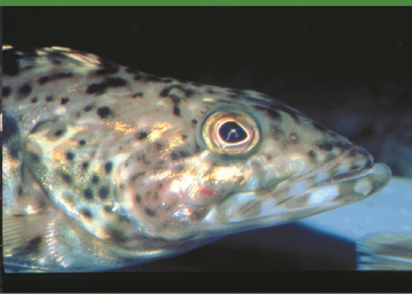
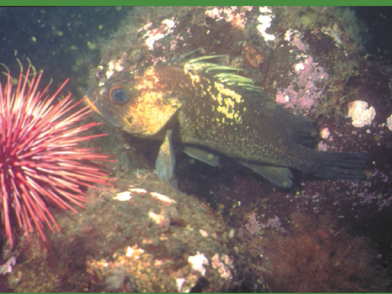


# FISHERIES ECOLOGY AND MANAGEMENT



Carl J. Walters and Steven J. D. Martell



# Fisheries Ecology and Management



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*CARL J. WALTERS AND STEVEN J.D. MARTELL*

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# C O N T E N T S

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<i>LIST OF FIGURES</i>	xi
<i>LIST OF TABLES</i>	xvii
<i>PREFACE</i>	xix
<i>ACKNOWLEDGMENTS</i>	xxi
 <i>PART ONE: CHANGING OBJECTIVES AND EMERGING ASSESSMENT METHODS</i>	 1
CHAPTER 1	
Introduction	3
1.1 The Role of Predictive Models	3
1.2 The Distinction between Fish Science and Fisheries Science	5
1.3 Approaches to Prediction of Policy Impact	6
1.4 Experimental Management	9
1.5 The Ecological Basis of Sustainable Harvesting	12
CHAPTER 2	
Trade-Offs in Fisheries Management	20
2.1 Trade-Off Relationships and Policy Choices	22
2.2 Short-Term versus Long-Term Values	25
2.3 Biological Diversity versus Productivity	31
2.4 Economic Efficiency versus Diversity of Employment Opportunities	37
2.5 Allocation of Management-Agency Resources	39
 <i>PART TWO: ELEMENTARY CONCEPTS IN POPULATION DYNAMICS AND HARVEST REGULATION</i>	 41
CHAPTER 3	
Strategic Requirements for Sustainable Fisheries	43
3.1 Harvest Optimization Models	46
3.2 Constructing Feedback Policies	49
3.3 Feedback Policy Implementation	58
3.4 Feedback Policies for Incremental Quota Change	61
3.5 Actively Adaptive Policies	63
CHAPTER 4	
Tactics for Effective Harvest Regulation	65
4.1 Tactical Options for Limiting Exploitation Rates	67
4.2 Managing the Risk of Depensatory Effects under Output Control	69
4.3 Tactics for Direct Control of Exploitation Rates	74
4.4 Regulation of Exploitation Rates in Recreational Fisheries	77
4.5 In-Season Adaptive Management Systems	79

4.6	Monitoring Options and Priorities	80
4.7	Maintaining Genetic Diversity and Structure in Harvested Populations	83
<i>PART THREE: USE AND ABUSE OF SINGLE-SPECIES ASSESSMENT MODELS</i>		87
CHAPTER 5		
An Overview of Single-Species Assessment Models		89
5.1	Objectives of Single-Species Assessment	89
5.2	State-Observation Components	91
5.3	Estimation Criteria and Measuring Uncertainty	95
5.4	Modeling Options	101
5.5	Using Composition Information	110
5.6	Dealing with Parameters That Aren't	121
CHAPTER 6		
Foraging Arena Theory (I)		124
6.1	Beverton-Holt Model for Stock-Recruitment	128
6.2	Alternative Models Based on Juvenile Carrying Capacity	132
6.3	Using Foraging Arena Arguments to Derive the Beverton-Holt Model	136
6.4	Implications for Recruitment Research and Prediction	147
CHAPTER 7		
Problems in the Assessment of Recruitment Relationships		151
7.1	Which Parameters Matter?	152
7.2	Predicting Reproductive Performance at Low Stock Sizes	158
7.3	Predicting Capacity to Recover from Historical Overfishing	160
7.4	The Errors-in-Variables Bias Problem	162
7.5	The Time-Series Bias Problem	165
7.6	Can Statistical Fisheries Oceanography Save the Day?	173
<i>PART FOUR: MODELING SPATIAL PATTERNS AND DYNAMICS IN FISHERIES</i>		179
CHAPTER 8		
Spatial Population Dynamics Models		181
8.1	Life-History Trajectories	182
8.2	Multistage Models	185
8.3	Eulerian Representation	188
8.4	Lagrangian Representation	193
8.5	Policy Gaming with Spatial Models	198
CHAPTER 9		
Temporal and Spatial Dynamics of Fishing Effort		200
9.1	Long-Term Capacity	201
9.2	Short-Term Effort Responses	204

9.3 Spatial Allocation of Fishing Effort	210
9.4 Mosaic Closures	223
 <i>PART FIVE: FOOD WEB MODELING TO HELP ASSESS IMPACT OF FISHERIES ON ECOLOGICAL SUPPORT FUNCTIONS</i>	 229
CHAPTER 10	
Foraging Arena Theory (II)	231
10.1 Understanding Foraging Arena Theory	232
10.2 Predicting Trophic Flows	236
10.3 Adding Realism (I): Foraging Time Adjustments	240
10.4 Adding Realism (II): Trophic Mediation	244
10.5 Ecosim	246
10.6 Representing Trophic Ontogeny in Ecosim	248
10.7 Single-Species Dynamics from Ecosim Rate Equations	252
10.8 Ecosystem-Scale Variation	254
CHAPTER 11	
Options for Ecosystem Modeling	256
11.1 Qualitative Analysis of Dominant Trophic Interactions	259
11.2 Qualitative Analysis of More Complex Linkages	270
11.3 Models That Link Dynamics with Nutrient Cycling Processes	271
11.4 Representation of Mesoscale Spatial-Policy Options	276
11.5 Individual-Based Size- and Space-Structured Models	283
CHAPTER 12	
Parameterization of Ecosystem Models	286
12.1 Parameterizing Models	287
12.2 Parameter Estimates from Experimental Data	289
12.3 Estimating Parameters from Mass Balance Snapshots	292
12.4 Challenging Ecosystem Models with Data	300
 <i>PART SIX: STRATEGIES FOR ECOSYSTEM MANAGEMENT</i>	 311
CHAPTER 13	
Marine Enhancement Programs	313
13.1 Things That Can Go Wrong	317
13.2 Critical Steps in Enhancement Program Design	326
13.3 Monitoring and Experimental Requirements	331
CHAPTER 14	
Options for Sustainable Ecosystem Management	334
14.1 Alternative Visions of Ecosystem Structure	335
14.2 Moving Toward Sustainable Ecosystem Management	344

**APPENDIX***Definitions for Mathematical Symbols***349****BIBLIOGRAPHY****355****INDEX****381**

## *L I S T   O F   F I G U R E S*

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1.1	Indecision as a rational choice during a fishery decline.	12
1.2	Variation in components of population change for pink shrimp on the west coast of Vancouver Island, B.C.	17
2.1	Trade-off relationships can often be usefully viewed as graphs of two value measures against one another.	23
2.2	The formal optimization of a linear or logarithmic objective function.	25
2.3	Trade-off relationship between the immediate and long-term harvest value, where fish abundance is high (“healthy”).	26
2.4	The same trade-off relationship between the immediate and long-term harvest as in figure 2.3, but where fish abundance is low (“unhealthy”).	27
2.5	Effect of complete closures versus low annual harvest rates on the potential recovery of the Newfoundland cod stock.	28
2.6	Possible trade-off relationships between a sustainable abundance of natural predators and fishery catches.	34
2.7	Distribution of intrinsic rates of population growth for 943 British Columbia coho salmon substocks.	36
2.8	The predicted mean annual total yield summed over the coho stocks in figure 2.7.	37
3.1	Examples of changes in fishing mortality rates for some major fish stocks in the North Atlantic.	44
3.2	A decision rule suggested by International Whaling Commission scientists for setting annual harvests of a whale population as a function of its estimated abundance.	47
3.3	Population-dynamics models with realistic recruitment relationships typically predict the relationship between average long-term yield and exploitation rate to be asymmetric.	49
3.4	Simulated barramundi population dynamics.	52
3.5	Simulated dynamics for the same barramundi population (and environmental “forcing pattern”) as in figure 3.4, maximizing the sum of $\ln(C_t)$ over time.	54

3.6	The barramundi example yet again, but with the age-specific vulnerabilities set to 1.0 for all ages to force the harvest of sub-optimally small fish every year.	55
3.7	Closed-loop or management-procedure evaluation involves simulating not just ecological dynamics but also the full decision loop from data gathering to policy implementation.	59
3.8	Example of optimum quota increments, and the resulting expected dynamic “flow” of quota and stock size over time.	62
4.1	Comparison of the best current estimates of the historical stock size of the Northern cod stock off Newfoundland to estimates and projections made by scientists in the late 1970s and 1980s.	66
4.2	Collapse of the Georgia Strait chinook salmon fishery was accompanied by a variety of sport-fishing regulations and a commercial troll-fishing closure.	67
4.3	Decision tree of tactical choices for trying to meet an exploitation-rate goal.	68
4.4	Bayes posterior probability distribution for the Northern cod vulnerable biomass ( $t$ ) in 1991.	70
4.5	Fish typically show considerable individual variation in growth rates.	84
5.1	Most stock-assessment models are built with the general systems notion that to analyze a set of incomplete data on any dynamic system, we must hypothesize (assume) at least two distinct types of “submodels.”	92
5.2	Variability and bias in the estimation of a key policy parameter (MSY) from three possible assessment models.	103
5.3	A simulated one-way-trip fishery development in which effort builds up enough to cause a severe decline in catch per effort, and apparent overfishing.	104
5.4	The simulated performance of three procedures for estimating optimum fishing effort and current exploitation rate for simulated data sets.	106
5.5	Performance simulations with an assessment procedure based on a delay-difference age-structured model.	108

5.6	Assessment models for the reconstruction of historical population changes using catch-at-age data can be solved either backward in time (VPA case) or forward in time (synthesis case).	113
6.1	Some of the ways that juvenile fish might moderate predation risk by hiding and moving.	125
6.2	Relationship between recruitment ( $R$ ) and initial numbers ( $N_0$ ) using equation 6.4.	130
6.3	A sampling of stock-recruitment relationships for a wide variety of fishes.	131
6.4	Comparing recruitment predictions using a numerical integration of equations 6.6a and 6.6b versus using the Beverton-Holt model.	135
6.5	Final body weights after one year of growth versus the initial stocking density for several small British Columbia rainbow trout lakes.	139
6.6	Abundance of age-0 to age-2 barramundi ( <i>Lates calcifer</i> ) in the Mary River, NT.	143
6.7	Moving predictions to larger scales.	148
7.1	The “stock-recruitment relationship” is best defined as a collection of probability distributions.	153
7.2	Lack of apparent spawning-stock size effect in stock-recruitment plots does not mean that the survival index $\ln(R/S)$ shows no effect.	159
7.3	A pathological errors-in-variables situation.	163
7.4	Stock-recruitment assessments should be treated with suspicion.	165
7.5	A simple way to visualize how time-series bias arises.	167
7.6	Plots of stock-recruitment information should include the “management” relationship ( $RS$ ) between the recruitment and spawning stocks “allowed” the same year.	171
8.1	A cartoon representation of a typical fish life-history trajectory.	183
8.2	Computational schemes for modeling life-history trajectories generally involve a nested or hierarchic structure of calculations.	185

8.3	For species that orient to fixed topographic features (bottoms, shorelines, etc.), we may need to model at least three distinct kinds of movements of individuals across spatial cell boundaries.	189
8.4	For each of the distinct reefs modeled in REEFGAME (fig. 8.5), a hydrodynamic model and larval drifter simulation was used to predict distribution of new recruits.	195
8.5	The REEFGAME model interface for simulating spatial organization of coral trout abundance and fishing on the Great Barrier Reef, Australia.	196
8.6	Boxcar representation of a run of salmon moving along the British Columbia coast and entering the Fraser River.	197
8.7	Estimates of the daily number of sockeye salmon passing an acoustic counting point in the the Fraser River.	198
9.1	Australian prawn and rock lobster fisheries are subject to strict license limitations and fishing seasons.	204
9.2	Individual fishers “see” fish abundance differently in deciding whether or not to fish.	206
9.3	Fishing fleets can differ dramatically in the form of their overall effort responses.	207
9.4	Combining effort, catch per effort, and mean biological surplus production responses to stock size can result in two quite different “bionomic equilibrium” patterns.	208
9.5	Catch history for the Peru anchoveta fishery.	209
9.6	Recreational effort responses, catch per effort, and calculated changes in fishing mortality rate components for the pompano fishery on the west coast of Florida, following a ban on commercial gill netting in inshore waters.	210
9.7	Many fisheries operate across multiple spatial sites or grounds.	211
9.8	Search processes by fishers can very often be modeled as a two-stage process.	216
9.9	Three qualitatively different predictions of the relationship between fishing effort and catch.	220
9.10	Catch-effort relationships for local areas within the Gulf of Carpentaria prawn fishery, northern Australia.	221



9.11	General pattern of variation in the predicted total (summed over sites) fishing effort $E_T$ as a function of the location-independent profitability $pr_o$ parameter used in IFD models for spatial-effort prediction.	223
9.12	Hypothetical distribution of stocks or species along a space-time gradient.	224
9.13	Optimum distribution of fishing effort for the three stocks shown in figure 9.12.	226
9.14	Distribution of effort and fishing-mortality rate by species in the B.C. groundfish trawl fishery, 1996.	227
10.1	A primitive three-level ecosystem with random distributions of algae, grazer, and predator on grazer.	233
10.2	Spatial organization of the same three-level ecosystem as the previous figure, but after the grazer species has evolved near-shore hiding behavior that reduces predation risk.	234
10.3	Further complication of the ecosystem in the previous two figures, due to an invasion of new species.	235
10.4	The relationship between predator abundance and predation mortality, and the relationship between predator abundance and food-intake rates.	238
10.5	Risk-sensitive foraging behaviors by prey fish imply a reversal of the predictions about predation impact.	244
10.6	Recruitment depensation can occur at low stock sizes.	249
11.1	Factors that would have either positive effects or negative effects on salmon production for an experimental logging program in the Carnation Creek watershed, British Columbia.	258
11.2	Effect of an increase in prey productivity on prey and predator abundances.	265
11.3	Predator-prey isocline structure for a prey species that is normally very rare.	268
11.4	“Trophic triangle” interaction, in which the juvenile survival of a dominant “benthic” species may be negatively impacted by a second “pelagic” species that is a prey of the adult of the dominant species.	269
11.5	Multiple-equilibrium structure caused by the bending of the predator isocline in a trophic-triangle situation.	270

11.6	Spatial boxes used in a detailed model of nutrient and biomass dynamics in Port Phillip Bay, Australia.	272
11.7	Ability of detailed nutrient cycling/biomass models to reproduce broad spatial patterns in algal abundance.	273
11.8	The possible qualitative outcomes of a lake-fertilization experiment that might favor one or both of the two competing zooplanktivores, <i>Mysis relicta</i> and kokanee salmon.	276
11.9	A typical spatial-grid prediction of an equilibrium ecosystem state using Ecospace.	281
11.10	Predicted equilibrium abundances and fishing patterns along a transect through a hypothetical marine protected area.	282
12.1	Traditional way of thinking about predictive models: enter the parameter estimates, make predictions.	288
12.2	A more powerful way of thinking about predictive models.	289
12.3	Changes in the stock biomass and growth efficiency for a simulated population that has a strong natural variation in recruitment and is subject to overfishing after year 50.	291
12.4	Effect of including the effects of the 1989 oceanographic regime shift on the ability of Ecosim to explain changes in monk seals following the development of a fishery on one of their prey, rock lobsters, in the Northwest Hawaiian Islands.	303
12.5	Ratios of the biomasses of various fishes in trawled vs. untrawled <i>Posidonia</i> beds off the coast of Spain, compared to Ecosim predictions of these ratios.	304
12.6	Sample Ecosim fits to time-series data for aquatic ecosystems.	307
13.1	Number of coho smolts released from hatchery programs and the total coho landings in the Georgia Strait, B.C.	321
14.1	Dynamic pattern of state-space transitions expected for a system in which a “dominant” species can be impacted at low abundances by a “depensator” species that can, in turn, become abundant only when the dominant declines.	338
14.2	Stationary optimum policy for the joint harvesting of the dominant species in figure 14.1, along with culling of the depensator species.	340

## LIST OF TABLES

---

1	An example of an age schedule for barramundi, where the grid represents rows and columns in a spreadsheet.	50
2	Catch numbers at age (in thousands) used for stock assessments on the Northern cod stock (2J3KL) off Newfoundland (data from Baird et al. 1992).	111
3	Mean parameter estimates from 100 simulated data sets where parameters were estimated using ordinary regression and maximum likelihood methods. True parameter values used to generate the data are: $\hat{a} = 2$ , $b = 0.5$ , $\sigma^2 = 0.3$ , and a constant fishing mortality rate $F = 0.8$ (note the true $F_{MSY} = -\ln(0.5) = 0.69$ ).	168
4	Maximum likelihood parameter estimates from $n = 100$ simulated data sets for unfished stocks ( $F = 0$ ), stocks fished at $F_{MSY}$ , and over-fished stocks ( $2F_{MSY}$ ).	169
5	Mean estimates of $\hat{a}$ , $b$ , and $F_{MSY}$ from $n = 100$ simulated data sets where recruitment anomalies are partitioned into two parts, known $w_t^*$ and unknown $\dot{w}_t$ . Considerable reduction in the estimate of $F_{MSY}$ occurs when independent estimates of $w_t^*$ explain $> 50\%$ of the recruitment variation.	171
6	Mean parameter estimates from $n = 100$ simulated data sets where 50% and 95% of recruitment variability are explained by the known environmental index ( $w_t^* = c\xi_t$ ).	172
7	Mean parameter estimates for $n = 100$ simulated data sets from two stocks with shared environmental effects. Shared effects would have to be a high proportion of the total variation in order to reduce bias in parameter estimates.	173



THIS BOOK IS intended as a text in upper division and graduate classes on fisheries-stock assessment and management. It aims to provide a broader review of assessment methods and policy issues than is available in existing texts on fisheries harvest management, like Hilborn and Walters (1992) and Quinn and Deriso (1999). It is not just a book of recipes for the analysis of fisheries data, and it is deliberately critical of the “science” of fisheries stock assessment as we have taught it in the past. It warns students that we have often been confused about nearly every aspect of that science, from its basic aims and objectives to the trust that we should place in our results and recommendations. That confusion has led fisheries scientists to do much work that is either irrelevant or damaging to the world’s obvious fisheries management crises. The book begins by asking the student to think about what we are trying to accomplish by presuming or pretending to “manage” fisheries, and it emphasizes that management is a process of making choices. There is no way to make choices without making at least some predictions about the comparative outcomes of the choices, and these predictions cannot be made without some sort of “model” for how the world works. Usually, management choice requires trade-offs among objectives, and these trade-offs need to be quantified in some way before we can make an intelligent choice or recommendation. This means that much of the book has to be about quantitative, mathematical modeling, and we make no apologies for demanding that people who would engage in fisheries assessment and management should at least be able to read and understand some basic mathematics.

There have been four really important developments in the decade since Hilborn and Walters wrote *Quantitative Fisheries Stock Assessment*. First, we have been able to look back more clearly on some spectacular fisheries collapses, like the cod of Newfoundland, and to understand a bit about the role that poor data and scientific assessment mistakes played in actively promoting those collapses. Second, there have been some substantial technical advances in the statistical and computational machinery of assessment, which allow scientists to build much more complex assessment models to account for more of the causes of variation in fisheries data and to measure uncertainty in assessments more accurately. But in our view, these advances have not dealt effectively with the causes of failure in the first place and, in fact, have diverted much working time and attention from the real problems. Third, thanks largely to the efforts of nongovernmental conservation groups, there is now strong public demand for sustainable fisheries and for protection of nontarget organisms and ecosystem functions, backed by the powerful threat of market sanctions. Fourth, we have finally begun to develop trophic interaction, food web, and ecosystem models that appear capable of making useful predictions about policy issues like marine mammal protection that were simply ignored in single-species assessment and policy recommendations. These models arise from the marriage of ideas from

evolutionary biology, in the form of what we are now calling “foraging arena theory,” with methods from ecosystem analysis about mass balance and historical reconstruction models, like Ecopath, that have helped organize rich sources of information on trophic interaction rates.

We think it is clear from these developments that students of fisheries assessment and management need to be conversant with a much broader set of issues and tools than have traditionally been provided in fisheries ecology courses. They need to learn to think in hierarchic terms about both broad strategic trade-offs and about the frustratingly detailed tactics involved in achieving these trade-offs. They need to understand the many things that can and will go wrong with analysis and modeling in a world where there will never be enough funding to get all the scientific answers that the public will demand. And perhaps most important, they need to understand how to embed analyses of fish dynamics in a broader analysis of the dynamics of the complex systems created by the linkage between fish, fishers, and the ecosystems that support them, and to construct such analyses by deliberately looking over a wide range of spatial and temporal scales. As Ludwig, et al. (2001) have eloquently argued, fisheries scientists need to be much more broadly educated in order to contribute more effectively to the development of sustainable fisheries policies; we hope that this book will contribute at least to the scientific side of that broadening.

*I haven't asked for much in this life, and Lord knows I've got it.*

(Al Bundy, in *Married with Children*)

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## PART ONE

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# Changing Objectives and Emerging Assessment Methods



## 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

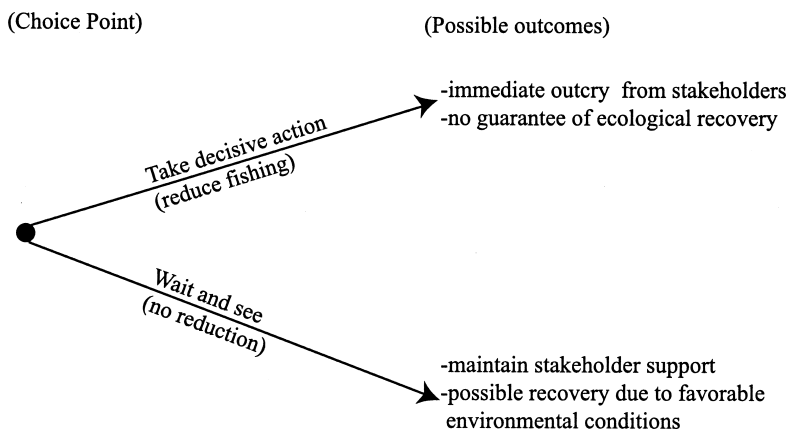


FIGURE 1.1: Indecision as a rational choice during a fishery decline. Viewed from a fishery manager's perspective in terms of a simple decision tree, it can be fully rational for the manager faced with either certain outcry from fishing stakeholders if decisive action is taken, or the possibility that 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

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

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  $D_t M_p/Z$ . ■

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  $R_t = s_{(j)t}f_tN_t$  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



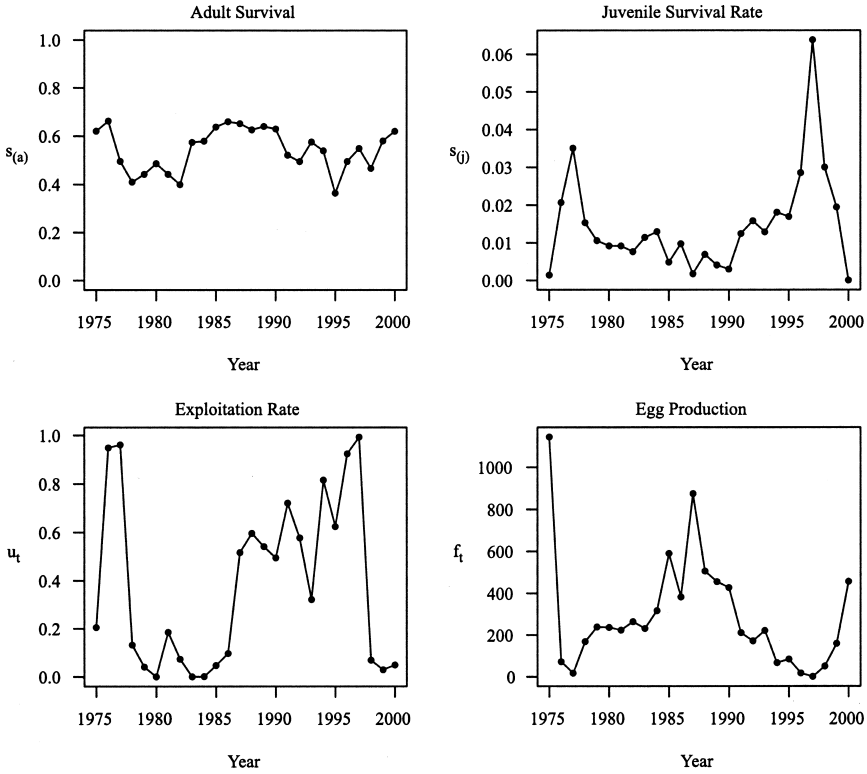


FIGURE 1.2: Variation in components of population change for pink shrimp on the west coast of Vancouver Island, B.C., from Martell (2002). These estimates were obtained by fitting an age-structured population-dynamics model to time-series data on relative-abundance, size-composition, and area-swept estimates 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.msos.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  $\times$  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 to 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).