation	Several equations	Many equations	One equation	Several equations	Many equations
Algebraic	Trivial	Easy	Essentially impossible	Very difficult	Very difficult	Impossible
Ordinary differential	Easy	Difficult	Essentially impossible	Very difficult	Impossible	Impossible
Partial differential	Difficult	Essentially impossible	Impossible	Impossible	Impossible	Impossible

operation of real ecosystems and/or their components', and the third is 'what is the relative importance of biotic vs. abiotic factors in determining the basic properties of species and of ecosystems, and their dynamics over time'. In addition there is the intertwined problem of whether or not the problem is correctly formulated. I next consider each of these points:

(1) For some reason, probably due to the earlier success of such techniques in physics and the mathematical rigor made possible by their use, most theoretical models have been developed using analytic mathematical approaches. But the number of mathematical problems that can be solved by routine analytical techniques are really very small (Table 1). One can argue that we are after the essence of a problem, and by its very nature the essence is rarely multifactorial, so that the limitations of using few equations are irrelevant. On the other hand, it seems to this field ecologist that to perceive of natural populations (etc.) as being importantly influenced by only one or two factors, and hence modelable using relatively few equations, is an absurd proposition, for there are so many interacting variables that influence each component, and then each component influences others. One can understand the difficulties and frustrations of attempting to put all of an ecosystem within a model, for then error in parameter measurement may negate the gains of greater inclusiveness. But to avoid the genuine complexities of nature by building an artificial world that must ignore complexities due to limitations of the chosen tools seems to me – as a matter of opinion – to be hopeless with respect to constructing models of real nature where nature is indeed complex. I always like Botkin's (1977) editorial "in praise of medium-sized models".

(2) Analytical models are solvable, and as such give predictions as a function of included mechanisms and input variables. It is an implicit assumption, I believe, that these mathematical solutions are equivalent to

ecological solutions. That is to say if the model predicts something, nature of necessity does the same, at least in a general way. If nature does not, and the problem is correctly formulated, then the formulation must be incomplete or the input or validation data must be wrong. In a metaphysical sense I have no idea as to why nature should necessarily follow our equations; and with the exception of the exponential equation (one of the very few theoretical formulations in ecology whose mechanisms seem real to me) applied to very limited and unnatural conditions in the laboratory, I just do not think that the fundamental premise that mathematical results are of necessity ecological results has been tested.

Rather I believe that our equations must follow nature. This gets into the messy area of whether all that we are doing is curve fitting. But we are not alone in this problem. Ohm's law, one of the bedrock equations of our sometimes guiding light discipline of physics, does not work at very low or high voltages where messy non-linearities dominate. Thus in a sense this 'law' is only an empirical best fit to data from a convenient range of conditions. Perhaps we are doing as well in ecology.

(3) Curiously, the majority of analytic models in use in ecology are almost completely biotic in their controlling factors. For example, a common starting point in many analytic models is that the distribution and abundance of a species is a function only of other species, as opposed to abiotic factors. It is rather curious that so much of analytical ecological modeling is almost completely composed of only biotic functions, for there is such a strong precedence for modeling abiotic factors in the discipline of physics, where analytical techniques have been very successful and which has served as a role model for many theoretical ecologists. In addition, abiotic factors are notoriously better behaved (and hence more subject to analytic modeling) than biotic processes. If physicists had to model electrons that behaved differently when they were hungry, they would probably be not much ahead of ecologists, and at some scales of prediction, perhaps they are not (Duncan and Weston Smith, 1978).

We have stated before a number of what I still consider to be the most pertinent aspects of this problem. Since I am unable to state these aspects any better now than then, I quote them from our previous paper (Hall and DeAngelis, 1985):

(1) A communication gap seems to exist between theoretical modelers, who use mainly analytic techniques in abstract models of systems or parts of systems, and more field-oriented ecologists, who, if they ever use modeling at all, confine their efforts to computer simulation models that differ radically in the spirit and approach from the abstract analytic models.

(2) Models have in general proved to be poor substitutes for specific empirical data, because biotic interactions seem to be recalcitrant to predictive models that are both general and accurate.

(3) Despite continued indications that certain models (e.g., logistic, Lotka–Volterra, stock-recruitment) are not suitable for most situations, many theoreticians and managers continue to use them.

(4) There is a frequent confusion of mathematical rigor with scientific rigor, for although mathematical rigor is essential for certain types of models it is often an irrelevant criterion for judging the virtue of a model vis-a-vis reality.

(5) There has been, in our opinion, a relative overemphasis on solving equations, and insufficient attention paid to which forms of equations represent nature with the greatest fidelity.

(6) The testing of the adequacy of models vis-a-vis reality seems to us to be poorly developed and often deliberately and arrogantly ignored (although this may be changing – *C.H.*).

OUR THEORETICAL MODELS ARE ALIVE AND WELL

The following section assesses the validity of a number of prominent models – the logistic growth curve; its derivative, the Ricker curve; and Lotka–Volterra predator–prey relations – in terms of their ability to represent the essential processes that they claim to represent, and also from the perspective of whether the empirical data that have been used in the past to ‘validate’ these models represent reasonable validation. These models are used extremely commonly, and probably represent the most generally accepted basic equations in ecology. They are taught in virtually every introductory ecology course – often as ‘basic truth’. I too did so in the recent past.

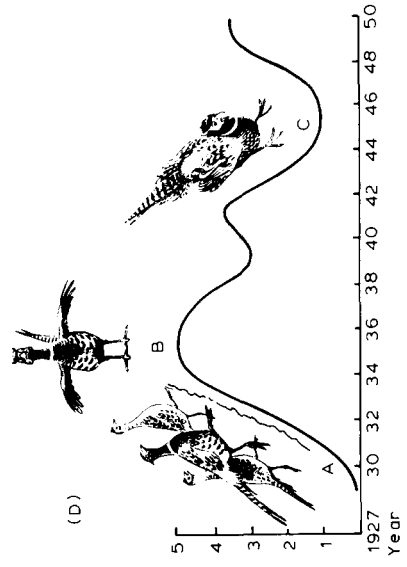
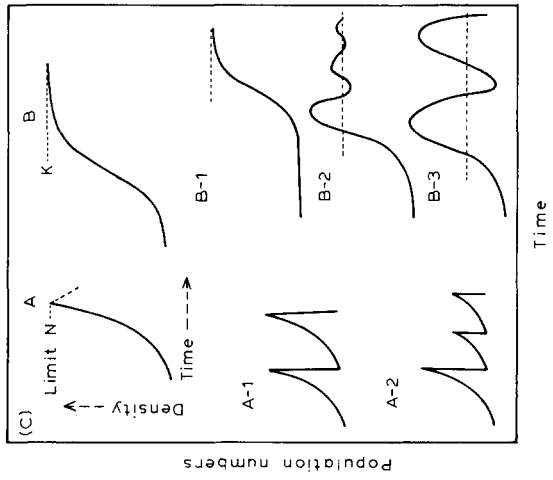
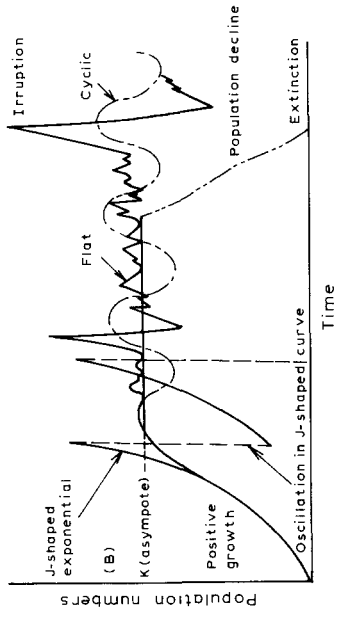
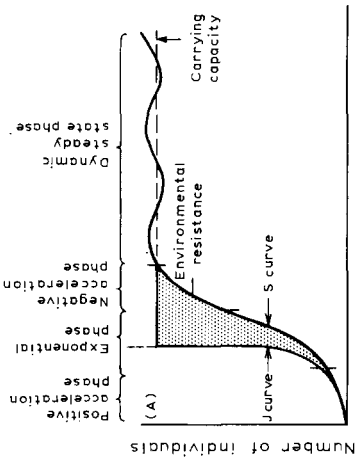
I was certainly taught these basic models more or less as ‘truth’ as a graduate student. Since there is no formal survey of what ecologists or managers do or do not believe, I undertook a series of informal surveys in the summer and fall of 1987. Half a dozen ecology and wildlife students at the University of Montana summer session (who in winter attended major universities from all over the United States) all said that they had been taught the logistic curve more or less as a basic law of nature within the past 2 or 3 years. Several were quite indignant that I was questioning what was so obvious to them! Then I queried three research biologists at Montana Fish, Wildlife and Parks. All three are bright, knowledgeable field biologists with Master’s degrees in fisheries or wildlife and additional background in ecology. All said that they had been taught the three models listed above more or less as ‘truth’. They also said that these models were used as the

basis for their day-to-day research and management programs, although they had been having trouble making their most reliable data conform to the theories. They felt that these ideas were even more strongly entrenched in many of their colleagues who were principally managers. My colleague, Dr. Jack Stanford, polled three wildlife managers for the U.S. Forest Service in the western United States and found that all used these models as the basis for their management programs. None had heard that any particular criticisms existed, although all felt that the basic model results could or perhaps should be modified by other factors. A poll of about 25 students and faculty at a seminar at Syracuse University found that about two-thirds believed that these three models were 'a good place to start' for analyzing and predicting populations, and none thought that they were a bad place to start.

And, of course, further development and use of these models can be found in a large number of recent and especially past issues of, for example, *Ecology*, *American Naturalist* and *Ecological Modelling*, as well as a number of theoretical (e.g. Vandermeer, 1981; Nisbet and Gurney, 1982) and management (e.g. Giles, 1978; Robinson and Bolen, 1984) books. It is a matter of debate as to whether the further complexities introduced into these newer and often very sophisticated elaborations of the basic logistic, Lotka–Volterra and Ricker equations are getting closer to truth in nature by adding on more mechanisms, or rather, as I believe, tinkering with completely inappropriate starting material. The important point is that I do not see validation criteria offered by which we can judge. In summary, although there is some evidence that these simple models are not as influential as they once were in the primary literature, they still seem to be enormously influential in the minds of at least most of our students and many managers of our natural resources.

THEORY AND REALITY: LOGISTIC, LOTKA–VOLTERRA AND RICKER MODELS

There are many ways to represent an initially rapidly growing but then saturating growth phenomena (e.g. Jassby and Platt, 1976). The most commonly used formulation amongst population ecologists is that of the logistic curve, the origin of which is attributed to Verhulst (Hutchinson, 1978). The logic behind the curve is simple and compelling, at least superficially. It is clear from many studies, both in the laboratory and in the field, that populations of both plants and animals have the capacity to grow exponentially, that is, to continue to increase at a relatively constant proportion of existing numbers of individuals as the population itself increases. Yet clearly the average populations of the world are not doing so (humans are an exception, at least temporarily). Environmental suppression of growth potential, that is, the suppression occasioned by direct and



indirect effects of crowding, seems a logical reason for why populations are not growing as rapidly as their reproductive potential allows. It seems logical that the more organisms there are, the more they will crowd each other in one way or another, and the less their growth potential can be realized. The particular mechanisms suggested are probably familiar to the majority of our readers, and can be found in, for example, Allee et al. (1950) or essentially any modern textbook in ecology or wildlife science. Figure 1 gives several examples of logistic curves found in textbooks, which treat them with varying but normally considerable degrees of credibility, at least from the perspective of what 'ideal' populations do. Other examples can be found in most other ecology and wildlife textbooks.

The following discussion is derived principally from the fascinating study of early mathematical ecology by Sharon Kingsland (1984). During the first third of this century a remarkable series of laboratory experiments was undertaken by Raymond Pearl at Johns Hopkins University, but also by Thomas Park and the Russian G.F. Gause. Pearl turned to the laboratory study of microorganisms after a fire had destroyed his life's previous work on empirical demographics. It is a curious speculation as to how the history of ecology might be different had that fire not occurred, or had Pearl turned his forceful personality to other endeavors.

Pearl was especially interested in the application of the idea of environmental resistance, and especially the logistic curve, to the prediction of human populations (Fig. 2). Despite some extremely strong criticisms from his colleagues that he was speculating far beyond the reliable bounds of either data or theory, he stubbornly advocated the generality of the logistic curve as a law of population growth – essentially equivalent to law in physics – for as long as he was professionally active. Other bright young ecologists came and went from his laboratory, sometimes initially endorsing the use of the logistic equation enthusiastically and then later repudiating it as a gross oversimplification of population growth. For example, the young Israeli naturalist Bodenheimer at first undertook studies that seemed to support the curve, but later became a strong critic of its too general application. This is especially interesting when we see Bodenheimer's work cited as support for the operation of the logistic curve in nature as late as 1978.

Fig. 1. A number of textbook examples of the logistic curve. (A) From *Living in the Environment*, 3rd Edition, by G. Tyler Miller, Jr., © 1982 by Wadsworth, Inc., reprinted by permission of the publisher. (B) From Smith, 1966, with permission. (C) From Odum, 1981, with permission. (D) From Smith, 1966, with permission.

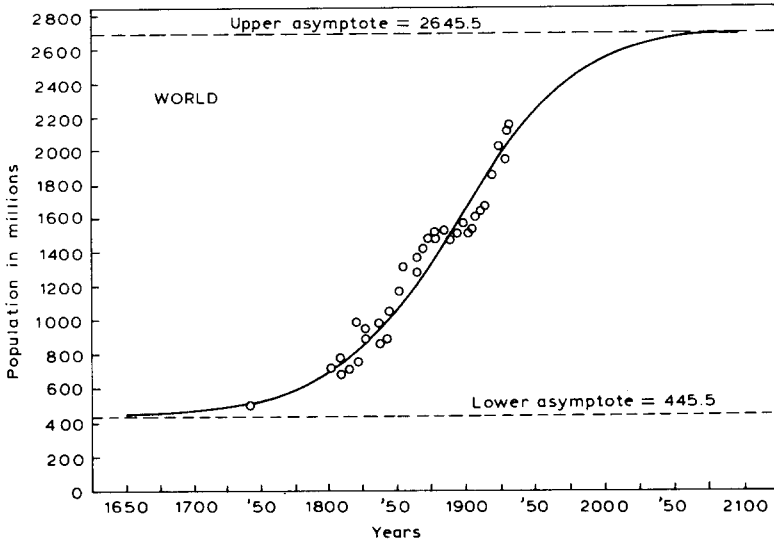


Fig. 2. Application of the logistic growth equation to the possible growth of the global human population (Pearl, 1936, as given in Allee et al., 1950). Since the present-world population is nearly double the asymptote of this curve it is clear that the projection was not too accurate. Probably the largest reason for this is that Pearl failed to foresee the tremendous impact that the industrialization of agriculture would have on the ability of this planet to sustain human populations.

I taught introductory ecology for many years at a major eastern university. Initially I taught the logistic formulation as more or less basic truth in ecology, but later I began to tell my students that I believed that there was no empirical evidence that I knew of that supported the logistic curve as a reliable explanation for the growth of any unmanaged population in nature. Each year the teaching assistants would respond with either interest or more frequently indignation, so I would then challenge them to show me a valid example. Many responded to this challenge, but they were unable to bring me even one example over the years that either of us thought was an adequate example, although certainly that may exist somewhere. Perhaps the readers of this paper know of such an example and would send it to me.

Yet purported examples exist in many textbooks and they need to be examined carefully. Several are given in Fig. 3. (It should be noted that these examples have a long history of use, and any possible misuse of them should in no way reflect upon the book's authors, who were simply using what was then – and perhaps still is – commonly accepted knowledge). Although all of these data appear superficially attractive, a closer examination of all curves shows that either:

- (1) The data are from the laboratory, where there is little doubt that the logistic curve at least occasionally represents the growth of some organisms (e.g. Fig. 3A and 3B).
- (2) The growth curve is for a population with a distinct temporal larval stage after which there are no additional recruits possible (e.g. barnacles, Fig. 3C).
- (3) The data are plotted on semilog paper to give the appearance of the logistic. This appearance disappears when the same data are plotted on a linear scale.
- (4) The lines' fit to the data reflect far more the scientist's eye and prejudices rather than the data itself (Fig. 3D and 3E). It is interesting to observe how the same (mis)fits to the data are reproduced, in this case, from one publication to another nearly 30 years later.

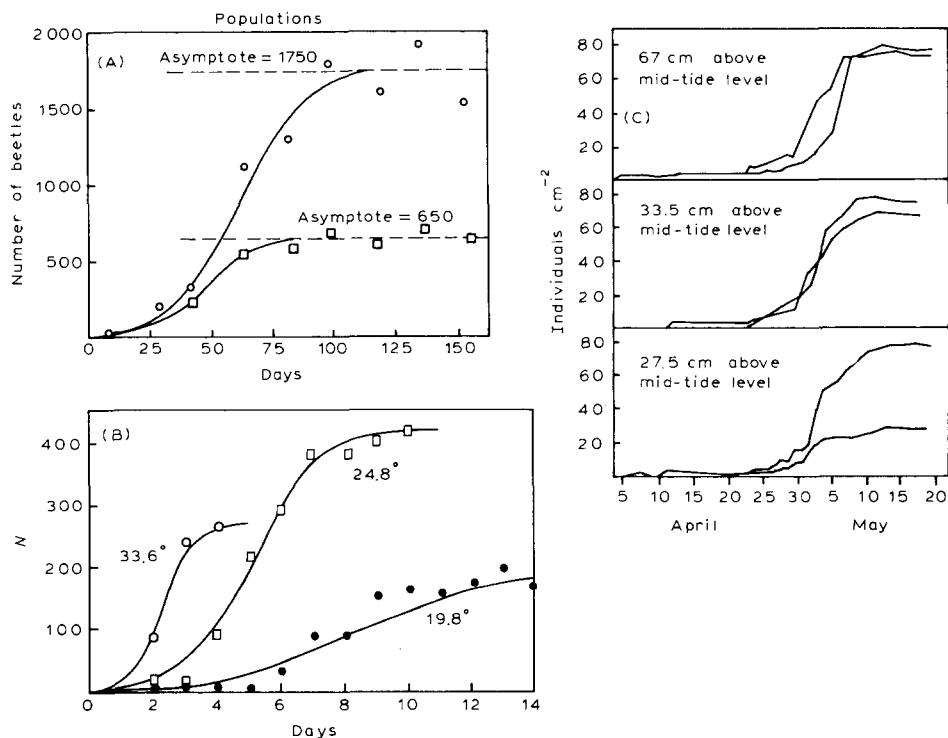


Fig. 3. Examples given in various textbooks to support the validity of the logistic growth curve as a predictor of populations in the laboratory and in nature. (A) Flour beetles, from Gause, as given in Allee et al. (1950). (B) Water fleas, from Tereio and Tanaka, in Allee et al. (C) Barnacles, from Connell, 1961, as given in Hutchinson 1978. (D) Argentinian antlions (from Bitancourt) and several types of bees (from Bodenheimer), as given in Allee et al.

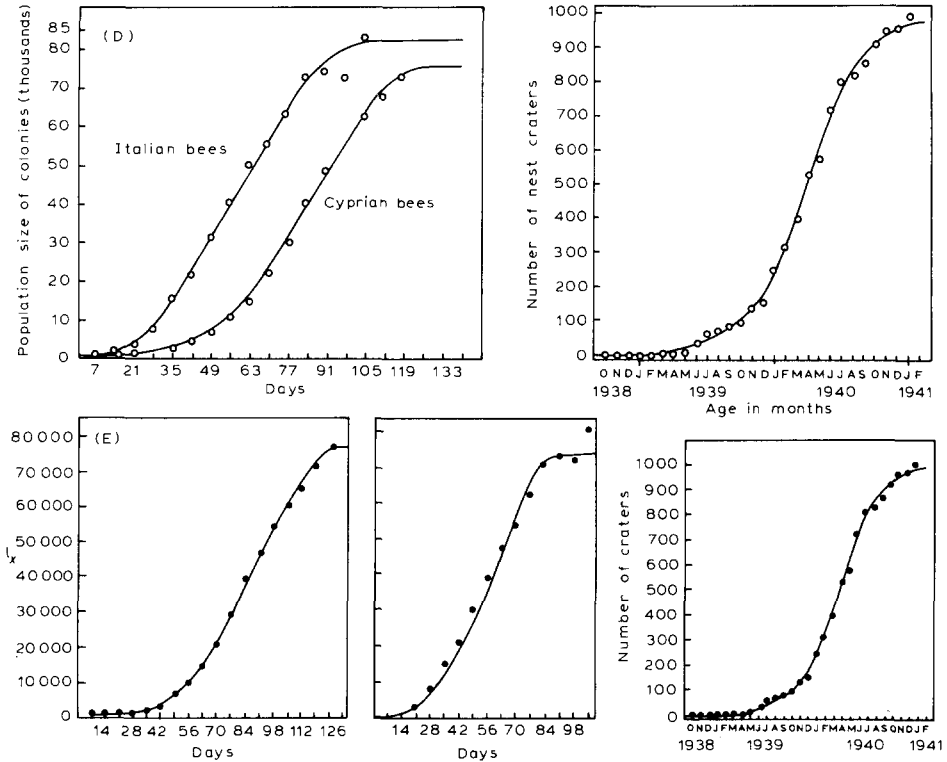


Fig. 3 (continued). (E) The same information as (D) as presented in Hutchinson, 1978. Note that in no cases in (D) or (E) does the logistic fit the final data points given better than a linear extrapolation. (With permission from Yale University Press, New Haven, CT.)

- (5) The data are for a human-managed population (sheep in Tasmania). We have no idea why the shearers of Tasmania chose to limit the population of sheep as they did, but it certainly does not reflect any natural control.
- (6) The relations are a fabrication. Suffice it to say that the majority of the logistic curves that I found in various texts had no data points at all associated with them or were drawn inappropriately over the data.

Perhaps the most famous example of the use of 'data' to support the importance of the logistic curve in nature is the population change over time of the deer herd on the Kaibab Plateau (Fig. 4). This was one of the most influential stories of my own early graduate education. The 'fact' that 'thinning' the deer herd (which were no longer thinned by natural predators which had been eliminated on the plateau) would have 'saved' the deer from the consequences of 'exceeding their carrying capacity' (which may or may not be true) was wonderful grist for the intellectual mill of young profes-

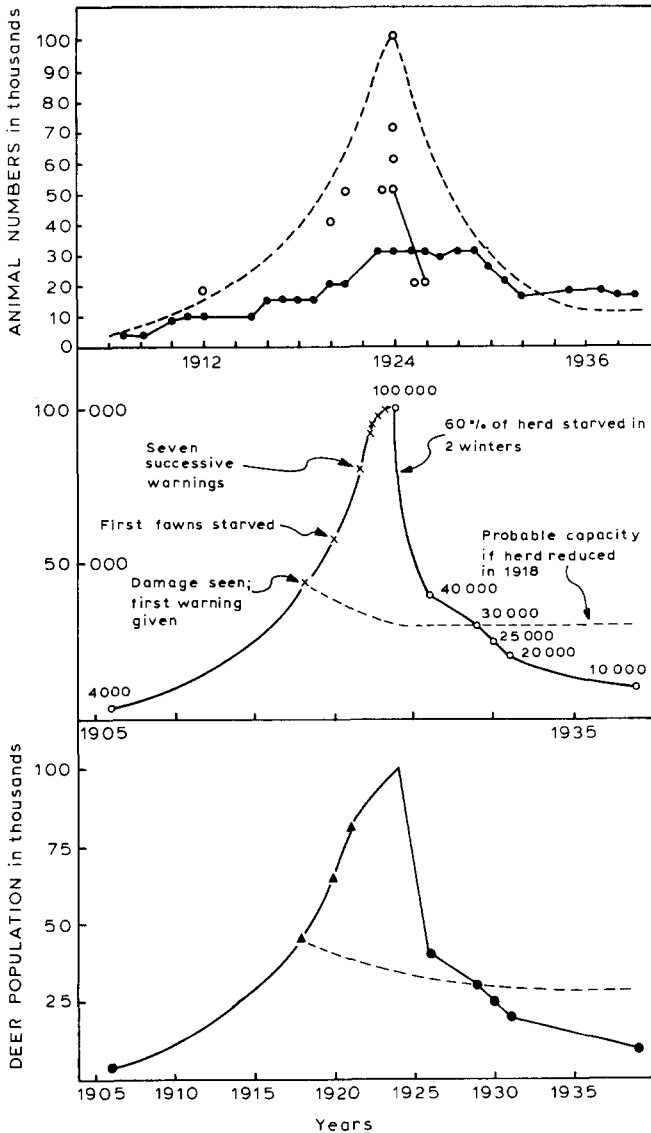


Fig. 4. Bottom: The Kaibab deer story as I learned it in graduate school. Top: The original presentation of the data. The linked circles represent the estimates of the forest supervisor and the other points represent the estimates of various visitors. The middle and lower graphs are found in later textbooks. See Colinvaux, 1973, for a more complete presentation. (Reprinted with permission of Wiley, New York.)

sional ecologists and wildlife managers who were, for the most part, also hunters. But the actual reliability of the data used to construct the Kaibab deer story seems extremely suspect. The apparent near-fabrications that

occurred as the same data were transferred from one publication to another has been thoroughly elucidated by Colinvaux (1973), and there is no need to repeat that here beyond the reproduction of his summary figure (Fig. 4).

It is quite remarkable to see these examples used again and again over the last 50 years with apparently so little questioning. I believe that the reasons are in large part sociological (see e.g. Dayton, 1979) but they remain outside the scope of this analysis.

Lotka–Volterra equations of the form:

$$\text{change in prey numbers} = (\text{intrinsic rate of increase}) \times (\text{prey number}) \\ - \text{loss to predation}$$

$$\text{change in predator numbers} = \text{gain from predation} - \text{natural losses}$$

are also among the most firmly entrenched of mathematical models in ecology. They are simple, intuitively appealing, mathematically tractable and interesting, and of potentially great utility in describing real populations. In addition, there is the appealing story of the mathematician Volterra's enchantment with this applied problem brought to his attention by the marine biologist D'Ancona, who was simultaneously enchanted with Volterra's daughter, his future wife. Lotka had derived similar equations independently and collaborated with Volterra. It is interesting to note that Lotka was more convinced that the key to understanding biotic processes was in energetics (Lotka, 1924), although his place in history has been far more firmly established, at least to date, by his association with these equations.

Many species in nature cycle, and so do coupled Lotka–Volterra equations solved over time. Since predation is dramatic and often readily visible to the human eye, there was an outpouring of interest in the possible explanatory utility of these equations for the observed cycles of nature. The most famous example, one that appears in most introductory textbooks in ecology, is the Canadian hare–lynx graph (Fig. 5). This graph, based on data from the Hudson's Bay fur returns, show strongly cyclic populations of hare and lynx that seem to oscillate in tandem. Many parts of the curves show that the changes in the lynx population seem to follow that of the hare. The solutions to coupled Lotka–Volterra equations behave mathematically in an extraordinarily similar fashion. This has been offered many times as substantiation of the operation of the Lotka–Volterra curves in nature.

Unfortunately, the story is not as neat as the superficial examination of the curve would have us believe. First of all, the changes in the lynx population sometimes precede those of the hare (Gilpin, 1973, incidently an ecological theorist), something that makes absolutely no mathematical sense unless hares eat lynx. Second, a closer look at the original data showed quite clearly that the two sets of population data were not from the same region: the hares were from Eastern Canada near Hudson's Bay and the lynx were

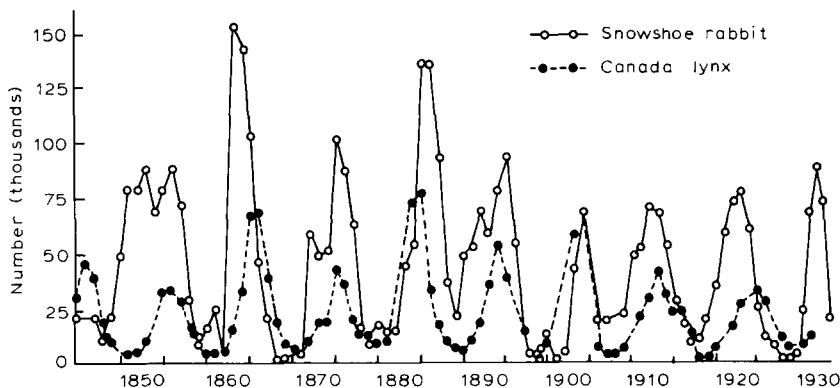


Fig. 5. Hare and lynx population dynamics as represented by returns to the Hudson's Bay Company (from Smith, 1980, with permission). See also e.g. Colinvaux, 1986.

from Western Canada (Finerty, 1979). The skins of the hare were not valuable enough to ship very far to the Hudson Bay Company's collecting centers, although those of the lynx were. Finally there is evidence that the hares on Anticosti Island in the Gulf of Saint Lawrence go through cycles similar to hares on the mainland, but there are no lynx on Anticosti Island (Elton and Nicholson, 1942, in Keith, 1963). Although it seems reasonably clear that some kind of cycles do exist for both lynx and hare populations (Finerty, 1980), the reasons for those cycles are not as clear. There seems to be some relation of the cycles to sunspot activity, but no one has proposed any connecting mechanisms. Weinstein (1977) has offered an interesting possible explanation for the cycles seen in the Hudson's Bay records as a result of sociological factors affecting trappers.

So again we must question the data that have been used repeatedly both explicitly and implicitly to support one of our most cherished theoretical models in ecology. I guess the lesson is that we must look much more critically at what we are willing to consider supportive evidence in ecology (see e.g. James and McCulloch, 1985), and we certainly should not accept supporting graphs for a theoretical model if the data points are not plotted. Such examples do not discount the possibility that such models are correct, nor do they necessarily discount the utility for some purposes of these theoretical models even if they are not an accurate reflection of nature. But they do tell us that these particular models cannot be counted upon to be accurate predictors or accurate representations, even as a 'starting place', of what is occurring in nature. I believe that this is so because the models do not have the correct mechanisms in them. Density dependence and predator control of prey (and the converse) are interesting ideas that certainly do occur, but that is very different from saying that they are routinely the only,

or predominant, mechanisms for determining population levels. Nevertheless these theoretical models are used continuously, even relentlessly, to extend theory and to manage natural populations. I next turn my attention to specific examples of the latter.

EXTENSION OF THEORY TO MANAGEMENT

It is perhaps excusable or even desirable for theorists to make up whatever world they wish to and then explore the consequences, for certainly much can be learned about nature (if it is later confirmed by appropriate non-trivial observations or experiments) from such an approach. A more serious problem may occur, however, when unproven theory is taken seriously by managers and used in ways that may have deleterious effects on real populations and ecosystems. This is not idle speculation. One of my reviewers (a wildlife ecologist) wrote initially that "Although wildlife managers carry these theories as part of their baggage, they fortunately don't use them that often." Later, upon returning from a Wildlife meeting, he amended that comment so that the later part read: "...unfortunately they attempt to use these models in the field and wonder why populations don't behave as they are supposed to." Smith (1985) found a beautiful field study marred by attempts to make populations fit density-dependent theories that were at odds with the data.

Since I know a little more about fisheries than wildlife management, I will focus on fisheries. A 'Ricker curve', named after Dr. William Ricker, a pioneer in salmon research and, incidentally, one of the better critics of the misuse of the curve that bears his name (e.g. Ricker, 1958), is based on the logistic curve in its derivation (Ricker, 1954). It 'says', in effect, that when spawning population numbers are high 'density compensation' will reduce substantially the number of young produced per spawning adult even to the degree that fewer total numbers of the next generation will be produced from large spawning populations than from medium-sized populations (Fig. 6). One readily observable mechanism for this is that when there were many spawners, the later females would disturb the redds (nests) of the earlier spawners. Another is cannibalism (e.g. MacCall, 1981, Santandes et al., 1983; Hyatt and Ringler, in press). But do these factors operate in real fisheries?

The Ricker analysis has been taken extremely seriously in the teaching of fisheries biology (e.g. Tyler and Gallucci, 1980; Pitcher and Hart, 1982 for a few of many possible examples). It has the supposed virtue of allowing one to both catch substantial numbers of fish while simultaneously enhance the numbers of future adult fish by harvesting 'surplus' adults that would have only depressed total production had they been allowed to spawn. It is

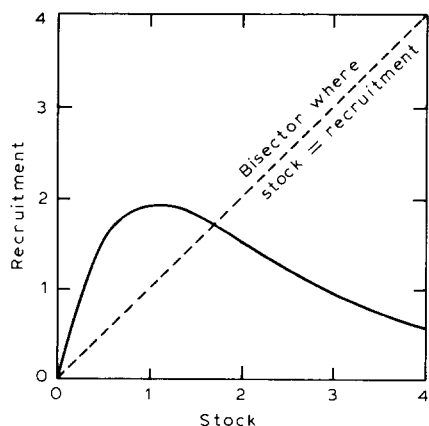


Fig. 6. Theory behind Ricker stock-recruitment dynamics. At low-stock (parent) population densities the young produced increases as the parents increase. But at higher-population levels, density compensation, of various forms, reduces the per-capita survival of the eggs laid so that at some point there are fewer young produced than would have been the case at lower densities of spawners.

probable that this ‘have your cake and eat it too’ aspect had a lot to do with selling the idea of its use to fishermen and to politicians.

The degree to which the Ricker curve is used in practice is more difficult to discern. Fletcher and Deriso (1986) wrote that despite the “perception of spawner-recruitment models as commonly accepted instruments of fisheries management” their survey showed “a universal rejection of such models” for actual management. Yet a half dozen managers that I queried all indicated that the Ricker curve was used routinely explicitly or implicitly to manage British Columbia Sockeye Salmon and other fish species. My colleague Karl English, who resides in British Columbia and works on British Columbia fisheries data, found it difficult to locate specific documents to substantiate this claim. He discussed the issue with Wayne Saito (Fisheries and Oceans, Canada) who said that since 1976 Ricker curves have been used routinely to manage Fraser River Sockeye and Pink Salmon stocks (such as the Horsefly River stock) especially for peak years (Karl English, personal communication, 1987). In Alaska the Ricker analysis seems to be used routinely for Sockeye Salmon: “escapement goals are established for many of our Sockeye stocks based on maximum surplus production from Ricker curves fitted to return from brood year escapement data.... Unfortunately the analyses that are conducted to set escapement goals are not formally published....” (Douglas Eggers, Chief Fisheries Scientist, State of Alaska Division of Commercial Fisheries, Juneau, November 1987). Dr. Eggers goes on to state that in addition to the Ricker analyses several other apparently very sophisticated techniques are used as

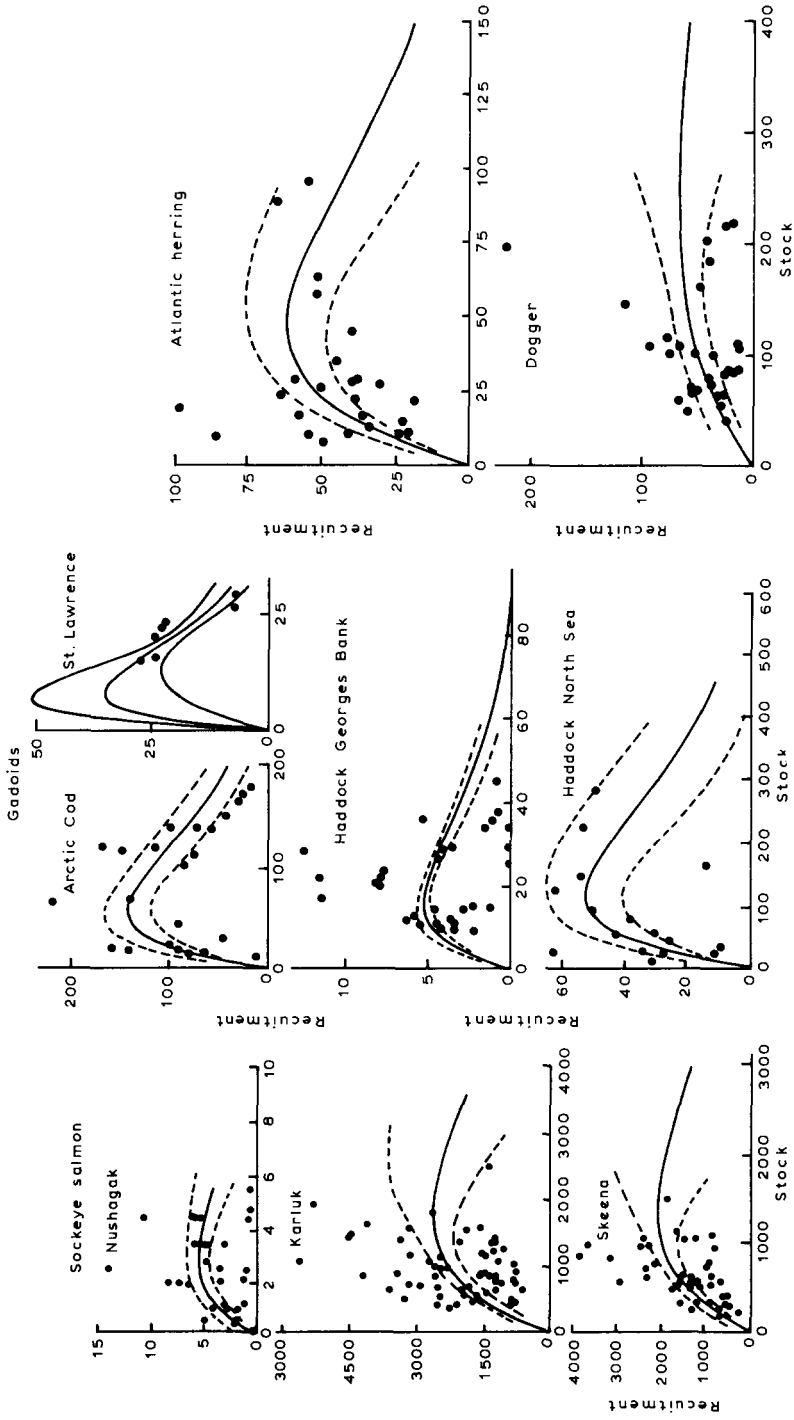


Fig. 7. Some stock-recruitment data and 'Ricker curve' lines fitted to them (From Cushing, 1973, with permission). The reader may wish to test the null hypothesis by drawing an horizontal line through the points.

well, that some of the data used for the Ricker analysis are in press, and that management is changing as new information is gained. Thus, although it is a little hard to pin down through publications the use of the Ricker curve, it clearly is being used formally in at least Alaska and British Columbia, and many investigators felt that it was used implicitly in many other fisheries. It is used explicitly in research papers recommending management strategies (e.g. Wespestad and Terry, 1984), although the fit of model to data generally remains dubious. The most recent fisheries management schemes for Alaska appear to use the Ricker curve very cautiously (e.g. Megrey and Alton, 1986).

Some consequences of the inappropriate use of the Ricker curve

One consequence of the use of the Ricker curve in particular (which can be used to support intensive fishing harvests and heavy fishing pressure in general) is that there has been little or no data to support the right-hand side of the empirically-derived Ricker curves (Fig. 7). Hence it is almost impossible to validate or examine the supposed decrease in production of young at high spawning stock densities. But when an exceptionally large number of Horsefly Sockeye Salmon happened to escape the fishery in 1985, there was no evidence at all of density-dependent depression in the production of young (Fig. 8A). British Columbia managers have responded recently by experimentally reducing allowed catches for selected stocks.

The consequences of actually managing real fish populations using the Ricker analysis where it is not well substantiated empirically can be very important and not necessarily what is expected. It is probably not too much of an exaggeration to say that the salmon have been managed now for many decades as if there was a surplus of potentially spawning adults that, were they not caught, would decrease per-capita production of their young because of 'density compensation'. But, in the meantime, the fisheries of British Columbia, and indeed the world, have been relentlessly industrialized, a fact that seems to have escaped the interest of theoretical fisheries analysts, despite its overwhelming importance (Hall et al., 1986). The total annual catch of British Columbia salmon can now be captured in just a few weeks of selected fishing in about eight locations. Fisheries management for British Columbia salmon now is devoted essentially to making fisherman inefficient through laws so that they do not catch virtually all the fish (Karl English, personal communication, 1987). There are probably very few stocks that have not had from perhaps 50 to 90% of the returning adults caught each year. As a result, most Ricker analyses are based on a cluster of points at medium to low spawning population levels with no information at all about higher population levels (Fig. 7). For every year since there have been

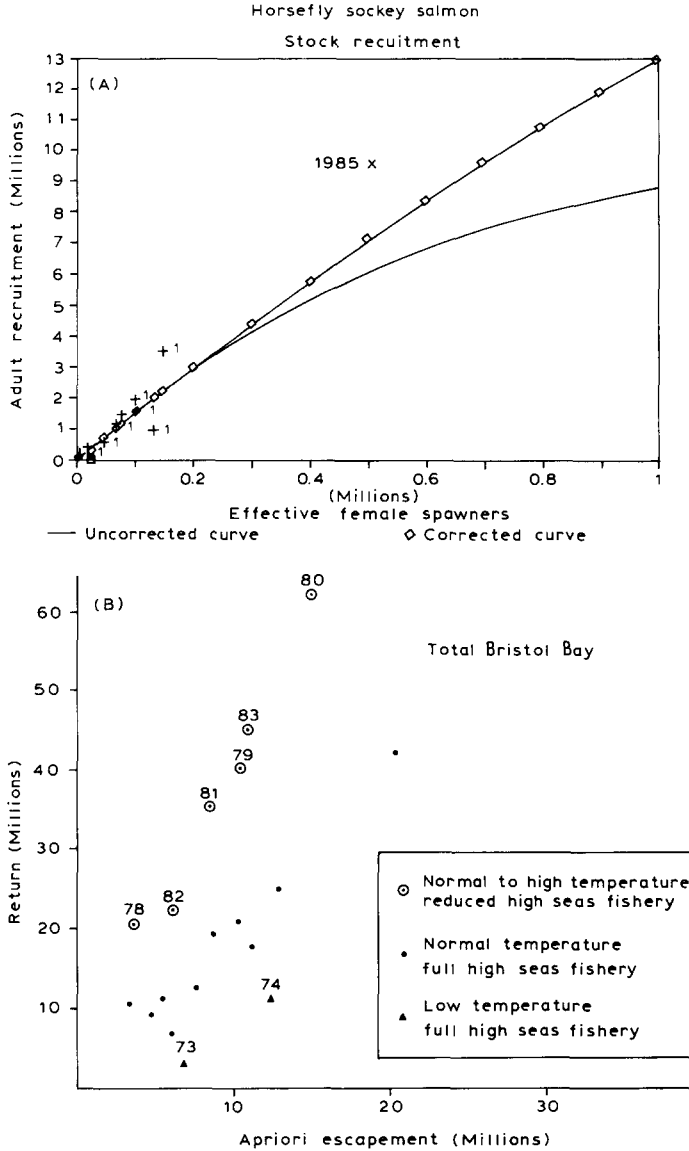


Fig. 8. Examples of where large numbers of spawners were 'let through' fisheries that had previously been managed to maintain populations of spawners at levels below which density compensation would occur. In these examples there was no evidence at all of density compensation with much higher escapement of spawners. (A) From Gazey et al., 1986, with permission. (B) From Eggers et al., 1986, with permission.

any records, these 'surplus' fish were captured by the fisheries whose managers were bent on maximizing the future production of young through optimizing the harvest.

Although we will never know for sure, probably what we consider 'high' population levels today are much lower than what existed before 1850, for there was extremely heavy pressure on most stocks for many decades before there were any attempts to gather data. And there is a different very important twist that is not a component of the Ricker, or any pure population dynamics, equation. In many areas the phosphorus brought back to the nursery areas from the sea in the bones of the adults that die after spawning is the major source of this essential nutrient to these generally oligotrophic environments. Thus, even where populations have been well managed according to the Ricker hypothesis, there probably has been a gradual depletion of phosphorus in many nursery areas. The adults that are a surplus from at least some population perspectives are not surplus from the perspective of their role in nutrient budgets. Because the number of fish that escape the fisheries now is much smaller than the earlier natural runs, it is hypothesized that in general salmon nursery areas are increasingly nutrient-impooverished compared to pre-fisheries times. This has actually been observed in the few areas where there are long-term nutrient records (e.g. Krokhin, 1975). But data in North America are scarce because fish are easier to count than phosphorus is to measure. So now, even if we let more salmon escape the fishery, they will spawn in generally less productive environments. It has been observed that growth and ultimate survival is less in these lower nutrient environments. In other words, even if we do accept the Ricker analysis as a good descriptor of the population dynamics of salmon, its short-term utility may mask ecosystem effects of the supposedly surplus adults, and the salmon will be overharvested. In the meantime the addition of nutrients to nursery lakes has had dramatically positive impacts on fisheries yields, indicating the importance of managing from an ecosystem as well as a population perspective (LeBrasseur et al., 1979).

Of perhaps greater concern, however, is the degree to which we have been willing to impose our theories on data that do not support them. Figures 7 are but a few of many examples that I found where theoretical curves have been drawn through data that do not support them. In effect, the null hypothesis that there is no relation between stock and recruitment (that is, that a straight line would fit the data as well as the curves drawn) has not been formally tested even though the fit of the data to the Ricker hypothesis is so obviously poor. In addition, the data itself are far from perfect, and there are biases in the way the data are handled that would often tend to make the data appear to fit a Ricker analysis better than it in fact does (Ludwig and Walters, 1981; Gazey et al., 1986). Salmon are relatively easy fish to count, or so it would appear. In fact there are many problems associated with the fish counts that have been used to derive Ricker curves used in management, including most obviously a failure to separate adult

fish of different ages when determining eventual recruitment (see Brown and Patil, 1986, for a consideration of the impact of uncertainty in parameter estimation on stock-recruitment analysis).

A salmon manager once told me that he had been managing salmon in Canada for three decades in a fashion that should have been increasing stocks, but that nevertheless the stocks had been decreasing. Since that time, there has been a very strong political movement in Canada to 'bring back the salmon' (in particular the popular sport silver and chinook salmon) in part through a massive and extremely expensive artificial propagation program. One rationale for this, perhaps not the dominant one, was that the problem to be avoided was density-dependent suppression of the production of little salmon on the spawning grounds. Enormous sums of money were spent to bulldoze lovely rivers into giant beds of perfectly machine-sorted gravel, where water flows and other factors are controlled closely. In addition, large hatcheries were established, and the birth of salmon in Canada has become as industrialized as their death.

To many the results of this program have been obvious and very desirable, for the fisheries seem to be no longer declining. What is not so obvious is that the huge numbers of hatchery fish may be depressing natural production as hatchery and natural salmon compete in fresh water and in coastal areas (Peterman, 1978), and especially as the fishing pressure on the remaining wild fish has intensified in response to the abundance of hatchery-reared fish. It is estimated that the hatchery stocks can sustain at least 75% and probably at least 90% harvest without affecting the ability of the hatcheries to produce more young salmon. Where hatcheries are successful, fishing is good and fishing pressure is very intense. Unfortunately, there is essentially no way to discriminate between hatchery and wild stocks in the sea, and that same fishing pressure is exerted upon wild stocks that can sustain only perhaps 50% harvest. The net effect is that the hatcheries have greatly increased the harvest rate on the wild fish that spawn in the vicinity of the hatcheries. Since the hatcheries were built on the best nursery rivers in the first place, the total impact on wild fish is probably very large but essentially unmeasured.

Meanwhile about a quarter of the hatchery fish stray to spawn in waters other than those of the hatchery, and the very delicately tuned genomes of specific wild salmon stocks (which home with much greater precision) are becoming increasingly swamped with genomes selected for survival in a world of concrete and Purina trout chow. This is probably the last decade that totally wild coho and chinook salmon genes will exist in large areas of British Columbia.

The largest of many ironies associated with this story is that it is possible that salmon production could have been increased greatly much more

cheaply and using natural stocks simply by dramatically decreasing exploitation pressure for a few years to allow much greater natural spawning. Of course we do not know for sure that this approach would have worked because we have never tried it, at least on a large scale. Where the salmon have occasionally outwitted the managers and returned in far greater numbers than the fishing fleet could harvest them, or at least the canneries could can them, we have seen no density compensation at all – but rather a far greater production of smolts and subsequent adult salmon (Fig. 8A and 8B). It seems to these eyes that we were so busy in the past attempting to draw density compensation lines through data that were probably telling us something entirely different that we never saw that a much less expensive and more environmentally sound way to rebuild salmon stocks was right in front of our noses. And we must ultimately lay at least part of the blame on the use of ecological theory in general and our unquestioning acceptance of the logistic curve concept in particular, because we have had data for years that did not support the theory if we had been willing to believe these data more than the theory. But too often we did not.

SUMMARY

I have given three examples here of commonly accepted and used ecological theories that in fact have very little data (perhaps none) from real populations to support their validity. I could have given additional examples. It seems to me that ecology is beset with fashion... grand theoretical concepts sweep in to our field from somewhere (let's see, what was it last year, diversity–stability, catastrophe theory, keystone species, island biogeography and the design of nature preserves or what?) Some of these theories are probably valid and useful descriptors of real ecological events at least some of the time, but almost all have been extrapolated in space and time far beyond any supporting information. Again and again evidence to the contrary has been ignored by the advocates of the theory, and very weak fits of model to data have been offered as strong support for the theory.

The take-home message, at least to me, from this analysis is that we as a discipline have been far too eager to grasp at data that appear superficially to support our most cherished beliefs, and that we have often not paid sufficient attention to data that have been trying to tell us something quite different. Somehow these models have taken on a life of their own, unrelated to empirical reality. Yet perfectly valid alternative theoretical approaches with a better fit of data to theory have existed since at least the time of Hjort (1918). As someone with an ecosystem perspective I believe that this overacceptance of certain simple models with inappropriate or very weak mechanisms has led us to pay insufficient attention – in fisheries and

elsewhere – to more complex ecosystem- or climate-oriented models that may have much greater predictive values (see examples in Sharp and Csirke, 1983, Hall et al., 1986). Why have we so often chosen to use the theoretical models even when they have obviously been failing us? I believe that much of the problem has to do with the complexity of the real processes of nature and our desire to find simple patterns. It is my own prejudice that eventually approaches based on thermodynamics will be much more powerful in addressing some of the issues presented here (e.g. Ware, 1982; Kitchell, 1983; Smith and Li, 1984; Hall, 1988), but obviously a much more powerful case must be made than has been done so far.

Finally most of us realize that there is a prestige ladder in most disciplines and departments where there often is a premium placed on the ability to do mathematical analysis. Meanwhile there has been great confusion amongst average ecologists between mathematical rigor and scientific rigor. One result is that ideas that clearly have at least some kind of rigor, even if it is inappropriate rigor, have been given far greater credibility than they deserve. This is not to belittle the importance of good mathematical rigor in the development of theory in ecology and elsewhere (see Caswell, this issue), but it, like any tool, has its place.

We must, I believe, tighten the link between the development of theory and the testing of that theory. If this is not done, then we should not accept that theory as ecological knowledge, but rather call it mathematics or by some other name. This does not mean that the theorists need to become experimentalists, but rather that any new theory be required to include non-trivial, non-tautological field validation or else suggest experiments or observations that could be done by someone else to (in)validate the theory (see e.g. James and McCulloch, 1985; Hilborn and Stearns, 1982). After such tests are rigorously passed then we can call the entire exercise, and the knowledge so gained, ‘ecological knowledge’. Such an approach can also be well exercised in other approaches to ecology, including field investigations.

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