EXCELLENCE IN ECOLOGY

6

O. Kinne, Editor

The late Frank H. Rigler
and Robert H. Peters

Science and Limnology

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Germany

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OTTO KINNE
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SCIENCE AND LIMNOLOGY

Introduction (Otto Kinne)

Frank H. Rigler and Robert H. Peters: A Laudatio (Jürgen Overbeck)

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To Ann and Antonella

Contents

Introduction

Otto Kinne

Ecology Institute, Nordbünte 23, D-21385 Oldendorf/Luhe, Germany

Science and Limnology is likely to become a milestone in ecological reasoning and research. Based to a considerable extent on unpublished thoughts and notes of Frank H. Rigler, and written by the winner of the Ecology Institute Prize 1991 in the field of limnetic ecology, Robert H. Peters of McGill University, Montreal, Canada, the book is enlightening, challenging and provocative. It is enlightening, because it views science in general and ecology in particular from unconventional angles; it is challenging, because it criticizes many of the ways in which ecologists think and approach their subjects; it is provocative, because the author presents an unattractive picture of present-day ecology and a harsh assessment of university education and research. Above all, *Science and Limnology* is a worthy companion to previous Excellence in Ecology books: it offers the well-written, concise and easy-to-read personal views of an outstanding performer in his field of expertise. Rob Peters has written this book as a professor in the best sense of that word. He professes his insights, beliefs and convictions with courage and honesty, and he considers his topics with care and a keen mind. His views reach far beyond the horizon suggested by the book's title, far into the realms of science history, philosophy and methodology; into the relevance of science to society; and into the centers where science is at home and where scientists are formed — the universities.

The essence of the message conveyed by Peters is this: ecologists have collected impressive amounts of observations and facts, but they have failed to sufficiently identify and formulate theories that go beyond the facts — theories that can be tested and that can predict. To aid in solving the many problems which press on modern human societies and in controlling and restricting the ever-increasing deformation of nature, ecological research must focus, more so than in the past, on empirical, holistic approaches that facilitate prediction. Peters insists that the failure of ecologists to produce useful predictions is not a consequence of the complexity of their subjects, but of the complexity of their approaches. He believes that his call for a more empirical, holistic strategy will be heard and accepted by ecologists and that it will help mankind to preserve itself and to save its environment.

ECOLOGY INSTITUTE PRIZE 1991

In Limnetic Ecology

Professor Robert H. Peters

(Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, PQ, Canada H3A 1B1)

has been elected by the Limnetic Ecology Jury of the Ecology Institute (ECI)
as the winner of the 1991

ECOLOGY INSTITUTE PRIZE

Professor R. H. Peters' contributions to the fields of limnology and ecology have been numerous and far reaching. His work on phosphorus cycling in lakes provides examples of excellent research illuminating a number of important aspects regarding the movement and availability of phosphorus in aquatic systems. His book "The Ecological Implications of Body Size" presents a powerful overview of the utility of allometric relationships for the study of ecological problems and for building ecological theory.

ECI Limnetic Ecology Jury 1991:

Professor J. Overbeck, Plön, Germany (Chairman)
Professor S. D. Gerking, Tempe, Arizona, USA
Professor G. E. Likens, Millbrook, New York, USA
Professor K. Lillelund, Hamburg, Germany
Professor J. G. Tundisi, São Paulo, Brazil
Professor D. Uhlmann, Dresden, Germany
Professor W. Wieser, Innsbruck, Austria

ECOLOGY INSTITUTE

The Director

Otto Kinne

Professor Otto Kinne

Oldendorf/Luhe, Germany, December 13, 1991

For Peters the essence of science is the creation, testing and use of theory. In the process of creating theory, induction plays an important role. It is here that inspiration and intuition enter the scene. While theory is the backbone of research, it can never be beyond doubt. Theories must be tested time and again. The prediction must be compared to further observation. Since scientific knowledge always remains hypothetical, the ultimate arbiter of scientific research is observation. 'The main goals of science are to make theories, to use theories to make predictions and to assess those predictions against observation' (p. 21).

Peters defines ecology 'as the science that predicts the abundance, distribution and other characteristics of organisms in nature' (p. 81). He deplores that ecologists have failed to appreciate the nature of their science: '... much of ecology is confused in its goals, uncertain of its thoughts, and inconsistent in its terminology.' Chapter V portrays ecologists 'as nonchalant about their tests, careless in their measurements, yet closed-minded in considering alternatives' (p. 77).

Turning to his main subject, limnology, Peters points out that the leading role this branch of science once played in ecological research was lost, largely because the assumption that ecological theory required an isolated microcosm was discovered to be a misapprehension. Based on the tools and information produced over many decades, limnologists are now turning to empirical theories that predict. Thus, modern limnology is becoming a leader again, this time showing the way towards predictive ecology.

Examining university research and teaching, Peters identifies shortcomings at every level, but he also makes suggestions for improvements and offers some practical advice. In regard to teaching science, he stresses again our failure to appreciate the significance and nature of theory. Reconsidering and contemplating science should lead to profound changes in research and in the ways professors teach students: 'Too much research is done for the same reason that a mountain is climbed ("because it is there"), and too little time is spent questioning the motives for doing so' (p. 179). On the other hand, deplores Peters, big science and societal power have separated professors from their ideals and goals, and thus almost destroyed the university as an intellectual retreat.

Ecology Institute Prize 1991 in the field of limnetic ecology. Reproduction of the prize awarding document

Excellence in Ecology Books

Published by the International Ecology Institute (ECI), the book series "Excellence in Ecology" (EE) is made available at cost price.* EE books are also donated to scientific libraries in Third-World countries. The books are authored by recipients of the Ecology Institute Prize. This prize honors the sustained high performance of outstanding research ecologists. Prizes are awarded annually, in a rotating pattern, for the fields of marine, terrestrial and limnetic ecology. Laureates are selected by a jury of seven ECI members appointed by the director. EE books offer the laureates the chance to publish their personal views on the state of the art in their fields of expertise and to bring to the attention of a world-wide audience their insights into the knowledge, problems and realities that form the biological basis for human existence.

EE books address fellow scientists, teachers, students and decision makers who must translate ecological information into practicable rules and laws for the benefit of nature and mankind.

The aims and activities of the Ecology Institute have been outlined in EE Book 3 (pp. VIII–IX).

In addition to the ECI Prize, the ECI awards an annual IRPE Prize (International Recognition of Professional Excellence) which honors a young (not more than 40 years of age) research ecologist who has published uniquely independent and/or challenging papers representing an important scientific breakthrough and/or who must work under particularly difficult conditions. The ECI also supports, via the Otto Kinne Foundation (OKF), promising postgraduates in environmental sciences in East European countries — especially in the fields of ecology, diseases of organisms, and climate research. The OKF aids postgraduates — without distinction of race, religion, nationality or sex — by providing financial assistance for professional travel, scientific equipment or published information. For details write to the President of the Foundation: Dr. J. Lom, Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic; tel. (+42) 38 41158, fax (+42) 38 47743.

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*Address orders for EE books to:
Ecology Institute, Nordbünte 23, D-21385 Oldendorf/Luhe, Germany
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Payment may be made via credit card (American Express, Visa, Euro/ Mastercard; please give account number and expiration date).
An order for the whole series is accepted at a 10% reduced price.
For book authors, titles and prices, consult pp. XV–XVII.

Nominations for ECI and IRPE Prizes (accompanied by CV, list of publications, and a statement why, in the opinion of the nominator, the nominee qualifies for the prize) are invited from research ecologists on a global scale. They should be sent to the chairperson of the respective ECI Jury, or, alternatively, to the ECI's director, who will then forward them to the chairperson. Eligible are all ecologists engaged in scientific research (except the ECI's director, the Jury's chairperson, and previous Laureates; Jury members nominated will be replaced by other ECI members). The Jury selects prize winners using the nominations received as well as their own knowledge of top performers and their own professional judgement.

Nominations for OKF Fellows, addressed to Dr. J. Lom (see above) and accompanied by a letter of support as well as a documentation of the nominees' performance, are invited from ECI members and members of the Editorial Staffs of the three international Inter-Research journals, *Marine Ecology Progress Series*, *Diseases of Aquatic Organisms*, and *Climate Research*.

ECI Prize Winners, Their Major Scientific Achievements and Their Books

Tom Fenchel (Helsingør, Denmark), ECI Prize winner 1986 in marine ecology.

Quotation of the Jury (Chairman: John Gray, Oslo, Norway)
The Jury found Professor T. Fenchel's contribution to ecological knowledge in a variety of research fields to be of the highest international class. In particular, the Jury cites his brilliant and uniquely important studies on the microbial loop which have opened up a fundamentally new research field. Professor Fenchel is, in addition, an excellent publicizer in his field of research with authorship of a number of standard works in marine ecology.

Book 1: Ecology – Potentials and Limitations. (Published 1987; price DM 67 plus postage and handling)

Edward O. Wilson (Cambridge, MA, USA), ECI Prize winner 1987 in terrestrial ecology.

Quotation of the Jury (Chairman: Sir Richard Southwood, Oxford, UK)
Professor E. O. Wilson is distinguished for his many contributions to different aspects of ecology and evolutionary biology. His life-time love of Nature, a theme explored in his book "Biophilia", has been particularized in his study of ants leading to major new insights on the evolution of castes and the operation of social systems. His seminal "Sociobiology", derived from this work, has founded a new branch of science, between ecology and the social sciences. With the late Robert MacArthur he was the originator of the modern theories of island biogeography that have contributed not only to the understanding of island biota, but to community and population ecology.

Book 2: Success and Dominance in Ecosystems: The Case of the Social Insects. (Published 1990; price DM 49 plus postage and handling)

Gene E. Likens (Millbrook, NY, USA), ECI Prize winner 1988 in limnetic ecology.

Quotation of the Jury (Chairman: William D. Williams, Adelaide, Australia)
Gene Likens is a distinguished limnologist who has made salient contributions to many fields of limnology. In 1962 he initiated and developed (with F. H. Bormann) the Hubbard Brook Ecosystem Study in New Hampshire. Comprehensive investigations in this study provided a model for ecological and biogeochemical studies worldwide. A major finding of the study was that rain and snow are highly acidic. "Acid rain" is now recognized as one of the major environmental hazards in North America, Europe and elsewhere. Elected to the American Academy of Sciences in 1979, and the National Academy of Sciences in 1981, Gene Likens is a highly worthy recipient of the 1988 ECI Prize in Limnetic Ecology.

Book 3: <u>The Ecosystem Approach: Its Use and Abuse.</u> (Published 1992; price DM 59 plus postage and handling)

Robert T. Paine (Seattle, WA, USA), ECI Prize winner 1989 in marine ecology.

Quotation of the Jury (Chairman: Tom Fenchel, Helsingør, Denmark)
Robert T. Paine has made substantial and original contributions to marine biology and to ecology in general. In particular the Jury mentions the discovery of the role of patch formation and properties of food web structure in shaping communities of sedentary organisms. These studies (of which several have become classics of marine ecology) have fundamentally changed the way in which we view marine benthic communities. This work has also served as an inspiration for innovation in the mathematical description of community processes and has had a lasting impact on our understanding of "landscape dynamics", of equal importance to the development of the science of ecology and to conservation ecology.

Book 4: <u>Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective.</u> (Published 1994; price DM 59 plus postage and handling)

Harold A. Mooney (Stanford, CA, USA), ECI Prize winner 1990 in terrestrial ecology.

Quotation of the Jury (Chairman: John L. Harper, Penmaenmawr, UK)
Professor Harold A. Mooney is distinguished for his studies of the physiological ecology of plants, especially of arctic-alpine and mediterranean species. He has explored the ways in which plants allocate carbon resources and expressed this allocation in terms of costs, benefits and trade-offs. This has given a quantitative dimension to the study of plant-animal interactions and acted to integrate physiological ecology with population biology, community ecology, and ecosystem studies.

Book 5: <u>The Globalization of Ecological Thought.</u> (To be published soon)

Robert H. Peters (Montreal, PQ, Canada), ECI Prize winner 1991 in limnetic ecology.

Quotation of the Jury (Chairman: Jürgen Overbeck, Plön, Germany)
Professor R. H. Peters' contributions to the fields of limnology and ecology have been numerous and far reaching. His work on phosphorus cycling in lakes provides examples of excellent research illuminating a number of important aspects regarding the movement and availability of phosphorus in aquatic systems. His book "The Ecological Implications of Body Size" gives a powerful overview of the utility of allometric relationships for the study of ecological problems and for building ecological theory.

Book 6: <u>Science and Limnology.</u> (Published 1995; price DM 74 plus postage and handling.)
Authors: The late F. H. Rigler and R. H. Peters

Dr. David H. Cushing (Lowestoft, United Kingdom), ECI Prize winner 1992 in marine ecology.

Quotation of the Jury (Chairman: John Costlow, Beaufort, NC, USA)
Dr. David H. Cushing has, for many years, made an enormous contribution to the field of marine ecology through his numerous publications and his original ideas. His work continues to be highly influential in fisheries and plankton ecology. Although first published over ten years ago, his pioneering studies on the dynamics of a plankton patch, the feeding of copepods, the 'match-mismatch' theory of recruitment and the climatic influences on plankton and fisheries remain of central importance.

Book 7: Recruitment in Marine Fish Populations. (To be published 1995/96)

Paul R. Ehrlich (Stanford, CA, USA), ECI Prize winner 1993 in terrestrial ecology.

Quotation of the Jury (Chairman: Harold A. Mooney, Stanford, CA, USA)
Dr. Paul Ehrlich's scientific contributions have been substantial and sustained. The quality and depth of his interpretation of environmental issues to students, the general public, and to policy makers is unrivaled. His concern for both environmental quality and environmental justice has rarely been matched. He has made fundamental contributions to the study of population biology utilizing butterflies as a model system. These studies have had a large impact on how we view the population structure of organisms and have provided important guidelines on the conservation of wild populations.

Book 8: A World of Wounds: Ecology and Human Predicament. (To be published 1995/96)

IRPE Prize Winners and Their Major Scientific Achievements

Colleen Cavanaugh (The Biological Laboratories, Harvard University, Cambridge, MA 02138, USA), IRPE Prize winner 1986 in marine ecology.

Quotation of the Jury (Chairman: John Gray, Oslo, Norway)
The Jury found the research of Dr. C. Cavanaugh on chemosynthesis – initially concerning hot-vent fauna but extended to other sulphide-rich habitats – to be highly original and to represent a major scientific breakthrough. Her hypothesis, formulated whilst a beginning graduate student, met severe opposition from established scientists with opposing views, but nevertheless proved to be correct. The Jury acknowledge Dr. Cavanaugh's brilliant and independent research in understanding chemosynthetic energetic pathways.

Karel Šimek (Hydrobiological Institute, Czechoslovak Academy of Sciences, 370 05 České Budějovice, Czechoslovakia), IRPE Prize winner 1991 in limnetic ecology.

Quotation of the Jury (Chairman: Jürgen Overbeck, Plön, Germany)
Dr. Karel Simek belongs to the generation of young limnologists in Eastern Europe who – despite lack of international information exchange – published, under difficult conditions, excellent contributions to the field of Aquatic Microbiology. He enjoys a high international reputation. Under the present, improved conditions Simek is likely to proceed even more successfully to new professional horizons.

Richard K. Grosberg (Department of Zoology, University of California, Davis, CA 95616, USA), IRPE Prize winner 1992 in marine ecology.

Quotation of the Jury (Chairman: John Costlow, Beaufort, NC, USA)
Richard K. Grosberg has not only published extensively on fundamental issues relating to marine ecology, but has also demonstrated his understanding of marine ecology through superb teaching of invertebrate zoology to undergraduate and graduate students. He is acknowledged as a leader in adapting molecular techniques for the study of marine larvae and in developing information on extraordinarily detailed mapping studies of the genetic structure of adult populations of marine organisms.

Nikolai V. Aladin (Zoological Institute, Russian Academy of Sciences, St. Petersburg 199034, Russia), IRPE Prize winner 1993 in terrestrial ecology.

Quotation of the Jury (Chairman: Harold A. Mooney, Stanford, CA, USA)
Dr. Nikolai V. Aladin is one of Russia's most eminent young ecologists. He has researched environments in the former Soviet Union, particularly in Kazakhstan where he and a small team have focussed upon the area of the Aral Sea. Dr. Aladin's studies were performed during a period of change, both in the patterns of organismic assemblages and in the political structure of his country. These studies were undertaken in his own time and at his own expense. It is only over the past few years that his studies have been officially supported and their value recognized.

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Terrestrial Ecology

Prof. T. N. Ananthakrishnan, Madras, India (1984)
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Dr. P. Ehrlich, Stanford, CA, USA (1994)
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*Following their receipt of the ECI prize, laureates are invited to join the institute's staff

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Prof. S. Ulfstrand, Uppsala, Sweden (1986)
Prof. E. O. Wilson, Cambridge, MA, USA (1988)

Limnetic Ecology

Prof. N. V. Aladin, St. Petersburg, Russia (1994)
Prof. J. I. Furtado, Washington, DC, USA (1985)
Prof. S. D. Gerking, Tempe, AZ, USA (1986)
Dr. J. E. Hobbie, Woods Hole, MA, USA (1986)
Dr. E. Kamler, Lomianki, Poland (1993)
Prof. W. Lampert, Plön, Germany (1993)
Prof. G. E. Likens, Millbrook, NY, USA (1989)
Prof. K. Lillelund, Hamburg, Germany (1985)
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Frank H. Rigler and Robert H. Peters: A Laudatio

Jürgen Overbeck

Max-Planck-Institut für Limnologie, D-24302 Plön, Germany

With the sudden death of Professor Frank Rigler in 1982, we, his friends and colleagues, lost a distinguished scientist and a leading limnologist with a broad field of interest and research.

Who was Frank Rigler? Born in London in 1928, he received his Ph.D. in limnology from the University of Toronto in 1954. He was married and had 5 children. Frank Rigler was Chairman of Biology at McGill University in Montreal, Quebec, Canada, from 1976 to 1981. His special interests were predicting the effects of nutrient enrichment on production in temperate and subarctic lakes. His laboratory was also long concerned with the status of ecology as a science and the role of ecological knowledge.

My first personal acquaintance with Frank Rigler was at the XIXth International Limnological Congress in Winnipeg, Canada, in 1974, where he gave a Plenary Lecture with the title *Nutrient Kinetics and the New Typology*. This lecture provoked an extraordinarily controversial discussion. Rigler began by saying that he doubted that studies on the details of the phosphorus cycle were really advancing our knowledge at all. There already existed an embarassingly large accumulation of facts in limnology. But scientific advance comes only when we think up a new theory that overcomes a difficulty experienced by the old theory. A qualified scientific theory must be — in the sense of Karl Popper — potentially falsifiable. Starting from this, Rigler presented, from a holistic point of view, nutritional-production limnology using the 'black-box' approach, which may give us predictive ability but no real understanding. Models are, by and large, purely empirical descriptions of correlations between state variables. However, they pose questions and the work of reductionists may suggest theories to answer these questions. It was indeed an extraordinary lecture, quite different from the usual way of presenting ecological results and systems.

Due to his early death, Rigler was unable to publish many of his ideas. In this connection I will cite a letter of Professor M. L. Ostrofsky, Meadville, Pennsylvania: “Rigler’s ideas about the nature of science, the requirements of ‘good’ science, and the role of ecologists in shaping public issues are not widely known. Rigler’s modesty prevented him from publishing many of his ideas until late in his career. Many of Rigler’s ideas have been placed before a larger scientific audience through the work of Dr. Robert Peters, Rigler’s most articulate student, friend and colleague. It would be of enormous significance if the full range of Rigler’s thoughts could be made accessible to a larger audience. I cannot think of a more timely subject for a book; the recent literature suggests that ecology is in the midst of a crisis of confidence and identity. I cannot think of a more appropriate individual to undertake the task.” The award of the 1991 ECI Prize in Limnetic Ecology to Robert Peters now offers the unique opportunity for realizing this project. This book, *Science and Limnology*, thus has two authors and two prefaces — a junior author’s preface and a senior author’s preface. Robert Peters approached the book as a “collaborative exercise, a collage in which Rigler’s enduring ideas are set within a matrix of my own writing to produce a contemporary essay about the science of limnology.” The basis of the 15 chapters is over 70 sets of notes and lectures covering 25 years.

Robert Henry Peters was born in Toronto, Ontario, Canada, on August 2, 1946. He received his Ph.D. in 1972. His doctoral thesis on regeneration of phosphorus by zooplankton — an issue which is still of great topical importance — was supervised by Frank Rigler. Highlights of Robert Peter’s academic career include post-doctoral fellowships in Pallanza (Italy), 1972–1973; in Vienna (Austria), 1973; and in Munich (Germany), 1974. He became Assistant Professor in 1974, Associate Professor in 1979 and Full Professor in 1986 at McGill University. He has published 125 papers, notes and reports, and authored a book on the ecological implications of body size. His current research interests center on material flow in aquatic ecosystems, zooplankton behavior, allometric relationships in autecology, and applied environmental management.

I hope that *Science and Limnology* will be as inspiring, uncommon and provoking for its readers as was the Plenary Lecture of Frank Rigler which I had the pleasure to attend and discuss 20 years ago.

Prefaces

Junior author's preface

To win an international prize is a wonderful and surprising event. A hundred other researchers could merit most prizes, and many worthy individuals go unrewarded in any prize-giving. Merton (1968) has called these unrecognized but worthy colleagues "occupants of the 41st chair", in reference to the many talented individuals who never won the honour of a place in the Académie Française, simply because the Académie is limited to 40 chairs. Deserving newcomers must await the death of present occupants, and some die before an opportunity arises, as did Descartes, Molière, Pascal, and Diderot. Because I know the unlikelihood of winning honours, the decision of the Ecology Institute to award me its 1991 prize in limnetic ecology was first a surprise, and then a source of great pleasure. It remains a reason for deep satisfaction and pride, as well as gratitude towards Professor Otto Kinne, Director of the Ecology Institute, Professor Jürgen Overbeck, Chairman of the ECI Jury, the members of the ECI Jury, the staff of the Institute, and the generous colleagues who lent me their support. Like most critical scientists, I am prone to self-doubt, and therefore I am all the more touched that not all of my ideas have been dismissed as either appallingly bad or, worse, frightfully dull. I am also humbled to find myself in the ranks of previous laureates whose contributions have been so much greater than my own.

I have an additional personal reason to be pleased with this prize. It has allowed me to complete a project that I have wanted to do for over a decade: to prepare the unpublished notes of Frank Rigler for publication. When Frank Rigler died in 1982, the world of limnology lost one of its leading thinkers. The loss was all the more tragic because most of his broader views on limnology, ecology and science were never published. His influence had been a personal one, spreading through conversation and occasional public lectures. As a summer employer and undergraduate teacher, as my doctoral supervisor, as my long-time colleague and close friend, and still as my conscience and model, Frank has been the major influence on my career and scientific development. He has played a similar role for other students, at levels ranging from undergraduate to senior scientist. For us all, conversation with Frank was a treasure, a model of clear thought, logic, penetration, relevance and simplicity. He taught us the nature of science, the power it gives its followers, and the burdens of responsibility it places upon them. He was a source of strength and inspiration, and he is sorely missed.

Rigler's natural modesty stopped him from writing about his larger views for most of his career. Soon after he finally began to write to a larger audience, his voice was stilled by cancer. His few philosophical papers (Rigler 1975a, b, 1982a, b) were powerful and controversial, but they exposed only a fraction of his ideas. Only those who knew his teaching at first hand, whether in university courses, in scientific lectures, in panel discussions, or in quiet talks, realize how much went unrecorded.

Rigler's vision and virtues are even more needed now, but my aim in preparing this book is not simply to reproduce the text of his lectures and unpublished notes. His notes were extensive and he was meticulous in preserving that material, but even good lecture notes are not publishable as they stand. I have instead approached the book as a collaborative exercise, a collage in which Rigler's enduring ideas are set within a matrix of my own writing to produce a contemporary essay about the science of limnology. This cannot be the book Rigler would have written, but because his spirit is so much a part of my everyday experience, it may approach a book we could have written together, had he lived. For me, the exercise has been profoundly rewarding. I have been able to reexamine the roots of my own views and to appreciate the rich earth from which they developed. I also discovered that many ideas I thought my own were actually foreshadowed in his writings.

I have chosen to write in the first person singular, and therefore I have created a non-existent author who is neither me nor Rigler, but some amalgam of us both. Use of the first person preserves that conversational tone of Rigler's lectures and confirms this book as a personal document. Use of this chimeric "I" sometimes results in incongruities since the pronoun clearly refers to only one of the two authors, but on the whole I like the device. At times, it even allowed me to see my ideas from a greater distance than I usually can.

The 15 chapters are based on over 70 sets of notes and lectures covering a quarter century. I have recast and resorted most of the material, but most chapters can still be appreciated separately. The book is arranged in a roughly chronological order based on an intellectual ontogeny or autobiography whose main lines apply to us both. The first three chapters deal with the development of a coherent philosophy of science based on the premise that science must tell us something about the natural world and the realization that not all science is directed to that goal. In Chapters IV and V, these criteria are used to force recognition that much of ecology and limnology, our own work included, is wanting. This revelation fostered a search for alternative models in limnology (Chapter VI), and ecology (Chapters VII and VIII) that eventually led to our adoption of empiricism (Chapter IX). The success of an empirical research agenda encouraged us to reassess the role of an education in science (Chapters X and XI), and provided a sharp tool in the evaluation of the science, whether in the context of society (Chapter XII), grant reviews (Chapter XIII), or historical analyses (Chapter XIV). The final chapter warns that we must be prepared to change the way we do our science. If we do not, someone else will change it for us.

There is a need for works that translate between the professional philosophers and the scientific practitioners in different disciplines, and at different levels of sophistication. The reader interested in the philosophy of biology already has a number of choices. Excellent reviews of the history of ecological ideas are available from Kingsland (1985) and McIntosh (1985). David Hull (1974) and Michael Ruse (1973) are philosophers who have written widely on the philosophy of biology and biological science. Rolf Sattler (1986) is a biologist whose book describes the important issues that biology presents to the philosopher. I even have a rather philosophical book of my own about ecology (Peters 1991a). These texts offer more sophisticated, more advanced, and usually less ecological treatments than this book.

Science and Limnology is intended to be an easy read. I have purposely used less referencing and adopted a less dense style than I would in a scientific paper. Rather than an authoritative review, it is meant to provide ecologists with a ready access to the history and philosophy of science. I hope it is sufficiently light reading that both the ecological researcher and the student can find a place for it in their schedules.

Senior author's preface

F. H. Rigler

This book is a personal essay expressing the biases of two researchers and promulgating their faith in an approach to limnological problems. As such, the book is little more than a sermon, and warrants consideration only if it is a reasonably good one. By a sermon, I mean an essay intended to inspire faith in an, as yet, undemonstrated and perhaps undemonstrable property of the universe in which the preachers implicitly believe.

Science and Limnology is not a monograph that presents new data or develops a new theory, nor is it a text that reviews the field. The writings collected here do not fall into one of these conventional categories for scientific works. However, if the reader has interests beyond normal scientific fare, then this contribution may be worthy of his or her attention.

Let us assume that the reader's definition of acceptable reading includes sermons, and evaluate this book as such. A good sermon has three important characteristics: (1) It must not be too long; (2) it must be internally consistent; and (3) it must be comprehensible.

Length: Each chapter is short and the different chapters are sufficiently independent, so that only a few pages need be read at a time. Part of the price of this independence is some disarticulation and a modest amount of repetition among the chapters. As a result, the book loses some impact and is longer than it needs to be. Unfortunately, the length of this book was entirely out of my hands, and the junior author must bear full responsibility if he has made a hash of it.

Consistency: I have fewer qualms on this point. We have both striven to maintain a logically consistent position throughout the book. Undoubtedly we have failed in this intention at many points, but we hope we are no less successful than many other contributions to the literature. In any case, we knew we were unlikely to succeed in total consistency before we began.

Comprehensibility: In a sermon, the need to keep the story-line clean is more significant than length or consistency. The message is very simple. The Baptist preachers (predictive or empirical limnologists) are trying to persuade the College of Cardinals (other biologists, ecologists and limnologists) that their lesser sect has its own valid sources of revelation. Since the Roman Catholics of science have considered themselves to be omniscient for such a long time, it will take the patience of Job and the logic and clarity of Thomas Aquinas to convince them that they can learn from others. We can hardly expect a mass conversion, but we may help prepare the ground for an eventual reformation.

The intent of the book is to convert those whose belief in traditional ecological approaches is weak, and to sow doubts in the minds of those whose belief is stronger. To do so, we show that some freshwater ecologists have achieved success by reflecting on the general nature of science and by developing models that are consistent with those reflections. We anticipate that a similar approach will apply equally well to other questions and to other systems. Indeed, a successful response to the environmental degradation of our planetary home depends on the widespread adoption of just such an approach. Thus, this sermon has an important message. It needs to be heard.

Prologue

I took advantage of being at the seaside to lay in a store of sucking stones. They were pebbles but I call them stones. Yes, on this occasion I laid in a considerable store. I distributed them equally between my four pockets, and sucked them turn and turn about. This raised a problem which I first solved in the following way. I had say sixteen stones, four in each of my four pockets, these being the two pockets of my trousers and the two pockets of my greatcoat. Taking a stone from the right pocket of my greatcoat, and putting it in my mouth, I replaced it in the right pocket of my greatcoat by a stone from the right pocket of my trousers, which I replaced by a stone from the left pocket of my trousers, which I replaced by a stone from the left pocket of my greatcoat, which I replaced by the stone which was in my mouth, as soon as I had finished sucking it. Thus there were still four stones in each of my four pockets, but not quite the same stones. And when the desire to suck took hold of me again, I drew again on the right pocket of my greatcoat, certain of not taking the same stone as the last time. And while I sucked it I rearranged the other stones in the way I have just described. And so on. But this solution did not satisfy me fully. For it did not escape me that, by an extraordinary hazard, the four stones circulating thus might always be the same four. In which case, far from sucking the sixteen stones turn and turn about, I was really only sucking four, always the same, turn and turn about. But I shuffled them well in my pockets, before I began to suck, and again, while I sucked, before transferring them, in the hope of obtaining a more general circulation of the stones from pocket to pocket. But this was only a makeshift that could not long content a man like me. So I began to look for something else. And the first thing I hit upon was that I might do better to transfer the stones four by four, instead of one by one, that is to say, during the sucking, to take the three stones remaining in the right pocket of my greatcoat and replace them by the four in the right pocket of my trousers, and these by the four in the left pocket of my trousers, and these by the four in the left pocket of my greatcoat, and finally these by the three from the right pocket of my greatcoat, plus the one, as soon as I had finished sucking it, which was in my mouth. Yes, it seemed to me at first that by so doing I would arrive at a better result. But on further reflection I had to change my mind and confess that the circulation of the stones four by four came to exactly the same thing as their circulation one by one. For if I was certain of finding each time, in the right pocket of my greatcoat, four stones totally different from their immediate predecessors, the possibility nevertheless remained of my always chancing on the same stone, within each group of four, and consequently of my sucking, not the sixteen turn and turn about as I wished, but in fact four only, always the same, turn and turn about. So I had to seek elsewhere than in the mode of circulation. For no matter how I caused the stones to circulate, I always ran the same risk. It was obvious that by increasing the number of my pockets I was *bound to increase my chances of enjoying my stones in the way I planned, that is to say one after the other until their number was exhausted. Had I had eight pockets, for example, instead of the four I did have, then even the most diabolical hazard could not have prevented me from sucking at least eight of my sixteen stones, turn and turn about. The truth is I should have needed sixteen pockets in order to be quite easy in my mind. And for a long time I could see no other conclusion than this, that short of having sixteen pockets, each with its stone, I could never reach the goal I had set myself, short of an extraordinary hazard. And if at a pinch I could double the number of my pockets, were it only by dividing each pocket in two, with the help of a few safety-pins let us say, to quadruple them seemed to be more than I could manage. And I did not feel inclined to take all that trouble for a half-measure. For I was beginning to lose all sense of measure, after all this wrestling and wrangling, and to say, All or nothing. And if I was tempted for an instant to establish a more equitable proportion between my stones and my pockets, by reducing the former to the number of the latter, it was only for an instant. For it would have been an admission of defeat. And sitting on the shore, before the sea, the sixteen stones spread out before my eyes, I gazed at them in anger and perplexity. […] And while I gazed thus at my stones, revolving interminable martingales all equally defective, and crushing handfuls of sand, so that the sand ran through my fingers and fell back on the strand, yes, while thus I lulled my mind and part of my body, one day suddenly it dawned on the former, dimly, that I might perhaps achieve my purpose without increasing the number of my pockets, or reducing the number of my stones, but simply by sacrificing the principle of trim. The meaning of this illumination, which suddenly began to sing within me, like a verse of Isaiah, or of Jeremiah, I did not penetrate at once, and notably the word trim, which I had never met with, in this sense, long remained obscure. Finally I seemed to grasp that this word trim could not here mean anything else, anything better, than the distribution of the sixteen stones in four groups of four, one group in each pocket, and that it was my refusal to consider any distribution other than this that had vitiated my calculations until then and rendered the problem literally insoluble. And it was on the basis of this interpretation, whether right or wrong, that I finally reached a solution, inelegant assuredly, but sound, sound. Now I am willing to believe, indeed I firmly believe, that other solutions to this problem might have been found, and indeed may still be found, no less sound, but much more elegant, than the one I shall now describe, if I can. And I believe too that had I been a little more insistent, a little more resistant, I could have found them myself. But I was tired, but I was tired, and I contented myself ingloriously with the first solution that was a solution, to this problem. But not to go over the heartbreaking stages through which I passed before I came to it, here it is, in all its hideousness. All (all!) that was necessary was to put for example, to begin with, six stones in the right pocket of my greatcoat, or supply-pocket, five in the right pocket of my trousers, and five in the left pocket of my trousers, that makes the lot, twice five ten plus six sixteen, and none, for none remained, in the left pocket of my greatcoat, which for the time being remained empty, empty of stones* *that is, for its usual contents remained, as well as occasional objects. For where do you think I hid my vegetable knife, my silver, my horn and the other things that I have not yet named, perhaps shall never name. Good. Now I can begin to suck. Watch me closely. I take a stone from the right pocket of my greatcoat, suck it, stop sucking it, put it in the left pocket of my greatcoat, the one empty (of stones). I take a second stone from the right pocket of my greatcoat, suck it, put it in the left pocket of my greatcoat. And so on until the right pocket of my greatcoat is empty (apart from its usual and casual contents) and the six stones I have just sucked, one after the other, are all in the left pocket of my greatcoat. Pausing then, and concentrating, so as not to make a balls of it, I transfer to the right pocket of my greatcoat, in which there are no stones left, the five stones in the right pocket of my trousers, which I replace by the five stones in the left pocket of my trousers, which I replace by the six stones in the left pocket of my greatcoat. At this stage then the left pocket of my greatcoat is again empty of stones, while the right pocket of my greatcoat is again supplied, and in the right way, that is to say with other stones than those I have just sucked. These other stones I then begin to suck, one after the other, and to transfer as I go along to the left pocket of my greatcoat, being absolutely certain, as far as one can be in an affair of this kind, that I am not sucking the same stones as a moment before, but others. And when the right pocket of my greatcoat is again empty (of stones), and the five I have just sucked are all without exception in the left pocket of my greatcoat, then I proceed to the same redistribution as a moment before, or a similar redistribution, that is to say I transfer to the right pocket of my greatcoat, now again available, the five stones in the right pocket of my trousers, which I replace by the six stones in the left pocket of my trousers, which I replace by the five stones in the left pocket of my greatcoat. And there I am ready to begin again. Do I have to go on? No, for it is clear that after the next series, of sucks and transfers, I shall be back where I started, that is to say with the first six stones back in the supply pocket, the next five in the right pocket of my stinking old trousers and finally the last five in the left pocket of same, and my sixteen stones will have been sucked once at least in impeccable succession, not one sucked twice, not one left unsucked. It is true that the next time I could scarcely hope to suck my stones in the same order as the first time and that the first, seventh and twelfth for example of the first cycle might very well be the sixth, eleventh and sixteenth respectively of the second, if the worst came to the worst. But that was a drawback I could not avoid. And if in the cycles taken together utter confusion was bound to reign, at least within each cycle taken separately I could be easy in my mind, at least as easy as one can be, in a proceeding of this kind. For in order for each cycle to be identical, as to the succession of stones in my mouth, and God knows I had set my heart on it, the only means were numbered stones or sixteen pockets. And rather than make twelve more pockets or number my stones, I preferred to make the best of the comparative peace of mind I enjoyed within each cycle taken separately. For it was not enough to number the stones, but I would have had to remember, every time I put a stone in my mouth, the number I needed and look for it in my pocket. Which would* *have put me off stone for ever, in a very short time. For I would never have been sure of not making a mistake, unless of course I had kept a kind of register, in which to tick off the stones one by one, as I sucked them. And of this I believed myself incapable. No, the only perfect solution would have been the sixteen pockets, symmetrically disposed, each one with its stone. Then I would have needed neither to number nor to think, but merely, as I sucked a given stone, to move on the fifteen others, each to the next pocket, a delicate business admittedly, but within my power, and to call always on the same pocket when I felt like a suck. This would have freed me from all anxiety, not only within each cycle taken separately, but also for the sum of all cycles, though they went on forever. But however imperfect my own solution was, I was pleased at having found it all alone, yes, quite pleased. And if it was perhaps less sound than I had thought in the first flush of discovery, its inelegance never diminished. And it was above all inelegant in this, to my mind, that the uneven distribution was painful to me, bodily. It is true that a kind of equilibrium was reached, at a given moment, in the early stages of each cycle, namely after the third suck and before the fourth, but it did not last long, and the rest of the time I felt the weight of the stones dragging me now to one side, now to the other. So it was something more than a principle I abandoned, when I abandoned the equal distribution, it was a bodily need. But to suck the stones in the way I have described, not haphazard, but with method, was also I think a bodily need. Here then were two incompatible bodily needs, at loggerheads. Such things happen. But deep down I didn't give a tinker's curse about being off my balance, dragged to the right hand and the left, backwards and forwards. And deep down it was all the same to me whether I sucked a different stone each time or always the same stone, until the end of time. For they all tasted exactly the same. And if I had collected sixteen, it was not in order to ballast myself in such and such a way, or to suck them turn about, but simply to have a little store, so as never to be without. But deep down I didn't give a fiddler's curse about being without, when they were all gone they would be all gone, I wouldn't be any the worse off, or hardly any. And the solution to which I rallied in the end was to throw away all the stones but one, which I kept now in one pocket, now in another, and which of course I soon lost, or threw away or gave away, or swallowed.*

Samuel Beckett (1950)

I Why Read about Science?

> "If, therefore, a scientific civilization is to be a good civilization it is necessary that increase in knowledge should be accompanied by increase in wisdom. I mean by wisdom a right conception of the ends of life."
>
> Bertrand Russell
> [*The Scientific Outlook* (1931)]

Scientists and students are busy. When one of them picks up a paper or a book, it is with the question, "Why should I read this?" That question is particularly trenchant for *Science and Limnology*. This book is not a text or monograph about freshwater ecology. It is a discourse on the relation of some of the most fundamental questions in the study of human knowledge to one scientific sub-discipline, freshwater ecology. It therefore offers few theories or concepts that busy ecologists might apply in their work or cite in an upcoming paper. Instead, this book addresses questions that most working scientists rarely ask: What is science? How does my field fit in? Does my research belong? What research is worth doing? How can I do it efficiently? Where should I look for ideas? What ideas are worth teaching? This book is an idiosyncratic and personal account of my struggles with these issues. It does not pretend to resolve all the problems, but it does outline how they affect my science. It offers a starting point for the contemplation of science as I see it. This chapter establishes the need for such contemplation.

Some Misrepresentations of Science

One indication of the need for such a book is the diversity of views among biologists in general and ecologists in particular about the nature of science. Some sense of this confusion can be had from the introductions to general biology texts. These texts provide an overwhelming amount of up-to-date biological information; that virtue is not in doubt. Introductory biology books also allow space to a few paragraphs that purport to define science. These varied descriptions suggest a flawed grasp of the nature of science (Table 1).

Table 1. Some lapses in descriptions of the nature of science in introductory texts in biology

The major principle underlying the experimentation step of scientific enquiry is that true hypotheses can never give rise to a prediction that can be proved false. (Weisz and Keogh 1982, p. 9)	Inductive Reasoning: A logical process in which a generalization is developed to explain several specific facts. Hypotheses and theories are formed by inductive reasoning. (Brum and McKane 1989, p. 38)
An annotated historical appendix, unique to this textbook among zoology and biology texts, lists key discoveries in zoology. (Hickman et al. 1984, p. viii)	Said briefly, a scientist determines principles from observations. This method of discovering general principles by careful examination of specific cases is called inductive reasoning. It first became important to science in the 1600's in Europe, when Francis Bacon, Isaac Newton and others began to use the results of particular experiments they had carried out to infer general principles about how the world operates. (Raven and Johnson 1992, p. 3)
The pursuit of scientific knowledge must be guided by the physical and chemical laws that govern the state of existence and interactions of atoms, sub-atomic particles, molecules and so on. (Hickman et al. 1984, p. 7)	A theory is a hypothesis that has been repeatedly and extensively tested. It is supported by all the data that have been gathered, and helps order and explain those data. (Keeton and Gould 1986, p. 4)
The ultimate goal of science is to understand the natural world in terms of concepts, interpretations that take into account results of many experiments and observations. These concepts are stated as theories.... The theory of evolution is one such conceptual theme. (Mader 1987, p. 14)	

The specific weaknesses of the entries in Table 1 will be clearer when the nature of science has been explored in subsequent chapters. For the moment, it is enough to signal the confidence, coherence, and regimentation of these quotations. They seem to show that science is a straightforward, rational process following a set of rules embodied in "the scientific method". What they really demonstrate is that biology is a naive and immature science that thinks too little about what it is doing and where it is going.

Since the writers of biology texts are usually respected scientists, we must hypothesize that biologists can succeed in science without worrying much about the general nature of their endeavours. Since less than 1% of their texts are dedicated to the nature of science, it seems fair to hypothesize that these leading biologists believe the general nature of science to be far less important than the thousands of biological details crowding the remainder of each text. And since these texts are adopted in hundreds of university courses, we can further hypothesize that most university professors of biology agree that the details of their science are far more important than science as a whole.

Confusion about the nature of science is not limited to occasional lapses in the hurried introductions of first year text-books. A review of the introductions to theses from research universities and of papers published in leading ecological journals will provide similar evidence. Too many introductions justify themselves by pointing at some missing information or uninvestigated phenomenon that then becomes the goal of the research program. Many biologists therefore act as though "science" consists of reporting previously unnoticed facts, and "original research" consists of doing something simply because it has never been done before. As I will argue below, the appropriate concern of science is instead the creation, testing and use of theory.

If professionals are little concerned with the general nature of their discipline, it is scarcely surprising that the popular press and electronic media are also confused about the nature of science. Some echo the professionals — they see science as a vast search for facts. They write as though all facts are found in one of two piles (Fig. 1). One, a small heap, consists of all known facts, and represents the present state of scientific knowledge. The other, a mountainous pile, represents the facts that science has not yet addressed. The purpose of science is therefore to move facts from the large pile to the small one until the large one is exhausted and the small one is immense.

Another popular conception depicts science as a sequence of discoveries. Newton discovered gravity in his orchard, Darwin discovered natural selection on the Galapagos, and Fleming discovered penicillin in his lab. In the same vein, the public hopes and expects that future scientists will discover cures for cancer, Aids, over-population, and depleted resources, and

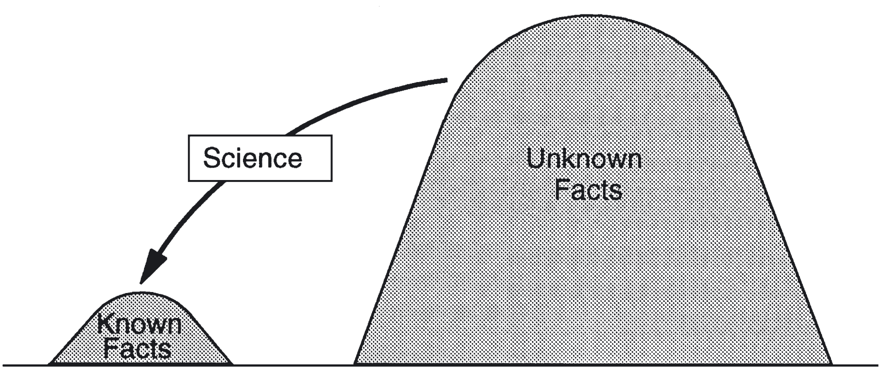

Fig. 1. The erroneous view that science consists of collecting previously unknown facts

historians can argue whether Priestly or Lavoisier was the discoverer of oxygen. This view sees science as a treasure hunt wherein important principles, concepts, theories and facts lie hidden by the artifices of stingy Nature. Particularly lucky scientists stumble across the truth; astute ones wrench truth from Nature's unwilling grasp with the right experiment or with a brilliant intellectual leap (Fig. 2). Others, the unlucky and the dull, overlook vital clues and wander into ignominy.

An indication that even scientists see science as the discovery of a preexisting natural order is provided by the basic protocol of many laboratory exercises in university teaching. A piece of apparatus is made available to a student and a question is posed. The student is required to do an experiment and is prompted to discover the law. The law to be discovered is one posited by a famous, usually long-dead, scientist. This protocol presents the experiment as the key that unlocks one of nature's secret boxes. When the box is opened, the principle pops out and the student makes the one discovery that was inevitable. If something else is found, the student has failed to repeat the great scientist's act of discovery, and (needless to say) the student is wrong.

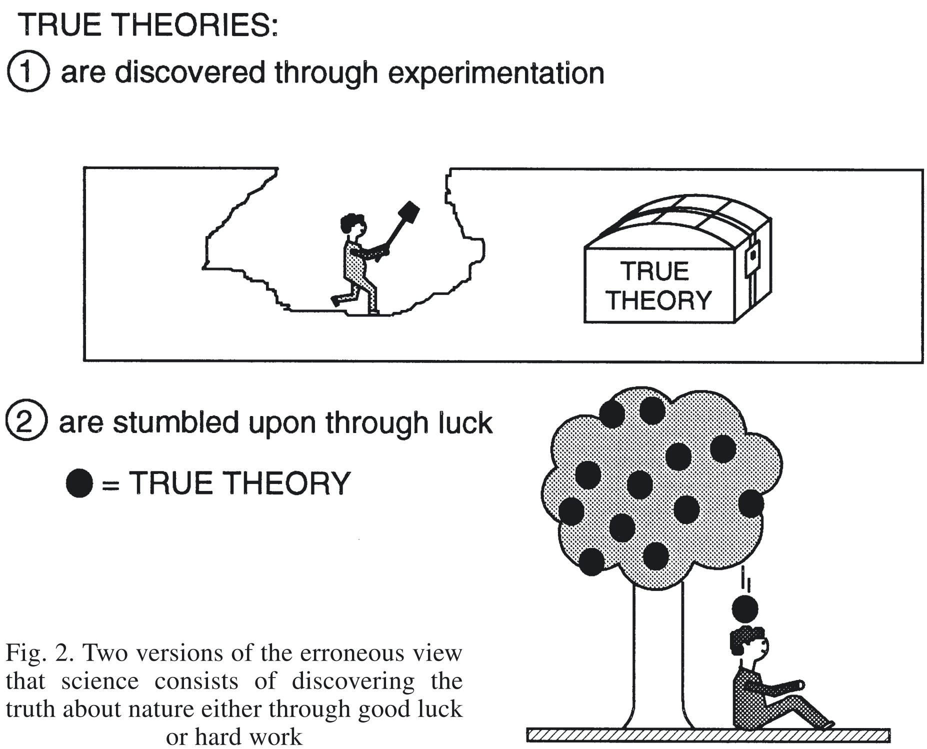

Fig. 2. Two versions of the erroneous view that science consists of discovering the truth about nature either through good luck or hard work

Still another view sees science as the application of the scientific method. Under this conception (Fig. 3), a scientist begins with a series of observations or facts, and the careful consideration of these facts results in an hypothesis. This process is called "induction". The scientist then deduces other facts from the hypothesis and "tests" the hypothesis by determining if the deduced facts are actually observed. If the observations differ from the expectation, the hypothesis is abandoned. If observation agrees with expectation, the scientist places a little more faith in the hypothesis and tests it further. As confirmations accumulate, the hypothesis gains in status, becoming first a theory and finally a natural law.

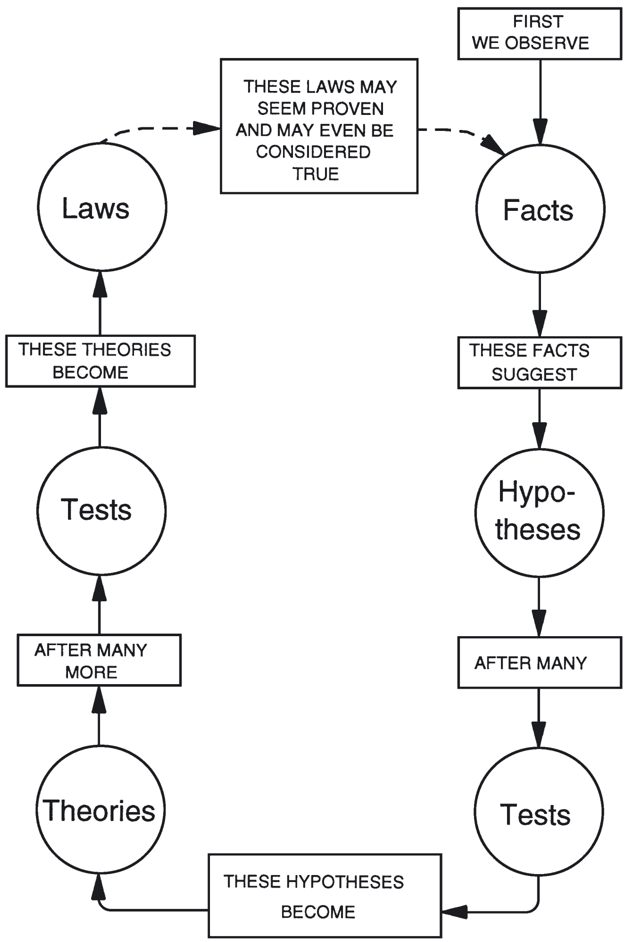

Fig. 3. An erroneous version of the scientific method, one that develops true theories and confuses fact with theory

This description is the treatment that appears in introductory texts. It seems a serviceable starting point, but it has a number of faults. In practice, the different elements in the scientific method are much more variable and much less methodical. For example, scientists often start with an hypothesis instead of observation; the inductive step may be no more logical than whimsy; many tests are often biased and flawed; negative evidence likely exists for every hypothesis, theory and law, but scientists ignore it; most scientists are never aware of a point in time when they made a discovery and many productive, important researchers are not aware of discovering anything at all; no theory can be considered "true" or above the threat of disproof in future tests; and falsification is rarely, if ever, unquestionably complete. To look at these seeming problems in more detail, I will have to define the basic elements of the scientific method.

Some Basic Distinctions

Facts and theories. First it is essential that we distinguish between facts and theories. If we do not do so, we will never understand science. Many scientists confuse the two. If we look at books or journals, we often see discoveries and laws treated as facts, as suggested in Fig. 3. For example, most biologists act as if evolution and the elemental table are facts, when they are really theories.

A fact is an observation, a datum or sense impression which has not yet been consciously interpreted and about which no scientific claim is being made. By itself, a fact is empty and useless, because it gives no basis for action. Parenthetically, one may object that such a pure fact probably cannot exist, that all observations are interpreted through our biological and cultural biases as soon as they are sensed. In other words, all facts are "theory-laden". A stricter interpretation would define a fact so that, as soon as it became more than empty and useless, the fact would be termed a theory. I accept this, but will not complicate discussion further for the time being.

A theory is a generalization that goes beyond the facts. It therefore makes predictions which are statements about facts we do not yet know. Consider a simple example. If I were to rise in a scientific meeting to state "it is not a fact that animals need food to grow", most of the audience would dismiss me as a lunatic. Nevertheless, it is not a fact that animals need food to grow. It is far more important. It is a theory. The facts are that the effect of starvation of a few individuals of a few species has been studied. Each of these individuals, when deprived of food, failed to grow, and instead wasted away and died. We do not know that other individuals of the same species would do the same. We

Table 2. Some facts about the lengths and weights of some babies

Baby	Length (cm)	Weight (kg)
Vic	39	11.864
Sarah	30	5.400
Eva	25	3.125
Adrienne	32	6.554
Mike	29	4.878
Julian	22	2.130
Elisa	37	10.131

can never know what every individual of every species that ever lived would do. Therefore, we are going far beyond the facts when we claim that all animals need food to grow. When we state a theory, we make a statement that we can never show to be true. We can however demonstrate that a theory is probably false as we shall see in the next section.

Induction and deduction. Deduction is the derivation of specific instances of a generalization. In simpler terms, deduction is the process by which we decide what predictions a theory makes. For example, suppose that we are interested in the growth of babies, that we measured and weighed a lot of them (Table 2) and that we had erected a theory (Fig. 4, overleaf) to describe the relationship between the weight (in kg) and length (in cm) of babies:

$$\text{Weight} = 0.0002(\text{Length})^3 \qquad (1)$$

Perhaps few would be willing to say we have made a discovery, but by developing an equation relating length and weight, we have created a theory, albeit a very simple and trivial one. There are other theories that would describe the data just as well; some of those may be much more comprehensive than Eq. (1), and they may offer deeper explanations, but I will postpone discussion of those complications. It is sufficient for the reader to accept that one characteristic of a scientific theory is that a theory offers the power to predict about specific cases on the basis of a more general statement. Most authorities concede the point.

The equation is a theory for two reasons. First we did not measure all babies, so we are claiming that we can extrapolate from our observations to babies we have never seen. Second we did not measure all sizes, even of the babies we did measure; so we are claiming that we can interpolate the weights that these babies had or will have at lengths we have not observed. When we go beyond the facts by extrapolating or interpolating, we have made a theory.

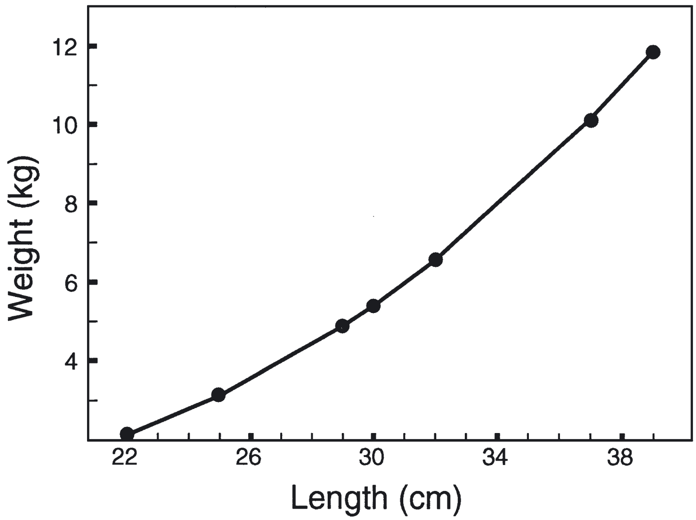

Fig. 4. A theory about the size of babies

The theory in Fig. 4 makes some very definite predictions. It says that for any baby we measure, there will be one, and only one, possible weight, that predicted by Eq. (1). This weight is a deduction from the theory. It is the logical consequence or implication of the generalization or theory. The important point is that a given theory makes specific predictions about unobserved instances, and that anyone who uses the theory will make exactly the same predictions. The theory may be wrong, because not all babies behave as it suggests, but that would not affect the claim that the relation is a theory.

Deductions allow us to test the theory to see if the predictions are correct. Given a theory, like Eq. (1), and some additional specific cases that were not used to build the theory, say Anna or Kate, we can make the required measurements of the babies' lengths, and calculate or deduce their expected weights. We can then test these predictions by observing the babies' weights and comparing them to our expectations. If Anna or Kate is lighter or heavier than we predicted, we would have falsified our theory and therefore we would have to revise it.

In describing the creation of a theory, I skipped over one of the most contentious parts, induction. Induction is the process by which we move from a set of facts to a theory or generalization. This is where intuition or inspiration enters science. The scientist looks at the facts and they, in some mysterious way called induction, suggest a generality to the scientist. Induction is not a logical process. It does not lead inevitably to one conclusion, but instead could lead to an infinity of possible theories.

The point that the same set of facts could inspire different researchers to entirely different theories seems hard for many people, including some scientists, to accept. I will therefore develop a ridiculously simple illustration (Fig. 5). The example will again deal with growing babies but this time, just for variety, we shall develop a theory about how fast babies grow. We will again begin by making a few measurements of weight (*W*, in kg) and age (*X*, in months), and after one month's work we might find:

Age	Weight
1	1
2	2

Now I need only sit back, contemplate the data and wait for an inspiration. After some time, I might hit on a more general pattern and propose a theory to describe the growth of a baby:

$$W = X \tag{2}$$

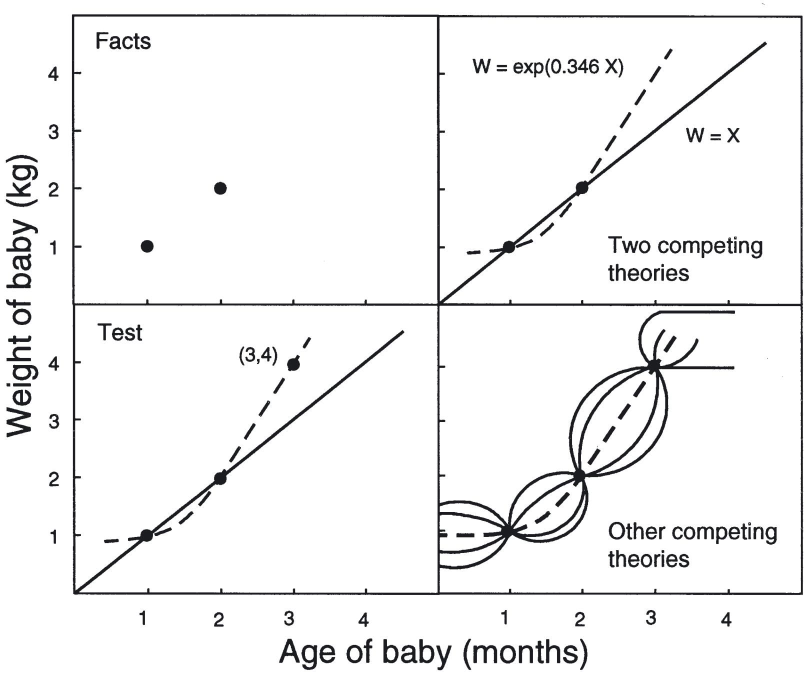

Fig. 5. The development of alternative theories about the effect of age on the weight of babies

A more sophisticated, or at least more mathematically competent, observer might instead propose another observation on the basis of the same observations:

$$W = e^{0.346X} \tag{3}$$

In fact there is an infinite series of relations, each representing a theoretical generalization, that could describe these data.

Logic will never tell us which of these simple theories best describes the growth of a baby, but we can logically deduce the consequences of the two competing theories. If Eq. (2) is correct, then $W = 3$ kg when $X = 3$ months. But if Eq. (3) is correct then $W = 4$ kg when $X = 3$ months. Assuming that we still have our baby, we need only wait until it is 3 months old to take the observation that will allow us to determine which theory makes the better prediction. If we find that $W = 4$ at $X = 3$, we can reject $W = X$ as the less useful theory. We thus know that $W = X$ is wrong, but we cannot therefore claim that $W = e^{0.346X}$ is correct. Someone else might look at the three pairs of data points and induce that:

$$W_X = X + W_{X-1} \tag{4}$$

where the subscripts indicate weight at the ages of X and X–1 months.

Since Eq. (4) fits the available data as well as Eq. (3), we cannot tell which of these two competitors, or of a host of other possible theories connecting the points, is right or wrong or even better. However, once again we can deduce the logical consequences of the competing theories. When $X = 4$, Eq. (3) suggests that $W_4 = 8$, but Eq. (4) would instead suggest that $W_4 = 7$. Once again, we must wait a month and make more observations to test these alternatives. Obviously, we will never reach the end of this process. We could postulate various wavy lines or step functions implying varying growth rates within each month, or an infinity of other possibilities that could join the four weights of the growing baby. In fact, no matter how many points there are, there will still be an infinite number of relations that could connect them together, and because we always use induction to arrive at the theory to describe these points, there can never be any guarantee that we have found the right one. In other words, we can never know if we have found the truth and therefore we should never claim that a theory is true in the sense that it is beyond doubt.

This is a profound discovery. It is one that Aristotle never made, Galileo rejected, and Newton dismissed. The widespread acceptance of the principle that we can never be sure of anything in science is one of the most revolutionary changes of the 20th century.

Empirical and explanatory theories. The theories I have used to illustrate this discussion are modest statements of trend that describe some data and could be used to predict future observations of the same kind. Many scientists are unwilling to call these statements "theories". I see this as only a problem of definition.

Like many who have considered the problem, I call any statements that make predictions "theories". This single term embraces two general types which I call "empirical theories" and "explanatory theories". Empirical theories are simple relationships based on observed patterns (e.g. allometric relations, species-area curves, the second law of thermodynamics) that make predictions by assuming that the future relations among the variables will resemble those in the past. Explanatory theories are grander, more comprehensive statements that not only make predictions, but also offer a comprehensible explanation of the phenomenon being predicted, like the size-efficiency hypothesis of Brooks and Dodson (1965), the trophic cascades of Carpenter et al. (1985), Darwin's theory of evolution by natural selection, and various theories of creation, like the big-bang hypothesis. Both empirical and explanatory theories play important roles in science.

The history of scientific achievement shows that theories develop in a characteristic sequence. First the scientist surveys the subject matter of interest, looking for patterns that might allow a prediction. This might be the swirling of stars in the night sky, or the occurrence of rain, or the production of certain chemicals in the lab. This search seems a simple step but it is just the opposite. The patterns we are seeking are invariably set among a vast collection of confusing and unrelated facts. These irrelevant observations often obscure the regularity of the system under study.

Once the scientist has perceived a regularity in the objects of study, and expressed this pattern unambiguously, an empirical theory has been produced. Empirical theories may be complex, but they are more likely to be simple *X*-*Y* relationships because such relations are so easy to perceive and to define. Thus the relations describing the weight of a baby from its age or length are theories. They are theories because they generalize from our observations and allow the prediction of weight from any value of age or length.

Empirical theories can be useful, but they have limitations. First, they make predictions only about the correlated variables. Thus, they can never generate unexpected predictions about other aspects of these entities or about other phenomena. They remain theories of relatively low generality. Second, they do not satisfy our desire to explain our environment; this sense of understanding seems to be a bodily need, at least for some researchers.

Empirical theories stimulate other scientists to explain why the theories work. With luck, someone will eventually replace the original empirical theory with an explanatory theory. Because this new theory relates the observed variables to other observations, it may make more predictions and thus be more useful. Given the limited predictive power of empirical theories, many scientists underplay their importance in science. Nevertheless, the history of scientific development shows that empirical theories are a crucial step toward explanation.

In summary, science is not about collecting facts or observations. It is the process of identifying, testing and organizing generalizations or theories that go beyond the observed facts and, in some sense, explain these facts as instances of a general pattern. Both empirical and explanatory theories are created by induction, an inspired guess that leads us to postulate some regularity in the universe. They are then tested by deduction that allows us to know what the theory predicts so we may compare its predictions to further observations.

The Importance of Science

Why should we care what science is? The reasons are clear. As citizens, we expect science to give us some grasp of the risks that we face and some measure of control over our fate. As taxpayers, we ultimately fund research, and so we must learn to scrutinize the growing demands of modern science for money and resources. As teachers and students, we need to know what science is so that we can teach and learn what is scientifically important, and disregard what is trivial. As scientists, we need a better knowledge of what we are doing, so we can use our resources well to confront the problems of science and humanity, so we can promote our vision to the rest of society, and so we can defend it from unjust criticisms. We cannot afford to be ignorant of the nature of science any longer. Society must learn what it can expect from science, and what it cannot.

There seems little call for a detailed defense of the thesis that science plays an important role in our civilization and therefore that the nature of science should be better appreciated. Like it or not, our food, shelter, health, our ways of life depend on science and technology. We may deplore this dependency as unnatural, dangerous, and unstable, but we cannot change the situation. Science has helped create the problems of the 20th century, but to throw away science at this stage in civilization would be a fatal error. We now depend on science so much that the solution to our dilemma will be scientific, whether it is civilized or catastrophic. We must use science for good, because we must use science. That will be easier if we know what science is.

Many humanists have taken the trouble to discover what science is. They often do a better job of explaining science than do the scientists. It may rankle scientists to turn to humanists to discover the nature of science. However, there is no reason to disdain their help.

The prologue to this book is an allegory of scientific research. It shows that the novelist and playwright, Samuel Beckett, had a keener appreciation of the nature of scientific enquiry than many scientists. There is science in Molloy's struggles with the problem of the sucking stones, in his abandonment of the vaguely felt, yet fundamental principle of trim, and in the inelegant (but sound) solution whose elaboration marked the end of both enquiry and interest. In all of this, Molloy gives a better picture of science than most introductory biology texts.

Jacques Barzun is another humanist who has concerned himself with science. His *Science: The Glorious Entertainment* is a milestone. In addressing C. P. Snow's (1963) concept of two cultures, Barzun writes about the need to appreciate science:

> The new science is for the public a Delphic mystery; it keeps the western intellect troubled but unenlightened, except for the practitioners themselves. Here we touch upon the grim deficiency of the scientific culture, which is also the first lesson to be drawn from our historical review: the fundamental lack in our mental and spiritual lives does not come from the trifling division between scientists and humanists, or between scientists and the whole of the laity; it comes from the fact that science and the results of science are not with us an object of contemplation.
>
> By common consent the sciences are taught in school and college; but everyone admits that this teaching is wasted on three fourths of those who are forced to endure it. For all the use or interest they find in "the science requirement" they might as well be required to take Greek or Latin: science remains to them a dead language. The belief persists that if sciences were better taught they might prove to be more titillating, but there is little agreement on how to teach them. And one reason for this is that to the teachers and practising scientists themselves science is rarely an object of contemplation. They teach therefore as if to intending professionals. (Barzun 1964)

Barzun's condemnation is well deserved. Somehow in a society that depends on science, we manage to turn off most students. How do we do it? We teach as we were taught, and we were taught "as to intending professionals." Given a choice, few professors would elect to teach any students other than those concentrating in biology, and most of us prefer to teach the details of our own narrow specialities. If instead we want to instruct a larger fraction of the general population about science, we must escape the traditions of our own training. We must find ways to make science meaningful to more people, without necessarily recruiting them to the profession. We must teach science as an object worthy of contemplation. I feel our only hope of doing so is to understand something about the nature of science. We scientists must step back from the welter of detail that bemuses us in our daily work and learn from enlightened humanists. If we can do so, we may be able to talk across the gulf that sometimes separates humanist and scientist, and across those that separate us from our students, our public patrons and our colleagues.

The Growth of Science

Derek de Solla Price (1986) dedicated much of his career to measuring the size of science. He showed that whether one measures science by the number of scientists engaged, the number of papers produced, the number of journals published or the number of dollars spent, one reaches the same conclusion: for the past 300 years, science has doubled in size every 10 to 20 years. In other words, science doubles about twice as fast as population (Fig. 6). This has some remarkable implications. One is that over 85% of all the scientists who ever lived are still alive. Another is that the scientific literature increases

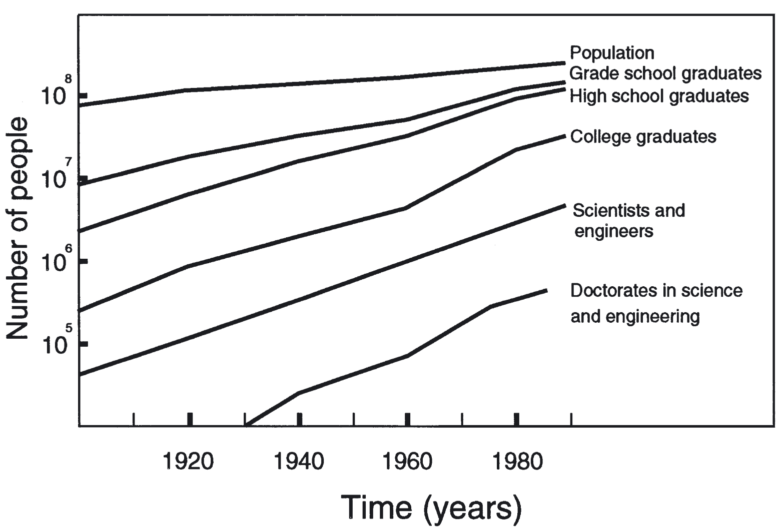

Fig. 6. A comparison of the growth rates of science and population in the United States. (Modified from Price 1986)

by about ten times over the course of an individual's career and has done so since its inception; we have always been awash with new work and we always will be. A third implication is that science has grown by encroaching on the rest of society.

The growth of science has demanded accommodation from working scientists. For example, we assemble in multi-disciplinary teams of specialists to teach and do research, we insist that scientists write, and that students read, even longer text-books, and we use the power of the computer and other machines in our data collection, data analysis, writing and publication. Many of us work nights, weekends, and holidays. We may focus our efforts more, and hone our interests to narrower specialties. Some ruthlessly excise erstwhile non-professional interests from their lives — hobbies, friends, family. Many scientists I know have already done these things, but we have not resolved our difficulties. We may only have made things worse. Science is growing faster than we can handle.

Obviously, science cannot grow faster than society forever. For example, if science does not slow down, every man, woman, and child in North America will have a Ph.D. by the year 2200. Whom, or what, will we teach then? Research now consumes 2 to 4% of the gross national product of most developed countries. If science were to continue to grow at present rates, this will increase to between 4 and 8% in another generation, and between 16 and 32% in another 100 years. There must be an upper limit and the explosive growth of science must eventually slow as that limit is approached. Since science already commands a large share of resources, we should expect to see the reduction in growth in the near future.

A slower rate of growth will present new problems, and require some hard decisions. For example, it is unlikely that society will fund all future mega-projects of all the disciplines, or meet all the demands of all the researchers. Eventually, choices will be made among many seemingly incomparable proposals. For example, we may have to decide if science is better served by a space station, a biotechnology complex, a mass accelerator, or an oceanographic vessel. We may have to compare the desirability of research into biodiversity with that into chemical pollution or crop yields. We may have to decide among sub-atomic physics, molecular biology, astronomy and limnology. To do that, we will likely have to know what science is, not just what interests its sub-disciplines.

Summary

I can now return to the question in the title of the chapter: Why read about science? First, a growing literature shows that science can be appreciated and understood as a process, rather than simply as a body of information, so that we can expect our reading to be profitable. Second, there are many indications that science is not properly appreciated. Introductory texts and graduate theses show that many biologists are unsure of the nature of science and the role of the scientist; I believe that an appreciation of science would make us better teachers and produce better students. There is also evidence that the fundamental components of research — facts, theories, tests, induction and deduction — are poorly understood by many members of society; a better grasp of these basics would allow the citizen to function better in a society that funds and depends on scientific research. It may also allow scientists to do their jobs better. Finally, we should learn what science is and what it is not, because the dynamics of growth of humanity and science imply that the traditional relations between science and society will soon change. Modern researchers and citizens are about to experience interesting times, and I believe that an appreciation of the nature of science will help them find a way out of the gathering confusion.

II A Brief History of Method

> "The great scientists ... represent to me a simple but impressive idea of science.... This, then, for me is science. I do not try to define it, for very good reasons. I only wish to draw a simple picture of the kind of men I have in mind, and of their activities. And the picture will be an oversimplification.... My criterion of demarcation between science and non-science is a simple logical analysis of this picture."
>
> K. R. Popper
> [*The Problem of Demarcation* (1934)]

Much of this book is premised on Karl Popper's distinction between scientific theory and non-scientific concept, his criterion of demarcation. According to Popper a construct qualifies as a scientific theory if it makes a potentially falsifiable statement or set of statements. These statements are called "predictions". The main goals of science are to make theories, to use theories to make predictions and to assess those predictions against observation.

Although Popper's views are widely known, they are not universally accepted even by philosophers, and their relevance is even less appreciated by many working scientists. For example, I was raised in a tradition that science discovers the truth, that only a scientist can understand science, and that philosophers and historians had nothing to tell the researcher. I came to realize the folly of that position through a consideration of the history of biology, a history that often reflects the stages of my own philosophical development and often those of other scientists. This chapter therefore uses an historical overview of biological thought as a device to appreciate Popper's criterion of demarcation.

Three Ways to Knowledge

For all the variety of human thought and endeavour, there are only three methods of gaining information about the universe: the intuitive method, the metaphysical method, and the scientific method. Each method is characterized by certain assumptions about nature and by criteria for judging insights that the methods produce.

The intuitive method is the oldest way of discovery. It assumes that no laws govern the behaviour of natural objects or, if there are laws, they can be repealed at any time by some greater organizing being or force. Given the fickleness of observable phenomena, the intuitive method puts little faith in observation. Instead, it holds that the only way to gain knowledge of lasting value is through revelation. Truth will be revealed to us if we put ourselves in so receptive a frame of mind that the organizing force can reveal its intentions. It is a corollary of this view that humans, by their own efforts, cannot gain any real understanding of the universe or hope to predict future events.

The second method, the metaphysical method, has been favoured by many philosophers. It assumes that the behaviour of natural objects is governed by a set of laws and that people can discover these laws by their own efforts. This method emphasizes the power of the human mind to see these laws. It begins with the search for premises that are obviously true and, by the use of logic, deduces natural laws from these axiomatic truths. Both the intuitive and metaphysical methods justify their insights by interpreting appropriate observations as instances of the perceived general truths.

Finally, the scientific method shares the metaphysicians' assumptions that the universe functions according to laws. Scientists differ from metaphysicians in that they rely not only on thought, but also on observation to define these laws. Science may therefore begin with observations, as suggested in Fig. 3, or with an idea. Wherever the method begins, scientists use their brains to produce a theory or law. Then they move to test the implications of theory against new observations. If the theory fails to predict well, the theory is changed and the new theory is tested in its turn.

The essential difference between the scientific method and the others is that the statements of science need not be truths. Science does not require its practitioners to perceive truth directly, nor does it accept that others can do so. In science, knowledge is always hypothetical, so the ultimate arbiter in science should be the testimony of observation, not the fervour of belief.

The three methods of enquiry are not necessarily applied separately. Time has allowed hybridization, and the history of science can be very usefully interpreted as the history of the interplay of these three methods.

Aristotle

We begin with Aristotle (384–322 BC) because science arguably began with the Greeks and Aristotle was the most influential of the Greek scientists.

We are only interested in his method of finding out about nature. When we look at how Aristotle did that, we find a curious blend of metaphysics and science.

Aristotle should be considered a scientist because he insisted on the importance of observations. For example, 2300 years ago it was commonly believed that the human embryo nourished itself by grasping the mother's flesh with its mouth and sucking. Aristotle ridiculed this idea because "anyone who takes the trouble to look" will see that the embryo is completely enclosed in a fluid filled bag; it could not possibly suck the mother's flesh (Bodenheimer 1953). Aristotle concluded that nourishment must enter via the placenta and umbilical cord (Fig. 7A, overleaf). This is what we still believe today.

Aristotle's argument for placental nutrition, although it concerned a small point, was a piece of science. He built on one theory — that all animals need nutrition — and one observation — that the fetus is enclosed in the amniotic sac — to conclude that the prevailing theory was false. He then drew on a further observation — that the umbilical cord passed from mother to fetus — to produce a generalization that concerned all human embryos: the embryo is nourished through the placenta and cord.

In considering the problem of placental nutrition, Aristotle appears to have thought very much as scientists do today. However, elsewhere in his writings, we encounter arguments that are almost meaningless to us. At those points, Aristotle blends science with his now strange metaphysics. A common property of all these now meaningless arguments is that they derive from "intelligible principles".

Aristotle's intelligible principles were really general statements, or if you wish theories, that seemed to be self-evidently true or axiomatic. They are like the obvious truths that characterize the metaphysical method of studying nature. For example, for Aristotle it was an intelligible principle (a) that the universe is perfect, and on a less general scale (b) that the circle is the perfect geometrical form. A consequence of these principles is that we should find circles everywhere. Aristotle did (Fig. 7B). He saw instances of these principles in the paths of the planets, in the cycle of birth, life and death and, since evolution or extinction would disrupt this perfect cycle, in the permanence of the species. Given this bias, Aristotle would not look for extinction or evolution of living species, and would probably have disregarded any observations relevant to those processes. As a result, he used his principles to deduce that species are permanent.

The argument for placental nutrition seems essentially scientific even today, but that for the permanence of the species is almost ludicrously incomprehensible. I have described these two instances of Aristotle's science to

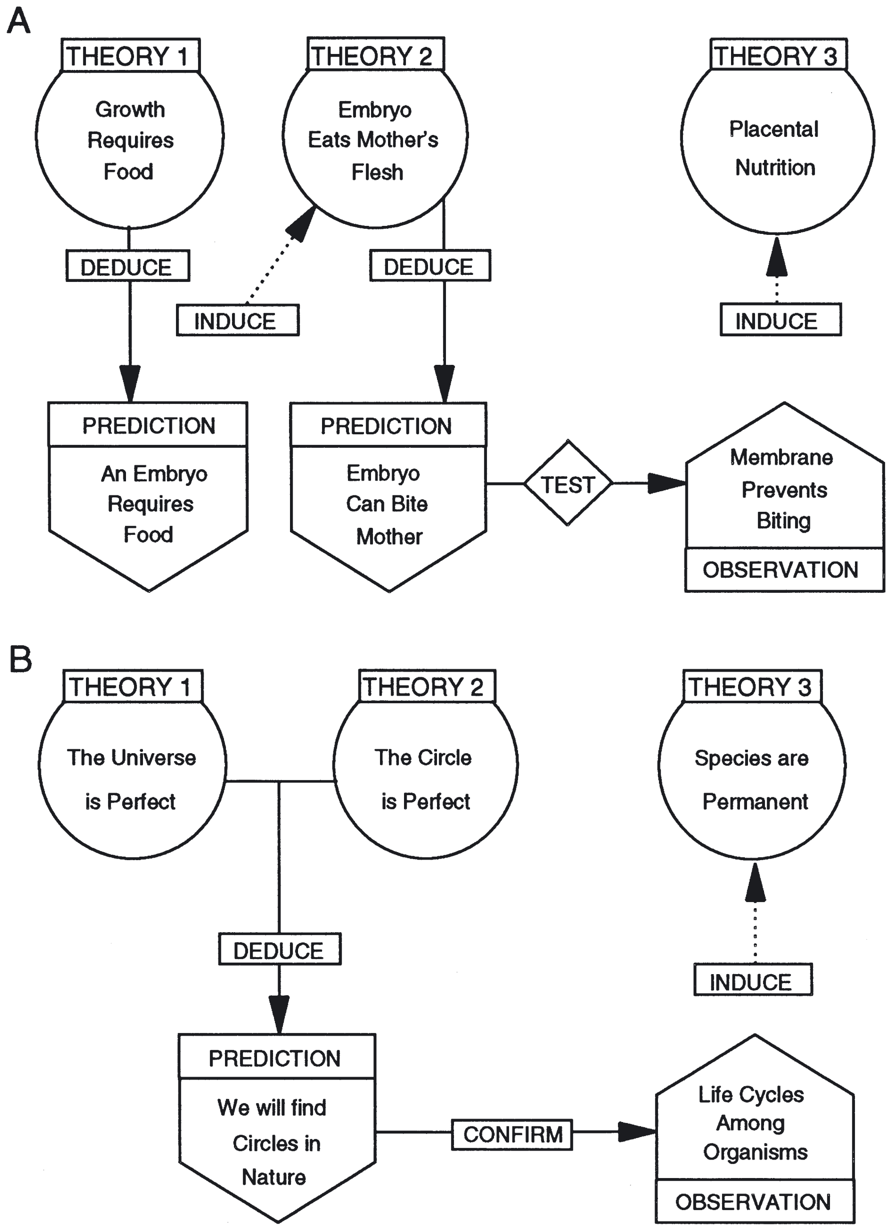

Fig. 7. (A) Aristotle's use of the scientific method in developing the theory of placental nutrition. (B) Aristotle's use of the metaphysical method in arriving at the theory of the permanence of the species

contrast the metaphysical and scientific methods of enquiry Aristotle used to understand the universe.

In both cases, Aristotle was confronted by theories of uncertain origin. Some, like the theory that the embryo sucked the mother's flesh, were presumably common-sense beliefs of the time. Others, like the theories that the universe and the circle are perfect, arose from his mind as intelligible principles. We cannot reject a theory because of its origins. We insist that the theory make predictions, but predictions can be deduced from both theories in Fig. 7. Both methods moved Aristotle to make other observations and to develop other theories, like those regarding placental nutrition and the permanence of the species.

The difference between the scientific and metaphysical methods lies in the way different practitioners link prediction to observation. Aristotle the scientist looked for observations that could be inconsistent with prediction. When they were inconsistent, he rejected the theory as false and moved to create a better theory. Aristotle the metaphysician looked for observations that were consistent with the theory because he wanted to illustrate the truth of his intelligible principles. Because the principles were not under test, he saw contrary evidence not as falsifying but as irrelevant. Since the intelligible principles were not open to change, the induction of the permanence of the species was not intended to be tested, but to extend the whole complex of theory and observation so that as much "knowledge" as possible would be consistent with the intelligible principles.

This explains why Aristotle's work is alternately meaningful and meaningless to us. When guided by intelligible principles, his work seems crazy, because it reflects the world view of a brilliant man who lived in an almost unimaginably different time and culture. Whenever he is free of these principles, whenever he saw no connection between the theories and the principles, his use of observations becomes "scientific" and valuable.

Deduction and Induction in the Age of Reason

Throughout the dark ages, Aristotle's ideas, beliefs and observations were accepted almost without question. In a sense, both his observational science and his metaphysics were treated as indubitable principles, so the distinction between the two methods of enquiry became blurred. When science began to emerge in the 16th century, there was a strong reaction against this metaphysical science. This reaction went in two diametrically opposed directions.

One faction is associated with Francis Bacon (1561–1626), an English philosopher and visionary, who also served as Lord Chancellor to James I.

Bacon recommended that we first purge our mind of wild theories and intelligible principles, and then carefully and systematically collect a mass of observations relevant to the subject of interest. From this material, Bacon thought we would induce a general theory, or two or three theories that could explain the observations. He supposed that we would then disprove and eliminate the wrong theories by careful observations and experiments. Bacon's method was characterized by its absence of intelligible principles and its emphasis on observation and induction. Subsequently, the Baconian method has been associated with the less tenable opinion that induction proceeds logically and certainly from masses of systematic observation to truth, but that is a perversion of his more complex views (Eiseley 1973).

Another approach was taken by the French philosopher and mathematician, René Descartes (1596–1650). Descartes was impressed by the certainty of mathematics, which advances step-by-step from one indisputable conclusion to another. Any claim to true knowledge outside of mathematics seemed dubious. He therefore concluded that we must bring order into chaos by applying the clear and certain deductive method of mathematics to philosophy and science.

Deductive science would only be possible if the deductions started from one or more very general and true theories. Descartes saw that the intelligible principles of Aristotle and his medieval followers had led only to confusion, and so devoted himself to a search for indisputable axioms that could form the basis for a true science. By rigorous thought, he arrived at two propositions he considered indubitable: I think, therefore I am; and God exists. Descartes' radicalism got rid of a lot of the spurious truths that had directed the science of Aristotle and his successors. However, Descartes also left us a one-sided view, still dependent on intelligible principles and still limited to deduction.

Both Descartes and Bacon greatly influenced subsequent views of science. Two schools of thought developed around their teachings. One tells us that knowledge is obtained by induction and the other relies on deduction. The resulting methodological debate eventually led to the newer and much greater question of whether it is possible to obtain true knowledge in any way at all. This terrible question undercut a basic assumption about the quality of knowledge and the goals of understanding. This was a turning point for science and humanity.

David Hume and Immanuel Kant both sought to answer this new question. In doing so, they came to very different answers. Each was extremely influential and each founded a philosophical tradition based on his answer.

David Hume (1711–1776) was a Scottish philosopher and writer. Interestingly (and somehow reassuringly) he thought his major philosophical treatise was a failure that "fell stillborn from the press" (Popper and Miller 1983). Before Hume, mathematics was considered a science, so analogies between the two were used to support the belief that science yields true knowledge. Hume instead separated the two, and so made that argument for the truth of science untenable. Hume then showed that induction did not give us certain knowledge.

I can only approximate the reasoning that led him to this belief. Philosophers differ about his arguments and I have no reason to suppose that I can do better than the professionals. Hume started with the demonstration that we know nothing about the external world. All we have are sensory impressions. Therefore we do not know that events in the external world regularly follow one another. We only know that certain sensory impressions follow each other in time.

For example, if a sequence of two events, P then Q, happens in the external world, we can never know it. All we experience, all we know, is a succession of sensory impressions, p then q. From these impressions, we infer the occurrence of the corresponding sequence of real events, P then Q. However this inference is a guess or induction. Because it is not certain, we can never know that the real events exist. We all sometimes experience this uncertainty when we become confused about whether a memory occurred in reality or in a dream. If we cannot know what events are real, we can similarly never know if there is a causal connection between P and Q. If there is no causal connection, then we can never be sure that Q or q will follow P or p. No matter how many instances of p then q we experience, we can never claim that we are sure that the next p will be followed by q. We have even less reason to believe that Q will necessarily follow P.

Hume concluded that the only systems about which we have true knowledge are artificial, like mathematics, and that we can never know when we have true knowledge about the universe. In the terms I have been using, there is no logical basis for believing that induction will ever lead us to a true theory about nature.

The great German philosopher Immanuel Kant (1724–1804) led the classical backlash to Hume. Kant argued that our knowledge of the external world does not merely come from Hume's sensory perceptions. For Kant, knowledge has two sources. There is empirical or *a posteriori* knowledge that comes after the fact, through our senses, as Hume agrees. But there is also *a priori* knowledge which is supplied by our consciousness independently of all experience. Of these two, *a priori* knowledge is by far the more important source.

In his *Critique of Pure Reason*, Kant argued that the most basic laws of nature can be discovered *a priori*, that is before the fact. Thus, discovery does not require science or empirical observation, it could be achieved by pure reasoning alone. In fact, Kant held that if we did not have these *a priori* laws for perception to play upon, we could not have any experience of the world at all.

With Hume and Kant, there appears to be a clear schism. Hume argues that the only source of knowledge is empirical but that it is not reliable, whereas Kant, Descartes and Aristotle found that reason is the most reliable, and perhaps the only, source of knowledge. Philosophers have not resolved this dichotomy, but natural scientists have tended to follow Hume. His denial of the possibility of certain knowledge was at first devastating, unacceptable, and even incomprehensible, but if scientists had instead followed Kant, they might have had to abandon observation and then they could scarcely claim to be natural scientists.

Logical Positivism

The philosophical direction that developed from Hume reached one extreme in the writings of Ernst Mach and his associates. These philosophers were known as the Vienna circle and their philosophy subsequently became known as logical positivism. Their history and ideas are explored by Phillipp Frank in his *Modern Science and its Philosophy* (1949) and his *The Philosophy of Science* (1957) upon which I depended in writing this section. At one time, I was deeply influenced by their writings. I no longer believe that they represent an end-point to philosophical development, because their philosophy is so extreme as to be completely unacceptable for many scientists. However, some of the findings of logical positivism still address contemporary issues in biology and so serve to show how thinking about science can help scientists to do their work. Just as importantly, the extremity of logical positivism prepares us to accept the more recent and useful position of Sir Karl Popper.

Hume viewed observations as only sensory impressions and held that theories suggested by these observations need not bear any relation to the laws of nature. Logical positivism suggested the situation might be far worse: Maybe there are no natural laws at all, for how would we know if there are? The regularities we perceive, and the explanatory theories we build around them, may be nothing more than a product of the scientists' minds. Perhaps the human mind demands the existence of laws, and scientists work in such a way as to satisfy that need. If so, the laws of nature may be no more than a definition of how scientists' minds work.

On causality. As an example of this argument, I will develop Phillipp Frank's attack on causality. Many scientists see causality as the cement of the universe; they hold causal connection among events to be the basis for meaningful pattern in the universe and contend that the description of these connections is the goal of science and the basis of theory. Frank attacks this fundamental assumption because, if he can topple that, the rest of our self-assurance about science and reality should follow.

Frank tried to show that the law of causality only exists because scientists act in such a way as to preserve it. In everyday words, we could express this law as "every event or effect has a specific cause". Frank states the law more rigorously: "If a State A of the universe is once followed by a State B, then whenever A occurs again, it will be followed by B". This pure form of the law can find no application in science because we can never know the state of the whole universe. But if we do not know the state of the whole universe, we can never be sure that some additional factor will not modify the State A so that State C follows instead. Frank feels that what we do is to reformulate the law as a more useful approximation: "If in a finite region of space, State A is once followed by State B and at another time by State C, we can make State B as similar to State C as we wish by increasing the size of the region of space we consider". This reformulation is more meaningful if we translate it into the everyday language of experiment: "If State A once appeared to be followed by State B and another time by State C, then our results were spoiled by an unknown and uncontrolled variable". To paraphrase Frank further, when we apply the law of causality to a finite biological system, the number of variables we control and the number of organisms we sample are determined by the amount of agreement we demand among our replicates, that is by how similar we require B and C to be.

Once he showed that the law of causality is rigorously valid only for an infinite system, Frank proceeds to a second argument. Even if we suppose the law to be valid for small, finite systems, there is still reason to doubt that it is really a natural law. Science begins with data and these data are sensory impressions. Our statements and generalizations must always refer to something we sense. We must be able to see them, touch them, smell them or something. Our laws and theories must therefore be translated, or at least translatable, into terms that have meaning in relation to what we observe. Whatever version of the law of causality we choose, the law refers to the state of the system. Frank defines this state in sensory terms as the sum of all perceptible properties of the system. However, when we find that some observation apparently violates the law, we invent unperceived, even imaginary, properties of the system to explain the contradiction.

Frank provides an example. Imagine two pairs of identical iron rods on a table. Both pairs are in State A. One pair simply sits there, that is State B. The other pair move towards each other — State C. To satisfy the law of causality, we say that the latter pair of rods had an imperceptible property called magnetism. Thus we conclude that the initial states were only apparently the same, and in doing so we preserve the law of causality. If we act this way, the law of causality will always be obeyed because whenever a system does not obey the law we invent as many fictitious properties as necessary to preserve the law.

Frank concludes that the law of causality no longer looks like a law. It is simply a definition. It defines the way we will interpret any situation in which A is not inevitably followed by B. If we treat causality as a law, we merely introduce a modern intelligible principle to science.

On new ideas. Frank's ideas on causality seem radical. After all, we have used the concept of magnetism since we were children, whereas discussion of States A, B, C and causality is unfamiliar and highly philosophical. Many biologists might be tempted to dismiss logical positivism as empty intellectualism. If this is so, an examination of Frank's views about how we convince ourselves of the truth of intelligible principles and general theories is appropriate.

His thesis is that a theory, when first introduced, is incomprehensible. We do not understand it and do not use it unconsciously as a premise in our thinking. Therefore, when a theory is new, we treat it as a theory should be treated, as a construct that may be "scientifically valid, but philosophically false". It is scientifically valid in that it makes more and better predictions than competing theories, and it is philosophically false because we do not believe it represents an eternal and self-evident truth. As we become more accustomed to the theory we begin to have more faith in it. Finally, we come to take the generality for truth.

Frank illustrates his point by reviewing how thinkers' attitudes to Newton's laws changed with time. Shortly after Newton published his theory of gravitation, the Irish philosopher and cleric George Berkeley (1685–1753) objected to it. He felt that scientists take a lot of trouble to apply, use and test their theories, but do not try hard enough to understand them. How can a theory be valid if we do not understand it? Berkeley saw that Newton's laws made good predictions, but found them incomprehensible. They were scientifically valid, but philosophically false.

The German philosopher and scientist Gottfried von Leibniz (1646–1716) also objected to Newton's theory. He wondered how a moving body could keep its direction and velocity with respect to empty space, and how bodies can exert a force on one another through empty space. For Leibniz, both experience and Aristotelian physics tell us that these elements of Newton's theory were in conflict with our perception of reality. For Berkeley and Leibniz, Newton's theory was philosophically false because it offended both reason and common sense. However, it was scientifically valid. Consequently, it was used by scientists and technologists for generations. It still is.

With the passage of time, Newton's theory was built into the thoughts of philosophers, scientists and educated laymen. It became assimilated and by the late 18th century, it had become philosophically true. For example, Immanuel Kant claimed to show that the law of inertia could be derived from pure reason and believed that, unless we accept the law of inertia as true, we will never understand nature.

In a few generations, Newton's laws changed from being philosophically false to being philosophically true. They eventually became a necessity of thought. This internalization was so complete that when Einstein showed that Newton's laws were scientifically incomplete, and even false, it was a stunning blow to the concept of scientific truth.

Sir Karl Popper

Logical positivism leaves us with the conclusion that science is not about the real world at all. It is a description of the way that scientists' minds organize sequences of sense impressions. As a philosophy of life and work, I do not find this very attractive. It removes many misconceptions, but offers little that one can use to improve one's science. However, it is a powerful device to free us of our own intelligible principles and to prepare us accept a different philosophy. Logical positivism helped us escape the view that science discovers the whole truth about nature. In doing so, it prepared the way for the views of Sir Karl Popper.

Popper was born in 1902 and trained as a physicist. In Vienna, he came to know the members of the Vienna circle and their ideas. His most influential work was *The Logic of Scientific Discovery*, first published in German in 1930 and in expanded form in English in 1959. He moved to England to escape Nazism and has since published many books and papers in English. Good summaries of the vast corpus of his works are available in reviews by Magee (1973) and Pera (1980), and in an anthology of his writings edited by Miller (1985).

Popper's contribution was to give scientists a beautifully simple scheme for recognizing and evaluating science. He accepts much of logical positivism, including the conclusion that a theory can never be shown to be true. Knowledge therefore cannot be a true understanding of natural laws; it is only the ability to look into the unknown to predict as yet unobserved events. These predictions are achieved by constructs that we call theories. Because science is the activity that generates such theories, science is the only source of such knowledge. Most importantly, the only good theory is one that has the potential to be wrong. If no conceivable observation could show the theory wrong, then the theory must predict every possibility and therefore would tell us nothing. In other words, to qualify as a scientific theory, a statement or set of statements must be potentially falsifiable. For example, the statement that human babies will weigh less than 15 kg could be wrong, so it is a theory. The statement that human babies will weigh something is not.

For Popper, scientists begin by creating a theory. It is irrelevant where this theory came from: principle, observation, revelation, intuition, induction, or simply a lucky guess. What is important is whether the theory identifies any potential future observations or facts as inconsistent with the theory, because the theory makes a prediction by telling us what facts will not be observed. We can then test the theory by comparing future observations with those facts. If unexpected observations are made, the theory has been falsified. If the facts agree with the predictions, we would be justified in using it again.

Popper's work has given us a clear working description of theories and facts. The former are the devices we use to make predictions and the latter are the instance that the theories predict. This great clarification should allow us to communicate better with both scientists and non-scientists, and to do better science. Because it is a scheme that deals only with the relation between theory and observation, and not with intelligible principles or philosophical axioms, we can use it, regardless of future philosophical changes. Indeed, much of the philosophical debate that has subsequently focused on Popper's work seems irrelevant to me as a working scientist. Popper has freed us from the philosophical fashions that make so much of Aristotle and other philosophers incomprehensible.

For me, Popper's work was a revelation. I was troubled by Hume's argument that induction was fallible and verification impossible, and could see no escape from the answer of logical positivism, that science was simply the creation of our minds to describe their own workings. I was not satisfied with science or philosophy.

Popper accepted the reality of the philosophical difficulties that I could not escape, but he also saw that these things did not matter. Science works regardless. What makes it work is its method and central to that method is falsification. As a working scientist I need no longer worry about being wrong, because it is irrelevant to ask if my theory is a true representation of the external world. I no longer need to ask if this theory is more true than that theory. I need only ask:

(1) Does it predict anything?
(2) Does it predict more than its rivals?
(3) Can I show that the theory is wrong?

Furthermore, I can do my science knowing that I have profited from a long philosophical tradition and that I base my thoughts on a current philosophy whose fundamental characteristics are not likely to change. Contemplation of the nature of science has made me a happier and better scientist.

III Normal Science and Pseudo-Science

> "It is the normal practise of scientists to ignore evidence which appears incompatible with the accepted system of scientific knowledge, in the hope it will eventually prove false or irrelevant. The wise neglect of such evidence prevents scientific laboratories from being plunged forever into a turmoil of incoherent and futile efforts to verify false allegations."
>
> Michael Polanyi
> [*Personal Knowledge* (1958)]

Popper's approach has many virtues, but his science is an abstract ideal. When Popper illustrates his ideas, he uses heroic figures like Newton and Einstein. Popper therefore gives a goal to strive for, but not a picture of what most real scientists do. His prescriptive definition of science must be tempered with a descriptive one that reflects better the reality of science as a human activity. Thomas Kuhn has provided one such description.

Real scientists, those who do day-to-day science, are also real people. They want recognition, they feel the pressures of society, and they suffer various limitations of intellect, temperament, resources, and opportunity. Such people probably comprise 99.9% of all scientists who ever lived, and this chapter examines their work. It begins with a review of the masterful work of Kuhn on the nature of everyday science, and ends by considering the reception of challenges to the scientific community, in light of Kuhn's ideas. This book, like many contemporary essays in the field, uses the word "science" in both Popper's prescriptive and Kuhn's descriptive senses, but the context should make my intention clear.

Kuhn's "Normal" Science

In 1962, Thomas Kuhn published what might be one of the most important books about science in this century, and certainly one that has had a continuing influence on me since I first read it in 1968. *The Structure of Scientific Revolutions* continues the process of uprooting our faith in science as an austerely intellectual search for greater truth about more phenomena. But instead of a reanalysis of the philosophy behind the scientific enterprise, Kuhn offers an historical reanalysis.

Many histories of science treat past research either as unsuccessful attempts to reach, or as necessary intermediary steps to achieve, contemporary ideas. Kuhn rejected that approach. Instead, he provides a new and unflattering model about what scientists actually do and have done.

An historical model of science. Kuhn posits that any branch of science cycles between long periods of "normal science" when scientists follow a dominant tradition or "paradigm" and short periods of crisis and revolutionary change when the paradigm is shaken and ultimately replaced. Kuhn also postulates an early pre-paradigmatic stage before the discipline emerges. That phase seems an appropriate beginning for a review of his model (Fig. 8).

Pre-paradigmatic science. The earliest members of a scientific discipline are at a considerable disadvantage, because the discipline cannot yet be well defined. There are no text-books to describe the material of the discipline, no courses to provide model answers to model questions, no scientific societies to identify the proud tradition that contemporary members of the discipline should respect and advance, no manuals of methods, nor any reviews of important questions.

The founders of a field are free of both the guidance and the constraints of tradition. As a result, there is usually a great deal of confusion and flounder-

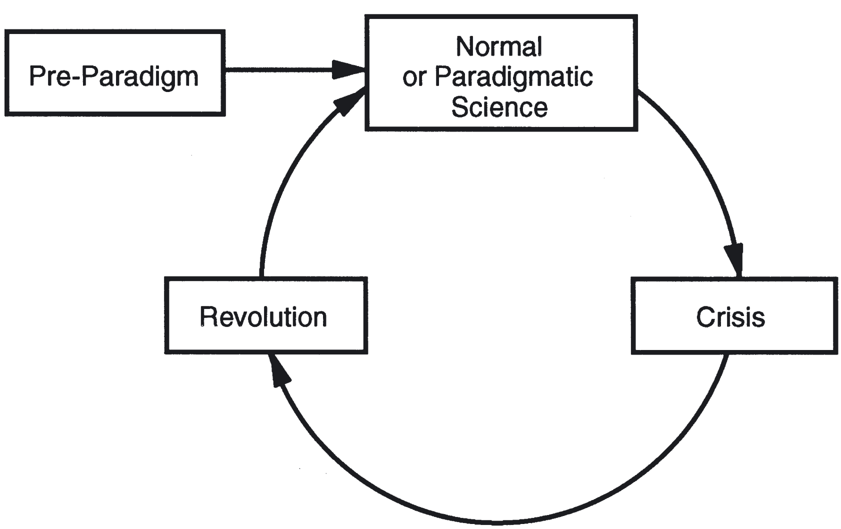

Fig. 8. A schematic representation of Kuhn's model of scientific revolutions

ing in the fledgling discipline. Terminology is inconsistent, methods are suspect and even the relevance of various observations is questionable. More positively, the field is very open because there is no constraining tradition. Different schools of thought compete and intellectual ferment is real. In the absence of specialists, researchers are drawn from many existing disciplines. To talk to one another, they must disseminate their new ideas in accessible language, and since contributions cannot assume a common intellectual base, books are an honoured device for communication. Relevant observations are often so simple, that the new discipline is even open to educated laymen.

Normal science. Eventually, researchers reach some modicum of agreement on the nature of the field. They embrace some view about how their corner of the universe works, at least in general terms, and this view dictates reasonable avenues of investigation. Working within this world-view, practitioners develop standards for education, research, and reporting. They come to accept certain questions as significant, and to ignore others as irrelevant. They produce intellectual leaders, text-books, courses, and learned societies, and these promote specific theories, applications, instrumentation, and methods.

In Kuhn's terminology, these common scientific traditions represent a paradigm or series of paradigms for the new field. Paradigms are what we refer to when we speak of Copernican astronomy, or Newtonian physics, or evolutionary biology. These paradigms not only tell scientists what to expect of the world, they also define legitimate subjects for future research and the methods for that research. In Kuhn's view, textbooks serve to propagate the paradigms of the field, and the purpose of scientific training is to indoctrinate a new generation of scientists to think and act like their teachers. Once the paradigm is so established that the practitioners in the field have a well defined research program, the field may be said to enter the phase of "normal science".

Before Kuhn, the accepted view was that science advances as a struggle between competing theories (Platt 1964). A winning theory is consistent with all relevant facts, whereas the loser is not. Kuhn instead argues that contrary evidence is available for every theory at all times, but that scientists unite behind their favourite anyway. Normal science therefore engenders agreement among researchers, not confrontation. One might wonder why science does not grind to a stop. The answer to this question sets Kuhn apart from other observers of science.

Kuhn suggests that an emerging paradigm is very limited in scope and precision. It is often more successful than alternatives only in solving those problems that a group of scientists have recognized as particularly acute. It out-competes the opposition and becomes established, not necessarily because it solves more problems, but because it promises to solve more. The allure for scientists is that the new theory provides more questions for them to address.

Kuhn's normal science is a mop-up operation as scientists attempt to realize the promise of their paradigm. "Normal scientists" are those who try to squeeze nature into the conceptual mould provided by their paradigm. Because no theory is perfect, they must often ignore, dismiss or simply not see anomalous observations. Thus normal scientists often seem to be striving to confirm their theories, not to test them. Kuhn suggests that even great figures act as normal scientists for most of their careers, and only rarely as revolutionaries. He believes that good scientists must always maintain an "essential tension" between conservatism and radicalism (Kuhn 1977). As a result, normal science is the business that occupies most scientists for most of their lives.

Kuhn identifies three classes of activity that typify normal science. Sometimes researchers who seem to be testing the theory are really looking for confirmatory instances and trying to show how useful the paradigm is. Other times they may be observing certain phenomena more carefully and precisely than ever before, because the paradigm suggested that such efforts may lead to new discoveries. For example, after Newton, more exact measurements of the position of the stars and planets allowed the discovery of other heavenly bodies; after Dalton, more exact estimates of atomic weights allowed the discovery of isotopes; and after Darwin, careful study of heredity led to genetic theory. The third activity in normal science seeks to resolve the theory's initial ambiguities and failings.

According to Kuhn, normal scientists do not revolutionize the field, and likely are never famous. Kuhn's answer to the obvious question about why they do their work is disturbing, yet it echoes Barzun's view of science as entertainment. Kuhn's normal scientists do their work because they enjoy puzzle-solving. They have a question which is certified as valid by the paradigm, they have a set of rules for solution that the paradigm has also specified, and they have a large part of the solution that the paradigm has again supplied. The motivation for science is the same as that for art, history, music and all the other activities that keep humanity occupied: our own disinterested curiosity, perhaps the one truly human activity.

Crisis and revolution. Kuhn's normal science sows the seeds of its own destruction. Eventually normal science ceases to provide us with interesting enough puzzles, so some scientists point to previously ignored anomalies as an indication that the old paradigm is in crisis and begin to look elsewhere for gratification. During this period of uncertainty, the anomalies may provide fodder for research within the old paradigm, so some workers rearticulate theory and practice to account for the now troublesome anomalies. Nevertheless, as more scientists become interested in observations that do not fit, the old paradigm begins to fragment. An alternative approach or paradigm eventually promises more fertile ground for future research. The old paradigm is abandoned, the new one takes its place, and a new generation of normal scientists begin the cycle again.

Kuhn ends with the question of scientific progress. In a Kuhnian scientific revolution, some problems that the old paradigm addressed may be dropped from consideration as uninteresting. Kuhn interpreted these shifts in interest as indications that different paradigms are incommensurate. Thus successive paradigms cannot be compared fairly, and there is no basis to claim that new paradigms are better than the old ones.

Kuhn's model makes science a very human subject, and very different from the intellectual discipline of the philosophers. His science is only "what scientists do", and is much closer to our everyday use of the word than Popper's heroic examples. Nevertheless, the differences between Kuhn and Popper are smaller than they may seem (Kuhn 1977). In particular, Kuhn's model is consistent with the philosopher's conclusion that we cannot recognize truth in science. Indeed, given the scepticism of modern scientific philosophy, we probably feel less that we understand nature than did most of our predecessors.

Criticisms of Kuhn's model. Despite the richness and even genius of Kuhn's book, some aspects of his model seem less sound. Although it is not my intent to review his position fully, I cannot leave the topic without pointing to some shortcomings.

The model implies that all sciences pass through a pre-paradigmatic stage. However, such a phase would be very difficult to identify in any area of human interest. Theories and paradigms existed in most areas long before the emergence of science. For example, before there was an evolutionary biology or a uniformitarian geology, there was a creationist paradigm, and there seems to have been some such paradigm since the dawn of humanity. Perhaps a pre-paradigm phase is only an illusion that one sees in retrospect.

Another criticism focuses on Kuhn's use of the scientific papers of normal scientists as evidence for his thesis. These papers often contain confirmatory tests of dominant paradigms. The authors' words suggest that they are pleased that their tests support the paradigm and that they did their work to protect that paradigm. However, when researchers write a paper, the rationale may have to be rephrased to fit the results. The introductions therefore present an idealized and flattering picture of scientific foresight, because any other introduction would confuse the purpose of the paper and confound the reader. If a scientist wanted desperately to overturn a paradigm but failed, the finished paper would almost certainly describe the work as a successful test of the dominant ideas in the field (Medawar 1990). Kuhn may have over-interpreted these politic misrepresentations as indicators of unthinking support for the dominant paradigm among scientists.

My final criticism is more general. Kuhn's book is short and readable, but this was achieved in part by excluding examples. Tests for his ideas are therefore difficult to devise because he provides so few models. Indeed, when one tries to identify a paradigm, a crisis, a pre-paradigm stage, or even a field of normal science, Kuhn's intuitively attractive concepts prove surprisingly difficult to apply. We discover that paradigms exists within paradigms, that hierarchies of normality, crises and revolutions make any identification of the current phase of a science ambiguous. Seemingly consistent episodes are therefore easy to find because the model is slippery and the observations malleable. For similar reasons, critical tests are rare (Cohen 1985).

Kuhn's model is therefore not without problems. Perhaps that is appropriate for a potential paradigm of the nature of science. After all, initial problems are what the model predicts.

"Pseudo-Science"

Kuhn's analysis helps resolve one of the continuing challenges to scientific researchers. It explains why most of us dedicate our lives to the resolution of apparently minor details of nature, rather than addressing glamorous questions of broad interest to society. Why do we not leave our laboratory benches to study alien abductions, holistic medicine, extra-sensory perception, or spectral apparitions? Kuhn's answer is that our scientific tradition identifies research on these topics as inappropriate. Such material can be called "pseudo-science", even if it passes Popper's criterion of demarcation, because it falls outside the Kuhnian model whereby science is largely what normal scientists do.

In this sense, pseudo-science is anything that purports to be science, but that the established scientific community does not accept as such. So defined, pseudo-science is not the delusional domain of a lunatic fringe. For example, Gregor Mendel spoke to the Brünn Natural History Society on two occasions in 1865 about his experiments with inheritance in plants; he published this work the next year and informed the leading scientist Karl von Naegli about the importance of the work in 1867. Nevertheless, as far as the world of science was concerned, Gregor Mendel did not exist. No one paid any attention to his work until 1900 when it was rediscovered simultaneously by three botanists (De Vries, Tschermak, and Correns) and Mendel became the father of Genetics.

What I am suggesting is that from 1865 to 1900, Mendel's work was pseudo-science, because it was treated as pseudo-science. For 35 years no one recognized it as science. It was simply ignored. There is nothing unusual about the treatment Mendel received. Most new ideas about science are ignored. No one gets excited about them, no one cites them, they just disappear unnoticed. That is the fate of most pseudo-science.

A further example demonstrates the other extreme of the scientific response to pseudo-science. In 1910, the German meteorologist Alfred Wegener became convinced that, 200 million years ago, all the continents were joined into a single super-continent he called Pangaea. Wegener promoted this theory for many years and it excited considerable debate amongst geologists until 1929. That year, at the Geological Congress, Wegener's theory was officially declared to be false, and so became pseudo-science for the geologists. Curiously, there was widespread, if tentative, acceptance of Wegener's views among biologists, even after it had been rejected by geologists; so a theory could be pseudo-science under one tradition while it was still science under another. There may be no right or wrong in science, but a very similar distinction is maintained between what the majority of scientists declare as interesting or uninteresting. That is the point of these examples of pseudo-science.

The year after his theory was declared false, Wegener himself disappeared in Greenland where he had gone to test his theory. The theory did not die. A number of new discoveries, like the lack of sediment in parts of the ocean floor and the mirror images of fossil magnetism on either side of the mid-oceanic ridges, eventually forced a complete re-appraisal. Today, the 'new' theory of plate tectonics is universally accepted.

This cruel and unfair treatment of new hypotheses is just what one should expect. According to Kuhn, we scientists spend most of our careers trying to patch up our leaky theories, modifying and mending them in the hope that they will one day fit the facts. As long as the theory holds the promise of being patchable, as long as it continues to provide interesting puzzles to keep us amused, there is no chance that the majority of scientists will reject it. We will cling to the established paradigm as tenaciously as a child clings to a favourite toy.

We will not reject a favourite theory simply because someone shows us a few embarrassing facts. Neither will we accept a new theory simply because some rebel champions it. There is a time for new theory, and that time is when our old theory has ceased to entertain us by generating new, but soluble, puzzles. This forces us to look to the anomalous observations that we had previously ignored as pseudo-science. Thus Mendel was a pseudo-scientist in 1865, but by 1900 his time had come. We were ready for a new toy.

The reverse of this reaction to a new theory is also part of the reception of pseudo-science. As long as we are content with the dominant paradigm, the theory it represents moves gradually towards acceptance as a universal truth. As such, the paradigm tells us what sort of experiments we can do, what methods we should use, what canons of evidence we will accept, and what form of publication we should use.

The initial reaction to the theories of Mendel or Wegener could be discounted as near-sighted conservatism that was eventually put right by forward thinkers. In that case, the examples would show the adequacy of scientific self-correction, despite the relativism of scientific truth and the dominance of the paradigm. This alternative explanation seems to posit that, although science was always wrong in the past (because no past theory has survived unchanged), modern science is right. I prefer the relativistic explanation, not just because it avoids hubris, but because it renders the scientific conservatism of the past more rational and comprehensible. The conservatives were not benighted disciples of error, but conscientious scientists working under other premises than those we use today. The lesson we should learn from Mendel and Wegener is to be more tentative in our conclusions about the validity of scientific theories.

Velikovsky. My last example of pseudo-science has not enjoyed the rehabilitation of Mendel or Wegener. It has always been considered pseudo-science and seems likely to remain so. My purpose in introducing such material is not to champion a failed cause, but to illustrate the resistance of science to new paradigms, the advantages and disadvantages of such resistance, and some of the mistakes that characterize a failed scientific revolution.

Immanuel Velikovsky was born in Russia in 1895. He studied abroad, but returned to Moscow to take a medical degree and subsequently practised medicine and psychiatry in Tel Aviv. After 15 years, he began a study of Akhenaton, Oedipus and Moses, during which similarities in the legends of different civilizations convinced him that a global catastrophe took place about 1450 BC. While seeking the cause of such an event, he discovered that neither Babylonian nor Hindu astrologers ever made mention of Venus among the planets, even though it is one of the brightest objects in the sky. He concluded that Venus did not exist during early human history.

The theory. From these and many more observations, all derived from ancient texts, Velikovsky developed the following theory and published it in *Worlds in Collision* (Velikovsky 1950). Our solar system originally had one less planet than it does now. Sometime before 1500 BC, a violent explosion on Jupiter gave birth to a massive comet that eventually became the planet Venus. About 1450 BC, this comet passed close to the earth, producing enormous tides, global heating, electrical discharges and a rain of hydrocarbons. These events are associated with the exodus of the Jews from Egypt. The comet then disappeared into space, only to return around 747 BC, when it collided with Mars. This collision brought the comet into planetary orbit as Venus but so perturbed the orbit of Mars that in 687 BC, Mars almost collided with Earth, causing one or more new global catastrophes. Although they may not have been so devastating as the upheaval of 1450 BC, they were enough to tilt the earth's axis by 10°.

According to Velikovsky, this theory explains many myths and legends, explains the absence of Venus from early astronomical records, and explains some of earth's petroleum deposits (as hydrocarbons from the planet's tail). He also believed that the theory predicted that (a) Venus would be hot, (b) its atmosphere would contain hydrocarbons, and (c) Jupiter would emit radio waves. Neither these predictions nor others are very clearly stated in the book. Nevertheless, Velikovsky believed that he had made these and other predictions, and that all of them proved correct (Anon. 1972).

Velikovsky followed *Worlds in Collision* with a second book, *Earth in Upheaval* (Velikovsky 1955), in which he gathered together a large number of biological and geological observations that he believed were consistent with his theory. He places before the reader a whole series of both well-known and obscure facts about vast bone heaps in the Arctic, about whale skeletons on hilltops, about erratic boulders found hundreds of kilometres away from their parent bedrock, about the food in the mouths of quick-frozen mammoths in Siberia, etc. These observations serve three purposes. First, Velikovsky wanted to convince us that many observations do not fit existing geological theory. Second, he wants us to accept that there was a recent world-wide cataclysm, and to change the date of the last ice age so that it will be consistent with the hypothesized approach of Venus in 1450 BC. Finally he wants to convince us that biological evolution could not have taken place by mutation and natural selection as Darwin supposed, but that it arose through mass extinctions caused by the cataclysms, followed by rapid speciation through multiple mutations caused by heat and radiation associated with the cataclysms.

The reception of Velikovsky's theory. At the time, Velikovsky appeared even more radical than he does now. His theories about rapid speciation predated the contemporary interest in discontinuous rates of speciation called "punctuated equilibrium" (Eldredge and Gould 1972) by a generation. His belief that single celestial events might control major turning points in terrestrial natural history predated current theories about mass extinction and meteorite impacts (e.g. Melosh et al. 1990) by 30 years. And his explanation of events in human history as the result of dramatic changes in their non-human environment was equally far ahead of its time.

Velikovsky managed to challenge the fundamental paradigms of four fields simultaneously. Not surprisingly, he was not well received. Most scientists simply and totally ignored his work. Some wrote damning criticisms of his book. Five of these critics had never read it. Other scientists brought such pressure to bear on his publishers (MacMillan) that they transferred the rights to the book to Doubleday and Company which was less easy to pressure because it published no textbooks. The unseemly condemnation of the author and his ideas by the scientific and academic establishment (de Grazia et al. 1966, Rose 1972, Stove 1972) made Velikovsky something of a hero during the 1960's. His book sales made him a millionaire, and eventually he was appointed to the Princeton Institute for Advanced Studies, where Einstein had worked. But he never found scientific respectability for himself or his theories.

Why did Velikovsky's theory fail to win support? If we accept Thomas Kuhn's view of science, it is clear that Velikovsky made a number of fatal mistakes. He failed to present scientifically acceptable evidence, he failed to present his work in the proper form, and he tried to revolutionize fields that were not ready for change.

Velikovsky's data sources were ancient texts, including the Bible. For him, observations like the parting of the Red Sea by Moses and the fall of manna on which the Israelites fed were anomalous facts that the dominant paradigm could not explain. For most scientists, these stories were simply irrelevant; they were not facts at all. Most scientists saw the history of their discipline partly as a liberation from such ideas. Scientists did not cite holy books; they used the theories of physics, the concepts of mathematics, and the resolving power of fine spectroscopes and powerful telescopes. Velikovsky's sources seemed a long step backwards. A serious work of science would be packed with tables, graphs and equations, but Velikovsky wrote 400 pages without any. By the standards of science, but not his own, Velikovsky presented no data at all.

Velikovsky also failed to examine any other explanation for the observations he presented. Although we scientists cannot hope to be unbiased towards our intellectual creations, we are expected to vet these ideas as carefully as possible by considering alternatives. Velikovsky passed this onus to the reader and thus sacrificed his own credibility.

Velikovsky also used the wrong style to present his ideas. Compared to the dry, impersonal writing of the professional researcher, his prose looks like sensational journalism. Moreover, Velikovsky chose to publish in popular books, rather than in scientific journals. Scientists have developed formal standards for communication, the scientific paper and the monograph (Kinne 1988), and are deeply suspicious of those who ignore those standards.

Not only did Velikovsky fail to present his theory effectively, he also chose to present it at the wrong time. According to Kuhn, a new theory can only be effective when the old paradigm has entered a state of crisis, when it has ceased to provide a bounteous supply of soluble puzzles. Unfortunately for Velikovsky, his books appeared when traditional sciences had more puzzles than they had scientists to solve them. Astronomy was still ecstatic about the giant telescope at Mount Palomar, and radio-telescopes were in the offing; the theory of stellar evolution was still fresh, the nuclear furnace was new, and the consequences of the red shift were being explored. Geologists were also delighting in a surfeit of new tools: deep-drilling for stratigraphy, magnetometry, seismographic surveys, and soon satellite pictures and remote sensing; intellectually, they dealt with the evolution of rock types and the discovery of new minerals, and were on the brink of the new theory of plate tectonics, a theory which would eventually address many of Velikovsky's objections. Biology was even healthier. Chromatography and the electron microscope soon led to the development of molecular biology; evolutionists were pursuing the possibilities of the new synthesis between genetics, natural history, selection and molecular biology. Scientists felt no need for a radical new paradigm, when normal science offered so much.

Finally, and perhaps most importantly, Velikovsky failed to give a clear and unambiguous description of his theory. He hints at its beauty, like a dancer behind seven veils, but the veils are never lowered. The theory is never apprehended. By any scientific standard, such vagueness is unacceptable.

Testing Velikovsky's theory. Kuhn's model explains the lack of interest in Velikovsky's theory, but not why the theory was ridiculed rather than being subjected to scientific tests. I therefore raise two further questions: "Can Velikovsky's theory be falsified?" And if so, "Why was it not tested?"

I believe that Velikovsky's theory can be tested and that if it had been tested, it would have been falsified. In a discussion of tree-rings in relation to the catastrophism, Velikovsky tries to convince the reader that no trees survived the cataclysm of 1450 BC and that there had been violent climatic changes in 747 and 687 BC. To achieve his first objective, he describes the dating of the giant sequoias of California, and concludes that "the most ancient of these started life after the year 1300 before the present era". This is advanced as evidence that no tree survived the "great catastrophe of the middle of the second millennium". He dismissed from consideration the oldest tree of all — the General Sherman — on the grounds that it had not been cut down. However, everyone knows that you can age a tree without cutting it down. In fact, the General Sherman tree had been aged in 1946 and its germination date estimated as 1550 BC ± 500 years. Thus there is a good chance that this tree antedated Velikovsky's great cataclysm. Since Velikovsky published, even better evidence against the great cataclysm has been found. A number of bristlecone pines have been aged and appear to have begun life between 2050 and 2950 BC.

A second category of tree-ring data can be used to test Velikovsky's theory. Annual growth varies with climate, so dramatic changes in the width of the annular rings might indicate climate change. Velikovsky found evidence for such changes that might represent the cataclysms of 747 BC and 687 BC (Douglas 1919), but failed to mention that even greater changes occurred many times in the life of these trees. Furthermore, he neglected to mention that very large annual fluctuations in tree growth are correlated with very slight differences in mean temperature and precipitation in the recent record. Thus we must conclude that there is no evidence for any major disturbances over the entire period from 750 to 660 BC. Similar evidence for the absence of cataclysms can be had from the record left in lake sediments.

If Velikovsky's theory can be falsified with observations like this, one must wonder why it was not done. I cannot speak for others. For myself I did not bother to publish these tests or to devise others because these ideas seemed so futile. Why would anyone want to disprove something that no one believes (at least, no one whose scientific opinion is worth having)? If someone claimed that Mars was made of Edam cheese, what joy would scientists have in disproving the theory? What place would they win in the estimation of their peers or in the history of science? As Polanyi suggested, the normal practice of scientists is "wise neglect".

IV The Ecologists' Disease: Two Personal Examples

> "In dealing with any aspect of limnology, as perhaps any other branch of science, it is impossible to avoid the thought that no work is perfect and that the greater proportion of published investigations are very imperfect indeed. Every one of us is at fault in some way or another, every one of us must attempt to achieve progressively higher standards in accuracy, scope and imagination."
>
> G. E. Hutchinson
> [*The Prospect Before Us* (1966)]

Ecologists have known for over a generation that something is wrong with the earth. There are too many people, too few wild places, too much waste, too little clean water, too many chemicals, too little food. These troubles make the life of an ecologist interesting, if depressing. We have been dragged from the quiet of academia to help solve the global problems of over-exploitation and over-population.

We have tried to respond effectively. Everywhere, universities and colleges have produced courses, programmes, chairs, institutes and faculties to deal with "human biology" and "environmental science". Some ecologists spend their evenings in legal challenges to proposed developments, political movements, and preaching to the public. Ecological researchers offer a dizzying array of new techniques, concepts and instruments to address our problems. A suite of learned societies have been formed and a host of new journals are being published. This is an exciting time because society desperately needs the services of good ecologists, drawn from the full range of science and beyond.

Nevertheless, for many ecologists, ecology has not provided the quest we sought. We entered the science because we felt a love for nature and the beauty of natural things, and because these things are under threat. Then, as soon as we were trapped in our careers, teachers confronted us with theoretical models, multivariate statistics, simulations and hypothetico-deductive frameworks. Our colleagues express horrified disbelief when we admit ignorance of eigenvalues, matrix algebra or Laplace transforms, and we naturalists hide our inadequacies like guilty secrets. It sometimes seems that we can only save the things we love by abandoning them in our work.

Even as we accept our inadequacy, we make another horrifying discovery. Different experts are equally confident, but they all have different ideas. At this point, we should feel bewildered.

My own bewilderment first caused me pain, but then it led me to wonder how much of what we call ecology can be considered scientific. Other ecologists are also questioning the relevance of ecological research, asking if their work is useful, and if they could be more effective. These questions spring from a deep disillusionment with the present paradigms of ecology. I am encouraged by such questions, because the present confusion is a sign that better times may be in store for us. I think ecology is ready for a Kuhnian scientific revolution (Kuhn 1962) and I see criticism as the goad that will push us to change (Peters 1991a).

I contend that the body of ecology is infected by a strange disease. The infection is not new, but its extent was unappreciated until our troubles were brought into the open by a set of unusual circumstances. Just as a heavy snowstorm reveals a blockage in the coronary artery of the hapless shoveller, the environmental crisis has revealed the unhappy state of ecology. The disease of ecology is that it is a science that lacks theories it thought it had. When we are asked to predict the impact of a new dam, or of an oil spill, or of chronic chemical contamination, we cannot do it.

This diagnosis can be illustrated with examples from the greater literature, but such critiques are available elsewhere (Peters 1991a, Schrader-Frechette and McCoy 1993), so I need not repeat that information. This chapter dwells on questions of lesser generality which arose in my own work. In part, I do this because I know that work better, so I can criticize it more easily. I also have a more subtle reason for self-criticism. I want to show that all ecologists carry the infection and to encourage others to be at least as critical of themselves as they are of others.

Science and Ecology

Our problems arise because ecologists do not seem to appreciate fully what a science should do. The job of science is to produce and examine a set of one or more statements, called theories. A scientific theory is a tool that specifies which of an infinite range of possible states are likely to occur, and which are not (Fig. 9). In other words, a scientific theory is a statement that makes a prediction and so tells us what we can expect to observe.

The most informative theories identify the likely future observations of the system precisely and completely. To do this, they must exclude most possibilities as unlikely. Thus the best theories are highly restrictive, and the worst are slightly restrictive. Constructs that place no restrictions on the future states of the system make no predictions at all and should not be called theories.

We may want to do more than predict. For example, we may want to explain or to understand nature. We may claim that we can do more, but those claims only demonstrate our naivety. Science cannot do more. The only way that we can demonstrate our understanding of nature is with predictive power; all else is opinion and posture. By ignoring that basic limitation of science, ecologists guarantee failure in their great endeavours, and direct attention away from what science can do, prediction.

Non-theories

Some ecological constructs are called theories because they tell us what might happen, even though they fail to identify what might not. As a result, every observation is either consistent with the general construct or irrelevant to it; no observation will falsify it. Such constructs are not theories at all. That they are given this status by ecologists reflects our failure to think about science.

The niche. The niche as a multi-dimensional volume in environmental hyperspace (Hutchinson 1959) is a familiar example of non-theory. This concept provides a model whereby we could order our observations about a

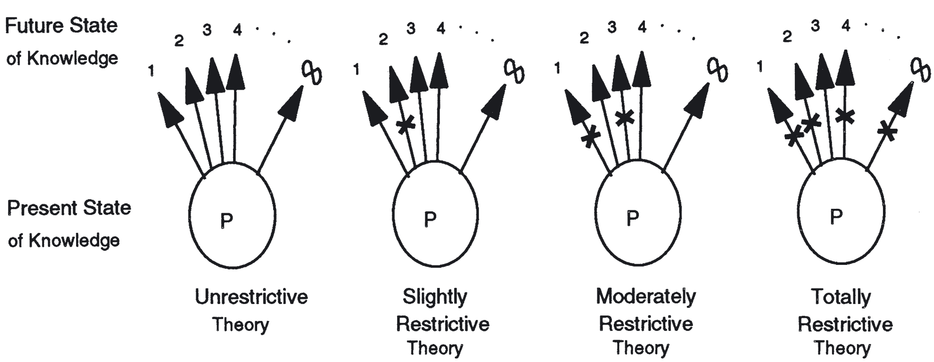

Fig. 9. A classification of putative scientific theories in terms of the degree to which they eliminate possible future states of the system as improbable

species' occurrence, or performance, as a function of some of an infinite number of environmental factors. Because the hypervolume has no definite shape, any form of the response will do. Because there is no minimum or maximum number of factors to be specified, any set of appropriate observations can fit. Because there are always other axes to establish, the niche can never be fully described, so seeming overlap between different species is not unexpected. And because the significance of any degree of overlap on any measured axis is unspecified, one is free to interpret overlap in any way one wishes. In short, any observation is consistent with the construct, and none is excluded. The multi-dimensional niche is wholly unrestrictive.

To assess a theory we must ask not "What facts are consistent with the theory?", but "What observations would be inconsistent with it?" That is Popper's criterion of falsifiability. If we focus where a theory may fail, we are more likely to find its failings, to seek improvements and eventually to develop better theories. But if we are interested only in showing how well a theory performs, we will focus on confirming instances and entrench that theory in the science, excluding alternatives and stultifying scientific advance. We must remember that an infinite series of relations (i.e. of theories) can fit any finite pool of data equally well (Chapter I), so confirmation is relatively uninformative about the validity of a theory. As scientists, we must seek the weaknesses of existing theory, so we can move to offer a better theory.

The competitive exclusion principle. The competitive exclusion principle provides a second case of an ecological non-theory. This principle goes under several names, but most students of ecology are exposed to it in the Lotka-Volterra equations. These equations ostensibly deal with the fate of two competitors, Species A and Species B, occupying the same habitat. The principle tells us that if you put two potentially competing species together either A will be eliminated, presumably by competition, or B will be eliminated, also by competition, or A and B will coexist, by sharing the habitat. A final case, where both A and B die out, is implicit but uninteresting. The principle is consistent with all possible outcomes; therefore it cannot be falsified and provides no information.

Hardin (1961) recognized that the competitive exclusion principle was unfalsifiable long ago, but he defended the principle as an aid to thought. For example, it has caused generations of ecology students to puzzle through the abstract algebra of the Lotka-Volterra equations, it has focused our thoughts and research on examples of coexistence of similar species, and it allowed us to organize observations of these examples within a common rationale, determining the resources over which competition is most intense, the likely mechanisms of competitive exclusion, or those differences in resource use that allow coexistence.

I pursued this example in my own work on the co-occurrence of calanoid copepods in Ontario lakes. Calanoids are minute crustaceans that constitute a major component of the zooplankton in most lakes, and in the sea. Hutchinson (1961) recognized that the co-occurrence of two or more species in the homogeneous habitat presented by the open water of lakes represented a major challenge to the exclusion principle. Co-occurrence of such similar animals in such a simple environment should lead to exclusion, but it does not. This "paradox of the plankton" became a classic example for limnological applications of ecological ideas (Hutchinson 1951).

My first approach to the problem was to establish its reality. To do this, samples were collected in over 100 lakes to determine the extent of coexistence among calanoid copepods in Ontario. Calanoids were found in 95 lakes and different species co-occurred in almost 3/4 of these. The animals were represented by four genera: *Senecella*, *Limnocalanus*, *Epischura* and *Diaptomus* (Table 3).

We first used the principle to rationalize and simplify our observations. The principle deals with competitive exclusion, but *Senecella* and *Epischura* are thought to prey on other zooplankton; we therefore eliminated those genera from consideration. As disciples of Darwin we had no difficulty in positing that ecological competition is a universal phenomenon or in accepting Darwin's statement that competition between closely related species is likely more severe. We therefore further limited our analysis to the most common and speciose genus *Diaptomus*, on the grounds that the others may be sufficiently distinct phylogenetically that they no longer compete with *Diaptomus*. This had the further advantage of directing our attention away from *Limnocalanus* whose little known food habits might include predation. *Diaptomus* is considered a filter-feeding herbivore, although its food habits in nature have actually been little studied. Subsequently, the genus has been divided into several genera. I will not use this taxonomic nicety, but it could be invoked to save the hypothesis.

Table 3. The number of lakes in southern Ontario in which each species of calanoid was found

Species	Lakes	Species	Lakes
Diaptomus minutus	70	*D. birgei*	2
D. oregonensis	69	*D. ashlandi*	1
D. sicilis	9	*Epischura lacustris*	49
D. reighardi	4	*Limnocalanus macrurus*	11
D. sanguineus	2	*Senecella calanoides*	5

After eliminating other genera from consideration, 92 lakes remain in the sample; these contain seven common species of *Diaptomus*, and these congeners frequently co-occur (Table 4). *D. oregonensis* and *D. minutus* occur together in about half the lakes, occasionally with a third species (*D. sicilis* in six lakes, *D. sanguineus* in two, and *D. ashlandi* in one). *D. birgei* or *D. reighardi* occasionally co-occur with *D. minutus*. This completed the first phase of study. Directed by the competitive exclusion principle, potential co-occurrence among congeners had been established and a scientific puzzle had been generated.

The second part of the study was directed at the mechanisms by which this co-occurrence was achieved, or equivalently, at the way species in the same lake divide their habitats so that apparent co-occurrence is not real. I will only give an impression of these results (Rigler and Langford 1967). Fig. 10 shows that the most common putative competitors, *Diaptomus oregonensis* and *D. minutus*, differ in their depths of maximum abundance, although there is considerable overlap and in some lakes their vertical distribution is virtually indistinguishable. When a third species is present, it consistently inhabits a deeper stratum than either *D. oregonensis* or *D. minutus*, although it may sometimes overlap with the two common species.

Our results are therefore consistent with the competitive exclusion principle: coexisting competitors do seem to divide their resources. However, we are not yet justified in concluding that spatial separation is sufficient to allow coexistence. The overlap between *Diaptomus oregonensis* and *D. minutus* seems great, yet these species co-occur in half of our lakes. We should therefore expect further differences between these species. Sandercock (1967) showed

Table 4. Frequency of associations in which the various species of *Diaptomus* were found to coexist

	Type of association									
	A	B	C	D	E	F	G	H	I	J
D. minutus	X		X	X	X	X	X	X		
D. oregonensis	X	X		X	X	X				
D. sicilis				X			X			
D. reighardi									X	X
D. sanguineus					X					
D. birgei								X		X
D. ashlandi						X				
No. of lakes	36	24	19	6	2	1	3	1	1	2

that the species are also temporally separated both in breeding and in diurnal migration. These differences are more substantial, and again lead to the conclusion that the two species coexist because they have divided their resources.

In short, our investigation of competitive exclusion in *Diaptomus* ended like all other investigations of the issue. Whenever two coexisting species are studied, we find ecological differences between them, and thus we support the competitive exclusion principle. When we find no difference, as when *D. oregonensis* and *D. minutus* had similar vertical distributions, we cannot conclude that the principle was wrong. That observation, like the supposition that both species use oxygen and phytoplankton, is irrelevant because the principle allows co-occurring species common use of many resources, provided they divide at least one.

The problem is not yet finished. We have not yet shown that these differences are enough to prevent competition. We might make further observations to determine other differences in resource use, we might determine limiting resources for *Diaptomus*, or we could manipulate the abundance of

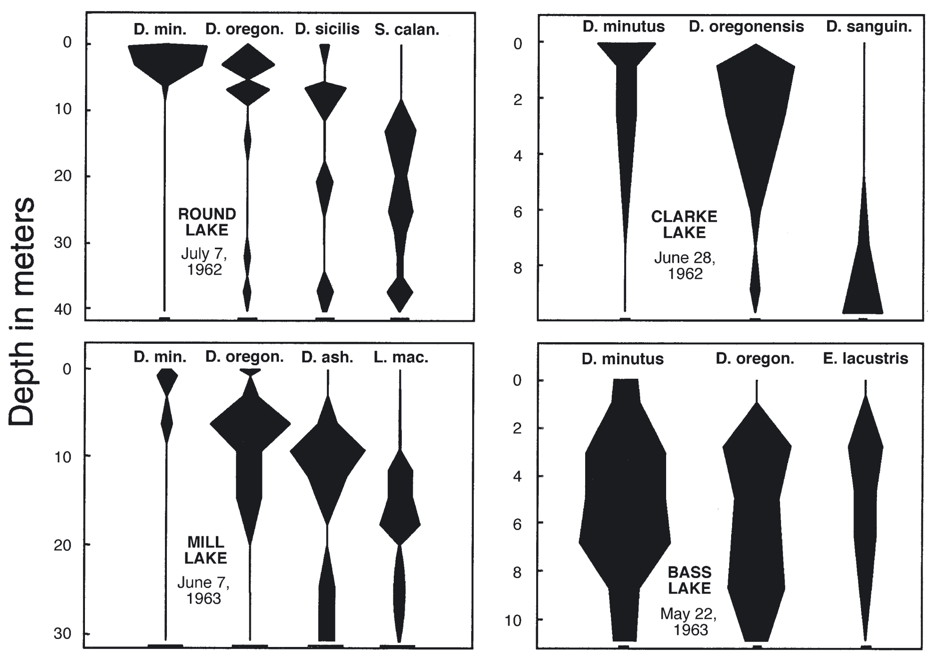

Fig. 10. Vertical distributions of co-occurring species of the calanoid copepods (genera *Diaptomus*, *Senecella*, *Limnocalanus*, *Epischura*) in several Ontario lakes. The length of the horizontal bars at the base of each polygon gives the scale since each is proportional to 5 copepods l^{-1}

one species to see how the other responds. The principle suggests much more work we might do. It acts as a fruitful paradigm.

I do not believe that any further studies would disprove the principle of competitive exclusion. In every case, the results would be confirmatory, or irrelevant. This is a serious flaw. When we deal with a predictive theory, we must be able to specify the observations that would be inconsistent with the theory. In the case of competitive exclusion, this is not possible. Our study, designed in light of the principle, could not have shown the competitive exclusion principle to be false.

Ecologists seem to like constructs that fit all relevant observations. Like Aristotle and his intelligible principles, we use observations to demonstrate the applicability of our ideas, to shore them up against criticism, and to extend them to new phenomena. As "theories", these generalities are completely safe, and completely uninformative. Unlike Aristotle the scientist, we do not use the general constructs to identify critical observations that might cause us to change our general ideas. Indeed, we cannot do so because the constructs are not susceptible to test. If we followed the simple rules of science, non-predictive constructs like these would have been eliminated years ago, and ecology would be less cluttered with nonsense.

Weak Theories

The best theories are those that tell us exactly what will happen by identifying only one future state among many as probable. In doing so, they identify the many other future states as improbable. We can call these highly desirable constructs "restrictive theories" (Fig. 9), because they restrict or limit the range of possible futures to a narrow range of probability. Such precise predictions are not common in ecology, but they can be found where a system is highly controlled or where the experimental manipulation is very large.

Ecology contains many theories which are only slightly restrictive. They might identify one or two future states that would be inconsistent with the theory. Other weak theories are simply quantitatively inexact. They predict trends: neonate size increases with maternal weight; species number decreases at higher latitudes; algae increase with nutrients; etc. These theories are predictive, but their predictions are so uninformative that the theories are virtually useless. They survive because ecologists do not demand better. Strong science recognizes that falsifiability and predictive power are relative, so each advance raises the standards for acceptable predictive power.

Evolution by natural selection. Other weak theories address only a limited range of phenomena, but are misleading because we act as though they addressed many more. For example, the theory of evolution by natural selection may be only weakly predictive. I say "may be" because I want to be generous. The principle may not be a theory at all (Slobodkin 1968, Peters 1991a).

Natural selection is characteristically invoked to explain or rationalize the variety of animals inhabiting the earth and their exquisite fit to their environments. In those contexts, there are four possible observations: maladaptation and extinction, adaptation and survival, descent with modification, and an evolutionarily stable state. These alternatives exhaust the possible future states, but no general statement of the theory of evolution allows one to predict what will occur in a given case, or the average response in a set of cases. Respecifications of the general theory may exclude some of these possibilities and therefore seem to offer predictions, but close analysis of those cases reveals only a narrower range of possibilities tautologically entailed by the particularities of the case (Peters 1976).

The theoretical status of natural selection apparently depends on some minor implications. Darwin thought that his theory would be shown false if any organ were found which existed for the benefit of another species. Ruse (1982) suggests that the theory of evolution predicts that some animals will be difficult to classify and that palaeozoic mammalian fossils will not be found. Whether or not these are predictions from the general theory is not under debate here (see Peters 1991a). Instead I want to point out that the absence of altruistic organs or the problems of taxonomists are not phenomena that interest evolutionary biologists. If the generality of evolutionary theory does not predict the phenomena of major interest, it is not theoretically relevant to those interests.

A construct is not valuable just because it can be made to yield a prediction. That only meets formal requirements of a scientific theory. Constructs can be theories and still fail to tell us anything we want to know. Popper's demarcation is only a bare minimum.

Weak theories are misapplied when they are used in situations where they eliminate no possibility. Like non-predictive constructs, concordances of weak theories and data are used to organize or "explain" unpredictable observations in terms of the generality, and to extend the sway of these non-predictive generalities. The frequency of such concordance is then used to defend the general construct in areas where its predictive power is negligible. The increasing popular technique of "hypothesis testing" in ecology (Fretwell 1975) often exploits this confusion to warrant weak theory, rather than to promote predictive power. The only protection against such abuse is to ask in every instance where a theory is invoked, "What observation would have falsified the theory?"

Concepts and measurement of phosphorus fractions. Because ecologists are uncertain about the nature of theory, they often seem to confuse theory with fact. Established, or merely familiar, theories are treated as if they were true, and therefore no longer worthy of the tests and scepticism that are the due of every theory. Alternative theories are regarded as contrary to facts, and falsifying facts are seen as erroneous theories. The effect is to entrench error and to slow the pace of scientific response and growth.

I became aware of my own confusion of fact and theory in an analysis of the various fractions that comprise phosphorus in lakes. Phosphorus fractions are traditionally identified operationally (Fig. 11). To measure the "total

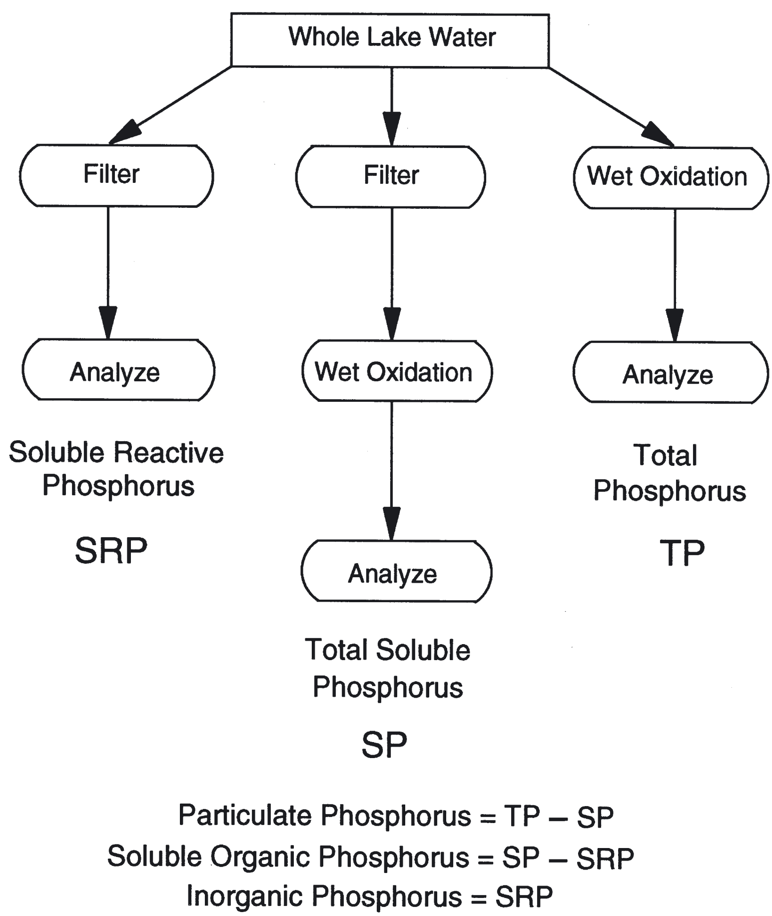

Fig. 11. The operations by which different fractions of phosphorus in lake water are characterized

phosphorus concentration" in a water sample, the organic material in the sample is burnt away by wet oxidation. All the phosphorus in the sample is thus converted to a soluble, inorganic form that reacts quantitatively with an acid molybdate reagent to yield a blue compound. The concentration of this blue compound is proportional to that of reactive phosphorus, so phosphorus concentration can be measured spectrophotometrically (Griesbach and Peters 1991).

If the sample is filtered before analysis, the phosphorus in the filtrate is taken to measure "dissolved" or "soluble" phosphorus in the lake water. Soluble phosphorus is analyzed in two different ways. If the sample undergoes wet oxidation before exposure to acid molybdate, the concentration of "total soluble phosphorus" is estimated. If the sample is exposed to acid molybdate without oxidation, the concentration of "soluble reactive phosphorus" is measured. The difference between total soluble phosphorus and soluble reactive phosphorus is the amount of soluble phosphorus liberated by oxidation and may be called "soluble unreactive phosphorus". The difference between total phosphorus and total soluble phosphorus is a measure of "particulate phosphorus".

Each of these fractions is subject to varying interpretations, but the most common are as follows. Because ortho-phosphate (also called PO_4 or inorganic phosphorus) also reacts with acid molybdate, without oxidation, soluble reactive phosphorus is usually considered to be PO_4; because orthophosphate is a prime plant nutrient, soluble reactive phosphorus is usually taken as a measure of available algal nutrient. Similarly, because soluble unreactive phosphorus is not ortho-phosphate, it is often considered to represent biologically unavailable forms of dissolved organic phosphorus. Particulate phosphorus is thought to be a mixture of the phosphorus bound to living and dead particles. Fresh water researchers now focus on total phosphorus (Chapter IX), but many workers still see soluble reactive phosphorus as particularly meaningful. Such considerations were apparent in the early work at the Experimental Lakes Area in Ontario (Armstrong and Schindler 1971), and still prevail in work by marine biologists and public health officers (APHA 1989).

I became interested in these fractions when I began to wonder about the biological availability of organically bound phosphorus, and sought a lake with high concentrations of soluble unreactive phosphorus for my experiments. The prevailing theory at the time was that soluble unreactive phosphorus concentrations were disproportionately high in tea-coloured lakes. Hutchinson (1957) had advanced this hypothesis to explain differences in the proportion of soluble organic phosphorus reported in lakes in Connecticut, Michigan and Wisconsin (Table 5, overleaf). However, when I tested this theory in Ontario lakes with different degrees of colour, I found similar

Table 5. The proportion (%) of total phosphorus in different soluble fractions and in particulates as reported for lakes in Ontario and the literature. (From Rigler 1964)

	Wisconsin (Juday and Birge 1931)	Michigan (Tucker 1957)	Linsley Pond, Connecticut (Hutchinson 1957)	Ontario* (Rigler 1964)
Soluble inorganic	13	11	9.5	5.9
Soluble organic	61	48	28.5	28.7
Particulate	26	41	62	65.4

*Grenadier Pond was excluded

proportions of soluble unreactive phosphorus in all lakes, despite changes in colour (Table 6).

When I was unable to produce the expected colour effects, I looked for alternative explanations, and noticed that previous studies had used different techniques to isolate soluble and particulate phosphorus. Juday and Birge (1931) had used a Foerst continuous centrifuge, Tucker (1957) had used three layers of Whatman filter paper and Hutchinson (1957) "a 35-second membrane filter". I postulated that the reported differences in the amount of soluble unreactive phosphorus might reflect these different methods, and tested my hypothesis by applying different techniques to water from the same lakes. I found that one could have almost any concentration of soluble organic phos-

Table 6. Water colour and the proportion of phosphorus in different fractions in Ontario lakes. SRP: soluble reactive phosphorus; SUP: soluble unreactive phosphorus; PP: particulate phosphorus. Colour is measured by comparison to the colour of platinum solutions measured in mg l^{-1}. (From Rigler 1964)

Lake	Total P ($\mu g\ l^{-1}$)	% of total P in each form			Colour (Pt units)
		SRP	SUP	PP	
Grenadier Pond	133	4.8	12.5	82.7	12
Heart	44	4.8	27.8	64.7	23
Teapot	33	5.0	29.6	65.2	42
Mary	27	6.8	25.0	68.2	11
Eos	18	4.8	28.1	67.1	162
Costello	12	7.2	28.8	64.0	30
Opeongo (South Arm)	7	5.5	31.7	62.8	20
Lake of Two Rivers	7	5.3	28.9	61.8	24
Found	5	7.8	30.0	62.2	6

Table 7. Effect of the method of separating seston from water on the percentage of total phosphorus appearing as soluble organic phosphorus. Values in parentheses are total P concentration in the lake. (From Rigler 1964)

Method of separation	Heart 8 Jul (38 μg l^{-1})	Mary 9 May (16.5 μg l^{-1})	Thompson 9 Dec (18.2 μg l^{-1})	Average
Foerst centrifuge	66	55	85	69
3-layer No. 44 Whatman filter	34	40	37	37
5.0 μm Millipore filter	32	42	52	42
1.2 μm Millipore filter	34	38	40	37
0.45 μm Millipore filter	21	39	40	33
0.22 μm Millipore filter	16	28	20	21
0.1 μm Millipore filter	15	26	13	18

phorus one wished by using the appropriate technique (Table 7). Apparently, the proportion of "particulate" or "soluble" phosphorus in a lake depends on the technique used, presumably because a continuum of small particles and colloids prevents any sharp distinction between the two fractions.

I had a very similar experience with soluble reactive phosphorus. Because soluble reactive phosphorus reacts with acid molybdate as if it were PO_4, it was assumed to be the major form of nutrient phosphorus in lakes. When I wanted to investigate the possibility that soluble organic phosphorus, measured as soluble unreactive phosphorus, was also a nutrient, I tried to strip the PO_4 from filtered lake water with an ion exchange column. To determine the efficiency of the column, I added a small amount of radioactive phosphate to the water before passing the water through the exchange column. When I analyzed the elutriate, I had a surprise. Retention of soluble reactive phosphate was high only when elutriate volumes were very small. When large volumes of water passed through the column, more soluble reactive phosphorus appeared in the elutriate. This did not seem to reflect exhaustion of the retention capacity of the column, because the efficiency of retention of $^{32}PO_4$ remained high. Soluble reactive phosphorus behaved more like soluble unreactive phosphorus than like PO_4 (Fig. 12, overleaf). This behaviour suggested that soluble reactive phosphorus was not a measure of available inorganic nutrient, and that the soluble phosphorus in lake water was almost all unavailable, despite its lability with acid molybdate, and the opinion of ecologists.

A further anomaly supported the view that soluble reactive phosphorus was not available to algae. When a small amount of PO_4 is added to lake water, it is rapidly taken up by the seston (Einsele 1941, Rigler 1956). Eventually, a steady state is established with 90 to 98% of the label in particles and the rest in solution. This process (Fig. 13) is most parsimoniously described as a two-compartment exchange between a small soluble compartment representing PO_4 in solution and a large particulate compartment representing the labile fraction of the total particulate phosphorus. This exchanging particulate compartment seems to consist of bacteria (Currie 1990) and might be presumed to represent 10 to 20% of the total phosphorus. If $^{32}PO_4$ is added to the soluble compartment, then at equilibrium, the ratio of radioactive tracer in particles to that in solution ($^{32}P_{part}{:}\,^{32}P_{sol}$) should be the same as the ratio between the pools of exchanging particulate phosphorus and ortho-phosphate ($P_{exchange}{:}\,PO_4$). This identity allows us to calculate the size of the exchanging particulate pool from the equilibrium distribution of tracer and the concentration of soluble reactive phosphorus (SRP), as an estimate of ortho-phosphate concentration:

$$P_{exchange} = SRP \times (^{32}P_{part}{:}\,^{32}P_{sol}) \quad (5)$$

However, when these calculations are made, the concentration of exchangeable particulate phosphorus is too large, sometimes several times larger than the total phosphorus concentration in the water. One of the measured values

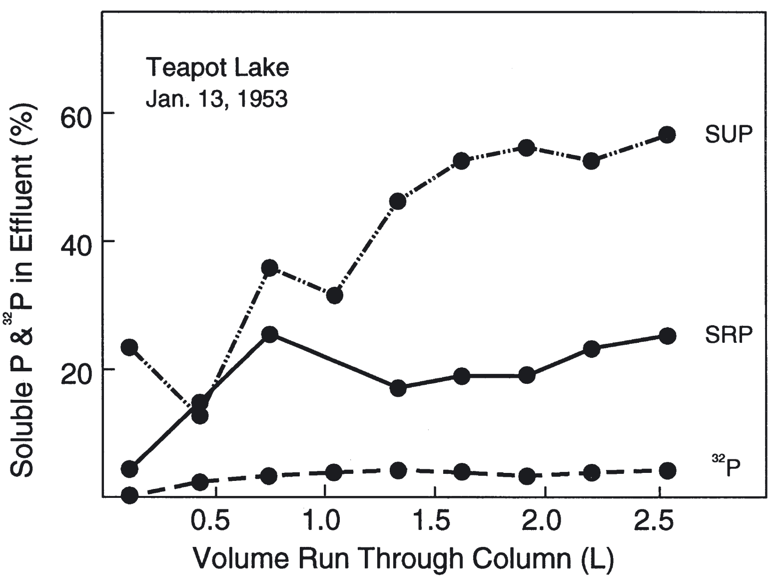

Fig. 12. Retention of soluble unreactive phosphorus (SUP), soluble reactive phosphorus (SRP), and radioactively labelled inorganic phosphorus ($^{32}P\text{-}PO_4$) when different volumes of filtered lake water are passed through an ion exchange column. SRP behaves like SUP and not like PO_4

must be in error, and the most likely source of this error is that soluble reactive phosphorus does not represent PO_4.

Subsequent experiments showed that the accepted technique vastly overestimates biologically available phosphate in lake water (Rigler 1966) and a number of authors have reached similar conclusions (Lean 1973, Peters 1977, Tarapchak and Herche 1988, Bentzen and Taylor 1991, Taylor and Lean 1991, Karl and Tien 1992). It appears that in phosphorus-limited systems, soluble reactive phosphorus is an irrelevant measure of nutrient phosphorus. Nürnberg has shown that the two are similar only where concentrations are high, above 10 to 30 mg m^{-3} (Nürnberg and Peters 1984).

This re-evaluation of various phosphorus fractions is not simply a history of methodological improvement. I see instead a typical programme of normal science whereby concepts, like available free nutrient, soluble but unavailable organically bound nutrient, and nutrient that is already biologically consumed, emerged from a dominant paradigm to set puzzles for the scientist. We wondered how we were to measure these concepts, and we assumed that the quantities we measured had the properties of the concepts: reactive phosphorus is available to algae or phosphorus that passes a fine filter is in solution. Working within the paradigm, I showed some inadequacies of current techniques, but did not question current concepts.

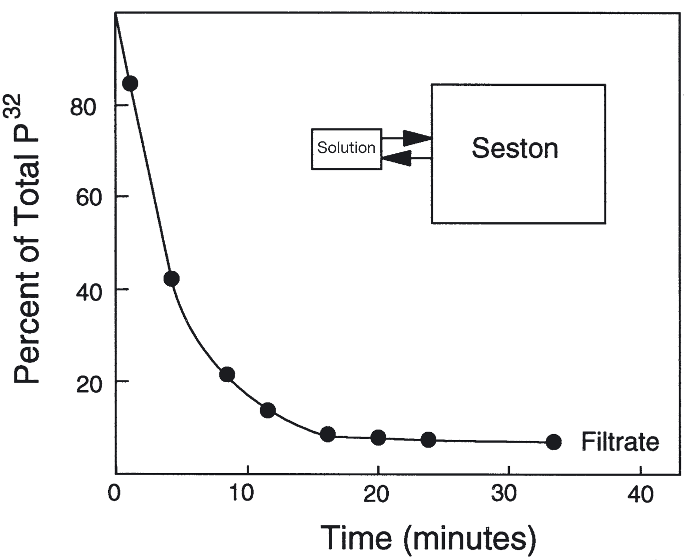

Fig. 13. A two-compartment exchange model to describe the plotted data showing rapid uptake of radioactive phosphate by seston in lake water, in the absence of any change in ambient level of PO_4 as measured by SRP concentration

Although I was pleased with the tests as pretty bits of science, I now recognize that the programme of research they represented was flawed. The programme confused the things I measured (e.g. soluble reactive phosphorus) with the concepts they represented (e.g. PO_4 and free nutrient) and the theories in which they were involved (e.g. algae can only use PO_4), until my mind slipped easily back and forth between fact, concept and theory, confounding and confusing these very different entities. I was trying to find a measurement that would correspond perfectly to a perceived truth, a paradigmatic concept, without realizing that I had no way of recognizing this correspondence if I found it. Apparently, I felt that the theory would arise almost automatically from the data, once the concepts were perfectly measurable. I now believe that those years of research, for all that they were interesting to me and productive of publications, would have been better spent if I had instead asked myself what theories could be built around the measurements I could make and what predictions these theories would yield. I might then have discovered much earlier that there was no theory waiting to use the concepts I was studying.

V Broader Symptoms of The Ecologists' Disease

> "The environ is a device to truncate the infinite time regressions and progressions propagating, respectively, inward toward and outward from the holon center. The truncation occurs at the border of the system to which the defining holon belongs, and hence the environ is also relative to this system. Accordingly, an environ is defined as a holon together with its associated within-system environment."
>
> B. C. Patten
> [*Environs: Relativistic Elementary Particles for Ecology* (1982)]

Confusion of concept, theory, and fact has made any assessment of ecology difficult, because the criteria on which scientific assessments should be made are obscured. The resulting fuzziness makes research proposals hard to judge, bewilders potential students, and obfuscates the few useful theories in ecology.

This chapter continues the examination of ecology that began in Chapter IV, and thus illustrates the disorder of ecology by pointing out some of the symptoms. I begin by discussing our difficulty in posing large questions that can be answered scientifically, because I believe that this difficulty has led to our interest in relatively uninteresting minor problems that can be easily addressed. I then examine the dissatisfaction, even contempt, that some ecologists seem to have for imperfect theories, for probabilistic statements and simplifications. Next, I consider our tendency to let untestable concepts grow unchecked and the characteristic lack of concern for scientific rigour in evaluating the theories we have. Finally, I consider the seeming incapacity of ecologists to use quantitative theory effectively. In all these examples, the underlying theme is that in ignoring the criterion of falsifiability, scientists discard or fail to grasp the touchstone of scientific quality. This fault has ramifications for the entire scientific enterprise.

Framing Scientific Proposals

I have generated two realistic, but artificial, introductions to research proposals or scientific papers to illustrate how easily we let slip the opportunity to pose relevant scientific questions (Table 8). These introductions might have introduced the two personal research topics discussed at length in the previous chapter. Both proposals begin by appealing to some large, generally desirable goal, like feeding the hungry or understanding secondary production. But both end by proposing a highly specific study whose relation to the grand goal is obscure.

Given this mode of operation, whereby the projected work does not strive to resolve the specified problem, almost any generally recognized societal or scientific problem will suffice as background for a scientific project. Instead of identifying a testable theory about the larger issue, typical ecological introductions point out that we need to understand, or that we are ignorant of, some component. We cannot know if this component is really important, because no theory specifies it as a critical element. Often there is only an allusion to some shared belief and that allusion allows one to introduce a specific topic (e.g. the relation between SRP and PO_4, or the distribution of *Diaptomus* in Ontario) under the aegis of a grand one (e.g. feeding the hungry).

The jump from grand science to little science is hidden by reference to our "ignorance" or our "need to understand". Such phrases are like the black-out of a theatre stage between scenes, for they allow a change of topic without any logical inter-connection. If that intellectual sleight-of-hand is not obvious, it shows us to be enured to such tricks. We no longer find them surprising or disruptive. We no longer question what they might mean. If we are actually ignorant, we cannot know enough to mount a scientific investigation. If we seek understanding, we should specify how we will know when this understanding has been achieved.

Once we accept the Popperian criterion of falsifiability, we know we are not ignorant because we can specify one or more theories that restrict the states that we are likely to observe. We would know when we have tested the original hypotheses because we can compare observed and predicted states. We would know when we have improved our original hypotheses, because we could specify states considered likely under the old theories that are unlikely in the new ones. And we would know that we have increased our understanding when these new hypotheses survive further rigorous tests. In the absence of hypotheses, introductions like those in Table 8 only indicate a topic that interests the proponent.

The Reception of Moderately Restrictive Theories

Ecology has a number of empirical theories which are only moderately restrictive. For example, given the average concentration of phosphorus in a

Table 8. Justifications for two programmes of normal scientific research in ecology. After an ethically strong introduction, we can justify almost any study by invoking our ignorance, the use of model systems, and the importance of understanding some fundamental part of the system. In neither proposal is it clear how the work will solve the important problem in the common introduction

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Introduction

The world is hungry for animal protein. Most protein for human consumption is grown on land, but this is inefficient, because farm animals compete with food crops for space and because of inefficiencies in the conversion of fodders to homeothermic tissue. The sea covers 70% of the planet but as yet produces only 10 kg of food per ha. Canada may have five million lakes that are even less productive. Intensive aquaculture can yield 100 times more food. There is thus great potential, if the factors that limit productivity in either fresh or salt waters can be relaxed. Of the two types of system, tractability and small scale argue that it would be more efficient to first assess the determinants of secondary productivity in lakes, and then to use these results as models with which to approach the limitation of productivity in the sea.

Proposal I

Nutrients usually limit the productivity of aquatic systems, yet the process by which a given quantity of free nutrient is transformed into consumable flesh is virtually unknown. Understanding this process will be the work of many scientists for many years, but an important first step is the accurate assessment of available nutrient. In lakes, phosphorus typically limits productivity and free phosphate is measured as soluble reactive phosphate (SRP) by exposing filtered lake water to acid molybdate reagent. A growing body of evidence suggests that SRP overestimates bioavailable phosphorus. This project reassesses the relation of SRP as a measure of free phosphate.

Proposal II

Calanoid copepods form the base of pelagic marine food chains and are arguably the most abundant organisms on earth. Yet they are only very imperfectly understood. In large part, our ignorance reflects the difficulty in sampling and studying wild populations across thousands of square kilometres of open ocean.

Lakes can be studied more intensively and at less cost. Since calanoid copepods are also important in lakes, the approximation involved in studying limnetic models of the marine system is not extreme. We can therefore use lakes to develop and test initial hypotheses about the structure and function of calanoid communities. Promising hypotheses will eventually be tested in marine systems, but initial probing and sorting of data and theories can be more efficiently followed in lakes than in the sea itself.

This programme will determine how congeneric species divide up a seemingly homogeneous environment. We will survey a large number of lakes to establish the degree to which species co-occur in different lakes and the amount of spatio-temporal overlap in their distribution within lakes. If co-occurrence is as prevalent as anecdotal and scattered literature accounts suggest, we will determine the likely factors that permit these animals to share their simple habitats.

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lake, it is possible to predict the mean chlorophyll concentration (Dillon and Rigler 1974a) to within an order of magnitude, and given the body weight of a *Daphnia*, one can make a similarly approximate estimate of its respiration rate (Peters 1987). These moderately restrictive theories predict a range of states, so the information they provide is probabilistic.

Probabilistic theories are good as far as they go, but we wish they went much further. If we are planning a picnic, we want to be told that there is no chance of rain, not that the chance is only 25%. Nevertheless, in the absence of alternatives, such moderately restrictive theories have their place. They tell us how well our science currently performs (as the explained variance), and they indicate how much more we have to do (as the unexplained variance).

Moderately restrictive theories are not viewed as useful by all ecologists. Some lament that the predictions are only approximate. For example, Shapiro (1978) and Benndorf (1987) focus on the uncertainty of chlorophyll concentrations predicted from phosphorus concentration in lakes. They are concerned because the chlorophyll concentration for a specific lake could lie well off the value implied by the mean trend, and still be consistent with the theory.

Others hold that such moderately restrictive, empirically based theories are too simple. For example, the abundance of zooplankton, planktivorous fish, piscivorous fish and spatial refuges can all be expected to affect chlorophyll development (Carpenter et al. 1985), yet they are not represented in predictive theories used for lake management (Chapter IX). The feeling that a model is insufficiently complicated also reflects the confusion between what contemporary science can offer and what we want. The critic posits the existence of a grand theory that describes the entire lake ecosystem and therefore predicts chlorophyll effectively. This dream is compared to our present limited predictive power. If one discards the existing theory when it loses to a phantom competitor, one is left with no theory at all.

These criticisms assume that explanatory theories spring fully formed from the mind of their creator. That is not the lesson of experience. In developing their theories of astronomy and gravity, Copernicus, Newton and Einstein drew on a tradition of recorded observation that dates back to the beginning of history. The table of the elements was basically the description of pattern in chemical behaviour; and the modern theory of the atom arose from painstaking measurements of absorption spectra. Theory begins with a search for pattern within the field of interest, passes to a rigorous description or quantification of that pattern and, finally, to the incorporation of the pattern into an explanatory theory. The idea that science can begin with comprehensive explanatory theories betrays ignorance of how science has always worked.

Still other critics complain that moderately restrictive theories do not tell us everything about the lake. For example, a theory that predicts mean summer chlorophyll tells us nothing about bio-accumulation of mercury (Lehman 1986a). Such complaints indicate a healthy desire for more and better theories. Such complaints are also disturbing because they indicate a general failure of ecologists to appreciate the nature of science and scientific theory. No theory can do everything. A theory that predicts chlorophyll will not predict contaminant burdens or algal taxonomy. A theory that predicts planetary motion cannot predict the natural fall of a feather nor the flight path of the bird that dropped it.

None of these counter-points to criticism should suggest that our current empirically derived, moderately restrictive theories approach perfection. They do not; replacements are needed and the current generation of theories should be discarded as soon as better alternatives are available. The moderately restrictive theories we have are only a step in the identification of pattern (Fig. 14). But if we do not make some first step, we will never reach the distant goals of better prediction and understanding for which so many of us yearn.

The Pursuit of Ecological Concepts

Science progresses towards better theories by comparing the abilities of competing theories to predict observations in critical experiments (Platt 1964). To make such comparisons, one must identify competing theories, and devise experiments that provide sound tests. In ecology, critical tests of competing theories are rare. Existing ecological theories are so little appreciated that most ecologists would be unable to identify one theory to predict

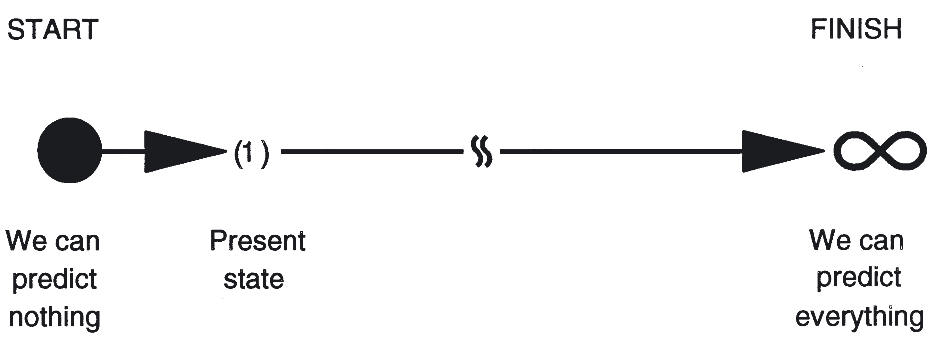

Fig. 14. At present, empirical ecological theory is far from where we hope to go, but it is a first step. (From Rigler 1982a)

a given phenomenon, much less two or more competitors. Unfortunately the response to this deficiency has not been a search for ecological theories and patterns.

Science uses theories to pinpoint observations of importance, and uses observations to test theories. Ecologists rarely think in these terms. Instead, we direct our thoughts towards abstract concepts that represent elements of a sophisticated (but incomplete) mental model of the system we want to study. If observations are used at all, they serve to confirm that the concepts act in nature. Ecologists thereby abandon the practice that distinguishes science and non-science, and our science suffers as a result. For example, that approach identified free nutrient as a critical component in the phosphorus cycle, and led me to two decades of work trying to measure a variable for use in a future theory (Chapter 4) rather than testing a theory. The pursuit of concept instead of theory is not just a personal failing. I share it with many colleagues.

The limiting factor. The history of ecology is filled with abstract discussions substituting for theoretical development. The concept of the limiting factor is a case in point. In 1840, Justus Liebig proposed his famous "law of the minimum". He was concerned with the growth of plants and had observed that a plant needs many different nutrients from the soil. If one of these nutrients was absent, the plant would not grow. He formalized his observations in the law of the minimum:

> ... if one is present in minimal supply, growth will be minimal. This is true no matter how abundant the other foodstuffs may be. Growth is then dependent on the amount of foodstuff present in minimal proportion.

At its inception, the limiting factor concept was applied only to the effect of mineral nutrition on the growth of individual plants.

The next step was taken by F. F. Blackman in 1905 who was also concerned with the factors controlling the metabolic responses of plants. However, he extended the concept beyond growth by considering other processes, like respiration, and non-mineral factors, like temperature. Moreover, Blackman described cases where high levels of the factor limited respiration, as high temperatures reduced plant respiration. Thus, in Blackman's work the initial concept of the limiting factor began to expand and change. It got muddled.

Shelford (1911) picked up Blackman's concept and applied it to the distribution of species: "The geographic range of a species is limited by the fluctuation of a single factor (or factors) beyond the limit tolerated by that species." Shelford thus extrapolated the concept from a factor constraining individual metabolism to one determining species' distributions. This extension may seem to offer wider application, but it also further inflates the concept and renders any precise use of the term increasingly difficult. Elton (1927) analyzed the geographic distribution of species more carefully than Shelford and concluded that "biotic limiting factors" could act in conjunction with abiotic limiting factors. Under that interpretation, a multiplicity of factors could act together, so the concept means little more than that the organism is affected by its environment.

F. E. J. Fry (1947) recognized the confusion gathering around the concept of limiting factors. The concept seemed ready to treat all environmental factors and all aspects of physiological and biogeographical response. To address the problem, he reintroduced some rigorous terminology. For Fry, a "limiting factor" was an environmental variable which regulates the metabolic rate of an organism by virtue of its operation within the metabolic chain. Thus nutrients, light, and oxygen could all be limiting factors, as Liebig had suggested, but Blackman's temperature, like pH, salinity, and humidity, could not. Fry called these factors "controlling factors" which were characterized by their ability to affect maximum and minimum rates, and all rates in between. Finally, Fry recognized "lethal factors" that operated at the extremes by killing the organism.

Fry's redefinitions were rigorous and rational but they did not stem the proliferation of conceptual meanings associated with the term. Eugene Odum (1954) also began with a definition: "Any condition which approaches or exceeds the limits of tolerance is said to be a limiting factor." Thus Odum's limiting factors are equivalent to Fry's lethal factors, and are nothing like Liebig's factors. However, when Odum uses the term limiting factor he obviously has many other definitions in mind. Sometimes his usage is consistent with his definition: "Fire is ... an extremely important limiting factor"; but at other points, his usage is similar to Fry's: "In the geological and physiological sense, the low concentration of CO_2 now existing is limiting to all land plants." Sometimes, he accepts that multiple limiting factors are at work, like Elton, suggesting that "in lakes, oxygen, nitrate and phosphate are limiting." Later he introduces a new conception of limiting factors by claiming that "on land ... wind exerts a limiting effect on the activities ... of organisms" and illustrates the point with an experiment where the growth form of an alpine plant was altered by a wind shield.

The limiting factor concept has continued to evolve. Hairston et al. (1960) apply the term to an environmental influence that determines the maximum population of a species. Limnologists refer to phosphorus as the factor that limits primary productivity of a whole trophic level, or the secondary productivity of a whole community. A glance at most contemporary ecology texts reveals simultaneous use of multiple concepts. Each application of the concept may be tied to observations, but these observations serve as confirming instances, not tests.

The end point of this development is that we can never hope to measure "the limiting factor". Ecological thinkers have associated so many meanings and ideas with a single term that no measurable property could ever correspond to all, and many different observations could correspond to one or more ideas. Such a multi-facetted concept cannot play a role in theory, and any construct that uses the concept, without rigorous redefinition and consistent subsequent use, cannot be a theory.

This history of limiting factors is not an isolated case. Conceptual expansion leading to terminological confusion and ending in unoperational concept clusters is the common fate of many ecological ideas (Peters 1991a). As a result, models that use such concepts cannot play a role in the formulation or test of ecological theory. Ecologists who work with these concepts are exiled to an untestable shadow-world that exists only in the imagination. The way to avoid this limbo is to insist that the entities we discuss be measurable components of predictive scientific theories.

Unconcern

Despite the developments outlined in the preceding section, some versions of the limiting factor concept are among the most cherished simple theories in ecology. Liebig's law of the minimum says that the growth of an organism is limited by only one substance at any one time. If more of that substance is added, growth will increase, but if any other substance is added growth will be unchanged. Extrapolation of the law to whole communities has had useful consequences for eutrophication abatement programs: tertiary sewage treatment and legislated changes to detergent composition have substantially reduced phosphorus loads to lakes and rivers. The law of the minimum has a strong intellectual appeal because it simplifies the theoretical problems of complex systems.

Multiple limitation in the sea. In 1974, Theodore Smayda, a highly respected oceanographer, published a paper in *Limnology and Oceanography*, the foremost journal in his field. This paper challenged the law of the minimum by concluding that in the nearshore waters of the western Atlantic Ocean, as many as five factors could concurrently limit the growth of a single clone of the planktonic alga *Thalassiosira pseudonana*.

Although Smayda's paper claimed to falsify a theory that had been accepted for 150 years, it generated no excitement. It went almost as unnoticed as Gregor Mendel's paper on inheritance. Each year, I look at the Science Citation Index to see how many times the paper has been cited and why. And each year it gains a modest few citations, a total of 40 by 1992, but no one seems to appreciate that the paper challenges one of the dominant paradigms in ecology.

Smayda's paper is an example of the fate of heretical ideas raised at the wrong time. Although Smayda's credentials, choice of journal and style of exposition followed accepted norms, Smayda's analysis was received with the same indifference as Velikovsky's (Chapter III). This was to be expected (Polanyi 1958, Kuhn 1962). Normal ecologists have quite enough puzzles to keep themselves busy, and see no need to upset the world-view that justifies those puzzles as scientifically interesting. Yet one would have hoped that some supporters of the law of the minimum would have rallied to defend their paradigm, if only because the prestige of the author and journal gave the contrary view some credibility. But no one cared.

There is an irony in this anecdote. If defenders of orthodoxy had attacked the paper, they would have discovered a fatal flaw. I chanced to study the article particularly carefully because I planned to use it in class as an example of a sound bioassay. When I examined the data, I found only one limiting factor, nitrogen. The paper compared growth rates in cultures where all nutrients were in excess with those from cultures where all nutrients but one were in excess, and found that the absence of any one of several nutrients might reduce growth below the rate where all nutrients are present in excess. Unfortunately, that finding is irrelevant to limitation in the field. The proper comparison is with controls to which no nutrients were added. Except for treatments where some toxicity was evident, growth rate increased above that in the no-nutrient controls control whenever nitrogen was added. If no nitrogen was added, growth rate was similar to those of the controls despite the addition of other nutrients (Fig. 15, overleaf). Here is another reason to suppose that the paper would have attracted serious attention, but again no one cared.

Most ecologists can point to other examples of flaws in experimental design or interpretation. This example is therefore only one among many. I do not intend to blame or discredit authors who have made mistakes in their scientific careers. We all do that and should expect to do so. I am instead concerned about a science which does not move to correct mistakes, that offers no resistance to challenges to its principles, and that does not read its own literature critically. Such nonchalance suggests a science deep in normality and far from revolution. If we need a revolutionized ecology to meet the environmental crisis, this evidence suggests that we are far from ready.

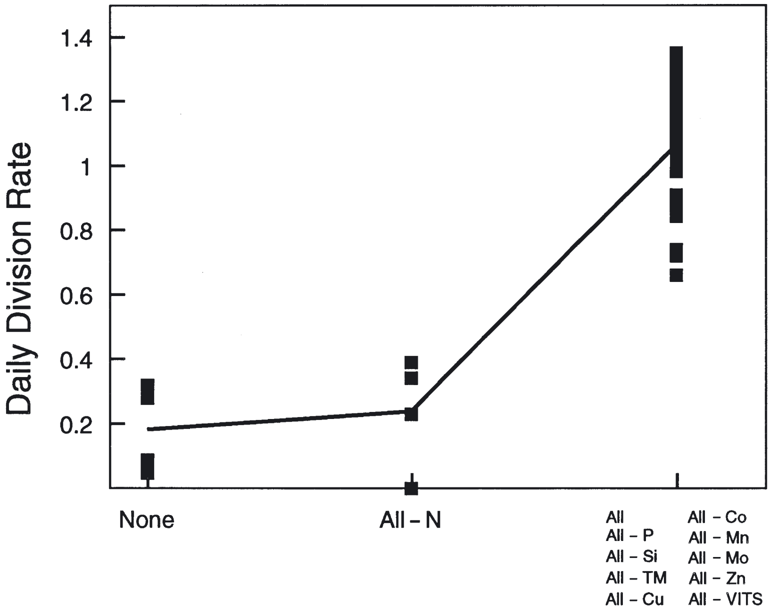

Fig. 15. Growth rate, expressed as a percentage of the maximum observed growth rate of the alga *Thalassiosira pseudonana* (clone 13-1) exposed to sea water amended with varying nutrient mixtures. Cultures which received all nutrients except nitrogen (All – N) grew no better than control cultures (None), whereas cultures that received nitrogen grew much better, regardless of deficiencies in other minerals. The variations among cultures that received nitrogen may indicate other deficiencies that are expressed only when nitrogen is available in excess. TM = trace metals, VITS = vitamins. (Data from Smayda 1974)

Inattention to Detail

Because ecologists are not used to working with theories, they often do not realize that strong theories and predictions provide important checks on poor measurements and miscalculations. If theory predicts one value for some fact and observation yields a different value, there is an anomaly. Such anomalies are fruitful. One might check the validity of the prediction, by recalculation, and the observation, by repetition of the measurement. This comparison allows us to identify human errors in both processes. If the anomaly persists, one has a potential falsification of existing theory and the basis for future scientific work.

In the absence of prediction, observational errors often go unnoticed and the necessity for theoretical development is hidden. Under these conditions, scientists lack a measure of validity, they may become sloppy and science may stagnate.

The calculation of secondary productivity. I became aware of this inattention in preparing a review of the methods of calculating secondary production (Rigler and Downing 1984). This section is a precis of that review. Secondary production has fascinated ecologists for much of this century (Downing 1984). Many theories have been advanced to explain it and many methods have been used to measure it. The basic concepts and techniques are simple. Nevertheless, I found myself amazed at the total confusion that surrounds these simple calculations. I worked through the literature in a futile search for good examples of production studies. All I found was one error after another.

I believe these errors arose because production biologists have been confused by the many complicated and sometimes erroneous methods described in the various instruction manuals and review papers to which they go for guidance. I suggest that if we were to address ourselves to the simple principle underlying the calculation we would not make so many mistakes. Furthermore, we would have more mental energy left over to devote to really difficult and interesting problems.

The production of a population is the total amount of tissue that population synthesizes during some interval of time. This production is a rate and has the dimensions of mass or energy per unit of time. A year is often taken as the unit of time, and for mass we might use fresh weight, dry weight, ash-free dry weight, carbon content, nitrogen content, etc.

To illustrate the principle of calculating production, let us consider a single cohort of an imaginary population (Fig. 16A, overleaf). It begins with a population of 10 individuals each weighing W_0. After an interval of time t_1, one of these individuals, now weighing W_1, dies. Its lifetime production is therefore $W_1 - W_0$. At a later time, t_2, another animal weighing W_2 dies, and its lifetime production may be calculated as $W_2 - W_0$. This process will continue until the last individual dies at t_{10} and its production $W_{10} - W_0$ is calculated. The total production of the cohort over the interval from t_0 to t_{10} is then the sum of the final weights ($\sum W_i$) less the initial weight of the population ($10 \times W_0$):

$$P = (\sum W_i - 10 \times W_0)/(t_{10} - t_0) \tag{6}$$

That is all there is to it.

Why then do we find whole books written on the subject of production, and within them a whole series of different calculations? There are a number of reasons that ecologists make such heavy going out of productivity calculations. One is that natural populations cannot be known as well as the imaginary cohort in Fig. 16A. As a result, we must replace individual animals with size classes, approximate the number of individuals in each size class and approximate the size limits of the class. The problems of approximation are real and merit thought.

A second reason for our difficulties in treating secondary production is that production ecologists erroneously believe there are three fundamentally different methods of calculating production from these data:

(1) increment summation
(2) mortality summation
(3) the Allen curve.

These methods are essentially identical. They differ only in the way they sum the weight increment over time (Rigler and Downing 1984). Each requires

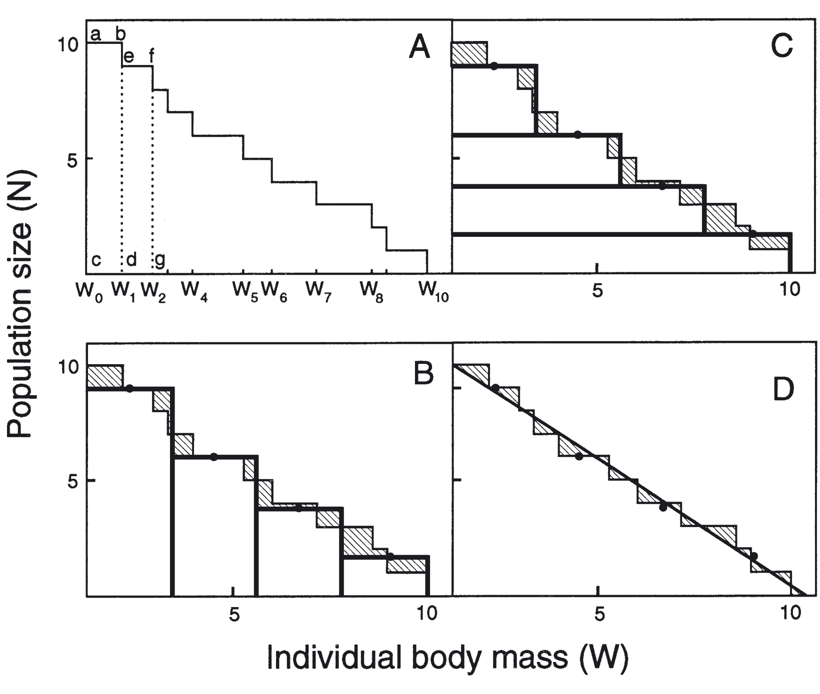

Fig. 16. (A) The exact calculation of secondary production by animals of known initial and final weights. When the first animal dies, the production of the cohort is the area of rectangle abcd; when the second animal dies, the cohort production is increased by the area of rectangle defg, and so on until all the animals are dead, and the total area under the curve is known. (B to D) Three variants in calculating secondary production of the cohort in panel A. Dots indicate four observations of population size and individual weight taken over the course of the cohort's existence and represent the means in a size class or over a time period. Heavy lines indicate the areas which are used to calculate total production and shaded areas are errors in estimation

that the population be divided into a number of size classes, and that for each size class one know N_i (the average number of animals entering size class i), $W_{min.i}$ (the mass of the average animal entering the size class), and $W_{max.i}$ (the mass of the average animal leaving that size class; this is also the mass of the average animal entering the next size class). Production is then calculated as

$$P = \sum N_i(W_{max.i} - W_{min.i}) \tag{7}$$

At this point, the interesting problems begin. Most real populations do not produce cohorts. When we measure the number of animals in a size class over time, we do not see a regular decline in numbers (Fig. 17), but a more or less erratic pattern of peaks and troughs as animals are born, grow and die. If the animals can be aged, they can be sorted by age class and treated as if they represented a cohort. If this is not possible, then production can be estimated from the number of animals in the size class (N_i), the upper and lower size limits of the class ($W_{min.i}$, $W_{max.i}$) and the average duration of that size class (D_i):

$$P = \sum N_i(W_{max.i} - W_{min.i})/D_i \tag{8}$$

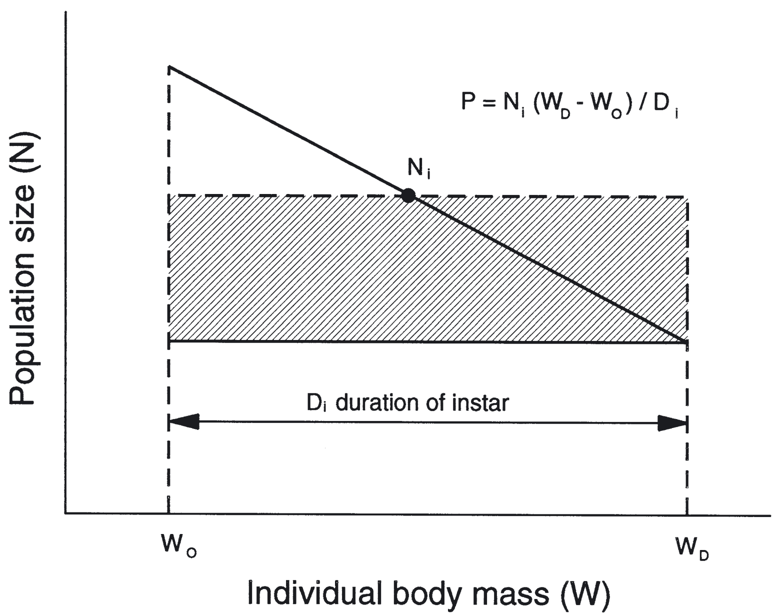

Fig. 17. Approximation of the production of a cohort, age- or size-class, or population based on a single estimate of N, estimates of minimum and maximum size (W_{min} and W_{max}), and estimated duration of the size class (D). The magnitude of the errors in this calculation depends on the schedules of mortality and growth over the period D, as well as on how representative the estimates of D and population size are

This equation is really an extension of the model in Fig. 16 pushed to the bare minimum of sampling effort (Fig. 17). It is an approximation to the extent that Eq. (8) departs from Eq. (6). For example, Eq. (6) assumes that the timing of growth and mortality are known for every animal, but Eq. (8) assumes that they can be approximated by averages. In fact, changes in the scheduling of mortality and growth over the interval D_i could cause significant errors in estimating production. For example, the production of animals that died before sampling to estimate N_i is left out of Eq. (8), and if these are many, then the equation underestimates production. Conversely, the equation assumes that animals alive at sampling survive to reach maximum size, and to the extent that they die soon after sampling, the equation will overestimate production. Finally, Eq. (8) assumes a linear growth curve, but if growth is exponential, most of the production will occur towards the end of D_i, when population is smallest; and again Eq. (8) will overestimate.

For fish or clams or humans or trees, D_i is easily measured, but for the host of tiny invertebrates that dominate aquatic ecosystems, this determination is not easy. Consequently, a number of so-called methods of calculating production are really disguised attempts to avoid measuring D_i. These attempts almost always lead to error and add to our confusion. I will give only one example: the size-frequency or Hynes method.

The Hynes method really excited stream ecologists because they could never sample their animals well enough to calculate D_i and, even when they had their samples, they could not identify the species. They were accordingly very pleased when offered a method that required neither D_i nor identification of species. This method is based on two implicit assumptions: that total development time equals one year for all species and that the development time of each size class or instar, D_i, is a constant. That is to say, the method assumes that animals spend the same amount of time in each size class. The Hynes method therefore does not overcome difficulties, it merely ignores them. But you cannot avoid measuring N_i, D_i, and $(W_{\max.i} - W_{\min.i})$. If you try, you will go wrong and confuse everyone else. More problems are discussed in Rigler and Downing (1984).

Let me summarize this section. Production has been considered important by a generation of ecologists. The method of calculating production is so incredibly simple that a child in elementary school could be taught it. Yet almost every zoologist who has calculated secondary production has done it incorrectly. There are similar errors in calculating primary production, and probably in most quantitative treatments in ecology. We can take a lesson from this example and that lesson contains both good news and bad.

First the good news. Ecologists are still frightened by the most elementary mathematics. Consequently we use the literature like a cook book: we look up a method and use it without understanding the principle behind it. I know personally that when I have to look at an equation and try to understand it, I usually fail. I give up, feeling frustrated and stupid. The lesson in this section is that if one has really tried to understand a paper and failed, the reason for failure may not be that one is stupid, but that the paper is wrong.

Now for the bad news. I think the persistence and frequency of error in the secondary production literature and in the rest of ecology shows that, by and large, ecologists do their research superficially and carelessly. We act as if we do not care about the validity of our results. We do not care because we are not testing theory, so that any value will do. This is a sign of the sickness in ecology.

We should all take pains to remove error and nonchalance in our own work. However, we should also be concerned with the cause of these symptoms. If we could understand their source, we would make an enormously greater contribution to our discipline. For me, the root of our problems is our disinterest in prediction. Predictive theories require accurate measurements to provide adequate tests and to avoid spurious anomalies.

Some Consequences

This chapter suggests that much of ecology is confused in its goals, uncertain of its strengths, and inconsistent in its terminology. It portrays ecologists as nonchalant about their tests, careless in their measurements, yet closed-minded in considering alternatives. It claims that ecologists do not recognize the few good theories they have, preferring to pass their time with weak theories and non-theories that substitute a form of explanation for prediction. It also claims that ecologists rarely try to make predictions, believing that some special property of their systems makes the common model for building and testing theories inoperable.

This is an unattractive picture. It is one in which few ecologists see themselves. Yet I believe it is the face we turn to the public, to the granting agencies, and to our students — with devastating results. In each case, a potentially friendly and supportive audience is baffled by arcane subject matter. Many turn away, feeling bored, frustrated, stupid, embarrassed and incapable. I submit that the fault is not with them; they have sensed the real nature of much of contemporary ecology.

Some students have such interest in ecology that they refuse to drop out. Those few survive to become professors and researchers. Unfortunately, they often do so by making the illogical jump from grand concerns to picayune experiments. When they do so, they become part of normal science. They accept the dominant paradigms of ecology and no longer see its anomalies and failures. They become us.

This process of acculturation explains the failure of ecologists to appreciate the nature of their science. We have all been brain-washed. To escape, we must step outside the comfortable limits of normal science to see what needs to be done, and to look back at what we are doing. We have to contemplate our science.

VI Why Limnology?

> "There is nothing — absolutely nothing — half so worthwhile as simply messing about in boats."
>
> K. Grahame
> [*The Wind in the Willows* (1966)]

Science has a way of overwhelming its participants. Fields of interest that fit within our scope during periods of youthful exuberance double in size every ten to fifteen years (Price 1986), and even rare demonstrations of personal competence invite additional duties. To succeed in their research, most contemporary scientists therefore have to dedicate themselves to the tasks at hand: experimental design, observation, data analysis, publication and reading in their specialty. One result is that scientists have little time to address philosophical generalities or to worry about how their efforts contribute to the larger body of science.

Our behaviour is justified if we believe that science is sufficiently self-correcting: a proper overall direction arises automatically from the process of thousands of researchers "doing science". A similarly blissful ignorance fosters the view that because any piece of scientific information is intrinsically valuable, there is no need to fit the piece we study into a larger picture. We may recognize the value of the long view, but too often our response is simple regret that we have not the time to think about it. None of this is acceptable. We must reject the notion that scientific forethought is an unnecessary luxury. To do otherwise is to deny the most fundamental of scientific tenets: that humanity can achieve some power over our destiny by thought and observation.

In this essay, I contemplate my own branch of science by trying to answer a question that has bothered me for some time: Why teach or study limnology? My answer is still only preliminary. I hope that by asking it, I will encourage others to complete the process of analysis for limnology and to extend that analysis to other branches of ecology, biology, and science.

What is Limnology?

Limnology is the scientific study of fresh waters. Within that limitation, its subject matter is broad. Limnologists may be physicists, chemists, mathematicians, geologists, hydrologists, engineers, or any of a host of other specialists. Limnology could involve studies of the evaporation rate of water collected by a pitcher plant, the thermal stratification of Lake Michigan, the chemistry of iron, etc. For biologists, like me, limnology is more restricted: limnology is the study of living organisms that inhabit fresh water. I will restrict it further and deal only with living organisms in lakes. The reason for this second restriction is partly personal, and partly convenient. I work with lakes and like them, and if I demonstrate that studying the biota of lakes has value then I will have demonstrated that limnology as a whole has at least that same value.

There are obvious practical reasons to study fresh water. Water is one of our most important and valuable resources. In Canada, many of us live in one of the most famous lake districts in the world: five of the world's largest lakes lie at our doorsteps, and millions of smaller lakes dominate the landscape of the Canadian shield and condition our lives. In the country as a whole, government figures suggest that fresh waters add 10 to 20 billion dollars to the economy every year (Science Council of Canada 1988). In the United States, extensive irrigation has allowed the deserts to bloom and feed a hungry world. In England, a tenth of the waters of the Thames passes down domestic drains on its way to the sea and at least as much again is used industrially. In the developing world, water-borne diseases are major killers. At a practical level, the need for limnology is obvious: fresh water is critical to industry, agriculture, health, and nature, yet it is in short supply and its quality is increasingly compromised. We must learn how to improve, to conserve and to use this precious resource (Likens 1992). That is the practical challenge for limnology.

Practical considerations are critically important, but they are not of central concern in this chapter. Practical issues are not used in universities to justify hiring a limnologist or offering a course in limnology. As university students and teachers, we should be primarily interested in science, and the reasons for hiring and teaching should hinge on the scientific value of the discipline. As students, we should be asking "What is science?" As teachers, we should be trying to answer that question. And as scientists, we should all be trying to make a contribution to the development of science.

What is Science?

Before we can ask "Why limnology?", we have to ask "What is this thing called science?" Since I have discussed the point in earlier chapters, I can answer arbitrarily here. Science is the process of making, testing and using theories. These theories are verbal or mathematical statements that make predictions, and thereby give a functional description of the world in which we live. I say “functional” because our theories need not give a “true” description of the world. In fact, philosophers have shown very convincingly that science cannot hope to give a true picture of the universe.

Our job as scientists is to produce a set of statements or theories that are consistent with each other and which make good predictions about future events and observations. In other words, the essence of science is in its theories, and the justification for any and every piece of research lies in its relation to a particular theory. If someone asks what you do, it is useless to answer, “I am an entomologist”, or “I am a limnologist”, as this describes only the tools of research. Insects and lakes are only the material used to test theories. A better answer would be “I am interested in gene theory” or “I study competition theory”, because this describes the ideas you wrestle with in your research. I define ecology as the science that predicts the abundance, distribution and other characteristics of organisms in nature. Biological limnologists, as freshwater ecologists, seek to predict these characteristics of organisms inhabiting fresh water. If limnology is to interest other ecologists, it must show them how the study of lakes relates to the tests and problems of other fields.

Now we can return to our original problem: “How do we justify limnology?” We now know that we can justify it only by showing how limnology allows us to test a scientific theory or a group of theories. In effect, we now know what to look for among all possible justifications and our search will be much shorter. We are looking for theories related to the study of organisms in their natural environment, and I will argue that lakes are a particularly good place to test those theories.

Ecological Theories

There are many theories waiting to be tested in ecology. We have theories about how individuals use their resources, about how predators interact with their prey, about how populations compete, about how food webs are organized, about how higher trophic interactions affect plants and about how variations in plant nutrients affect predators. In short, we have many, many theories about how organisms interact with their environment.

Where will we test these theories? What constitutes the environment? How extensive is the population? or the community? Do we consider the assemblage of species in the whole world as “living together”? Are there practical limits to the system we wish to study? Perhaps it is hard to imagine that an Australian earthworm and a North American beaver share any resources, but does this mean we should treat continents as our units? If not, how do we carve the world up into ecological units? Are we actually justified in dividing it up at all? These questions have always been thorny ones for ecologists and they show no sign of resolution. Modern chaos theory has given the problem new respectability as "the butterfly effect" whereby small causes may have grand effects, as the reverberations from a butterfly's wing in Africa may determine weather patterns half a world away (Gleick 1987).

The ecosystem concept. Ecologists believe that we can and, in fact, must divide the world up in order to study it. We call this "the ecosystem concept". The idea that we could identify lakes as discrete ecological units was formulated back in 1887 by Steven Forbes in *The Lake as a Microcosm*. This article had such a strong influence on amateur as well as professional biologists, that it was reprinted at least twice and is still cited in the literature. Forbes begins his paper:

> A lake is to the naturalist a chapter out of the history of a primeval time, for the conditions of life there are primitive, the forms of life are, as a whole, relatively low and ancient and the system of organic interactions by which they influence and control each other has remained substantially unchanged from a remote geological period.
>
> The animals of such a body of water are, as a whole, remarkably isolated — closely related among themselves in all their interests but so far independent of the land about them that if every terrestrial animal were suddenly annihilated it would doubtless be long before the inhabitants of the lake would feel the effects of this event in any significant way. ...It forms a little world within itself — a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp.

Forbes makes a number of interesting points in this short section of his paper, but I want to draw attention to only two: organisms in a lake are unaffected by those on the land; and the ecological processes in a lake are so primitively simple and the scale of these processes is so small that the lake system can be easily comprehended.

These two ideas have been very influential. They have attracted many ecologists to work on lakes, and convinced many limnologists that the study of lakes is more likely to be rewarding than the study of streams. If the organisms in the lake are isolated from events and organisms on the surrounding land, then characteristics of the lake alone must determine the properties of the lake system. If lakes are simple systems, they will allow us to see general ecological principles in action. Thus a lake provides ecologists with a simple model system in which to test their ideas.

Forbes and his followers saw that it was possible to divide up the biosphere into little, self-contained units in which all ecological processes could be observed. He called this unit a microcosm, but many terms have been used for this concept. Nowadays, everyone uses the term ‘ecosystem’. English-speaking writers usually attribute the term to Tansley (1935), but Remmert (1980) mentions that it was introduced by R. Woltereck a decade earlier and the concept is older still.

An ecosystem is an ecological unit comprising living and non-living components interacting to produce a stable system. An ecosystem might be a forest, an area of grassland, a stretch of desert, an oceanic island, a temporary pond, an alpine meadow, a lake, or any other piece of the biosphere. The ecosystem has become a basic unit for ecologists, just as the atom is a basic unit for chemists and the species is a basic unit of taxonomists. Since the ecosystem is considered to be the smallest unit in which all ecological processes occur, it may be the functional unit of the biosphere (Odum 1971). If so, ecologists must eventually test their theories in ecosystems, and until a theory has been shown to be relevant in a real ecosystem, its relevance to ecology is speculative.

Why limnology? Now we can return to our original question: Why study limnology? And since I have explained why we should study the ecosystem, our original question can be resolved to

“Why study this particular ecosystem?” Why not offer a course in grassland biology, forest biology or even urban biology? The answer, if there is one, should be that the lake has properties that make it a more suitable ecological tool than other ecosystems. At least at first sight, lakes offer many advantages for testing theory, and I believe that these advantages explain much of the early interest in limnology by ecologists. So let us now look at some characteristics of a lake that make it a better model ecosystem than many others.

A terrestrial ecosystem. Instead of looking at lakes in isolation, let us first consider a wood bordered by grassland (Fig. 18, overleaf) to see the limitations of terrestrial ecosystems as objects of study. The wood seems a self-contained ecosystem; it includes a whole assemblage of plant species not found in grassland, and many mammals and birds found there do not enter surrounding grassland. Within this woodland, nutrients are cycled, energy is fixed and degraded, predators prey and plants reproduce. It is an ecosystem.

But let us look more closely. Ask how the oak interacts with the beech. Do they share nutrients or energy? Would removal of beech affect the oak in any way? One can always argue that there might be an effect. Perhaps some squirrel that depends on nuts from both trees is hiding them together so their offspring compete. My point is not whether there are or are not interactions, but only that some of these interactions appear weak and tenuous. It is easy to imagine that interactions within the woodlot are no stronger than those between the beech tree and the nearby shrubs or grasses at the edge of the adjacent grassland ecosystem.

Now consider large herbivores or predators associated with our ecosystem. How do we handle the fox that hunts mice and insects in the wood, the grassland and the adjacent woods across the valley? What do we do about the male robins that come from miles around to spend each night in a bachelor tree, leaving behind little heaps of concentrated nutrient? We seem to be running into problems with our terrestrial ecosystem. Its boundaries have become so blurred that we begin to wonder if it is really there at all.

Finally, consider the practical problem of sampling a terrestrial ecosystem. Except in the very special cases where the researcher can count and measure each individual, every ecological study begins by sampling the populations of some species. In a forest, this is not easy, for each group requires special techniques. Plants are not evenly distributed and must be sampled in randomly selected quadrats, deer may be sampled by aerial surveys, mice by capture-recapture with live traps, soil invertebrates by Berlese or Tullgren funnels, moths by night-lighting, and other insects by sweep-sampling or groundsheets. Estimates for mobile species are often affected by emigration and immigration, and some measures of abundance are only indices that cannot be compared to each other.

This hypothetical example and its suite of rhetorical questions highlight the problems of applying the ecosystem concept to real ecosystems. Interactions, such as the sharing of energy and nutrient, between any two organisms within same ecosystem are sometimes less than those between two organisms

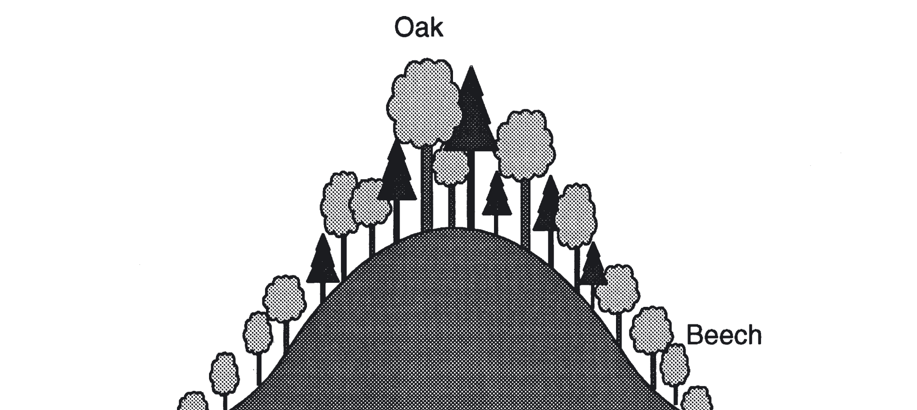

Fig. 18. A woodland ecosystem

in adjacent systems. Animals migrate from one system to another and we must decide where they belong. The transition from forest to grass may be so gradual that it is difficult to say where one ecosystem begins and the other ends. An added difficulty is that the assemblage of species in the oak-dominated hilltop differs from that in the beech-maple forest lower on the slopes; one is always tempted to divide the single ecosystem further.

A limnetic ecosystem. The confused and complex situation of the terrestrial ecosystem contrasts sharply with the apparent simplicity of a lake (Fig. 19). The first difference is that the lake has definite boundary: a step in one direction puts you in, and a step back gets you out. Some animals, like kingfishers and frogs, cross the boundary, but because conditions change so abruptly at the water's edge, most do not. Boundary-crossers are much less common than on land.

The second difficulty we encountered with a terrestrial ecosystem was that it is sometimes more difficult to show interactions between individuals within one ecosystem than between individuals in adjacent systems. Now look again at lakes and see if this difficulty exists (Fig. 20, overleaf). The lighted, well-mixed, surface layer of a lake is called the epilimnion. It is here and in the upper portion of the next layer (the metalimnion) where most photosynthesis takes place. The photosynthesizers in this ecosystem are not trees, but minute algal cells, 1 to 200 μm in length. Now consider cells at two positions (A and B) in the epilimnion, and ask if we can expect interaction. Because the wind continuously stirs the epilimnion, the algal cells there can be compared to lumps of vegetable in a stew. Each leaks organic material into the medium and each absorbs the flavour of the others. If you stir long enough each lump will bump into every other lump. We can therefore conclude that interactions are potentially very strong and that all cells compete for nutrients and energy. A related advantage to this stirring is that it imposes considerable horizontal uniformity on the system. Just as we have less trouble distinguishing boundaries, we are also less tempted to divide the system further.

The third difficulty concerned sampling terrestrial systems. Now consider lakes. The plants are microscopic, many cannot swim against the current and

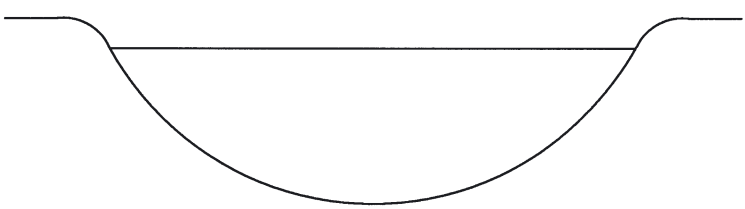

Fig. 19. A lake ecosystem

their horizontal distribution will usually be sufficiently uniform that a single vertical series of samples will give a good estimate of biomass (Hanna and Peters 1991). Zooplankton are more mobile and may be affected by wind so vertical samples must be taken at different positions in the lake (Langford and Jermolajev 1965, Prepas and Rigler 1982), but this is still a simple procedure. Sampling fish is a more onerous exercise, but because migration is negligible, the method of capture-recapture is probably valid.

There are other advantages to lakes as systems of study. Aquatic communities are dominated by minute organisms with short lifespans; such organisms can respond almost instantaneously (at least to the human observer) to disturbance, so the influences of an unknown history are presumably much less than in terrestrial communities, and the likelihood of encountering a quasi-steady state seems larger. If we avoid the discontinuities associated with the surface and the mud, the lake community is more homogeneous than the forest or grassland, so that sampling can be less intensive. Horizontal changes are small and existing vertical gradients in light, temperature and oxygen are gentle and predictable.

I will stop here because my object is not to convert all ecologists to limnologists. I am not proselytising for limnology, but for a way of approaching research. A scientist's job is not to make measurements that no one has made before, it is to construct and test theories. Science always begins with theory, whether with a theory that needs testing or with groups of facts that should be related by a theory. You should try to discover where your interests fit into the scheme of things in science by showing how your pet theory is related to other theories. When you test predictions of your theory, look for the system — whether a cell, a species or an ecosystem — that makes your job simpler.

A difficulty arises because aesthetics almost always enter into biological research. We are biologists because animals or plants happen to please us. One researcher likes fish and finds them beautiful, but hates birds; another is

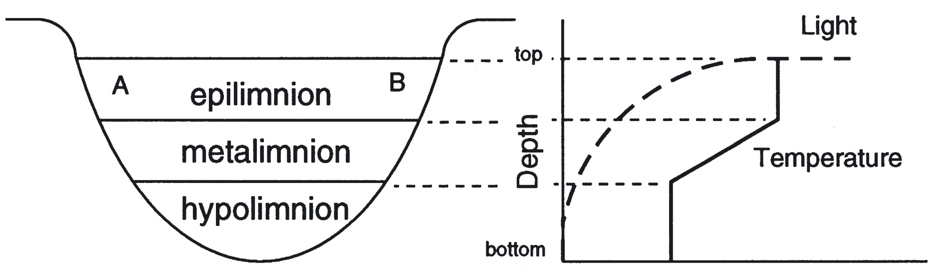

Fig. 20. Gradients in light and temperature in the lake ecosystem. A and B are two distant points in the epilimnion

just the opposite. Personally, I find lakes and the organisms they contain aesthetically pleasing. Obviously, one should not try to test a theory with inappropriate material, however fascinating you think it to be; but equally obviously, we will not give up the subject we like to work on for one we find repulsive, just to test a theory. If we begin with the subject matter, we must ask what biological theory or theories can best be tested with that pet material. Thus we still look for the theory before we start making measurements.

Ecological theories relate an object of particular interest to its environment. In lakes, both the object and its environment are easily defined. This practical detail, coupled with the theory that the lake ecosystem is easier to understand, made the lake ecosystem an important tool in the search for and the testing of ecological theory.

A paradigm shift in limnology. This argument for limnology explains the interest of early ecologists in limnology, but not its current role. Some of us still see limnology as a vital field, providing leadership to the rest of ecology. However, for many scientists both inside and outside limnology (Jumars 1990, Wetzel 1991), limnology has lost its central position in ecology. Therefore I want to end this eulogy to my beloved science with a further suggestion.

The early lead that Forbes gave to limnologists allowed us to discover the limits of the ecosystem concept before other ecologists. The idea of the lake as a microcosm now threatens to be restrictive rather than instructive. Limnologists who have gone beyond that paradigm are now poised to enter a new, more powerful phase of scientific development in which limnology will once again be a major branch of ecology.

The lake is not a microcosm. In Europe, limnologists were less influenced by the beauty of Forbes' English (Elster 1958). Some held similar views (Pearsall 1932), but others disagreed. Thienemann (1926) stressed the role of lake morphometry in determining the composition and abundance of organisms in lake communities. A deep lake would be unproductive and rich in oxygen; shallow lakes were instead productive and their deeper waters were deficient in oxygen. Both types of systems would have the flora and fauna appropriate to their respective conditions. Naumann (1930) instead argued that lake properties were determined by the geology of their basins.

At first, limnologists on both sides of the Atlantic were little concerned with the impact of the land on lakes or with the evolution of lakes under these impacts. Because the life of lakes is long relative to our own, we first thought of lakes as we first thought of species, as permanent. Then paleobotanists began coring bogs to reconstruct the history of terrestrial vegetation, and found that bog sediments contained the remains of open-water algae. This discovery forced us to extend our time scale and to admit that lakes change and die. We began to think of the evolution of lakes as similar to the life of a star: A lake is created in a catastrophic event such as the advance and retreat of a glacier; it develops strength as it slowly accumulates nutrients; it ages as sediments accumulate; it gradually fills, becoming shallower and richer; and it finally dies in a eutrophic burst of productivity before it is transformed into a meadow of sedges and grasses. This view of lake evolution was basically consistent with the ideas of Thienemann.

As the human population increased, human observers first on the shores of Swiss lakes (Ambühl 1960, Thomas 1969) and then on the shores of North American lakes (Beeton 1969, Edmondson 1969) began to see changes within their own lifespans. We had to admit that the evolution of a lake was not so slow as we once thought. In fact, only a few lakes, like Baikal, Titicaca, and the African Rift Valley lakes, antedate the pleistocene. The rest are only 10000 to 100000 years old. The inhabitants of these lakes cannot be the remnant from a distant past. Moreover, we had to admit that climate and humanity could hasten the aging process and affect the properties of the evolving lake. We began to realize that lakes were not isolated systems. They were very much influenced by what happened on land. We became interested in predicting these processes, and much of the current support for limnology is directed to predicting the effects of development in the drainage basin on the properties of the lake.

Evidence against the hypothesis that lakes are isolated ecosystems is now everywhere. The watershed and airshed bring nutrients that set the limits of biomass and production (OECD 1982) but also bring mercury (Håkanson et al. 1990), lead (Evans and Rigler 1985), PCB's (Macdonald and Metcalfe 1991, Taylor et al. 1991) and acid (Neary and Dillon 1988). In most lakes, planktonic primary production is insufficient to meet the energetic demands of even the plankton, let alone the benthos and fish (del Giorgio and Peters 1993), so energy subsidies are required from the littoral or the catchment. The modern lake is not a microcosm.

From Forbesian microcosm to empirical holism. Limnologists had elected to follow what Forbes calls "the *a priori* road" whereby we begin with bold conjectures about nature. There is no harm in such a first step. Problems arose because we did not see this process as only a first step to the identification of hypotheses for testing. We instead treated some conjectures as inspired guesses at intelligible principles for ecology. Such principles were accepted as true. Since they did not need to be tested, they were above the scrutiny of scientific criticism. With hindsight, we can be more critical; what we see is that many of the positive attributes of lakes as study sites were illusory. No measurements showed that the lake was more isolated than a forest or grassland, that its inhabitants were more primitive, that its interactions were simpler, or that its scale was smaller. We had accepted our conjectures as descriptions of reality, rather than hypotheses for testing, and we built and tested hypotheses within the framework of that preconception. In other words, we confused our most fundamental theories about the environment with facts.

The change in perception that saw limnology move from the view that lakes are isolated microcosms to the view that they are part of a larger unit including their drainage basin and airshed represents a shift in the paradigm of limnology. Eventually, the old paradigm failed because it could not address the new problems of pollution, so its initial flaws became more obvious. This change should entail reassessment of the advantages of lakes for the testing of ecological theory.

The loss of limnology's privileged position among ecological testing grounds also has another, more hopeful message for limnologists. The Forbesian view that lakes were specially appropriate for ecological study because they were distinct ecosystems was also a trap. The rationale that led us to expect to see the principles of ecology more clearly in lakes also implies that the lessons learned in lakes would not easily apply to other ecosystems. This limitation was not a problem because limnologists found few principles and because the premise that all ecosystems were similar was not treated as a theory, but as a metaphysical doctrine. In any case, we can now see that lakes may not differ from other ecosystems, so our limnological experience may have broader relevance.

It is counterproductive to think of paradigms as right or wrong. For all its faults, the old Forbesian paradigm played an important role in the evolution of limnology. For many years, it attracted scholars to work on lakes and it allowed these researchers to treat lakes in a consistent and characteristic way. Because the lake was seen as a homogeneous entity, limnologists came to characterize the ecosystem with a few state variables. In the water, we measured phosphorus concentration, chlorophyll concentration, zooplankton biomass, conductivity, and pH. In the sediments, we measured organic content, redox potential, metal levels and density of macrobenthic invertebrates. Such data represent the measurements made by a whole generation of limnologists.

Regardless of the status of the lake ecosystem concept, we can use past measurements to construct new theories about lakes. When we do this, we use the time-honoured approach that scientists have always used: we identify a system of interest, we look for regularities in the behaviour of the state variables describing that system, we express this regularity qualitatively, and then we may seek to explain these patterns.

For example, Richard Vollenweider (1968) sought patterns in lake eutrophication. He saw a pattern in the loading of nutrients (P and N) to a lake and the degree of eutrophication, and developed a simple model to describe the pattern. This approach has since been used repeatedly to provide simple empirical descriptions of nature (Peters 1986, Seip and Ibrekk 1988). For a small group, this process has become a new paradigm, based on empirical holism and called "ecometrics" (Håkanson 1991) or "predictive ecology" (Peters 1986; Chapter IX).

If lakes are no more isolated than other ecosystems, there is no reason to suppose that this approach is limited in its effectiveness to lakes. It should and does apply to forests (Box 1981), grasslands (East 1984, McNaughton et al. 1989), seas (Nixon 1988, Iverson 1990) and rivers (Morin and Peters 1988, Hoyer and Canfield 1991). It should apply everywhere we take the trouble to measure state variables, to examine those measurements for pattern and to express those patterns quantitatively (e.g. Fig. 21). Since robust patterns beg explanation, the last step to explanatory theory will follow almost automatically. Limnology continues to give leadership to ecology, because it has demonstrated that ecology can be a predictive, empirical science.

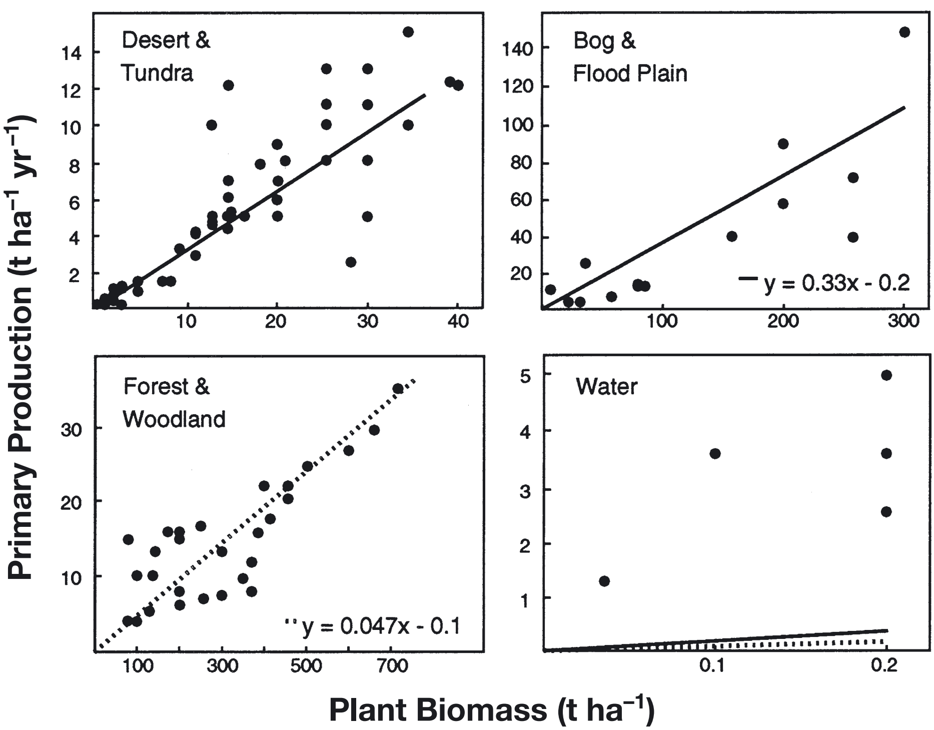

Fig. 21. Relation between plant biomass and primary production in terrestrial and aquatic systems. One regression applies to both the upper panels. Both it and the regression for forest and woodlands are reproduced in the panel for aquatic systems. (From Peters 1980)

Limnology and marine science. I hypothesize that limnology achieved its current predictive power (e.g. Table 9) because it passed through a Forbesian period whereby different systems were characterized by a few measurements. We have now forsaken the idea that lakes are isolated ecosystems, but in doing so, we discovered that those measurements have an independent value. The importance of limnology's Forbesian past can illustrated by comparing the developments in limnology and oceanography.

Oceanographers have typically led limnologists in breaking new ground, rather than vice versa. For example, in my own fields of interest, oceanographers developed techniques to measure phosphorus (Atkins 1923), identified zooplankton feeding as worthy of study (Pütter 1909), and provided the first effective techniques and estimates of filter-feeding (Gauld 1951). Therefore if limnology has stolen a step on oceanography, it is not because freshwater scientists are usually first off the mark.

Differences in the evolution of the two subdisciplines are not imposed by the nature of their material. Marine systems offer most of the practical advantages as lakes. Their boundaries are distinct, much of the biota consists of minute organisms in a homogeneous, three-dimensional habitat with little structure and few gradients. They are sampled in similar ways and similar measurements are compiled. The open sea even appears more isolated from

Table 9. Selected regressions describing the relationships between total phosphorus concentration (TP, mg m^{-3}) and other lake characteristics; n: number of lakes. (From Peters 1986)

Dependent variable	Units	Equation	r^2	n
[Chlorophyll]	mg m^{-3}	$Y = 0.073\,TP^{1.4}$	0.96	77
Transparency	m	$Y = 9.8\,TP^{-0.28}$	0.22	87
[Phytoplankton]	mg wet wt m^{-3}	$Y = 30\,TP^{1.4}$	0.88	27
[Nanoplankton]	mg wet wt m^{-3}	$Y = 17\,TP^{1.3}$	0.93	23
[Net plankton]	mg wet wt m^{-3}	$Y = 8.7\,TP^{1.7}$	0.82	23
[Blue-green algae]	mg wet wt m^{-3}	$Y = 43\,TP^{0.98}$	0.71	29
[Bacteria]	millions ml^{-1}	$Y = 0.90\,TP^{0.66}$	0.83	12
[Crustacean plankton]	mg dry wt m^{-3}	$Y = 5.7\,TP^{0.91}$	0.72	49
[Zooplankton]	mg wet wt m^{-3}	$Y = 38\,TP^{0.64}$	0.86	12
[Microzooplankton]	mg wet wt m^{-3}	$Y = 17\,TP^{0.71}$	0.72	12
[Macrozooplankton]	mg wet wt m^{-3}	$Y = 20\,TP^{0.65}$	0.86	12
[Benthos]	mg wet wt m^{-2}	$Y = 810\,TP^{0.71}$	0.48	38
[Fish]	mg wet wt m^{-2}	$Y = 590\,TP^{0.71}$	0.75	18
Average primary prod.	mg C m^{-3} d^{-1}	$Y = 10\,TP - 79$	0.94	38
Maximum primary prod.	mg C m^{-3} d^{-1}	$Y = 20\,TP - 77$	0.95	38
Fish yield	mg wet wt m^{-2} yr^{-1}	$Y = 7.1\,TP^{1.0}$	0.87	21

the land. Of all the ecological sub-disciplines, marine biology seems the most likely to resemble limnology, yet in some respects the two sub-disciplines are poles apart.

There are differences between lakes and oceans. The sea is salt, the scale of the oceans is greater, sampling is more expensive, biological diversity is higher and so on, but none of these differences seems crucial. A more important distinction between lakes and oceans is the number of discrete sites. There are vast numbers of lakes. My home province of Quebec has a million lakes larger than 10 ha in area and, next door, Ontario has half a million more. There may only be seven seas.

The great number and small size of lakes offer the advantage that limnologists can manipulate lakes to test our theories (Schindler and Fee 1974; Elser and Carpenter 1988). In the sea, one could use estuaries, bays (Håkanson and Wallin 1991) and fjords (Aure and Stigebrandt 1990) as natural units for replicated measurements and experimentation, but this approach has only proven popular in the marine littoral (Paine 1977).

The large number of lakes is a misleading statistic. That alone need not impose different frames of reference on fresh and salt water researchers. There are more lakes than seas, but those many lakes cover less than 1% of the area of the oceans, contain less than 0.01% of the ocean volume, and are spread less evenly across the earth's surface. In some important ways, the ocean offers more sampling sites than lakes. Even the discreteness of lakes may be more apparent than real, for most lake districts bind their lakes together by common patterns of geology, climate, and land use. In any case, the distinctness of lakes and the inter-connectedness of the seas are relevant only as properties of our theories about these systems. If the theories do not work, then the properties are irrelevant.

Because oceanographers could not delimit small distinct areas to study, many of them adapted a different form of the ecosystem concept. Rather than characterize each area with a few state variables, they tended to treat each study area as a unique assemblage that required detailed description of its components, likely in terms of a simulation model. Oceanographers felt the collapse of the microcosm view less. They did not normally work at the level of the ecosystem, but at a lower level of organization, with ecosystem components. They experienced neither the discomfort of paradigm change nor the benefits of a fresh outlook. Instead, marine biologists continued to treat their material as an aggregate of many sub-systems, each of which has to be individually described. This view is discussed in the next chapter. For the present, it is enough to note that, without the Forbesian frame of reference, marine ecologists could not see their data as state variables characterizing a system, and therefore their systems remained difficult to characterize or to compare.

Why limnology — an answer. In summary, limnology originally played a leading role in ecology because limnological systems seemed optimal for testing contemporary ecological theory. The suggestion that the limnetic pelagial might be a microcosm attracted some of the brightest minds in ecology to consider limnological examples. Terrestrial ecologists were less drawn to the approach because their ecosystems were less clearly connected internally; marine biologists were not attracted because their potential ecosystems were less obviously isolated from other parts of the ocean. Neither group was able to agree on how to identify the system they should study or on what measurements characterized their systems. Confident in the definition of their ecosystems, limnologists moved ahead to describe their ecosystem with state variables that characterized the whole.

Subsequent development revealed anomalies and flaws in the limnological paradigm, and many of the concepts it encouraged have been shown to be untestable or erroneous. If limnology is no longer leading all of ecological theory, it is because its earlier success was premised on the misapprehension that tests of ecological theory required an isolated microcosm. Since this is no longer tenable, ecological theories are equally testable in many systems and limnology has lost some pride of place. Thus to much of ecology, limnology seems to have slipped from its once pivotal position (Jumars 1990, Wetzel 1991).

Some limnologists learned from the experience to move beyond the microcosm concept. The information and tools that developed under the old paradigm allowed researchers to step boldly into a new phase of growth based on measurable state variables and prediction of whole system properties. Although our original conceptions of lake system limits were flawed, and although we are uncertain what the new limits should be, the holistic measurements we took still describe our lakes. Even if we can no longer define the system, our holistic measurements function as the basis of empirical theories to predict lake characteristics.

Science does not depend on what we think about reality or about the state variables we use. Science depends on how well these variables function in theories to make predictions. Some limnologists learned this when their paradigmatic conception of reality crumbled, but related empirical theories continued to predict. Predictive limnology is a flourishing sub-discipline (Peters 1986, Seip and Ibrekk 1988), and limnology is once again showing the way, this time towards a new science of predictive ecology. And that is why we should teach and study limnology.

VII Reductionism versus Holism: An Old Problem Rejuvenated by the Computer

> "The meaning of this illumination [...] did not penetrate at once, and notably the word trim [...] long remained obscure."
>
> Samuel Beckett
> [*Molloy* (1950)]

The subject of this chapter has been ignored for such a long time that the key words in the title are nearly meaningless to most biologists. These words may even give the impression that I will deal with the history or philosophy of biology rather than with its science. That is not my intention at all, for I am neither an historian nor a philosopher. My only reason for being interested in the history and philosophy of science is that these disciplines may teach me to do my science, ecology, more effectively.

Ecology is a branch of science that is, or at least ought to be, very important to society. We need ecological predictions and we need them now, yet ecology has failed to produce the predictive theories we need. If asked why, most ecologists explain away our failure by the extreme complexity of our subject matter and the youth of our discipline. I do not deny these explanations. They may be right. However, the intractability of our subject matter is not the only barrier to ecological progress. There is also something peculiarly unproductive about the approach we ecologists have taken to study our subject matter.

The Place of Philosophical Debates in Biology

The theme of this chapter is that we ecologists have been working inefficiently because we ignored philosophical debates that involved a few biologists a century ago. We working scientists ignored the biophilosophers because we never understood what they were talking about. Indeed, they did not understand it themselves. The advent of the computer has re-invigorated some of these old, semi-philosophical questions, and forced us to restate them in such a way that they become meaningful to experimental ecologists. I will illustrate the problems this creates with some of my own work with ecosystem ecology in the high Arctic and with the autecology of zooplankton feeding. Finally I will suggest that if we learn the lesson such examples provide, we may become more effective. The point of the chapter is to suggest that the discovery of ecological systems and the introduction of the technique of systems analysis into biology require us to reevaluate the ecologists' approach to science.

Molloy and the principle of trim. Before describing the history of our debates I will give an example of what I mean by saying that we did not understand our own arguments. This statement would seem strange to philosophers and historians because they work with words, and are expected to use them rigorously. However, scientists tend to be less interested in words than in phenomena. Consequently, when a scientist looking at nature gets a brilliant idea, the immediate problem is to express the idea in words. Until this is done, there will be no convincing others of the brilliance of the idea.

My illustration comes from the writings of Samuel Beckett — a writer most remembered for his deep understanding of the human tragedy. I believe he had an equally deep understanding of science, as shown beautifully by the incident of the sucking stones in his novel *Molloy*, which forms the prologue to this book.

Molloy, crippled, destitute and lost, rests (to the extent that he could ever rest) on the sea shore. There he sucks wave-washed pebbles to relieve the pangs of hunger and thirst. Yet he is totally engrossed in the problem of distributing his sixteen sucking stones among his four pockets such that he can suck them each in rotation. He goes through several unsatisfactory solutions until finally he has an insight. He can obtain his goal if he sacrifices "the principle of trim" and distributes the stones unevenly among his pockets. At this phase in his research, Molloy exemplifies my point, that scientists have trouble expressing their discoveries, in the quotation that begins this chapter. Molloy was convinced he had made a great discovery and he expressed his discovery in a word: "trim". However, for a long time he did not know what he had discovered, nor why it was aptly described as "sacrificing the principle of trim".

This inadequacy did not deter Molloy. Neither does it deter the biologist who has found something great but cannot explain it. This I believe was the situation with a few biologists who took part in the debates of the 19th century. Their insights were important, but unfortunately the words they used left the great mass of working biologists unmoved.

Vitalism and mechanism. The debate I want to discuss is the debate between the holists and the reductionists. Because this debate has become incredibly confused, I will also give some of its history and show how it evolved.

Aristotle is again a good starting place. Among his many ideas about the nature of living things, he believed that the difference between living and non-living things was due entirely to the fact that the living things possess a soul. A simple consequence of this belief is that we cannot expect to learn anything about life by studying a dead body. Neither can we learn anything about life by studying a hand or a liver or some other organ removed from a living body. This philosophy (perhaps "faith" is a better word) was called vitalism (Table 10).

Vitalism dominated biology until the 18th and 19th centuries, by which time physiologists had wrought a slow, initially unnoticed, change. Incited by René Descartes (1596–1650), they began to treat living things as if they were physico-chemical machines. For example, Hermann Boerhaave (1668–1738) and George Martine (1702–1741) argued that the vital warmth of the human body is produced by the friction of red corpuscles rubbing on the walls of arterioles. A century later, Gustav Magnus conducted experiments with blood removed from the body, analyzing the results of his experiments as if blood were merely a physical fluid (Mendelsohn 1964). Theodor Schwann (1810–1882) extracted the active principle of gastric juice from the lining of the stomach with acid, and then showed it could be precipitated as if it were simply a chemical substance (Bodenheimer 1953).

Table 10. Fundamentally different approaches to the study of biology

Vitalism:	Life depends on the presence of a soul.
Mechanism:	Living organisms are simply complex physico-chemical machines.
Organicism:	Life depends on organisation; each level of increasing complexity of organisation can only be described in terms of laws appropriate to that level.
Reductionism:	The proper approach to the study of complex phenomena, like life, is to decompose this complexity to simple components. In many cases, these components can then be shown to be instances of general physical and chemical laws.
Holism:	Complex systems must be treated as whole systems, because the process of analysis inherent in reductionism destroys the basis of their integrity.

The story of vitalism ends in France in the middle of the 19th century in a little cellar in Paris, where the great physiologist Claude Bernard (1813–1878) had a table which he called his laboratory. Bernard did a very simple experiment. He killed a dog and removed its liver. He then inserted a tube into the hepatic portal vein and perfused water through the liver. He analyzed the water emerging from the liver for sugar and found glucose, but in time no more sugar came out. He had washed out all the available sugar. He then left the liver in a warm place for several hours, once again perfused it, and found more sugar. Bernard concluded that the liver could make sugar from another compound and he called this hypothetical precursor "glycogen".

This experiment was terribly important in its day. It showed that animals can change one compound into another, it helped Bernard develop the idea of internal control, which became one of his greatest contributions to science, and it showed that an organ can have more than one function (Larner 1967). The experiment was even more important because biologists of the time accepted it as valid.

Bernard had drawn conclusions about the functioning of a living organism from an experiment done with a part of that organism separated from the rest of the body. For the two thousand years after Aristotle, this approach had been totally unacceptable to most biologists. Everyone had known that the only difference between a living organism and a dead organism is the soul, which conferred life and left the body at death. Thus a dead animal or animal part could tell us nothing about life.

By Bernard's time, biologists were no longer unanimous on this point. A growing number were treating organisms as highly complicated machines. The biologists promoting this new approach were the mechanists who saw life as a complicated physico-chemical process, and Bernard's experiment marked the triumph of this scientific revolution. The real significance of Claude Bernard's experiment was that it was the last shot in the battle. With this experiment, the mechanists won the war and vitalism was never again an acceptable paradigm for biologists. With Claude Bernard, the revolution was over and most biologists rejected vitalism for mechanism.

Organicism and holism. Our story does not end with the mechanistic revolution. It begins there. Some biologists accepted that biology could best progress without postulating a soul, but not that living things were only perambulating bags of chemicals. These biologists argued that the components of living things are organized into living systems, and that the properties of these systems could not be predicted from a study of their parts. This new idea was a modification of vitalist thought. It differed from vitalism by substituting organization for soul and by asserting that we could learn to understand living things, but only if we studied them intact. This view came to be called organicism. The organicists produced the idea that is central to this chapter.

The new trend began with Xavier Bichat (1771–1802) who was obsessed by the variability of living systems. Physico-chemical systems were dependable and their behaviour reproducible, but biological material was unreliable and variable. From this hypothesis, he argued that biological systems must have something extra. Their behaviour must be governed by new, still unknown, peculiarly biological laws (Mendelsohn 1964, Hall 1969).

Lloyd Morgan (1923) improved on Bichat by inventing the idea of "emergent properties" whereby each level of complexity has its own laws. An important consequence of this idea is that if we want to develop theories about matter at a particular level of complexity — like a cell, an organ or a whole organism — then we must study the cell, the organ or the whole organism, not its parts. This is because the whole cell (or organ or organism) has properties that its component parts lack.

At the beginning of the 20th century, the opposing forces had regrouped and the mechanists had changed their names. The descendants of mechanism became "reductionists", because they believed in breaking up the system they intended to study. The battles that raged, unnoticed by most biologists, were first between the vitalists and mechanists and then between the mechanist-reductionists and organicists. It was the organicists who had something to say but were unable to find a way of saying it. Just as "trim" meant something to Molloy, "emergent properties" meant something to the organicists. Unfortunately, it meant nothing to most working biologists.

In the 20th century, their words began to gather more meaning and began to be applied not just to living organisms but to ecological work as well. The first advance was made by Ludwig von Bertalanffy (1950, 1952) who suggested why living systems might have emergent properties. Von Bertalanffy said the important characteristic of organisms is that they are systems, that is to say they comprise "a complex of elements in mutual interaction". The behaviour of a system depends on all interactions amongst all the parts, and so the interactions are as important as the parts. If one part is removed, the interactions between it and other parts are broken. This was much more convincing than the vague talk about emergent properties, and in recognition of the advance we changed the names of the protagonists for the last time to holists and reductionists.

Reductionists and holists were debating a real and significant question about scientific knowledge, but we hear little about their dispute today. I believe biologists lost interest because the opposing forces were just too unequal to make a battle worth fighting. The holists were few and far between, so the reductionists just ignored them. Consequently, most of us are reductionists by default. We accepted an approach to which we were conditioned without ever questioning our belief or knowing that there is another viewpoint.

Holism and reductionism in ecology. Most ecologists were oblivious of these questions. We were mostly concerned with predicting and controlling the abundance of particular species, because we wanted to know, for example, if fishing would deplete fish-stocks, or how different forms of pollution affect organisms we care about. Our interests were therefore largely directed to individual species, and we hoped that a single factor would be of overwhelming importance for each species.

Many ecologists behaved as if the distribution and abundance of a species could be predicted from physical and chemical factors alone, and early field work was largely directed at the relations between individual members of a species and their physical or chemical environment. Researchers therefore sought to establish the response of an organism to temperature, humidity, pH, salinity, etc. Given this emphasis, it is scarcely surprising that autecology was a major branch of ecology or that the limiting factor was the most popular concept. The emphasis on autecology even allowed plant and animal ecology to develop as separate disciplines in different university departments, as if animals and plants did not interact.

The autecological approach was appealingly simple, but it did not work well enough. Researchers therefore increasingly emphasized biological interactions, like competition and predation. This interest marked an implicit recognition that biological interactions can be more important than physicochemical factors.

The American botanist F. E. Clements (1916) moved decisively beyond autecology when he wrote about plant communities as superorganisms. He has since been thoroughly abused for this. I think the attacks against him were unjust, but I recognize that he made two fatal mistakes: he was suffering from the Molloy syndrome and he was too far ahead of his time. If Clements had "penetrated the meaning of his illumination" and if he had read von Bertalanffy, he would have said something like this: "The community is a system, and in this respect, it resembles an organism. But it is more complex. It comprises the interactions among many organisms, and in that sense, the community is at a higher level of organization than an organism. This is what I mean by superorganism". Similar ideas are currently accepted as elements in hierarchical thinking (Allen and Starr 1982, O'Neil et al. 1986). But, alas for Clements, he did not say it right, and he has been a bogey-man for politically correct ecologists ever since.

Nevertheless, gradually and unconsciously, we began to change. We admitted the food chain among our fundamental concepts, and when faced with results like Hardy's (1924) study of the complex feeding relations of the herring, we admitted that the food chain was unrealistic and changed to food webs, implicitly accepting the idea of multiple interactions. We stopped separating plant and animal communities, and began to talk about ecosystems. We slowly came to realize that in ecology we are not dealing with isolated entities but with one or more highly organized systems in which the parts interact with and depend upon one another.

The concept of the ecosystem led to a problem. Most ecologists had developed a tradition of studying bits and pieces, but had no idea of how to fit our bits and pieces together. Then, two developments outside of ecology made it possible for us to deal with complex systems. These were systems analysis and the computer.

What is Systems Analysis?

I can explain systems analysis best with a simple example (Fig. 22). Take a tumbler of water containing plant nutrients. Shine a light on it. Put in some algal cells and add a few water fleas to eat the algae. This is a system: algae, nutrients and *Daphnia* all living together and dependent on each other. If we know the quantity of each component and the interactions between all the

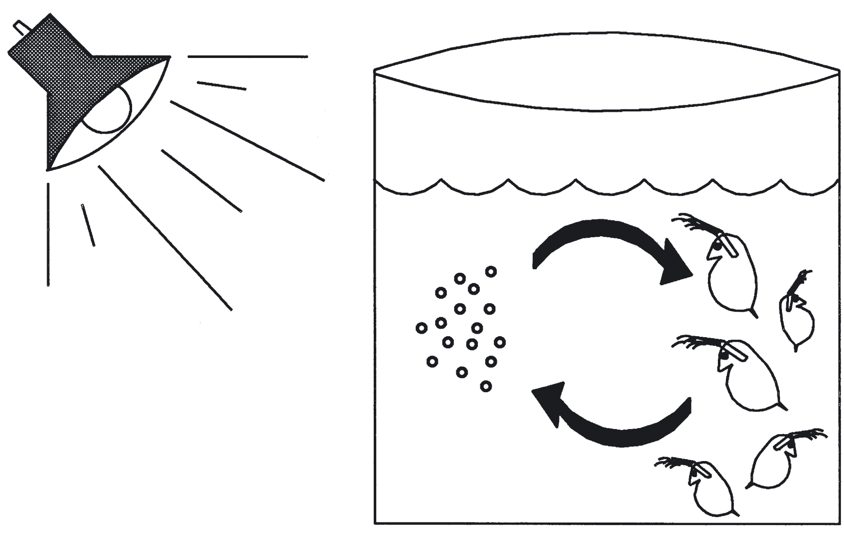

Fig. 22. A simple system consisting of an external energy source (light), a primary producer (algal cells), herbivores (*Daphnia*) and their interactions

components, then we can use a computer to do an incredible amount of simple arithmetic and so calculate the amount of each component or "state of the system" at any time in the future. This approach was taken by many ecologists who accepted that ecology deals with complex systems. It is called "systems" analysis because it seeks to decompose the working natural system into parts for study, and then to recreate that system as the sum of these interactions. In the example of Fig. 22, the interactions I must measure are feeding rate as a function of animal size and algal abundance, uptake rate of plant nutrients as a function of nutrient concentration, and the rate of nutrient excretion by the animals.

There is a catch. To succeed, I must measure all components and all interactions. If I leave out *Daphnia* or omit excretion, or if I measure one interaction erroneously, my model will not work any better than a watch without its tiniest cog-wheel. To do otherwise, to presume that we can either leave some elements out of our model or model only the significant interactions, presupposes that we can somehow identify the important processes *a priori*.

Failures since the time of Aristotle should have taught us that appeals to "intelligible principles" or the "*a priori* road" of assumptions about nature are not effective. If we are to dismiss some interactions as unimportant, we must first study those interactions in detail. Unfortunately, that effort is exactly what we are trying to avoid. Moreover, partial representations involve a possible contradiction because the appeal of mechanism and reductionism is their capacity to represent "what's really happening", so that we will "understand what's going on". If we ignore much of what is really happening, then the apparent strong point of the reductionist-mechanist position is already lost. Any argument would only be a methodological debate about how thorough the holist position should be.

Even in a simple system, the possibility of modelling all the interactions is small. For example, we perhaps should consider the excretion of different elements or compounds separately. Perhaps our model should have a place for the bacteria in the daphnid's gut and the epibiotic organisms living on its shell. Perhaps the modifying effects of time of day, or light levels or temperature or age of the culture should be considered. Perhaps there are important interactions among the algal cells. Neither these specific problems nor the general question of when we should stop analyzing the system has been resolved.

We are not satisfied with systems consisting of a few species and their physico-chemical environment. We need to describe large ecosystems, and to do so we must gather larger and larger teams of scientists and technicians to work on each ecosystem. For example, in Russia, a team of 150 scientists worked on a single reservoir for three years. This trend to more ambitious projects is also exemplified by large scale international programs, like I.B.P. (The International Biological Programme) of 1965 to 1975, or the contemporary JGOFS (The Joint Global Ocean Flux Study) and WOCE (World Oceans Circulation Experiment).

To appreciate the difficulties that systems analysis presents in the treatment of these large systems, we must consider the data that ecologists are gathering and the uses to which these data are put. Imagine the moderately simple ecosystem represented by the biota of a temperate lake. In round numbers, this might include 200 species of plants, 100 species of herbivores, 100 species of carnivores, 50 species of bacteria, 200 animal species that cannot be attributed to any trophic level, and 100 species of detritivores. This community of 750 species is simpler than it might be. Likens (1992) estimates that there are at least 850 species in Mirror Lake, New Hampshire (USA) and Elton (1966) suggested that Whytham Woods in England might contain 5000 species of metazoans. To model such systems we must describe these communities. Such a description might take the form of a compilation of the biomass, the rates of birth, growth, and death for each species, and the interactions (predation, competition, etc.) among these species. We might further describe the effect of variations in light, temperature, nutrients, etc. on these components and their interactions. We could then build these parts of the system into a model system in our mind (Fig. 23, overleaf).

The arrows in Fig. 23 show only the predator-prey interactions. In a real description of the system, every component potentially interacts with every other one. Therefore if the number of components (n) equals the number of species, n = 750 and the potential number of interactions = n(n–1). This average lake has 561 750 potential interactions among its components. (The calculation assumes that the effect of Species A on Species B must be described separately from the effect of Species B on Species A, because that situation seems more plausible to me; if the interaction is instead bidirectional, the number of arrows will be halved.) Now imagine that we have our system arranged in our minds where all 561 750 interactions are indicated by arrows. The human mind cannot keep track of all these interactions. To predict the effect of any disturbance on our system, we have to use the technique of systems analysis and its characteristic tool, the computer. What should we do next to make this possible?

There is no need for details. It is sufficient to note that systems analysis requires us to quantify every interaction, under the entire range of environmental conditions that we expect to encounter. If each interaction requires only one person-year of effort, this description will require centuries even for a large team. In passing, I note that I spent over four years developing a theory that describes only 50% of the variation in a part of a single interaction: phosphorus excretion rate by *Daphnia rosea* (Peters 1972, Peters and Rigler 1973). Other arrows linking zooplankton, their food and the resources upon which that food depends were studied almost as long with almost as limited success by other doctoral candidates in the same laboratory (Chamberlain 1968, Confer 1969, 1972, Haney 1970, Lean 1973). I conclude that full description of an entire ecosystem is so great an effort that we will never complete the task. In fact, we won't even try. The job is just too big.

Some problems with proposed solutions. The previous section established that it is impossible to specify the current state and interactions of the components of complex ecological systems. The problem is not a philosophical issue but a purely practical limitation (Wimsatt 1980). Simplification seems a practical solution, but a few moments' reflection shows that this is not the case.

Identifying the components. Most biologists prefer to work on individual species, and when systems models have been built, they normally depend

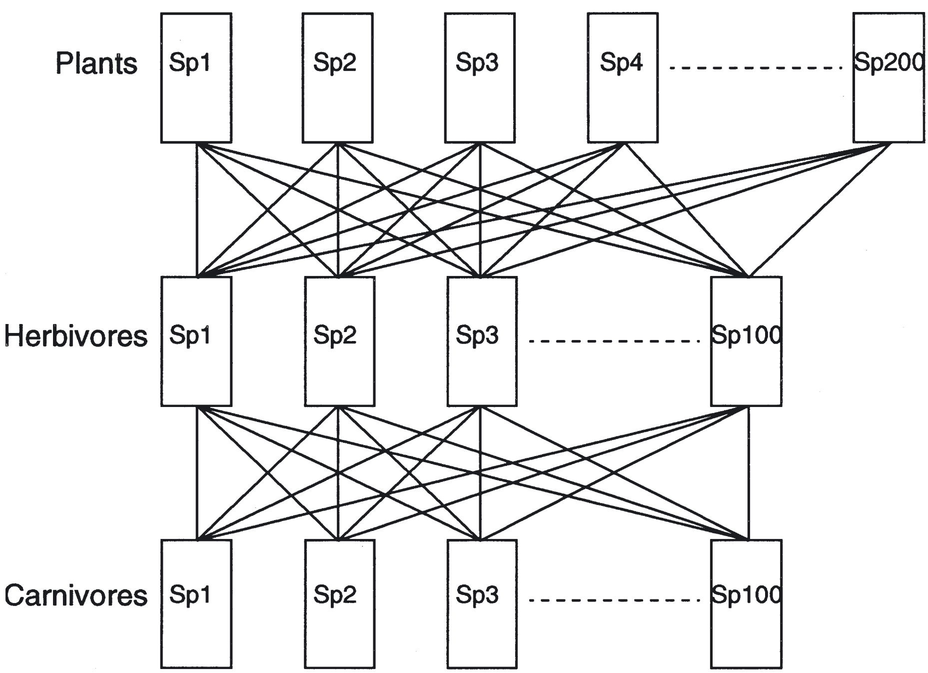

Fig. 23. A hypothetical lake ecosystem consisting of 200 species of primary producers, 100 species of herbivores and 100 species of carnivores. Arrows indicate potential trophic interactions, and not shown are 50 species of bacteria, 100 species of detritivores, 200 species that could not be classified to a single trophic level, and all non-predatory interactions

heavily on autecological work done at the species level. Unfortunately, we do not know the number of species in any natural ecosystem. Study after study has shown that the harder and longer one searches, the more species one will find. Thus we can never know how many components comprise the system.

One can seem to address this problem in a number of arbitrary ways. For example, one could propose that the system is characterized well enough when the rate of increase in species number per unit of additional effort falls below some specified value. Unfortunately, approximations like that will not do. There are many cases in which obscure components play important roles in structuring their communities: *Opuntia*, the prickly pear cactus, is held in check by the now rare *Cactoblastis* moth in Australia; in Africa, intestinal parasites of tse-tse flies apparently protect the Serengeti from over-exploitation by debilitating human agriculturalists with sleeping sickness. Currently small or rare members of the ecosystem cannot be excluded from a systems analysis on the grounds that such components never play an important role.

Aggregation. One way to simplify the system is to lump different species of similar organisms into a smaller, more tractable number of functional groups. The trophic level approach (Lindeman 1942) is one such attempt. The description of the planktonic community of primary producers in terms of chlorophyll concentration might be another. Unfortunately, aggregation is rarely easy or effective in systems analysis. To determine which organisms are functionally similar members of a community, we must determine their relations to the rest of the community, but this was the difficulty we were trying to escape. Whether we aggregate the data or not, we are required to create a tiny theory for each member of our system in which we hypothesize how that member relates to every other component. Since we can hardly expect to create 561 750 correct theories, we must build error and approximations into the systems analysis model. Since these errors will be propagated with each calculation (Beck and Halfon 1991, Peters 1991a, van Straten and Keesman 1991), we cannot expect that the model will work.

Interactions. We have not seen it all yet. One last problem poses even more difficulties than either simplification or aggregation. Consider how the ecologist usually quantifies interactions between system components. Occasionally these are estimated *in situ*, but more often than not this is impossible. Therefore the two interacting components to be studied are isolated and their interactions are measured in the laboratory. For example, when we measure the feeding rate of a water flea as a function of the abundance of its food, we isolate the flea and one type of food in a beaker where we can easily vary the food supply. Then we take the rates we measured and apply them in our model.

This procedure is effective only if no component of the natural system acts directly on the interaction we are measuring. If there is such a component, our lab values will not apply to the natural system. Obviously such modifying interactions are common: the presence of noxious algae may cause the water flea to reduce its ingestion rate of palatable species (Burns and Rigler 1967, Burns 1968), the absence of vitamins may make the water flea less capable of utilizing assimilated food (Provasoli et al. 1970), and feeding rates change with temperature and time of day (Haney and Hall 1975). Since most interactions are modified by the environment in which they occur, we must study the animals *in situ*, and we must study each interaction intensively. We cannot escape the massive work-load that systems analysis of any natural ecosystems imposes (Rigler 1982a). But since we cannot do that much work, the applicability of systems analysis is so limited as to require reassessment of the approach.

Two Personal Experiences

The impossibility of really analyzing a system and of synthesizing the parts into a computer model is rarely appreciated. Most of our research is designed to allow us to analyze the bits of a natural system that interest us, leaving the remainder for others and assuming that someone else will solve the problems of putting the big picture together. I no longer accept this view because I have seen the magnitude of the problem of creating a system analysis model. I encountered these difficulties in many aspects of limnology, but I will illustrate the problems with two aspects of my work which differed very much in scale: the Char Lake Project and the analysis of zooplankton feeding.

The Char Lake Project. Some years ago I became involved in the study of one of the simplest lake ecosystems in the world, Char Lake located on Cornwallis Island in the Canadian High Arctic. This study was not undertaken because the lake seemed an ideal site for systems analysis, but we justified our research with a conceptually similar argument. We hoped that we could exploit the simplicity of Arctic systems (Table 11) to increase our chances of learning something about lakes in general. In retrospect, this justification seems lame, but at the time it was quite convincing.

The Char Lake Project also represented part of Canada's contribution to the International Biological Programme in which 50 countries participated in over 140 different projects. Each project involved a team of biologists working together for up to five years. At the time, IBP provided an unprecedented level of funding, international communication and communality of purpose.

In many ways and despite its eventual shortcomings, the period of the IBP was a golden age in ecological research.

The ostensible reason for the IBP was to determine the limits of productivity of the earth and thus to determine its capacity to meet human needs. Teams of scientists were to measure productivity all over the earth, and the composite of their results was to represent this global overview. Most of us felt that this was too simple a goal and sought to measure primary, secondary and tertiary production and the associated biomasses and energy flows as well. We hoped that by focusing our attention on this previously little studied set of properties, and by standardizing our techniques as much as possible, we might discover a theory relating these properties to others such as light, temperature or nutrients. This hope now seems naive.

Regardless of the reality of our hopes, the same data were to be used both to estimate production and to try to understand production processes. A large team was required for this work because the objective was to study everything in the system.

Only a few members of the IBP were directly involved in simulation modelling. The others sought to identify the components of the system, and then to quantify each component and interaction. When these had been measured in sufficient detail, the various components were to be pieced together as a predictive model in a computer simulation.

There are reasons for comprehensive data collection, other than systems analysis. Indeed, the larger part of the IBP teams doubted that systems analysis would resolve the problems of ecosystem ecology. That group acted as though ecology (and presumably science) consists in the organized and systematic collection of data that the scientific community considers important. Presumably few members of IBP were pure Baconians, subscribing to the discredited view that theories arise automatically from a sufficient quantity of

Table 11. The depauperate fauna of a high Arctic lake, Char Lake, relative to that typical of a temperate lake

Group	Number of species	
	Char Lake	A temperate lake
Vertebrates	1	20
Planktonic crustaceans	1	10
Planktonic rotifers	1	15
Diptera	7	150
Nematodes	24	?
Other benthos	13	100

good data. However, many would have accepted the view that the collection of good data is justification enough.

Other researchers may have joined a team project because they believed that they were working on the single critical and tractable component of the ecosystem. The subject of their interest would repay study because, when this component was understood, we would be able to predict the observations that other members of the team had conveniently made (Fig. 24). A corollary of this egocentric view is that the subjects studied by others would prove less easy or valuable. The weak point in this argument is the lack of consensus about which process was the controller, and the individual assurance that each of us had chosen to study the critical interaction whether that be nutrient load, primary production, excretion, predation, or whatever.

Regardless of its rationale, the team approach made reductionists of us all, even if we did not know the term, because the team was trying to assess the

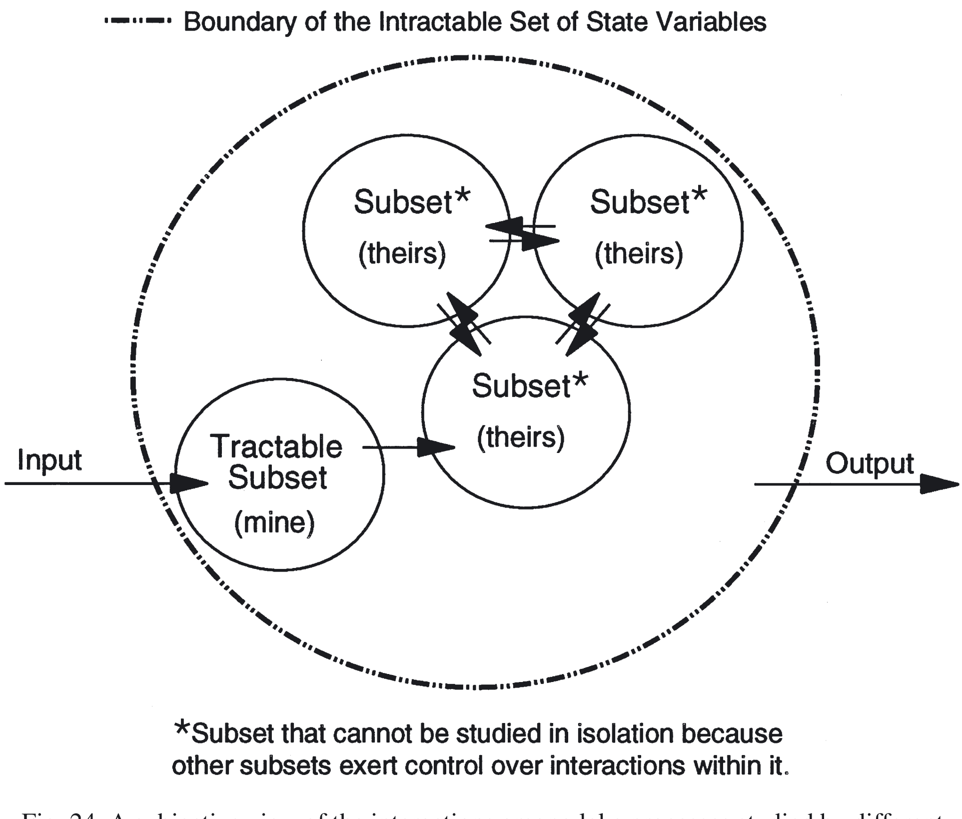

Fig. 24. A subjective view of the interactions among lake processes studied by different reductionists in the same team. (From Rigler 1975a)

whole, but the individuals were studying the parts. The approach also made us all systems analysts, whether we touched a computer or not, because we could not hope to put all our studies together except in some form of computer model.

Problems in the components of reductionism. The problems of building a computer model for an ecosystem are rarely apparent to anyone except the modellers. The present generation of models is so complex that a description of all the adjustments, guesses and theories that went into model development cannot be given in the space of a scientific paper. As a result, these presentations are usually impossible to assess (Rigler 1976). Instead, I will simply describe some of the results from our own work that made the simulation of Char Lake impossible.

So far, I have written as though the species was the smallest component that one would include in a systems model. However this is a gross over-simplification. For example, although all the fish in Char Lake are Arctic char (*Salvelinus alpinus*), these animals are not all equivalent. A few were cannibalistic giants, whereas the rest of the population fed largely on benthos. The single crustacean zooplankter, *Limnocalanus macrurus*, has 11 different instars or developmental stages, some of which are so different that they were once classified as a separate genus, all of which differ in their feeding capacities. Thus the complexity of the system is not necessarily reflected in its species list.

If we could identify the components of the ecosystem, we would then seek to estimate their biomass. Such estimates have preoccupied ecologists for many years. Most of us recognize that the size of a wild population can rarely be estimated within 50% at any one point in time and that population size normally fluctuates by an order of magnitude over time (Connell and Sousa 1983, Peters and Wassenberg 1983, Schoener 1985, Pimm and Redfearn 1988). For example, when we used nets to make a capture-recapture estimate of the fish population in Char lake, we estimated a population of 15 000 char. However, when we counted the fish on the spawning beds, our estimate rose to 50 000. Apparently, marked fish were more easily recaptured than unmarked fish, so our recapture rate was high and our population estimate low. Although we are justified in claiming that the initial estimate was low, we cannot assume that our spawner count was right.

Finally, our modelling, whether conceptual or computed, required estimates of the various rates of energy flow through the members of the community. In a general sense, this was unsatisfactory because each component was analyzed to a different degree and with different methods. A great deal of effort was directed to the zooplankton, largely because the plankton were the simplest part of this simple system and because many of us were primarily planktologists. Unfortunately, most of the energy flow in this system went through the benthos, which was less studied and more difficult. For example, none of the 24 species of nematode could be cultured and there were no *in situ* methods for these organisms. The energy budgets of our most speciose taxon could not be studied.

Some holistic successes within the Char Lake Project. These many difficulties should not obscure the successes of the project, but because most have been reviewed elsewhere (Rigler 1978), I will only mention some examples here. At the level of the whole system, Welch (1974) was able to measure community metabolism by using the ice-covered lake like a huge dark bottle through the dark Arctic winter. Welch and Kalff (1974) developed techniques to measure bryophyte-dominated benthic production in the lake and showed that 80% of all primary production in this lake was benthic. They also showed that nutrients limited algal biomass in the Arctic, just as they do in more temperate regions (Kalff and Welch 1974). At a smaller scale, work with rotifers (Rigler et al. 1974), chironomids (Welch 1976), *Mysis* (Lasenby and Langford 1972) and char (Holeton 1973) showed that these Arctic populations were not especially well acclimated to their cold environment, but behaved like southern representatives of the same species at the same temperature; this finding is a major challenge to a generation of autecology. With respect to zooplankton feeding, careful examination of the guts of the crustacean zooplankton showed that these calanoids did not digest diatoms, unlike their marine counterparts (Kibby and Rigler 1973). Careful use of well-designed sediment traps showed that *Limnocalanus* produces only one faecal pellet per instar; contrary to general belief, the faeces of this animal are not bound into a pellet and so most of the faeces might not have been lost from the water column, but rather resuspended.

The common thread through these results is that all address different systems of interest. The lake, the benthos, the animals, and the faecal pellet were treated as separate systems, albeit systems of very different scales. Thus successful projects focused on a phenomenon for its own sake and not because the phenomenon was the sum of its component processes or because the process played a role in a larger system too. Holistic analyses by individuals or small teams succeeded, whereas systems analysis of the entire project based on reducing the whole to parts that were studied separately failed.

Zooplankton feeding. My experience with zooplankton feeding seems poles apart from the scale of the Char Lake Project. However, decades of research into this single element in the systems analysis of any lake show conclusively that estimations of the parameters for transfers among different lake compartments are uncertain. I can illustrate this point best with research on zooplankton feeding, because I know that work well. Indeed, I believe that zooplankton feeding rate estimates are among the best measured of all ecological rates (Rigler 1971, Peters 1984). Unfortunately, even the best estimates leave much to be desired as system parameters.

Individual variation. If one measures the rates of ingestion of a number of animals, whether these be *Limnocalanus* in Char Lake or *Daphnia* in the lab, one finds that the animals do not all behave in the same way. Some eat at a very high rate, others at a much lower rate, and others are in between (Fig. 25; Turner et al. 1993). When we try to describe these data we often use the average rate, assuming that our experimental conditions captured nature effectively and that the most representative rates are somewhere in the middle of our measurements. Alternatively, we could decide that the experiment sometimes disturbs the animals, and that the correct rate is the maximum observed in the experiments. There is however convincing evidence that some experimental protocols starve the animals before feeding, and that starving animals feed at greater than normal rates. Perhaps the low values are most appropriate. In any case, we do not know the rates at which animals feed, so the rates we use in our simulations are hypothetical and uncertain.

Environmental factors and their description. There are other problems. Early work on zooplankton assumed that they filtered food from a constant volume of water per unit time. If this was so, filtering rate would have been a constant, and ingestion rate would rise directly with food concentration (Gauld 1951). Subsequent studies showed that filtering rate was constant

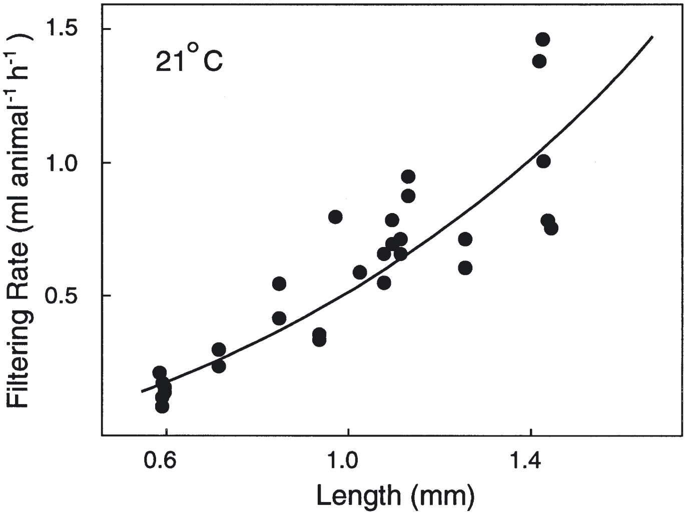

Fig. 25. The effect of size on filtering rate in laboratory study of *Daphnia*. (Peters unpubl. data)

only at low food levels (McMahon and Rigler 1965) and declined at increasingly higher food concentrations. Ingestion rate is instead roughly constant when food is abundant, and varies with food levels when they are low. Many different curves can relate ingestion rate to available food, but three are preferred (Fig. 26) because they relate to three basic types of predator functional response identified by Holling (1959). The differences among these curves are critical to some systems analysis models, but the data for zooplankton have never been good enough to distinguish which model is best. Indeed, where enough data and enough statistics have been brought to bear on the problem, the best fit can support any of these three curves, and more besides (Downing 1981).

Lab measures and field applications. Even if zooplankton feeding in the laboratory could be effectively described, application of the description to nature would still be problematical. For example, Haney (1973, Haney and Hall 1975) has shown that in nature animals follow a marked diurnal cycle in feeding rate, and approach rates measured in the lab only around dusk and dawn; so our lab rates may be even poorer approximations of field behaviour than we all fear.

Still another source of error is the use of relations and measurements in the literature to convert measured lengths and counts into estimates of population biomass. Schmidt (1968) has shown that variations in food level can change

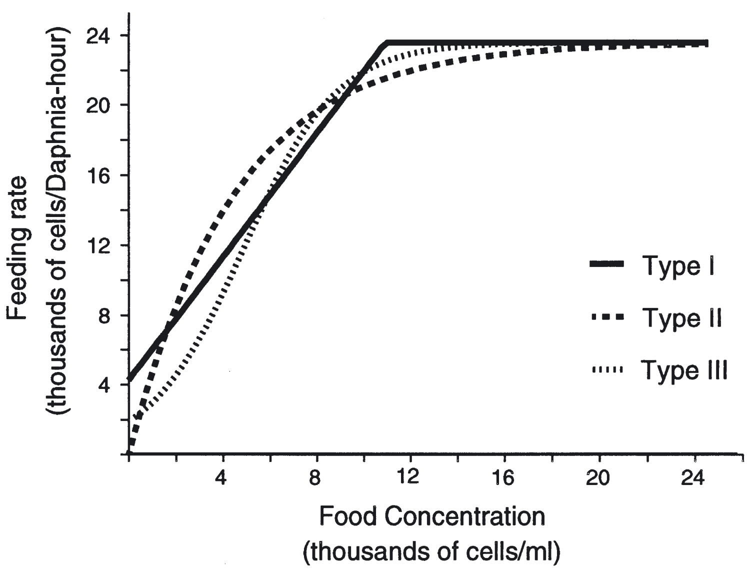

Fig. 26. The effect of food concentration on ingestion rate of *Daphnia*. (From Porter et al. 1982)

an animal's weight two-fold, and many of the discrepancies in estimates of weight specific rates in the literature might represent no more than the error due to an inappropriate length-weight relation. I once surprised myself by generating negative weights for *Daphnia* simply by "correcting" my measured weights for the egg mass, in turn estimated as the product of egg number and an average value for egg weight. Egg size can vary considerably with age and food level (Glazier 1992), so no such easy step is justified.

Other organisms. One last example can demonstrate the problem of employing these rates in a simple model. Jassby and Goldman (1974) measured potential and actual growth of phytoplankton, and calculated mortality by difference. They then estimated mortality due to sedimentation and to grazing and found that the sum of these two processes was much less than the calculated total mortality. They concluded that natural cell death is the main cause of phytoplankton mortality. If they are correct, their analysis demands a complete revision of the way we think about lakes. But is it right?

If we look more closely at their grazing calculation, we see that they took data for the filtering rates of individual cladoceran and calanoid zooplankton and summed these to get community grazing rate. This process ignores yet another odd discrepancy in feeding studies. Haney (1971, 1973) developed a technique to measure the grazing rate of zooplankton communities and individual crustacean zooplankton *in situ*. He found that the measured total grazing rate is much higher than the summed total of the individuals. Apparently, rotifers, nauplii, protozoans, and other organisms ignored in the analysis of Jassby and Goldman (1974) are responsible for much of the phytoplankton mortality. We cannot leave inconvenient animals out of our analyses simply because they are less studied and therefore presumed to be less important.

I could go on, but I think I have given enough examples to show that every aspect of feeding behaviour of zooplankton is uncertain. I conclude that, although the data are uncertain enough to encourage more study of zooplankton feeding, they are not nearly good enough to be used in systems models. Ecologists have developed a flourishing scientific sub-discipline to address the feeding behaviour of zooplankton, and this work by and large treats the animals as wholes, not as the sum of many mechanisms. However, that excellent work cannot be combined reliably into reductionistic models of lake ecosystems.

The Reality of Systems Analysis

Systems thinking now dominates ecology. It has convinced us quite rightly that a reductionist theory must embrace all significant components of the system and all significant interactions between these components. We should also recognize the futility of trying to measure all those components and interactions. Those who attempt to quantify them (as opposed to those who build the interactions into a simulation model) will be overwhelmed by the number of phenomena that need to be described quantitatively long before the simplest ecosystem can be modelled.

Modellers have accepted this limitation and are usually content to fill the gaps with interactions patterned after Michaelis-Menten kinetics, with arbitrary but reasonable constants, and empirical relations. Patten (1975) even argues that we do not need good data for systems analysis, because the models work perfectly well without good data, so long as we refrain from testing them against observation. However, if we wish to apply the model, we always take short-cuts, replacing reductionistic descriptions with arbitrary rules or empirical relations of at least some components. When we do so, we imply that reductionism is inadequate.

One result of our recognition of these limits is the disorientation of experimental ecologists. We do not have enough faith in the systems analysis models. On the other hand, we have lost our traditional, if naive, belief that there is a key interaction and the ecologist fortunate enough to stumble on it would produce the theory we seek. We have lost faith in our ability to generate useful theories. Consequently, there is a large element of 'going through the motions' in contemporary studies of ecological interaction.

This raises some interesting questions. Why do we do it? Why are zooplanktologists satisfied with bad estimates of every vital parameter? And why are other ecologists similarly satisfied? I think the reason we expect so little from science is that we have not yet realized that our job is to predict not to describe. We have not yet come face-to-face with our failure to do effective ecological science. If we had effective, interesting, ecological theories we could be testing them, and they would dictate the accuracy required of our measurements. In the absence of theories, we can be as careless as we like.

Conclusions

Now I think we can see what the computer has done for us. It has turned a vague, semi-philosophical question of apparently little relevance to the working biologist into a practical, methodological problem. The computer gave reductionists the tools required to approach an ecosystem as the sum of its parts, and it allowed us all to discover that these tools are, and will always be, inadequate. When ecologists realize what has taken place, they will take renewed interest in the long-forgotten debate between holism and reductionism, and this time the debate should have a different resolution.

There are two morals to my story. First, if ecology is to develop quickly into a science that develops by testing its theories, we must recognize the limitations of reductionism and put more effort into the holistic approach to living systems. To make predictions about the future states of a system, we must study the properties of that system, not those of its parts. Secondly, philosophers and historians of science could play an important role in the development of science. But to play this role, they must learn to communicate with working scientists. They must find the right words with which to convey their insights. This may mean that they must learn enough about day-to-day science to convert their insights about the methodology of science into a language scientists understand.

VIII Sources of Ecological Creativity

> "Science proceeds by revolution and not by addition, pure and simple."
>
> Claude Bernard
> [*Le Cahier Rouge* (1860)]

Philosophers of science have long distinguished between "the context of discovery" of theory and "the context of justification". The former, which is the topic of this chapter, is concerned with the sources and modes of scientific creativity. The latter deals with the evaluation of existing theories. Although both phases are important to science, most writers treat questions about justification, rather than questions about the nature of scientific discovery.

Justification has received more attention for two reasons. First, it is the public phase of science (Peters 1991a). Scientists are obliged to provide scrupulously honest accounts of the tests of their hypotheses, but they need not explain what inspired those tests or hypotheses. In fact, the rational developments of an hypothesis or test described in the introductions of scientific papers are usually part of the context of justification and bear little relation to the actual events surrounding the creation of the theory (Caws 1969). As a result, the scientific literature does not lend itself to the study of creation. Second, justification has received more attention because it has attracted and yielded to the great philosophers of science, from David Hume to Karl Popper. The same thinkers have placed far less emphasis on creativity, allowing that discovery is a personal matter best left to the individual scientist and his or her muse (Popper 1934).

The Challenge of Creativity

This uneven emphasis on creation and justification should be a matter of some concern for working scientists. The evaluation and application of existing theories is relatively straightforward. We are by and large competent technicians, distinguished by some modest originality, above average intelligence, and a highly specialized education. This combination allows us to function effectively in the context of justification. Our problem is more likely to be the creation of clearly stated theories that are interesting enough to warrant the effort of justification.

The problems of how to identify the hypotheses that will receive the weight of our highly developed evaluative abilities should be addressed by those philosophers who deal with the context of discovery, but that literature is not very helpful in practice. Many of the writers who treat scientific creativity are visionaries who think that the object of their studies is too sublime to be fully grasped (Caws 1969). As a result, their writing deals with concepts that are too ill-defined for application. For example, we learn from Koestler (1969) that there is a ripeness to ideas, but we are given no advice about how we are to find these ideas or how we can compare maturities of ideas once they are found. Koestler also tells us that we may expect a creative flash of insight, but not how we can precipitate such a “Eureka act”. Most accounts of scientific creativity give space to genius, imagination, and intuition (Morris 1966). The problem for working scientists is not that we mistrust the value of these intangibles, but that an appeal to them is no help in our day-to-day work (Caws 1969). Like most scientists, I recognize I have too little of these virtues, and I gain nothing on being told I need more. What would be useful are instructions about how to make my little store of imagination grow, or at least how to use it effectively. The metaphors are simply unhelpful in that regard.

Sociologists of science have approached the problem of creativity by placing science and scientists under the microscope and examining creation as a phenomenon. They examine the lives of distinguished scientists to determine if some similarity of education or environment might explain their stature. From such studies, we learn that Nobel laureates tend to come from the middle class, studied with other Nobel laureates and worked at only a select few universities (Zuckerman 1977). Francis Galton (1875), one of the first to work on this topic, noted that distinguished scientists tended to be the eldest child, had lost one parent before the age of ten, and had become strongly attached to the other. Galton also emphasized the role of family and heredity in genius. There is some indication that left-handedness may be more common among great scientists. Unfortunately, this information comes too late for most of us. Our genetic dispositions, childhoods and formal educations are already set in an unredeemable past.

There are some hints as to what we might do to be more creative. Caws (1969), following Galton, suggests that creative scientists are critical of current views in the science and suspicious of dogma. Koestler (1969) suggests that we not resist new ideas, but try to prepare our minds to accept them. We should consider alternatives (Chamberlin 1890, Platt 1964). The notable success of scientists who switch fields suggests that periodic changes in research topic are likely beneficial too. These steps are suggestive, but far from a cookbook for creativity.

In considering this literature, I came to the conclusion that it has limited meaning for most scientists because it deals primarily with scientists of heroic dimensions: Galileo, Newton, Einstein, and Darwin. Even the sociologists of science limit themselves to such distinguished individuals that the relevance of the conclusions for the rest of us must be suspect. For example, Zuckerman (1977) deals with Nobel laureates, but figures in Price (1986) show that only one in every one to ten thousand scientists can hope for such achievement. What are the rest to do?

It can be argued that the research of the bulk of scientists simply does not contribute to their science (Glaser 1964, Cole and Cole 1972). Statistics show beyond the shadow of a doubt that the literature is dominated by a relatively small number of scientific authors. These are the leaders who write most of the papers, fill most of the best journals and receive most of the citations. At the other extreme, there are a large number of authors who write but one or a few papers, who are never cited, and who are relegated to lesser journals with tiny readerships (Price 1986). The rest of us, mid-level career scientists, could accept that we are unlikely to contribute creatively (Cole and Cole 1972) and resign ourselves to the important role of the audience that gives the great scientists the recognition they have earned (Merton 1968). However, most scientists legitimately hope to do more.

The Existing Literature as an Inspirational Device

Medawar (1967) suggested that scientists almost always draw their inspiration from the literature of their science and their own scientific observations. Falling apples, swinging chandeliers, and slopping baths are therefore as atypical as instances of scientific insight as Newton, Galileo, and Archimedes are atypical of scientists. Most of us do not write revolutionary papers that redimension our sciences, and even scientific revolutionaries do so rarely. Instead, most research is directed to solution of “puzzles” thrown into relief by the paradigms of our sub-disciplines (Kuhn 1962, 1970).

Most of the remainder of this essay elaborates Medawar’s position using the ecological literature. My concern is to provide models for scientific creativity that are more familiar and more functional for the majority of working scientists, by providing more typical and more prosaic examples of the discovery of pattern in nature. Although I have no authority to judge their applicability beyond ecology, I would be surprised if scientific creativity in other disciplines were remarkably different.

Dissection. The most common approach to the identification of relevant problems in ecology has been the dissection of large things into manageable parts. For example, the literature identifies many processes as important: the phosphorus cycle in lakes, the productivity of forests, and the interaction between plants and herbivores. Since these topics are too vast for a single research project, we study some component of the total process that is interesting and that we are competent to handle — plankton in a beaker, stomatal gas exchange, or the feeding preferences of moose.

Fig. 27 provides a model of the rationalization for such studies (Rigler 1982a). The model provides a rationale for an almost limitless number of small studies providing bits of previously unknown information about the world around us. It can be used over and over again so as to help scientists find new topics for research, and so continue playing the game. Science of

X is a very

[abundant / unusual / important] type of [community / species / ecosystem].

Although similar [species / communities / ecosystems] have been studied,

as have some aspects of X

[(references, to demonstrate knowledge of the literature)],

X's [feeding / production / physiology / Pb content / et cetera] has not.

Therefore I chose to study

[one of the last set].

Fig. 27. The safe and easy game of ecology. Scientific research programs can be identified by choosing some population, species, community or ecosystem as X, and then selecting the appropriate words and phrase in brackets. (From Rigler 1982a)

this sort is not particularly challenging, but it may be essential for normal science.

Mechanism. Mechanism is a special case of dissection. Mechanistic analysis arranges other components of the system explicitly in flow diagrams and simulation models, or implicitly as a mental construct in the minds of the project directors. The object of study is important only because it is an essential part of the whole. This device was effective in realizing the aims of NASA and the Manhattan project, where a final, tangible goal was well recognized and the parts were developed for this application.

Mechanistic analysis has also produced a number of fine descriptions of various ecosystems (e.g. as part of the International Biological Program). It seems to have been less successful in this area, perhaps because the problems the ecological teams were to confront were less clear than bombing the enemy or walking on the moon.

Although this essay is most concerned with indicating some of the ways that working ecologists find their problems, the preceding chapter obliges me to point out a difficulty with mechanism. The rationale assumes that the importance of the process does not lie in the isolated parts, but in the whole. If the program is to succeed, someone must eventually put the disconnected parts together. This synthesis has proven remarkably difficult (Brown 1981).

Dichotomies and categories. Dissection and mechanism are reductionistic approaches to theory building in ecology, but there are holistic alternatives. One of these involves a thorough classification of the phenomena and subsequent hypothesis about the characteristics of the classes. For example, Robert MacArthur repeatedly identified extreme behaviours and then used these extremes as dichotomous categories for the classification of less extreme behaviour of the same type (Schoener 1972, Kingsland 1985). Thus we have opportunist and equilibrium species, generalist and specialists, and coarse- and fine-grained environments. A similar approach takes the extremes as the poles of an axis, as in the r–K continuum in life history theory. In all cases, the approach involves two steps: first an identification of the defining categories or axis, then an examination or comparison of the different characteristics associated with the resulting categories or ranks.

There is no reason to limit this approach to dichotomous categorizations. Southwood (1988) advocates a trichotomous division of the habitat in terms of disturbance, adversity, and biological interaction. MacArthur (1972) believed that future developments in ecology would depend on a two- or three-way categorization of the habitat and its potential inhabitants such that ecological theory would take the form: in environments of type B, organisms of type X will have characteristics P, Q, and R. The biome approach goes further still.

Analysis of variance. Categorization is often qualitative, but an analogous quantitative approach is available. This uses the power of common statistical procedures to identify tentative patterns which can then be evaluated by further tests. Again one selects a significant topic from the literature, but now interest is limited to quantitative estimates of the process of interest. For example, primary production may represent the productivity of lakes and fish catch that of the sea. One then collects as many estimates as possible and estimates the variance. The variance quantifies the extent of our ignorance and is addressed by determining what other factors explain a significant fraction of this variation. Qualitative factors are assessed by expressing these variables as simple categorical variables and applying analysis of variance (ANOVA) to determine the explanatory power of the categorization. The effects of continuous variables can be estimated by regression techniques, which are themselves minor variants of ANOVA, and mixed models with both categorical and continuous variables can be developed with analysis of covariance (ANCOVA). Downing (1991) found that 50 % of the statistical comparisons between ecosystems used one of these variants; a further 40 % relied on visual inspections of graphs or tables, which are simply the non-statistical analogues of ANOVA. This empirical approach has been particularly effective in developing nutrient response models in limnology (Peters 1986) and allometric models in autecology (Peters 1983, Calder 1984).

Extensions, additions and modifications. Almost all relations in ecology are unsatisfying because the uncertainty of prediction is too large, because the domain of the relation is too small, or because the original work suffers some potential bias or other shortcoming. These limitations have long been fruitful areas for new research. For example, the phosphorus-chlorophyll relation first proposed by Sakamoto (1966) was improved by Dillon and Rigler (1974a) who expressed the relation statistically, showed that it applied outside Japan, added more lakes to the data base, and, following Vollenweider (1968), related it to the problem of phosphorus abatement. Since then, more than 60 relations (Peters 1986) have been added to show that the relation holds or to modify it for use under a variety of conditions or regions. Such modifications suggest different mathematical forms for the relation (Straškraba 1980, McCauley et al. 1989, Prairie et al. 1989), different parameters (OECD 1982), different measures of algal biomass (Nicholls and Dillon 1978), and additional variables (Smith 1982, Canfield et al. 1984). Some authors have concentrated on developing the largest possible data set (Canfield and Bachman 1981), others on explaining the variation in the existing sets (Carpenter et al. 1985).

Similar developments have occurred in allometry. Beginning with Rubner's study of respiration in dogs (Kleiber 1961), there has been a consistent tendency to increase the range of weights, the number of species, and the number of higher taxa represented (e.g. Benedict 1938, Brody 1945, Hemmingsen 1960, Pagel and Harvey 1988). Robinson et al. (1983) considered temperature as well as size; McNab (1980) has suggested that life styles and food habits be considered too. Some few champion other models (Economos 1979, Smith 1980, Seim and Saether 1983) and many have argued for different statistical treatments (Zar 1968, Jolicouer and Heusner 1971, Harvey and Mace 1982, Ricker 1984, Pagel and Harvey 1988). Moreover, successful models, like the phosphorus-chlorophyll models and size-metabolism models, have encouraged the development of similar models predicting other responses from the same independent variables or from correlates of these variables (Peters 1983, 1986).

The amazing fertility of extension, addition and modification is not limited to large scale regression analyses. Indeed, limnologists have so long insisted that each lake and each species is different, that we can safely claim to be doing science simply by repeating earlier research in a previously uninvestigated region, or with a slightly different organism, or at a different time of year. Extensions to new domains, additions of new variables, and modifications to existing analyses and models are all implicit elements in the model for normal research in ecology in Fig. 27.

Technologies. The application of a new technology to the traditional problems of aquatic ecology is another way to generate a research problem in ecology. This allows us to profit from advances in our sister sciences including the traditional areas of electronics, analytical chemistry, mathematics, and statistics, but also molecular biology, bioengineering, and computer science. For example, we can now work at higher levels of sensitivity in the analysis of the contaminants of our waters, we can identify the genetic structure of our study populations, and we can collect and analyze data at a rate which was unimaginable only a few years ago. We can only expect these fruitful interactions to grow. Those ecologists who are technologically competent can therefore look forward to long, profitable, and potentially much cited careers dedicated to the translation of advances outside of ecology to ecological applications.

Complications. Still another mode of creation in ecology has involved the further complication of existing theoretical models by allowing greater complexity. The history of the logistic curve and its descendants provides an example (Hutchinson 1978, May 1981). The logistic is itself a modification of the equation for exponential growth over time (t) of a population containing N individuals, where r is the growth rate constant:

$$\delta N/\delta t = rN \tag{9}$$

The logistic sets an upper limit to this population by assuming that population growth may be described as sigmoid growth to an asymptote (K) so that the rate of increase slows as the asymptote is approached:

$$\delta N/\delta t = rN(1 - N/K) \tag{10}$$

When it became apparent that few populations grew according to this formula, the formula was complicated by the addition of other terms to include other factors. Thus, the basic equation could be modified (Hutchinson 1978) to accommodate the lag whereby population growth at time t is a response to population size at time t–1:

$$\delta N/\delta t = rN(1 - N_{t-1}/K) \tag{11}$$

Alternatively, one could presume that the asymptote varied in time and thereby replace K with a function of time, or a function of resource supply.

This was developed further by Lotka and Volterra to treat the effects of a predator population (containing P individuals):

$$\delta N/\delta t = Nr(1 - N/K) - \alpha NP \tag{12}$$

$$\delta P/\delta t = -Pd + \beta NP \tag{13}$$

where αNP describes the decline in prey growth as a result of predator-prey encounters. The growth of the predator population is instead assumed to represent a balance between the predator death rate, d, and some positive function of predator-prey encounters, βNP. These equations can be elaborated much further (May 1981).

A further set of equations based on this model were developed by Volterra to describe population growth of the ith species as a function of both its own population size and the effect of 1 to j competing species, each characterized by a competition coefficient α_{ij}:

$$\delta N_i/\delta t = r_i N_i (1 - N_i/K_i - \textstyle\sum_j \alpha_{ij} N_j/K_j) \tag{14}$$

This led to the very rich conceptual developments of MacArthur, Levins, May and others, treating communities as matrices of mutual competition coefficients.

Since an infinite number of equations could replace the simple relations of Verhulst, Lotka and Volterra, these developments could go on indefinitely. Moreover, since there are also an infinite series of alternatives to these simple models, we could expect to see creative programmes in ecology eventually developing parallel to the logistic mainstream.

Not all complications need be so mathematical. Some can be largely qualitative. For example, models of zooplankton filtering rate (Chapter VII) began with the assumption that the animals were simple pumps and filters. Gradually researchers have uncovered a far greater range of complications showing that the feeding rate is sensitive to temperature, pH, oxygen, food particle concentration, particle size, particle type, experimental methodology, animal feeding history, age, size and so on (Peters 1984, Lampert 1987). Similar developments could be sketched for any physiological process. Another limnological example, but one which invokes community ecology, is provided by the size efficiency hypothesis (Hall et al. 1976, Peters 1991b, 1992) which began as a rather straightforward case of predator-mediated competition between large and small animals (Brooks and Dodson 1965), but which has subsequently been developed, extended, and complicated by considering the effects of invertebrate predators and their vertebrate predators (Dodson 1970), of food particle size, of starvation resistance in juveniles (Tessier and Goulden 1987), of interference due to larger particles, and of differential capacities to avoid entanglement (Webster and Peters 1978, Gliwicz and Siedlar 1980, Porter and McDonough 1984). The paradigm has built on the original broader base of Hrbáček et al. (1961) to include a host of top-down effects (McQueen et al. 1986) and may be considered a forerunner of biomanipulation (Shapiro and Wright 1984). Ecologists thrive on complication and therefore an easy step to creativity is to develop still another flourish for the existing models.

The Danger of Conventionalism

It is not my intention to describe all the ways that ecologists come to their new ideas. Instead of developing this list further, I want to end by considering a problem that results if these are the only models for creative developments in ecology and to point to a potential solution to that difficulty.

The flaw is that these developments are all based on the overriding paradigms and dogmas of contemporary ecology. If we use any of these models we further entrench prevailing ideas. Therefore before we continue any line of development we should invoke our critical capacities to determine if that line merits development. In some cases, including limnological models of lake nutrient-response models and autecological models based on allometry, I think a fair evaluation would encourage such development. These are good theories with considerable promise for growth and application. In other cases, the logistic and competition theory being two, conventional creativity has led to many publications and citations, but not to predictive power or the resolution of problems that such power allows. I suspect that the normal creative modes of ecology sometimes simply extend the life of constructs which have not borne fruit in the past (Brown 1981) and are unlikely to do so in the future.

The traditional questions and topics of our science can be fruitful sources of inspiration for new research. They can also be intellectual traps. We risk entrapment when we allow the science to become so self-defined that the only interesting questions are those which we have always asked, but failed to resolve. This is the final retreat to scholasticism, it is part of what Pramer (1985) called "terminal science", and it is the opposite to Medawar's (1967) conception of science as "the art of the soluble".

Creative Alternatives for Normal Ecology

If we are to escape from the trap of terminal science, we need a means of introducing new questions. At first, this may seem to require a higher level of creativity than the techniques mentioned above, but there are some ways of finding new questions which need not lie outside normal science.

Syllogisms and analogies. One spectacularly successful technique to encourage creativity is that of Hutchinson (1978; see Kingsland 1985 for discussion). This consists in the identification of a syllogism — that is of some logical, usually algebraic or graphical, model — from some area outside of ecology, and application of this syllogism to a problem in ecology which is hypothesized to be analogous. This approach appears in analogies of ecology with economics, game theory, physics and genetics. It is frequently used in competition theory, optimality theory, and evolutionary theory, and has been characteristic of the powerful school of ecological thought dominated by Hutchinson, MacArthur, and their intellectual descendants (Fretwell 1975, Brown 1981). It is especially useful for those who have interests and abilities which extend beyond ecology.

The process has two relatively independent phases. The logical implications of the model are elaborated in a deductive phase. Since this elaboration is a purely logical question, this phase requires no empirical input and therefore this is a major activity for theoretical ecologists. Once the deductive phase is well advanced, the research enters a hypothetical phase in which the model is hypothesized to apply to some ecological phenomenon. Identifying such a phenomenon may prove difficult or impossible, and some of these logical models leave the theoretician with a solution in search of a problem, like the logistic and its descendants.

Because this approach is based on analogy and metaphor (Oster 1981), it is only as good as the degree to which the analogy holds. In practice, the analogy is rarely perfect and considerable ingenuity may be required to fit some ecological observations to the logical model (Maynard Smith 1972). However, even if the model cannot be applied to nature, its logic may become a part of theoretical ecology. For example, this seems to have happened to the theory of limiting similarity, whose terms cannot be applied to nature (Brown 1981) but which remains a favourite point of discussion for theoretical ecology (Abrams 1983). Sometimes, as in optimal foraging theory (Beatty 1980, Stephens and Krebs 1986, Gray 1987), one may be in a position to decide which model applies to a particular case only after making the observations that the models purport to predict. Such models only tell us what we already know.

The syllogism has proven a useful prod to ecological creativity, but it has also introduced a series of logical arguments into ecology which are either impossible to apply to nature, or can only be applied after the fact. These are the tautologies that confound ecological texts, courses and journals, and slow the development of a powerful science (Peters 1976, 1991a).

A return to application. There is another way to stir the creative juices of ecologists and thereby help them to isolate appropriate research problems. This also involves material from outside the traditions of the science, but it has been less widely recognized than syllogism and analogy.

I suggest that we step back from our library desks and lab-benches, that we put aside our field notes and learned journals, and instead take a long look at our lakes, our seas, our forests and our fields. We should ask ourselves what are the most obvious, first questions that we would put to such a system. We might wonder, for example, if the water in a lake is good to drink or if it is warm enough for swimming. We might wonder what fish live there, where in the lake they are found, how many we can catch, and if they are safe to eat. We may have other concerns like how much water we can drain from the lake for agriculture or how the fish will respond to water level controls, industrial development, and acid rain. There are a host of questions like this, questions we once asked, but of which we lost track in the course of the professionalization and professorization of the science.

Often, we have turned our backs on these obvious questions to ask questions like “How many eggs does a copepod carry?”, ”What is the successional sequence of algal species in the lake?”, “What are the names of the animals which the fish have in their stomachs?”, “How fast is radioactive phosphate absorbed by the plankton?”, and “How much does a water flea excrete?”. These may be important questions. We may need to know these things to answer the obvious questions. Whether this is so or not, we have lost the connection between these obvious questions that first attracted many scientists to ecology and many contemporary ecologists to their specialities, and those which our scientific training has subsequently encouraged us to pose.

The benefits of practice are widely recognized. De Solla Price (1986) made the point in a general context in his last paper, *On Sealing Wax and String*. Box (1976) argued that the interchange of theory and practice was an essential element in the genius of R. A. Fisher. Vollenweider (1968) showed that it is possible to contribute powerfully to limnology, while ignoring the traditions of the science. Application is more scientifically valuable, more socially essential, and more intellectually challenging (Rigler 1975a, 1982a, b) than most of normal science.

Therefore my last suggestion to increase our creativity is a simple one. It is to return to the questions of the layman, or better to the questions of a child. In doing so, we may be able to see our subjects with fresh eyes, lighting again the creativity that effective science demands, and simultaneously helping confront the ever-growing problems of humanity.

IX Empirical Limnology

> “No scientist is admired for failing to solve problems that lie beyond his competence. The most he can hope for is the kindly contempt earned by Utopian politicians. If politics is the art of the possible, research is surely the art of the soluble. Both are immensely practical-minded affairs.”
>
> Sir Peter Medawar
> [*The Art of the Soluble* (1967)]

In previous chapters, I defined science and theory to emphasize the importance of theory in telling us what the world is like. According to Popper, science does this by telling us what the world is not, so that we can discount logically possible observations that the theory tells us are unlikely to occur. I then detailed my growing unease as I searched for such theories in ecology and instead discovered that many ecological constructs were not very informative in this sense. I looked for guidance to my speciality and to the general field, but was again disappointed. They did not seem to measure up, either to Popper’s criterion of demarcation or to the growing environmental challenge. Initially, my disillusionment was profoundly disquieting, but eventually it led me to resolve the issue by putting aside the traditional topics of my research to focus on socially relevant, holistic, empirical studies of lakes. That change in approach is the topic of this chapter.

Social Demands and Scientific Supply

For many years, eminent ecologists have warned that the present course of society will lead to certain disaster for civilization. For the most part, society has ignored them.

I was never an eco-preacher — I am much too selfish about research time — but generally I support that mission and I have wondered why the excellent arguments of our leading ecologists were ignored. I resolved the issue, at least in my own mind, by recognizing that the questions ecologists were answering differed from those society was asking. The eco-preachers made predictions about the fate of the biosphere, but society was asking questions about populations and ecosystems. Ecologists would eagerly argue for global restructuring of the economy, culture and politics, but were often mute in discussions about cleaning a river or managing a fish stock. The ecologists argued, with some justification, that biospheric questions were more important. Society wondered, equally legitimately, why it should accept ecologists' solutions to big questions, when it was apparent that ecologists could not resolve local issues.

This ecological credibility gap grew when society realized that most ecologists had not been trained as biospheric experts. Ecologists trained to address much smaller questions, yet, when asked to make a specific prediction about a particular population or ecosystem, we could rarely do it. Even more rarely did we agree with one another.

The standard reply to a request for advice was in effect, "Give me $100 000 per year for twenty years to study the issue and I'll tell you what happened." Society caught onto this trick pretty quickly. Instead of asking one ecologist, it asked a suite of *n* ecologists, and out of the *n* different guesses that resulted, it picked the guess that was most economically or politically expedient. This tactic simply obfuscated the process of finding scientific solutions to societal problems, delaying science by confusing both researchers and society.

My discovery that ecologists' answers were mismatched with society's questions led me to a personal choice to start predicting what society wanted to know. My decision to change research directions after many years was hard, but I found it even harder to develop useful theories. I could, with modest intellectual effort and considerable hand-waving, invent a new theory, but I could not guarantee its success in application. I therefore focused on finding the approach most likely to create a "useful" theory. In this context, "useful" means predicting what society wanted to know.

Pessimists and Optimists

There seemed to be two distinctly different methods of attacking a scientific problem, which I shall call, for the present, the way of the optimist and the way of the pessimist. They can be distinguished by the way they address difficult scientific problems. The optimist says "I am going to solve it." The pessimist says "It is not soluble in its entirety, therefore I will solve a little bit of it."

Imagine that each school wanted to predict when an alarm clock would go off so that they might control this device to their advantage. The optimist would study the behaviour of the clock under a variety of conditions and look for regularities or patterns. The pessimist, believing that the clock could never be really understood that way, would instead offer to take the clock apart: "I will study each screw, and each cog wheel. I will take apart the cogs and see how they are made, I will study the shape of the teeth, and the scratches on the casing; I will look at the structure of the brass, steel and lead. Then I will begin to study the interactions between and among these parts, and slowly, painstakingly, I will come to understand the clock." Given the information at hand, we have no way of knowing which approach is better. The scenario supposed that we could not predict the clock's behaviour, and as long as this is so, we cannot judge the success of the different approaches. Any choice between them is whimsical, unless we can appeal to a broader experience. We need a theory of scientific development.

Testing the alternatives. Luckily for me, I once taught a course on the history of biology, and I was able to cast my mind over examples of the invention of past theories. To my delight, I discovered that they all came about in the same way.

If we were to look over the history of branches of science that have achieved successful theories, we would discover a remarkably consistent story. It runs as follows:

(1) identify the system about which you want to make predictions;
(2) observe the behaviour of that system and look for pattern;
(3) express the pattern rigorously and, if possible, quantitatively to yield an empirical theory;
(4) try to explain why the theory works, with an analytical or explanatory theory.

Thus Copernicus built on patterns that had been observed by astronomers from Babylonia to Tycho Brahe, and Newton "only" completed the quantitative description of those patterns begun by Kepler and Galileo. That archetypical scientific advance did not reach the status of explanation until a new generation saw it as philosophically true (Chapter III). Dalton saw that chemicals combined in fixed ratios, Mendel tended his peas, and Darwin visited the Galapagos. Even the most elegant analytical theories began as humble empirical patterns.

This is not to say that the discoverers of pattern had no preconceptions or working hypotheses. They undoubtedly did. Nevertheless, the initial work was observational and the first achievement was the identification of patterns in those observations. Consequently, most of the creative approaches of normal ecology (Chapter VIII) aim to detect pattern. That is an appropriate focus for a young science.

One of our problems in ecology is that many ecologists have decided that this standard scientific strategy is inappropriate for ecological systems. Ecologists have placed their trust in alternatives. Perhaps the most popular has been reductionism or mechanism, whereby we dissect a system we see as too complex and study the parts in isolation. An alternative technique, less used but still much honoured, is the "*a priori* road" (Forbes 1887) whereby we intuit bold hypotheses for subsequent test. Still another technique creates elaborate intellectual universes and ecosystems of concept or algebra and then seeks parallels between those intellectualisms and the real world. These approaches are popular and attractive, but the weakness of ecological theory in the face of the environmental crisis argues tellingly against them.

Holists and reductionists. I have made two important points. Successful investigators did not begin by dissecting the system of interest; and the original theories did not pretend to convey understanding. In other words, historical evidence suggests that the way to construct theories has been holistic and empirical. There is really only one way to create new theory and that is the way of the optimists.

My perception that there were two ways to create theory was based on a misapprehension. The source of this misapprehension was also revealed by our collective experience in building ecological theories. After a pattern had been identified empirically, other investigators were inspired to explain why this holistic theory worked. They might tear the system apart and relate the behaviour of the whole to the behaviour of the parts. They might attempt to rephrase the theory in words that conveyed understanding, and if successful, they might gain far more credit than the empiricist who first described the pattern. The pessimists then were not trying to build a new theory or to offer useful new predictions. They were trying to explain theories that already existed. Like many ecologists, I had confused the two processes and now see my early years in research as a misapplication of the pessimist's piecemeal approach to the creation of new theory, rather than to the explanation of existing theory.

In more conventional terms, the ecological optimists are called "holists" and the pessimists "reductionists". In general, scientists are much happier with a reductionist, explanatory theory than with an empirical, holistic theory, even though both may be equally predictive. As a result, most researchers approach their material as reductionists. However, since I was concerned with producing predictions that contemporary ecological theory could not give, there was no reason for me to work like a reductionist. My decision was therefore to reject the reductionist approach and to become a holist and an empiricist. Thus after twenty years, I stopped being a scientific pessimist and became an optimist.

What to Predict?

Once I had decided to hunt for a theory, I had to decide what the theory was going to be about. What system would I study and which of its properties would I predict? The system would clearly have to be a lake, because I had no expertise about anything else. At the time, there were a number of questions people asked about lakes: Is it green? Does it smell? Are there fish in it?

At first, I balked at the idea of addressing topical issues in society. The professor in me, the old scientist, grey, wrinkled, and paunchy, wanted to say “No, you must stick to pure science because only basic research yields new theories.” The concerned scientist, interested in society’s problems and society’s image of ecologists, countered by asking how I could hope to close the credibility gap if I insisted on making predictions that were irrelevant to society.

Luckily, history again came to the rescue. The old professor was wrong. Many contributions to scientific theory come from attempts to answer society’s questions. Astronomical theory arose from our perceived need for a calendar. The earliest chemical theory arose from our desire for eternal life and for the ability to convert base metals to gold. More recently, the germ theory of disease and our theory of spontaneous generation arose because Louis Pasteur was hired to find ways to cure diseases of grapes and wine. Claude Bernard, motivated by a desire to cure diabetes, developed our theory of homeostatic internal regulation. The best examples of useful theories in ecology that I knew were models developed to predict commercial fish catch by D. S. Rawson (1955) and later by Dick Ryder (1965, 1982). Thus we have plenty of evidence to show that new theories can come from applied problems.

The problem of which property to predict remained. Society wants predictions about many properties of lakes: taste, toxicity, algal abundance, oxygen levels, contaminant fates, fish harvest, and so on. How does one select amongst these properties? An answer to this question was given most succinctly by the Nobel laureate P. B. Medawar (1967) in a review of Arthur Koestler’s book, *The Act of Creation*. Medawar answered Koestler’s accusation that scientists ignore the important questions by saying that these questions are too difficult. Successful researchers deal with soluble problems. Here was the answer I was looking for. I should try to make predictions about the easiest problem I could identify. For a variety of reasons, most of which concern personal competence and logistic support, the most tractable problem of societal interest was the problem of predicting algal abundance.

A Research Program in Holistic Empirical Ecology

How green is my lake? I had decided that we needed predictions. The history of biology showed that the holistic, empirical approach was most likely to produce the requisite theory. Algal abundance looked easy, so that was my first target and I did not mind in the least that society was interested in that result. My approach would be to search for repetitive patterns in the algal abundance of lakes and then to correlate these patterns to other lake properties, so that in future we would be able to predict algal abundance from those properties.

The twin perils of complexity and reality. At this point, I had to be careful not to fall into a dangerous trap. I must not allow myself to be distracted by all the fascinating complexities of the system. For example, it was tempting to start by counting all the species and races of algae in a series of lakes; or I might have instead begun to speculate about the relation between the property I wanted to predict and other equally unpredictable properties, like the relation between zooplankton and algae. These questions, and many others, are quite capable of engaging armies of limnologists for generations.

To avoid such traps, I very quickly decided that the measure of algal abundance for my purposes was the concentration of chlorophyll *a*. This choice seems dangerously simplistic to the modern limnologist who knows that different algal divisions contain different pigments, and that the chlorophyll: biomass ratio can vary enormously within a single algal species (Nicholls and Dillon 1978). Indeed the choice is even more simplistic because we are not even measuring chlorophyll *a*. All that I was trying to predict was the absorbtion of a particular wavelength of light by the pigments extracted from the particles collected in a sample of lake-water.

The decision to study chlorophyll extracts put me in danger from another trap, that I might become stalled in a lengthy consideration of the reality of my measurements, just as I had once studied the reality of phosphorus fractions. I escaped both pitfalls by applying a holistic, empirical approach. The holist avoids dissection of the problem (i.e. the prediction of total algal abundance) into its components (e.g. the prediction of algal species abundance). The empiricist focuses on measurable properties. The amount of green colour to be extracted from lake-water by a rigorously defined method is a measurable property of the lake. To keep my mind focused on the right approach, it would probably have been useful to say that I was trying to predict greenness rather than algal abundance. Not surprisingly, that was what society wanted to know because that is what people see.

Success — the phosphorus-chlorophyll relation. I was now ready to look at the data and find patterns in the greenness of lakes. Whenever one starts such a search for pattern in nature, the obvious place to begin is the published literature. When I did so, I discovered the problem was even more easily solved than I hoped, because much of the work was already in the literature waiting to be used.

In a study of 40 Japanese lakes, Sakamoto (1966) showed that, where the ratio of total nitrogen concentration to total phosphorus concentration was at least 12:1, chlorophyll concentration is closely correlated with total phosphorus. I immediately began looking for other lakes to test this relationship. I found work by Deevey (1940) in Connecticut, by Edmondson (1969, 1972) in Lake Washington, and by others elsewhere in North America. All of them fit very well on Sakamoto's plot. Peter Dillon (1973) confirmed the applicability of this relationship in a further series in Ontario, and Wolf Scheider (1978) did the same in a series of much smaller lakes. All the data fit the same relationship (Fig. 28).

Twenty years ago, the phosphorus-chlorophyll relation was a revolutionary discovery, so counter-intuitive (Elster 1958) that for a time it seemed unpublishable. Since then, the basic positive response has been confirmed so many times that the relation is taken for granted. Some even say that the relation is tautologically true, although I have never seen the deductive proof that claim implies. Instead, I think the imputation of tautology indicates that the

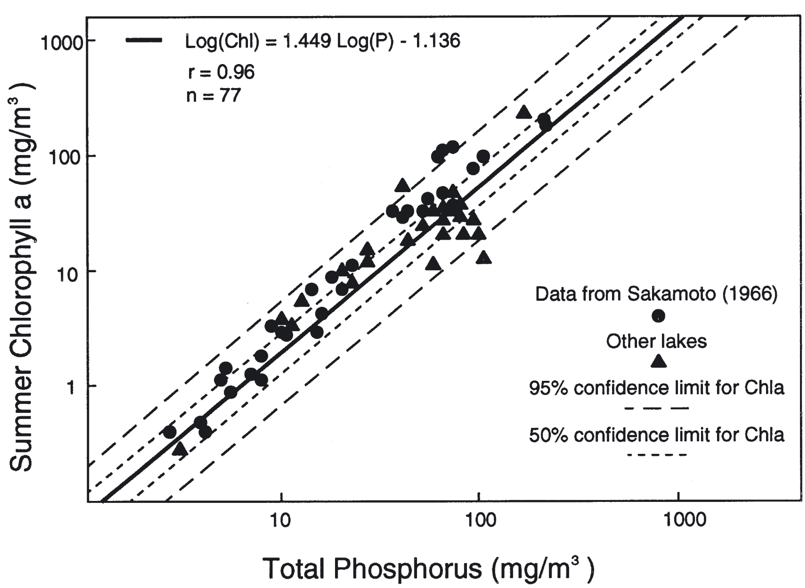

Fig. 28. The phosphorus-chlorophyll relationship in lakes. (From Dillon and Rigler 1974a)

relation is now considered self-evident. The phosphorus-chlorophyll relation has become philosophically true, because it now is what we expect.

Phosphorus concentration. At first, we misinterpreted the data in Fig. 28 as a correlation between total phosphorus concentration at spring overturn and mean summer chlorophyll, but now we would see this as a relation based on seasonal mean of the phosphorus concentration. In either case, this is not a particularly useful relationship because it is as much work to measure phosphorus as it is to measure chlorophyll and because there is no indication in the correlation that we could manipulate chlorophyll by manipulating phosphorus. However, if we could predict phosphorus concentration from some other easily measured property we might be getting somewhere; and if we could relate mean phosphorus concentration to the quantity of phosphorus entering a lake or something similar, it would be more useful still.

Vollenweider's basic model. In 1969, Richard Vollenweider published a model for substance budgets in lakes that purported to predict the concentration of any substance in lake water. The model is extremely simple. It treats lakes as if they are open systems, each consisting of a single compartment in steady state (Fig. 29). For the present discussion, the model can be specified to predict average lake phosphorus concentration ([TP], in mg m^{-3}):

$$[TP] = L/(q_s + \sigma z_m) \tag{15}$$

where L (mg m^{-2} yr^{-1}) represents the annual load of phosphorus to the lake's surface, and the other terms may be thought of as correction factors for other processes. Mean depth (z_m, in m) corrects for the depth over which the load must be distributed; the term for areal hydrological load of water to the lake's surface (q_s, in m^3 m^{-2} yr^{-1} or m yr^{-1}) corrects for loss of phosphorus through the outlet, and the sedimentation coefficient (σ, yr^{-1}) corrects for the sinking of phosphorus from the lake water to the bottom. If it worked, this model could be combined with the phosphorus-chlorophyll regression (Fig. 28) to predict the effects of phosphorus abatement and enrichment on the greenness of lakes.

Modifications and reformulations. Vollenweider's model appeared to work very well for total phosphorus in relatively unproductive lakes, but not in highly eutrophic lakes. However, the model had a more important flaw. It required an estimated sedimentation coefficient to describe the net rate of phosphorus sinking, and this constant is very difficult to measure directly.

Our solution was to reformulate the model slightly, replacing the hard-to-measure sedimentation coefficient with a "retention coefficient" so that all terms were measurable (Dillon and Rigler 1974b). If the total amount of phosphorus entering the lake from all sources is J (the phosphorus load in mg yr^{-1}), and the total amount of phosphorus leaving the lake via the outflow is J_{out} (also in mg yr^{-1}), the retention coefficient (R) is defined as the fractional loss

$$R = (J - J_{out})/J \tag{16}$$

R is therefore the net fraction of the incoming phosphorus which is apparently lost to the sediments.

Given R, J and an estimate of the net amount of water flowing into the lake from all sources (the hydrological load, Q, in m^3 yr^{-1}), one can predict [TP] in the lake water as

$$[\mathrm{TP}] = (J/Q)(1 - R) \tag{17}$$

Eq. (17) simply states that lake phosphorus concentration is equal to the volume-weighted mean phosphorus concentration of all sources of water and phosphorus (J/Q), corrected for net loss of phosphorus ($1 - R$). Dillon (1973, Dillon and Rigler 1974b) then showed that this formulation could effectively predict phosphorus concentration in lakes. These results were subsequently confirmed in a set of smaller lakes by Scheider (1978).

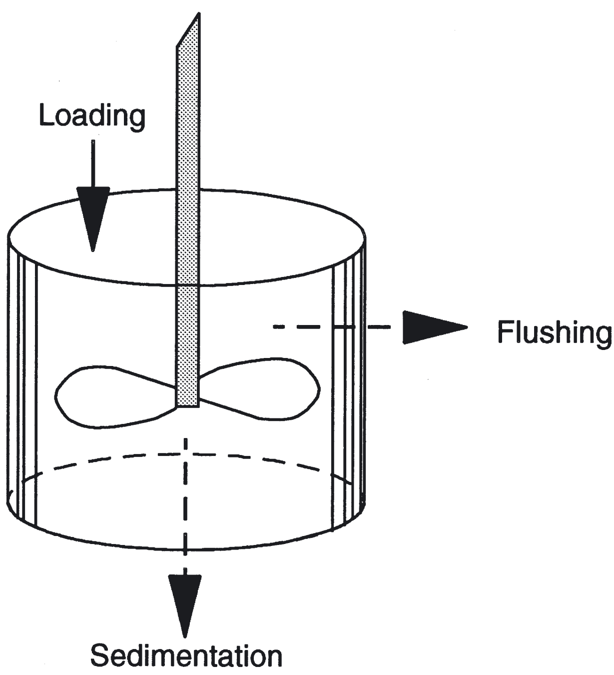

Fig. 29. The lake interpreted as a simple continuously stirred mixed reactor in which the internal concentration at steady state is the result of a single source, the inlet, and two sinks, the outlet and the sediments. (From Reckhow and Chapra 1983)

Predicting the components of the model. Unfortunately, the model described by Eq. (17) is useless for many practical purposes. Because estimates of J, Q and J_{out} require vast field programmes, they are far more expensive and time consuming than measurements of [TP]. An estimate of Q requires estimates of the sum of the annual flows of all the i tributaries to the lake (Q_{t1}, Q_{t2}, ..., Q_{ti}), the sum of the water inputs from each of j "precipitation events" (Q_{p1}, Q_{p2}, ..., Q_{pj}), less evaporation (E) from the lake surface:

$$Q = \sum Q_{ti} + \sum Q_{pj} - E \tag{18}$$

An estimate of J requires estimates of the total phosphorus concentration associated with these various inputs from tributary streams ($[TP_{ti}]$) and precipitation including dry fallout $[TP_{aj}]$:

$$J = \sum Q_{ti}[TP_{ti}] + \sum Q_{pi}[TP_{aj}] \tag{19}$$

And estimates of R require all this plus an estimate of [TP] and water flow in the outflow. Obviously, the approach would be much more useful if we had a way to predict these components of the phosphorus mass balance. If this were possible, we might be able to predict how green a lake would be with minimal field work, perhaps without even visiting the lake. This became our goal (Dillon and Rigler 1975).

Q was the easiest of all the components of the budget to estimate. Because the quantity of water in streams is important for many purposes, hydrologists had been measuring water flows for years and government sources were able to provide maps describing the average annual flows of water per unit area of drainage basin for all of Canada. The same sources provide estimates of evaporation from and precipitation onto lake surfaces. Analogous agencies can provide the same information for other jurisdictions. We simply had to assume that future flows would resemble past ones and we were able to predict the components of Eq. (18).

Predicting the phosphorus concentrations associated with this water was more difficult, because that characteristic had been measured less frequently. However, Dillon and Kirchner (1975) were able to collect enough estimates from the literature to provide average figures for the amount of phosphorus exported per unit area of watershed, given contrasting patterns of land use and geology (Table 12). The values were only averages, the scatter is high, and some land uses are not addressed, but the data were then the best available. As this approach eventually proved powerful, subsequent authors (Reckhow and Simpson 1980, Prairie and Kalff 1986) have improved and extended it.

Because P load is calculated as the product of hydrological load and phosphorus concentration, Eq. (19) requires estimates of the phosphorus in precipitation and dry fall ($Q_p[TP_a]$). Dillon (1973) estimated an average value for this "aeolian input" (77 mg m^{-2} yr^{-1}), and we were surprised to find that in many of our lakes rain, snow and dust could be the major source of nutrient (Rigler 1974). Because there were many opportunities for error in our estimates of aeolian input, Renata Gomolka (1975) took a much more careful look at the phosphorus associated with rain and dust. Her work showed that much of the phosphorus collected by shore-based funnel traps overestimated the amount that falls on the lake surface. Nevertheless, her estimate (37 mg P m^{-2} yr^{-1}) still identified the air as the major source of phosphorus for many undeveloped lakes with small catchments. This still seemed counter-intuitive, but subsequent work has confirmed both the magnitude of this input and its biological reactivity (Peters 1977).

Eq. (19) has no adjustment for the number of people living in the lake's drainage basin, yet we know from physiological studies that animals the size of human beings release about 0.5 kg P yr^{-1}. In other words, each additional human occupant of the drainage basin has the same effect on phosphorus load to the lake as an additional 10 ha of undisturbed watershed. Thus, to adjust for the phosphorus in human sewage in occupied watersheds, one must add 0.5 kg P per occupant to the sum in Eq. (19). If the population uses high phosphate detergents, the per capita phosphorus load should be increased to 1 kg per person per year. These same values allow us to calculate the effect of proposed developments and cottaging on the phosphorus load to a lake. The effectiveness of the approach has been confirmed in subsequent studies relating the number of people living in a catchment and phosphorus output (Mosello et al. 1978, Dillon et al. 1994).

Precept and observation in models of retention. Although we might be able to predict J and Q, the annual loads of phosphorus and water respectively, we could not use Eq. (17) to predict total phosphorus concentration without an estimate of the retention coefficient, R.

Table 12. Phosphorus export coefficients for contrasting bedrock geologies and land use patterns. Listed values are the means and ranges, in mg m^{-2} yr^{-1}, of observed annual losses of phosphorus in all forms expressed per unit area of drainage basin. (From Dillon and Kirchner 1975)

Geology	Dominant land use	
	Forests	Forests + pasture
Igneous	4.7 (0.7–8.8)	10.2 (5.9–16)
Sedimentary	12 (6.7–18)	23.3 (11–37)

To predict retention, Kirchner and Dillon (1975) first fit a regression model to estimates of R from the whole lake phosphorus budgets in Dillon's doctoral work and the literature. The model described R as a complex function of the annual hydrological load expressed per unit of lake area ($q_s = Q/A$, in m yr^{-1}). Although the regression fit the data as well as possible, extrapolation beyond the data set suggested that retention would be less than 100% in lakes with no outflow ($q_s = 0$). Since this seemed impossible, they chose a second, semi-empirical model that was consistent with the expected retention of 100% when q_s was zero, at the cost of a slightly poorer fit to the data:

$$R = 0.426 \exp(-0.271\, q_s) + 0.574 \exp(-0.00949\, q_s) \tag{20}$$

Dillon and Kirchner's model made sense, but it did so by sacrificing descriptive power for preconception. Such trade-offs may sometimes be necessary. However, in this case the semi-empirical model (Eq. 20) proved less effective in predicting retention in lakes with low values of q_s (Fig. 30). Ostrofsky (1978) developed a series of empirical models that performed better, although they did not predict 100% retention where outflow was zero:

$$R = 0.201 \exp(-0.0425\, q_s) + 0.574 \exp(-0.00949\, q_s) \tag{21}$$

Ostrofsky succeeded by sacrificing preconception for descriptive power.

Other retention models. Subsequent authors have developed a series of regressions and other models to handle phosphorus retention, either explicitly like Eqs. (20) and (21), or implicitly in variations on Eq. (17). For example, the widely recognized international program of eutrophication research summarized by Richard Vollenweider and Joseph Kerekes (OECD 1982) recommends:

$$[\mathrm{TP}] = (J/Q)/(1 - \tau^{0.5}) \tag{22}$$

where τ is the lake turnover time (yr) calculated as lake volume divided by annual hydrological load ($\tau = V/Q$). In other words, $1 - R = 1/(1 - \tau^{0.5})$. Nürnberg (1984) compared a series of possible models and settled on:

$$R = 15/(18 + q_s) \tag{23}$$

Nürnberg also showed that existing models performed poorly in lakes that developed anoxic deep waters, apparently because anoxia increases the rate of phosphorus release from the sediments. For such lakes, Eq. (23) should be corrected by an additional term for internal phosphorus load (J_{int}) calculated as the product of the area of anoxia, the duration of anoxia, and the rate of P release from anoxic sediments:

$$[\mathrm{TP}] = J(1 - R) + J_{\mathrm{int}}/Q \tag{24}$$

Holistic tests of the predictions. All the theories predicting the concentration of phosphorus in lakes would count for nothing if lakes did not respond to higher phosphorus concentrations by becoming greener, and by developing other symptoms of eutrophy. When I changed my research directions to pre-

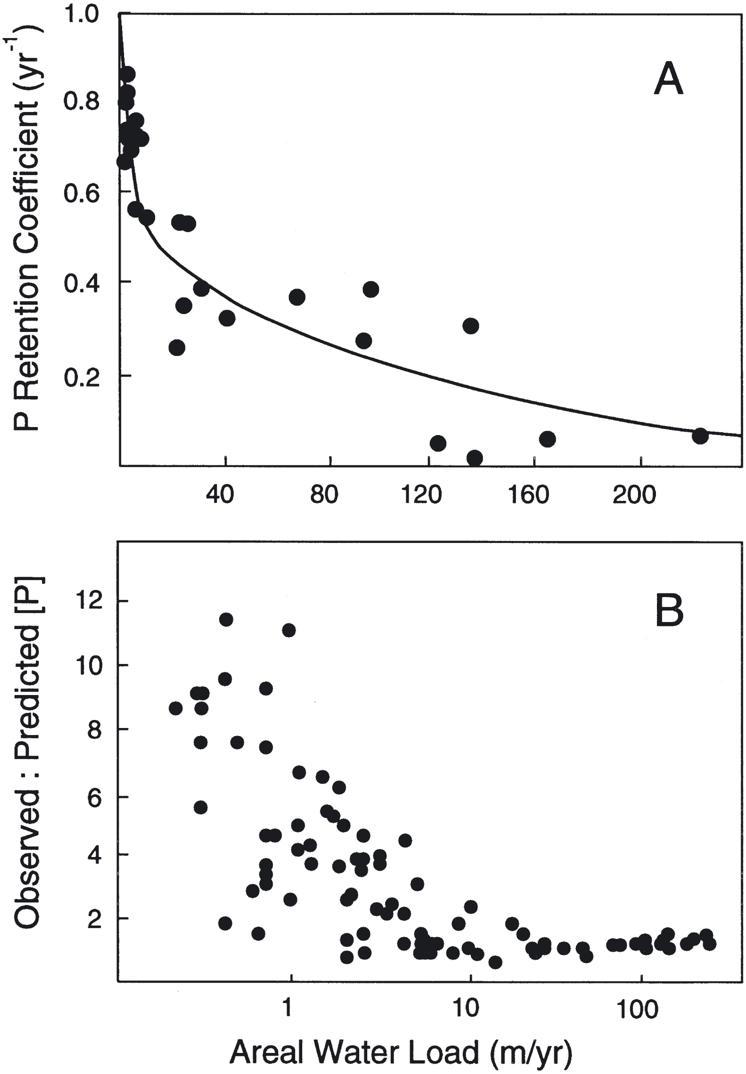

Fig. 30. The failure of precept as a guide in empirical modelling. (A) The model for retention of Kirchner and Dillon (1975) made sense in that it was required to predict 100% retention of phosphorus in lakes with no outflow, but it overestimates retention (B) where hydrological load is small (Ostrofsky 1978)

dictive limnology, a considerable body of evidence already suggested that lakes eutrophied in response to phosphorus, but much of that work was open to criticism and re-interpretations. For example, the classic work of Edmondson (1970, 1972, Edmondson and Lehman 1981) detailed changes in Lake Washington, including phosphorus and chlorophyll reductions, after sewage was diverted away from the lake. These observations could be interpreted as the parallel effects of some common, but unmeasured, cause. The bulk of laboratory work suggested that phosphorus was limiting, but there were exceptions and the problems of scale hampered the transfer from lab to lake.

Some whole-lake studies appeared to support the role of phosphorus in the eutrophication of lakes. Schindler's dramatic experiments with nutrient addition to lakes showed that massive additions of phosphorus made a lake green (Schindler 1971, 1974, 1978). In Sweden, early implementation of phosphorus abatement programs began to yield positive results (Forsberg 1987), and projects elsewhere also showed promise (Sas 1989). However, fortunes were at risk, both to the public purse in terms of the cost of tertiary treatment, and to the soap and detergent industry which had invested heavily in the production of high phosphate detergent, so phosphorus abatement met active resistance.

I recognized the need for more whole-lake tests of the models, but I was generally unable to convince my traditional sources of funding that such money would be well spent. Twenty years ago, Canadian agencies, that is to say my peers in science, had such faith in the necessity and efficacy of traditional approaches that they saw little of value in whole-lake experiments and were appalled at the costs of field surveys that sought patterns among many lakes. This attitude still prevails at the world's most important source of research funds, the National Science Foundation of the United States. As a result, American ecologists are actively discouraged from empirical, holistic research in ecology. Since American scientists are among the best supported and best respected in the field, this antipathy is one of the greatest stumbling-blocks to the development of effective ecological theory.

Interestingly, applied branches of government in Canada were less reluctant to accept the lessons of our research. Indeed, we were startled at the speed with which our results were implemented in phosphorus abatement programs. As dusty academics, we had always believed that government and politicians ignored our advice out of perversity, ignorance or self-interest. Instead, the public clamour for action on eutrophication was so loud that politicians were desperate for applicable solutions. As soon as we had something concrete to offer, they proved more than ready to listen and to act.

In the past, ecologists had failed to give advice that could be applied. For example, our traditional advice on eutrophication was essentially to reduce phosphorus loads to zero. Since that goal was impossible, our advice was ignored. The new models allowed cost-benefit comparisons and showed that effective abatement was practicable.

I eventually succeeded in finding support for whole-lake experiments, but only from an unconventional source, The Department of Indian and Northern Affairs, and then only under the condition that I work in the Canadian Arctic. The department wanted a scientific basis for land use regulations in the north. Since I was now committed to the idea that lakes fit a common pattern, I saw little immediate need for remote testing, but I was prepared to make a virtue of necessity by testing the applicability of southern models on lakes lying in permafrost. In this work, we essentially repeated Schindler's whole-lake phosphorus addition experiments, but rather than raising phosphorus concentration an order of magnitude in a single lake, we added only enough phosphorus to double the initial phosphorus concentration of several different lakes. To our delight, the lakes responded like southern lakes. Our initial surveys showed that the phosphorus-chlorophyll relation in these lakes was no different from those established in southern lakes. Phosphorus addition to some of these waters resulted in higher phosphorus concentrations, and the chlorophyll levels responded by increasing as expected (Smith et al. 1984).

The growing school of empirical limnology. According to Kuhn (1962), programmes in science succeed because they generate more puzzles for scientists to solve. Thus, to predict the greenness of lakes, my group was led to predict phosphorus concentration of lakes. Those studies in turn led us to predict retention and the components of the phosphorus and hydrological budgets, and eventually to test the corpus of existing theory with experiments on Arctic lakes. It proved a fertile area of research.

The Arctic work was more novel than I had anticipated. The limestone basins of the area held a surprise: the hydrological budget depended so much on subsurface flows that Q could not be estimated. As a result, models like Eq. (17) have limited application in such sites. There is still work to do there, and at every other stage of the research.

I do not think that our success with the prediction of chlorophyll is a lucky fluke. I see it as a successful test of the theory that science begins with holistic study and empirical identification of patterns in nature. The same approach should work elsewhere, on other problems in ecology and limnology, and so it has. I will therefore conclude this section with some further tests of the efficacy of holism and empiricism in producing simple ecological theories.

Hypolimnetic oxygen deficit. Trout (*Salvelinus*), whitefish (*Coregonus*) and walleye (*Stizostedion*) are among the most prized game-fish in Canadian lakes. Because these fishes prefer cold temperatures, they are often confined to the deeper water of lakes during the summer months. Because they are adapted to well oxygenated waters, they die if the oxygen concentration falls below 2 to 3 mg l^{-1}, and because eutrophication often results in hypolimnetic deoxygenation, fish-kills are among the most noticeable and unwelcome effects of eutrophy. As a result, there was a particular need for models that predicted oxygen concentrations in lakes. In addition, because anoxia enhances phosphate release from the sediments, a model to predict the extent of anoxia should allow improved predictions of internal load. Welch (1974) and Lasenby (1975) had already developed relations for oxygen concentrations under the ice on frozen lakes, and Jan Barica (1984) had developed models to predict fish-kills in hypertrophic prairie lakes and sloughs. We still needed relations for stratified lakes in summer.

At the time, limnologists depended on ideas developed by the founders of limnology: Thienemann, Strøm and especially Hutchinson. They had developed three hypotheses about the development of the hypolimnetic oxygen deficit:

(1) Hypolimnetic oxygen consumption is the result of oxidation of organic material settling out of the surface waters.
(2) The quantity of this organic material is directly proportional to the rate of organic production in the surface waters.
(3) The rate of hypolimnetic oxygen consumption is proportional to the amount of organic matter settling into the hypolimnion.

Since hypolimnetic oxygen consumption depended on the amount of material settling through the upper surface of the hypolimnion, the rate of hypolimnetic oxygen consumption was expressed as the average rate of decrease in the mass of dissolved oxygen under a square meter of the hypolimnetic surface. This is called the areal hypolimnetic oxygen deficit (AHOD, in mg O_2 m^{-2} d^{-1}).

The three hypotheses listed above were generally accepted in limnology, and were supported by a series of estimates of hypolimnetic oxygen consumption in lakes of different trophic state by Hutchinson (1938). Unfortunately, no limnologist was able to confirm Hutchinson's results for other lakes. Forty years later, Jack Cornett, a graduate student at McGill, succeeded where other limnologists failed. He showed why no one had been able to reproduce Hutchinson's results, he falsified the model under which Hutchinson had worked, and he pinpointed the source of this failure as the third of the listed hypotheses.

Cornett was able to do so for two reasons. He doubted the premises of Hutchinson's model, whereas others accepted them without reservation; and he used the absolute retention of phosphorus (calculated as $R \times J$) as an index of the amount of organic material falling into the hypolimnion. The second point is important because it allowed Cornett to estimate organic load in many more lakes than would otherwise have been possible. Cornett's model (Fig. 31) shows that the AHOD is a function of the absolute retention of phosphorus, the mean temperature of the hypolimnion, and the mean depth of the hypolimnion.

Cornett did not stop at this point. He recognized that AHOD was not really what we wanted to know. The hypolimnion is not homogeneous with respect to oxygen concentration. If we wanted to know what part of the hypolimnion was anoxic and what part was still habitable by fish, we had to estimate the volumetric oxygen deficit (VOD) in each stratum. Apparently we had agreed to look at a substitute variable (AHOD), even if this was not what we wanted to know, and for many years we were content with this substitution because it showed what determined hypolimnetic oxygen in principle, even if not in practice. Eventually, Cornett was able to develop a model which did predict VOD and therefore could predict the concentrations of oxygen in the water, the variable in which we are actually interested (Fig. 32, overleaf).

Other phosphorus response models. A number of workers reasoned that if phosphorus influenced chlorophyll so profoundly, it should affect other com-

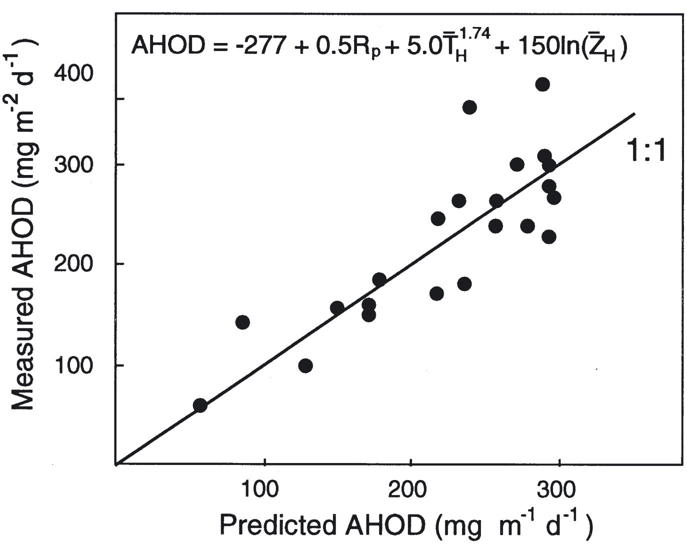

Fig. 31. Predicted vs observed estimates of areal hypolimnetic oxygen deficit. R_p = absolute retention of phosphorus, $\bar{T}_H$ = mean temperature of the hypolimnion (°C), $\bar{Z}_H$ = mean depth of the hypolimnion (m). (From Cornett and Rigler 1979)

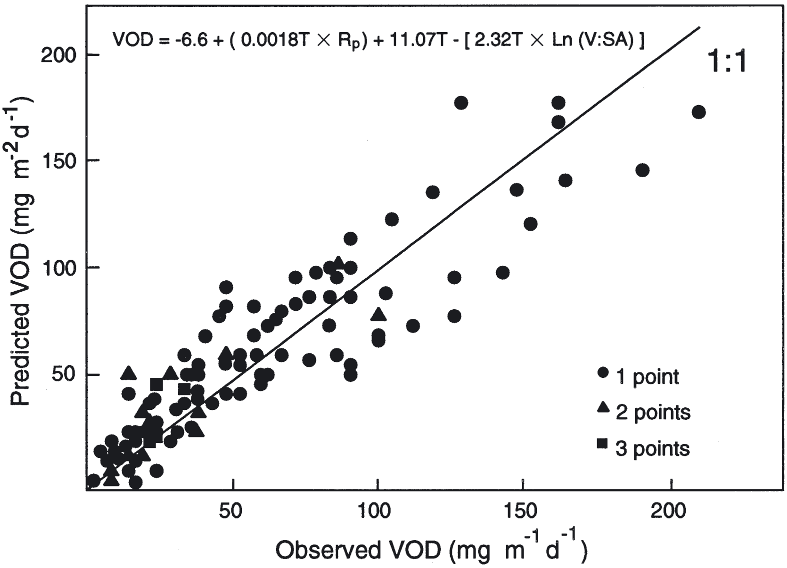

Fig. 32. Predicted vs observed volumetric rates of oxygen consumption in different hypolimnetic strata. T = temperature (°C), R_p = absolute retention of phosphorus, $V{:}SA$ = ratio of stratum volume (m^3) to sediment area (m^2) contacting that volume. (From Cornett 1989)

ponents of the lake community too. No doubt some of this work is simply an analogue of the existing regressions, whereas others are based on a deep conviction about how lakes function. The source of the researchers' beliefs is not at issue in theory creation. What is noteworthy is that such general success has been achieved in developing empirical, holistic theories, that the ecological characteristics of lakes are more predictable than those of any other community.

I would need a much larger review than this to do justice to all of predictive limnology. I can, however, briefly indicate the scope of that work. Models now exist to predict fish standing stock (Hanson and Leggett 1982), zooplankton biomass (Hanson and Peters 1984, Pace 1986, McCauley et al. 1988), bacteria (Bird and Kalff 1984), benthos (Rasmussen and Kalff 1987, Rasmussen 1988), and the distribution and biomass of epiphytes (Cattaneo 1987) and macrophytes (Chambers and Kalff 1985, Duarte and Kalff 1990). Other models predict primary production (Smith 1979), planktonic respiration (Ahrens and Peters 1991, del Giorgio and Peters 1993) and fish harvest or yield (Hanson and Leggett 1982, Downing et al. 1988, Godbout and Peters 1988). Antoine Morin developed models to predict the biomass (Morin and

Peters 1988), production (Morin et al. 1988a) and ingestion (Morin et al. 1988b) of black flies living in streams. Still other general relations exist to predict the production of aquatic invertebrates and fish (Downing et al. 1988, Plante and Downing 1989, Morin and Bourassa 1992). Other models predict characteristics of sediments (Rowan et al. 1992), macrophytes (Chambers and Kalff 1985, Duarte and Kalff 1990), and periphyton (Cattaneo 1987).

None of these relations are perfect, but none of us expected perfection. What is far more surprising is the speed and the ease with which empirical theories were developed for a broad range of limnetic phenomena. This rapid success gives me hope that many ecological questions can be similarly resolved, and that useful, credible ecological theory is generally possible. If so, we may see a generation of applied ecologists who, like physicians and engineers, have valuable skills to offer, and a generation of ecology texts that are more similar to engineering handbooks than to philosophical treatises. Perhaps then humanity will be worthy and capable of the planetary stewardship we have assumed.

Summary — A Future for Ecology

In summary, the failure of ecology to produce useful predictions was due not to the complexity of the subject, but to the complexity of our approach. It took me twenty years to become dissatisfied with the traditional approach and to identify an alternative. However, when I changed course, it took less than a decade to see the results of the new approach put into practice and to see the rapid success of the approach in addressing a whole range of limnological phenomena. The process has just begun and I am fully confident that the field will continue its rapid expansion for many years to come. After all, even the best of the current models leaves great room for improvement. Eventually, these patterns may be ready for the next step in science, reductionistic explanation, but for the time-being our needs are such that I am still putting my faith and my effort in theory creation. I am optimistic that an empirical, holistic approach will be widely embraced by ecologists because society needs help to preserve itself and its environment, because ecologists want to be useful, and because the empirical, holistic approach is the approach that works.

X An Education in Science: Evaluation

> "The instruction at Edinburgh was altogether by lectures, and these were intolerably dull..."
>
> Charles Darwin
> [*The Autobiography of Charles Darwin* (1876)]

The thrust of my argument to this point has been that scientific knowledge is knowledge of a special sort. It uses theory to identify which of the possible observations are unlikely. The ecology we teach and learn often fails to meet that criterion, yet there is an alternative. Predictive ecology uses an holistic, empirical approach to identify pattern in nature. This search for pattern has been an early step in the development of all scientific theory. Better still, the identification of pattern is a simple process that uses time-honoured scientific tools and that lies within the grasp of most working scientists. Even without genius, we can create a more incisive ecology by thinking about the science we do.

One element in this introspection is thinking about the way we teach ecology and biology. Because one generation of scientists teaches the next, it is imperative that we consider our present paradigms and methods of teaching, their past success and their future place in education. We have to teach better than we were taught or have taught.

On Advising Teachers

Perhaps the most arrogant act a teacher can commit is to advise others how to teach. What is merely a weakness on the part of a student, parent or administrator is a sin for the teacher because the teacher alone knows how much harder it is to teach well than to give good advice. We teachers know how easily a lesson, conceived like a beautiful dream in the solitude of our office, becomes a nightmare when presented in class. And although we can dash off an eloquent description of our philosophy, methods and objectives in an evening, we rarely, perhaps never, produce a course that actually achieves those objectives. As a teacher, I should know better than to give advice about teaching. Nevertheless, I yield to the temptation to do so because I believe that it is time for a change in the teaching of ecology, of biology, and of science. The curriculum we inherited from 19th century Britain is no longer appropriate to producing the scientists we need.

Even as I set aside my aversion to advice about teaching, I still face daunting questions like "Is it possible for us to become better science teachers than we are now?", "Have we reached the limits imposed by our own ability and education?", and "What remains to be said about a subject that has been worked and reworked by generations of professional educators?" I cannot answer these questions with authority. When I teach, I merely profess my beliefs about science to a small group of select students. I therefore have neither the training nor the experience one expects from a teacher of pedagogy. I only have faith — faith that there is always more to be said and faith that we can always do better. Secondary schools could do a better job of preparing students for science programs at university, and universities could do a better job with the students they get. Those of us who are teachers must ask how this can be achieved.

The Goals of a University Education in Science

To begin, we should ask what we are supposed to be doing for our students. In other words, what is the purpose of a university training in science? I see only two purposes for scientific education, one a question of practical detail and the other a question of general grasp, but I recognize that these are stressed differently by different people.

The first purpose is practical. Students expect the university to prepare them for a career and therefore they want what they call a marketable degree. Legislators and taxpayers want the university to produce the technicians and managers necessary to keep a highly industrial, technological society running smoothly. The objectives of both interest groups can be met by providing students with a certain number of specific skills, by giving them the ability to learn new skills and by instilling in them the confidence to use their abilities.

University teachers sometimes reject the practical demands of students or society because we think them inconsistent with the goals of a true university. We therefore spend little time explicitly teaching students the details of doing things. Instead, we seek to develop a general understanding of the field, presuming that the practical skills needed to solve specific problems will somehow follow automatically. Unfortunately, the evidence for this coupling of general grasp with specific capacity is not strong, and many graduates are frustrated that their general education gives them so little ability to do anything concrete.

Our disinterest in teaching people how to do things reflects a long-standing tradition that science is an aesthetic and contemplative activity, not a practical one. Many thinkers in ancient Greece eschewed experiment, perhaps because their manufacturing skills were too rudimentary to test their sophisticated ideas or because manual labour was appropriate only for slaves (Macaulay 1852, Russell 1931, Medawar 1984). In the great British universities, the traditions of scientific thought and discussion grew out of the humanities and arts. Applied science and engineering were left to more practical men outside of academia (like James Watt or Josiah Wedgwood), so that manual skills were undervalued. Until this century, many English scientists were independently wealthy gentlemen who saw the study of nature as purely intellectual. They devised and used experiments, but the labour and critical technical skills were provided by unsung technicians (Price 1986). The contemplative tradition in science has a long and noble lineage, but it was an error. We are wrong to treat science only as a matter for the mind.

Universities have always had some pedestrian, practical goals and always will. Now, when the doing and teaching of science are more expensive than ever before, universities depend totally on society. University teachers must therefore serve the state and the students. We must teach them how to do things. As a bonus, we will find that we also produce better scientists, because we will produce people who can do their science, not just think and talk about it.

I do not mean to suggest that the university is nothing but a service institution. It is and must be a subversive element in society. Its professors should preach an anti-materialist, anti-establishment, and sometimes anti-religious doctrine. As the university trains students to be useful tools of society, it should also tempt them with a vision of total self-indulgence: a life in science, a life dedicated to inquiry into the workings of the material world. As we train our students, we should try to change their values, to make them more interested in the generalities of nature than in the details of making money.

Since our subversion rarely succeeds, university scientists were much happier teaching the violent rebels of the 1960's than the docile herds of the late 70's and 80's. Students in the 1960's seemed so much less interested in the demands of society, that we teachers thought we had at last succeeded in our subversive agenda.

Strategies for Teaching

The teacher tries to provide an overview of major findings of the contemporary discipline, to initiate the student into the paradigms of science, and to show the student how the findings of the discipline apply to relevant observations. Some of these strategies will teach students about the theories of the science, but others can conflict both with that intention and with the expectations of student and society. Yet, because university teachers rarely specify either the goals or the strategies of education, they lack explicit guides in the preparation and presentation of their material. Instead, teachers try to do everything simultaneously and science courses become self-contradictory, confused, and confusing. It is therefore a useful exercise to consider what strategies might achieve the various goals of education.

Empowerment by theory. Theories allow anyone to derive identical deductions from the same, specified information. They have to be used with care, because they provide the power of science to control our environment and our lives. However, they are not statements that should be kept out of the hands of the unwary or the uninitiated (i.e. the students). Instead, an initiation into the use of theory should be the core of an effective education in science.

In practice, the application of science is necessarily a question of detail. It requires a knowledge of theories of very low generality to select appropriately among competing constructs, to choose the appropriate techniques to monitor a particular situation, to use these techniques well, to assess the results of this monitoring, and to find alternatives that offset any adverse effects suggested by assessment. Part of our education should teach this process through paradigmatic examples of good practice and ecological success.

Students also need to learn theories of greater generality. Grand theories provide models for less general theories and contexts for specific actions. Students must therefore learn the grand theories of science, like the laws of thermodynamics or gravity. There are also theories of intermediate generality that link the grand theories to observation and that provide broader, less precise predictions about the phenomena of nature for non-specialists. The student should master some of these intermediate theories too.

A scientific education also transmits the traditions of searching for and testing theories. It describes some of the successes of theoretical discovery and application, and outlines the failures of current theory. In Kuhn's (1962) phrase, it provides paradigms for future practitioners.

An education in science should teach students how to use some subset of existing theory, provide them with the skills needed to find other extant theories, and cultivate their abilities to build, apply, disseminate and judge future theories. If we taught our students about theory and theories, our graduates would find they have skills to sell, society would find they have the requisite technicians, and science would find it has a new generation of able practitioners. A student who has had such an education would know some of what has been done and what remains to do, would know a series of examples of good scientific practice, would see how techniques condition and interact with theory, and would have a basic set of theories that allow application of knowledge to some of the problems of society. Such a student would have been empowered by his or her scientific education.

Understanding through explanation. Scientific knowledge is predictive and theories are the constructs that make predictions. I would like to be able to claim that an education in ecology is based on theory, but no such claim is justified.

If one searches the indices and tables of contents of current ecology texts for references to "theory", one is struck with how rarely the word is used. When it is used, the word almost invariably denotes a highly academic construct which makes few, if any, predictions. Most ecology courses, texts and teachers try to describe the contemporary science, and therefore do not stress the role of prediction and theory. Because ecologists often do not recognize the central role of theory in science, we do not yet have the theories we need, we do not teach the few theories we have, and our students would be unable or unwilling to learn them if we did. In short, courses teach what ecology is, not what it does or should be.

Many ecology teachers have adopted a strategy designed to produce a sense of understanding, rather than a mastery of ecological theory. In providing a sense of understanding, science makes us feel "at home" in the universe and so performs a role similar to that of religion, art, and an assortment of other human activities. These activities succeed by giving us the feeling that we understand and control events in our lives, even if this is not so. In religion, the rituals associated with the winter solstice appear to bring longer days and, eventually, spring. In art, the irrationality of poetry may seem to explain events and feelings we do not understand at all, like love, beauty, laughter, and grief. And in science, an educated student can expound at length about the causes of the weather, the impact of pollution, and the future of AIDS, even though the phenomena may be totally unpredictable. In all fields, the importance of understanding is not whether we actually control events, because we certainly do not, but to make us feel less at the mercy of unknown powers and forces.

To promote understanding, teachers try to explain relevant aspects of the universe using the constructs of their discipline. In principle, these explanations should demonstrate that a given observation could have been predicted, and thus that the observation was an instance that could have been deduced from a more general theory (Hempel 1962). In practice, the elements of explanation are a hodge-podge (Peters 1991a). By offering alternatives to predictive theory, the search for understanding usurps the rightful place of whatever theories we have, and hides our ignorance with word-play.

Putative explanations based on non-predictive statements are no more than *post hoc* rationalizations. Because the human mind can explain any finite set of observations in many ways, such explanations are always possible and plausible. Given the advantage of hindsight, *post hoc* explanations can fit the available facts exactly, whereas predictions from theory are unspecific statements of probability. So long as we only compare explanations for data that have already been observed, *post hoc* rationalizations appear more precise and attractive than scientific explanations.

To distinguish *post hoc* rationalization from scientific explanation, one must ask if any observation would have invalidated the explanation. Because *post hoc* rationalizations are specific and complex, they need only explain what occurred. Alternative observations are easily explained away by differences in the details of each case. In contrast, scientific theories not only predict some observations, they also prohibit others. The theory would be falsified if these other observations were made. This asymmetry has the regrettable consequence that *post hoc* rationalizations are difficult to remove from the field, so they tend to accumulate in the literature. Theories, and explanations based on theories, can be falsified and forgotten. In ecology, non-scientific explanations provide students with poor examples, and hide the fact that we can predict relatively little and then only imperfectly. This is most regrettable because, if we recognized the extent of our scientific ignorance, we would also see the many opportunities for improvement that ecology offers.

We likely find non-scientific understanding seductive, because we are unwilling to admit how little we control our environment. If we accepted predictability as the criterion for scientific knowledge, we would realize that most of the decisions that govern our lives are not scientifically justified. Economics is a predictive swamp, politics a scientific quagmire, social interaction a bog of intuition, and so forth. If we recognized the limits of our predictive and manipulative power, our already deep sense of helplessness might become unbearable.

The explanatory role of understanding may reflect a deeply seated human need, but that feeling must not hide the importance of predictive power. An obsession with understanding draws potential researchers away from science, and the desire to explain makes scientists reluctant to accept Popper's predictability criterion as the demarcation between science and non-science. Instead of confronting scientific short-comings, educators frequently disguise them with words of explanation and a sense of understanding. This preserves the status quo and social serenity, but confounds the advance of science because it obscures the problems that scientists should address.

Paradigmatic indoctrination. A common strategy in teaching is to indoctrinate the students to think and act like their teachers. This is the point where we teach as to "intending professionals" (Barzun 1964) and where students are introduced to the over-arching paradigms of normal science (Kuhn 1962). Teachers know that future researchers will not live or work in a vacuum. Would-be scientists must be recognized by the leaders in the field and by peers, or they will never have a chance to practice science. As in art or in any creative field, a would-be innovator must play by the rules that govern the community. Scientific innovators must address questions that are of interest to their community, they must design their experiments in the appropriate manner, and they must analyze the data by accepted methods, even if this means going to extremes, like applying advanced statistical tests where none is necessary. Fledgling scientists must publish in accepted journals, even though these are read by only a handful of professionals, and they must write in the accepted style, even though that style is pompous, dull and nearly incomprehensible. New scientists must be indoctrinated to do all these things or their work will not receive a fair hearing.

If we want our students to succeed in science, part of our effort must be to teach them to conform. However, conformity holds the danger of stagnation. When a discipline can no longer meet new demands placed on it by society and by its members, the field is in crisis. New solutions and approaches outside the normal paradigms are sought, and eventually a new paradigm may be found to treat contemporary concerns. Progressive science therefore needs the occasional revolution (Kuhn 1962).

I believe that environmental degradation has revealed the inadequacy of traditional ecological theory. Ecology needs a revolution, but the processes of critical assessment and radicalization that precede revolution are frustrated by indoctrination into contemporary ecological paradigms. At the end of their education, too many students simply accept the foundations of their science, and the only problems they can find to study are minor elaborations of current paradigms. We teach people to be normal scientists, but we may need a revolution to meet the challenges of contemporary ecology.

Disciplinary description. A description of findings in the discipline is a part of all strategies: teaching theory, developing understanding, inculcating paradigms, or promoting revolution. However, theory is only part of description, and in ecology usually a minor part. Even upper level courses may describe contemporary science as a body of incontrovertible concepts, logical truths, and law-like facts. Students are encouraged to believe, rather than to question the corpus of science. As a result, even senior undergraduates and graduate students see science as virtually complete and consequently rather uninteresting. To the converted, contemporary science seems unlikely to change.

An Evaluation of Teaching in Biology and Ecology

To summarize the chapter to this point, I have suggested that teachers should strive to prepare students for careers, to prepare technicians for the state, and to infect some young minds with the passion for science. If we are doing our jobs well, students graduating with a B.Sc. should be fluent in the use of a body of scientific theory and method, and they should be confident in their ability to learn more skills and theories. Those who go on to research need these same attributes, but they also need an appetite for scientific thought and investigation.

A simple example will show how well I think we are achieving the practical goals of higher education in science. I recently had to hire a technician and my advertisement attracted five graduates from the undergraduate program in biology at my university. To select among them, I thought to use a test to determine if the applicant could follow routine analytical procedures. I asked each applicant how he or she would prepare a one molar solution of sodium chloride and how they would dilute that stock to 0.1 M. I thought this task would present no difficulty because our undergraduates are required to complete several courses in chemistry, and the applicants were allowed to use any books they wished. What astounded me was not just that none could answer the questions directly, but that none could describe how they might go about finding out how to answer them. Apparently, they could not apply what they had learned and were so unconfident in their abilities that they could not teach themselves either old or new material. How will they meet the challenges of the current marketplace, much less of the next millennium where they would spend most of their lives?

Nurture or nature. If our students are not as capable as we would like, we can blame their genetics (them) or their environment (us). The only fruitful approach is to blame ourselves.

The material society sends to be educated must be basically sound. During rare historical periods of exceptional intellectual achievement, small populations have produced many more masters and geniuses than numbers alone would suggest possible. One need only compare the architecture and sculpture of Periclean Athens, the painting of renaissance Italy, the literature of Elizabethan England, or the music of 19th century Germany with the products of our age. These societies contained only a few tens of thousands of potential contributors, many of whom lived in poverty, ignorance and squalor compared to us. Yet they achieved much more than the well-fed, leisured millions who make up contemporary mass society. If we cannot succeed in educating scientists, it is more likely because we, as a society, spoil the material we have, than because we receive spoiled material.

Even a few hours with a pre-school or kindergarten class is enough to show that most young children have ample wit and intelligence. Even later, after the schools have done their worst, they still deliver superior students to the universities. For example, Harmon (1961) analyzed the secondary school IQ's of eventual winners of doctoral degrees in different fields (Table 13), as revealed by U.S. Army General Classification Test (AGCT) scores. These results show that we can be elitist in thinking about education.

Both lines of evidence, the usually untapped potential of humanity and the demonstrated intelligence of our students, imply that the failure of a science education is more likely to be institutional. High IQ's and native ability are not enough. Indeed, most of our doctorates in science do not succeed in their discipline. De Solla Price (1986) has shown that of all the contributors to a field in a given year, a fifth never publish again in the same area and a further third never publish again in any field. More than half the contributors to a science do so only once and then drop out. Only a fifth of the initial contributors become the core of researchers who are major contributors to the science over the longer term. We are not using our material well.

The problem with textbooks. If biologists are uncertain about the nature of science, they cannot be expected to direct students effectively. This uncertainty is echoed in the cursory descriptions of the nature of science offered in introductory textbooks (Chapter I), but is also apparent in the body of the textbooks, in courses and in more advanced monographs. When teachers are

Table 13. IQ scores as recorded in AGCT tests of high-school students who eventually earned doctoral degrees in different fields. (From Harmon 1961)

Discipline	IQ
Physics	140
Mathematics	138
Engineering	135
Geology	133
Arts & Humanities	132
Chemistry	132
Biology	126
Education	123

uncertain about the field, they are unlikely to deliver clear messages about what is important to their students.

Evidence of the teachers' uncertainty about what is important can be seen in the vast welter of information that typifies contemporary texts. Most introductory textbooks in biology or ecology are huge undertakings stretching over hundreds of oversized pages. Even these vast texts soon prove insufficient to contain all our important findings so new, even larger editions appear at regular intervals (Table 14).

No instructor can seriously suppose that students will absorb more than a tiny fraction of this material. The texts therefore cannot teach, and they are scarcely authoritative enough to be reference works. They serve mainly as samplers of biological thought, providing a place for most major currents in the discipline. Publishers approve of this format because such a text will likely touch on the special interests of the professors who select the texts. The

Table 14. The growth of textbooks in ecology and biology (as measured by number of pages, n) with successive editions (as indicated by the year of copyright, y). Page sizes also tend to increase in subsequent editions, so this table under-represents growth in the contents of these texts. Names are those of the authors. Editions were selected according to availability in the McGill University library system

			Biology texts				
H. Curtis	y	1968	1979	1983	1989		
	n	854	1043	1159	1192		
W. T. Keeton	y	1967	1972	1980	1986		
	n	955	888	1080	1175		
C. A. Villee	y	1960	1962	1972	1977	1985	1989
	n	615	625	915	980	1206	1412
P. B. Weisz	y	1959	1963	1967	1971	1982	
	n	796	786	886	656	1009	
			Ecology texts				
C. E. Krebs	y	1972	1978	1985			
	n	694	678	800			
E. P. Odum	y	1953	1959	1971			
	n	384	546	574			
E. R. Pianka	y	1973	1978	1983	1988		
	n	356	397	416	468		
R. Ricklefs	y	1973	1979	1990			
	n	861	966	896			

teacher, recognizing the impossibility of teaching all of contemporary biology (or ecology or limnology), can assuage the inevitable sense of inadequacy with the thought that the subject is dealt with somewhere in the text. Interested students could always pursue the topic there, but the indigestibility of the material must discourage all but the most dedicated (or insensitive).

Texts do not have to be so comprehensive. The best overview I have ever read of then contemporary biology was *The Ideas of Biology*, a pocket-sized paperback less than 200 pages long (Bonner 1962). T. H. Huxley (1880) developed a text for biology that dealt only with a single model animal, *The Crayfish*. Both authors succeeded because they ignored the imperative to present everything, and chose to display their ideas clearly and effectively with highly selected examples. The student could then use these ideas to organize other facts and other theories. Contemporary textbooks may begin with similar aims, but they become cluttered by a seemingly inevitable accretion of biological detail. Each new edition becomes more bloated as the authors add information to bolster and illustrate their original conception of the science (Table 14). Unfortunately the result obscures that conception. The secret of great teaching lies as much in what is left out, as what is left in.

The problem with courses. The swelling texts are only indicators of teachers' confusion about biology. The same process occurs in the design of university courses, as I can illustrate with another personal example.

Some years ago, the government of Ontario decided that the present biology course for senior secondary school students was old-fashioned and that it had to be jazzed up to appeal to modern students. A committee was formed and a number of zoologists were invited to provide ideas. We talked and argued all evening. Finally, a good friend of mine announced that he had the solution and began to outline a new course. Other committee members added material that was dear to their hearts, and eventually a new biology course was developed. This is a quite typical ontogeny for an introductory course, and I suspect that it has been repeated many times in both secondary schools and universities. Nevertheless, the final product was a recipe for disaster.

The "new course" my friend helped design for high school students was actually the course he was then giving to first-year university students. In proposing that a university course be offered to high school students, he overlooked the fact that university students had only 18 classroom hours a week, so they had much more time to think about the subject than students spending almost 30 hours a week in secondary school. Moreover, he ignored the reality that a university professor might have only 5 contact hours a week, whereas colleagues in secondary school had 25. In addition, my friend was a highly trained and brilliant biologist who later became president of a major university. This combination of native ability, professional training, and reduced teaching load should have afforded him greater success in his course than might reasonably be expected of the average high-school teacher.

The real situation was even worse. Because the two of us were working very closely, I attended many of his lectures, and I repeatedly found he had serious difficulty understanding some of the concepts he was trying to teach. Therefore the new course began with subject matter that a good professor found difficult, yet the course would almost certainly be taught by less competent teachers to more harried students. I think it extremely unlikely that most students would find that such a course would pique their interest in science.

My moral is that we cannot teach everything. There is too much for one course or one career. Instead, we must use a limited set of materials and examples to show our students how to learn and how to teach themselves.

Repercussions for graduate training. Not surprisingly, the lack of focus that characterizes undergraduate texts and courses reappears in the research proposals that students make soon after entering graduate school, and in the theses they write at the end of their formal education. Students who are not trained to cherish scientific theory are less capable of formulating testable hypotheses for their own research. Too often, students set off "to assess the impact" of some perturbation, "to determine the importance" of some process, "to understand the role" of some organism or "to shed light" on a phenomenon. These woolly generalities provide little direction and convey little meaning. They hide an unwillingness to specify what variables will be measured and what responses are expected. They show that one has not thought about what one can and should do as a scientist.

The challenge for graduate students is therefore to rise above the generalities of undergraduate education by identifying a much more specific, immediate goal for graduate research inside a larger context, as an early step to a long-term goal. This process requires that the generalities be replaced with highly simplified hypotheses about the relations between operationally defined variables. It is however not enough that a prediction be made about some phenomenon; the relations and predictions should also be scientifically or societally relevant.

So little is known about so much that there should never be a dearth of good scientific projects. If there seems to be, it is because students are poorly prepared for the process of hypothesis formulation and testing. The store of proper paradigmatic examples is low, the testable implications of the science they know are few, and their graduate instruction, the antidote to an unsatisfactory undergraduate experience, is weak.

Graduate students in ecology too rarely recognize the futility of a science that cannot predict. Their long experience with non-scientific "explanation" has crushed the curiosity, doubt and frustration with ignorance that should give impetus to science. They see their task as the development of discursive explanations for an accepted set of observations. Instead they should identify an hypothesis that could have predicted those observations and set out to test its predictions. Others assume causal relations in nature and set out to prove the validity of their assumptions, rather than testing what the relation predicts. Still others study things simply because they were previously undescribed. Small wonder if after five years of studying inward-looking, often dead-end projects, the graduated Ph.D. leaves the field.

A lesson from the literature. The problem of trying to do too much is not limited to formal education. Some years ago, I had occasion to read Alfred North Whitehead. I found it a humbling experience. Like many great thinkers, Whitehead had recorded a very large number of interesting ideas. There was no need for the ideas to be correct, and because correct ideas are very rare, most of them were not. However, great intellectuals, like Whitehead, are arrogant people (otherwise they would not have the confidence to spend so much time writing), so they produce a vast volume of writings. To do justice to this material would take years of study, and so almost all readers are inadequate to the task put to them by the world's leading intellectuals.

The fault does not lie with the busy reader alone. Great writers have written far too much. The same idea may be flogged in different guises in dozens of books. Padding appears everywhere. The great thinker may develop a literary style that is at times outstandingly good, but at other times obscure. And the reader, overawed by the writer and by the obscurity, style and quantity of the material, is simply incapable of sorting out the useful bits. Consequently, reading becomes superficial, works are labelled thought-provoking (although there is rarely time to pursue the provoked thoughts), the writer's fame spreads, and more, ordinary mortals feel compelled to read the great man's works. Even the writer may be fooled and feel encouraged to broaden his field. For example, although I was struck by Whitehead's earlier work, I find his later, more popular, philosophical writings to be so nearly meaningless as to be incomprehensible. Eventually, even Whitehead exceeded his ability.

This raises a problem. How much time should the would-be reader devote to the work of a man like Whitehead? A year would surely be far too little, yet there are many others who merit study. What is the busy scientist or student to do? The only answer must be to use teachers who can interpret the work for other professionals, as Magee (1973) and Pera (1980) interpreted Popper. Science requires incisive teachers at all levels.

XI An Education in Science: Prescriptions

> "It is this union of passionate interest in the detailed facts, with equal devotion to abstract generalization which forms the novelty in our present society.... This balance of mind has now become part of the tradition which infects cultivated thought. It is the salt which keeps life sweet. The main business of the universities is to transmit this tradition."
>
> A. N. Whitehead
> [*Science and the Modern World* (1925)]

In the previous chapter, I described the roles we expect our education system to play, I gave a simple observation suggesting that there is scope for improvement, I identified shortcomings at every level, and I suggested that, in teaching science, the critical issue is our failure to appreciate the nature of theory.

The interesting question is "How can we do better?" I am going to approach this question in a way that is somewhat foreign to professional educators, but more appropriate to a working scientist and teacher. I will ask "What makes a good scientist?" and "Can we modify our approach to education in any way so as to produce more or better science?" This has the distinct advantage of bringing the discussion closer to my own experience as an undergraduate instructor, a graduate supervisor, and a university administrator.

The Undergraduate Program

Let me premise this discussion with the observation that the public's love affair with universities has grown cold. University professors will have to grow accustomed to more meagre moral support, less lavish budgets, and poorer facilities. Our traditional teaching methods will have to change.

We should not expect that any substantial fraction of the teaching staff at a university would agree on a particular solution or collective action to these challenges. Professors are free-thinking, angular individuals who are too convinced of their own righteousness to be much influenced by someone else's prescriptions for better teaching. This is how it should be. It would be equally vain to hope for an institutional response to our difficulties. The unhappy mass of university educators are pulling the administration in a hundred different directions. Experience at two universities has taught me the virtual impossibility of an imposed, general solution to the problems of university education.

The only easy modifications that university teachers can impose on education involve their own courses. Chapter X indicated where some changes are needed, and this chapter indicates some that I try to apply in my own teaching. There is no point in advocating the general introduction of these suggestions, so I offer them for other teachers to use or ignore as they see fit.

The problem of confidence. Over a century ago, Francis Galton (1875) showed that almost half the members of a group of eminent scientists were either the eldest or only child in their family (Table 15). This remarkable observation has since been confirmed and extended. A very high percentage of our best scientists were the eldest or only child (Table 16), they lost one parent by death (Table 17) or divorce, and they were lonely, rather asocial children (Roe 1953). These observations should not suggest that, to produce researchers, we should identify bright children before they reach 10 years of age and isolate them from their parents. No one advocates such extreme measures because they would be both morally wrong and ineffective. Roe (1953) makes the point that about 25% of homeless men also lost a parent before the age of 10. Most bright orphans do not achieve scientific fame.

The critical characteristic of the bright orphans who do develop into researchers is that they are very self-confident and self-reliant with respect to their interactions with the material world. (Their social interactions are much less successful, but perhaps that is more incidental to their scientific achieve-

Table 15. The birth order of eminent English scientists in the 19th century. The families of these 99 individuals were large, averaging 6.3 children per family, so the chance of the eminent scientist being the first or only child was much less than the observed frequency of almost 50%. (From Galton 1875)

Birth order	Number of scientists
Only child	22
First born	26
Middle children	36
Last born	15
Total	99

Table 16. Birth order of 64 eminent American scientists of the 20th century. Fifteen only children are included among the first born. (From Roe 1953)

Birth order	Number of scientists
1	39
2	13
3	3
4	3
5	2
6	2
7	2
Total	64

ment.) Family circumstances develop in them the belief that they can do and understand things. This belief is critical to success as a scientist.

For those bright children who are not fortunate enough to be orphaned before the age of 10, we teachers should help develop this same confidence. Present science curricula may be intended to achieve that goal, but unfortunately, they are rarely designed in a way that will achieve their intentions. The main problem is that our science curricula expect far too much of the students. They try to be too good. Unrealistically high goals teach students that they cannot do science, and massive texts show that there is too much material to master. Students are therefore trained to pass exams by learning lectures, so they learn to rely on authority rather than reflection, reading and experience. As a result, university courses rarely teach students to use or to improve what they have memorized, and certainly do not encourage students to be confident in their ability to criticize, to use or to do science. The great-

Table 17. Percentage of future eminent scientists who lost a parent in childhood through death. The expected values for college students would be 6.3% before 10 years of age and about 10% in total. (From Roe 1953)

Future field	Age at parent's loss: < 10 yr	> 10 yr	Total
Biologist	25	0	25
Physicist	13	9	22
Social scientist	9	18	27
Total	15	9	25

est weakness of our present system is that it does not give students confidence in their abilities.

De-enrichment and dis-integration. Universities and departments like to present comprehensive programs and integrated courses, perhaps because such organization implies a mastery of the material. Unfortunately such an approach misrepresents biology and ecology. Neither discipline consists of monolithic sets of theories. There is no over-arching theory of great generality that ties together all of modern biology or ecology in the sense that every theory is a refinement or specification of the general theory. If we insist on teaching as if there were a single science of biology or ecology, or a central core of crucial facts, we misinform the students about biology and insure our own failure as teachers of science. There is instead a heterogeneous collection of hypotheses with different scopes, variables, formats, domains, and successes. Indeed, there are so many of these theories of low generality that they could never fit into a single degree.

If we wish to give students a realistic view of our science we must teach its theoretical structure. This requires that we give them a dis-integrated view, one without a unifying central theory. They must learn that theories in plant ecology can be falsified or confirmed without impinging on theories of hormonal balance, that one can be a good physiologist without mastering population genetics, and that success in eutrophication control does not insure equal success in controlling macrophytes or predicting the yields of terrestrial herbivores to hunters.

Since we cannot expect students to see the generalities of science if they are constantly harried and bewildered with the particularities of its subdisciplines, students with intelligence and an interest in science require a factually impoverished or de-enriched program. Teachers might try to cover one-fifth of the subject matter in most contemporary courses, but ensure that everything taught in one course reinforces and uses everything taught in other courses. This would allow students time to contemplate the nature of science in general and their material in particular. Not all students would do so, but at least those who wanted to could. The others would be no worse off than they are already. A de-enriched biology course would cover very little factual material, but it would show students how to apply knowledge from other courses and it could build their confidence, graduating students who think "I can do biology".

I would teach a few aspects of some homely subject, like limnology or physiological ecology. These are beautiful subjects with which to introduce biology because so many aspects can be quantified, and because they depend on the mathematics, physics and chemistry the students have already learned. In the laboratories, I would concentrate on a few basic skills in mensuration, analysis and handling of biological material using phenomena that are susceptible to study. Students can easily design and build a water bottle to sample at depth or a Secchi disc to test general theories. They can build and use respirometers to measure oxygen consumption by poikilotherms at different temperatures and levels of activity. They can design and build the equipment necessary to investigate factors limiting the growth of algae. They can learn to do biology, and thereby learn to do science. If they do not do so, they will be lost regardless of the number of facts, concepts and observations they accumulate. Having done so, they can learn most details about the biology they need for their careers on their own.

I would also include a hefty dose of the history and philosophy of science in university training. That material is essential to give students the breadth and vision to appreciate their science. Philosophy can be a tool to help students find optimal strategies in learning and research. It is also a handy weapon for students to defend themselves against the inevitable attacks from traditionalists.

There are topics which I would no longer teach. For example, the theory of evolution by natural selection is a subject that still confuses professionals, and one that cannot be related to most of the physics, chemistry or mathematics that the students are learning or have learned. It is unlikely that university courses will save many fundamentalist students from their ignorance, and open-minded students can learn most of what they need from a host of splendid books on evolution, or even from the public press and electronic media. Above all, neither scientist nor student can do much with the theory of evolution by natural selection because it makes so few predictions. This "theory" may satisfy the students' urge to understand their world in some emotional, visceral way, but such a sensation is not science. Teaching students to seek that form of explanatory gratification is a disservice to their training as scientists.

I would also avoid some of the exciting new fields, like biochemistry and biophysics. If they are to be mastered, these fields require a background in mathematics, physics and chemistry that few biology students have as undergraduates. In any case, evolution, biochemistry and biophysics will still be taught by the many professors who will remain with the old curriculum, so there is no need for me to repeat that material.

A de-enriched and dis-integrated program will impose difficult decisions on the teacher. The material chosen for the course must be carefully selected, but no general theory exists to identify relevant material within the sea of biological detail. The criteria could not be those used by the writers of textbooks, trying to touch all the bases of a huge and complicated field. Nor could the criteria be those used in so much of contemporary ecology, tying conceptual argument and extreme detail together with a sense of understanding. Training different ecologists will require different criteria of biological relevance.

Hierarchical themes for undergraduate education. In the absence of central theory, relevance in biology or ecology depends on the scientific demands of society and pedagogy. Material for a course can be selected because society is interested; for example, we might teach about diseases, conservation, pollution control, plant production or human population growth. Material may also be selected because it teaches an effective way to do science. If we were less concerned to detail all the fruits of scientific investigation, we might introduce students to particularly creative modes of thought, to recurrent patterns in the development of theory, to effective criticism of scientific ideas, to effective tests of theories, and to appropriate responses to both the confirmation and falsification of theory in such tests. Students would therefore face a series of different examples of scientific and societal problems that have been addressed, more or less successfully, at different scales and levels of biology.

Such an approach necessitates "hierarchical thinking" (Allen and Starr 1982, O'Neil et al. 1986). The students should learn that similar problems expressed at different scales may yield to different, even contradictory, solutions. For example, annual mean concentrations of zooplankton and algae are positively related across communities (McCauley and Kalff 1981, McCauley et al. 1988), but inversely related in microcosms (Novales et al. 1993) and over a single season in a single lake (Lampert et al. 1986, Sommer et al. 1986). Phosphorus may be important in lakes (Peters 1986), but marine systems may depend on nitrogen or iron (Price et al. 1991). An effective course should therefore draw examples from a range of phenomena and biological levels to illustrate differences and inconsistencies in our knowledge (Fig. 33). Within one hierarchy, the student should be introduced to theories of high generality, which allow predictions of a crude sort but at a very general level, and theories of low generality that allow more precise predictions about questions of specific interest. For example, one can make crude estimates of production per unit biomass from body size alone for all animals and protozoans, but if the question is restricted to a single species or population, more precise and often more complicated relations may be necessary.

The theories of production in Fig. 33 predict similar variables, but at different levels of generality. They coexist because they have different domains of application. They can be independently falsified or confirmed because they fall at different points in a hierarchically differentiated science. Similarly, theories about respiration or ingestion can be resolved at different levels, again more or less independently of parallel hierarchies. For example,

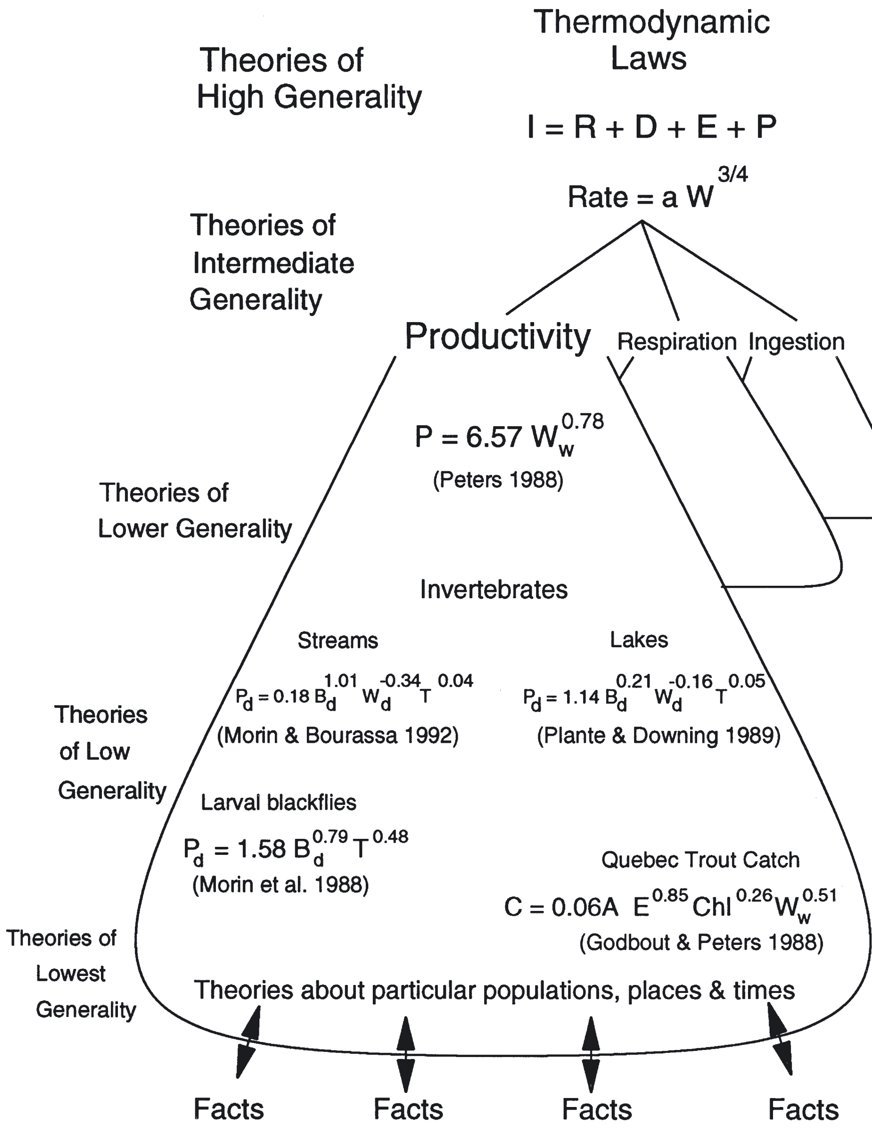

Fig. 33. One system of theoretical hierarchy that may be used to structure biological education. The figure shows the relations among theories dealing with productivity, at various levels of generality, predictive power, and specificity, the relationship of these theories to other hierarchies dealing with other phenomena, and the relation of all these hierarchies to still more general theories, like the laws of thermodynamics. I, R, D E, and P (ingestion, respiration, defecation, excretion and production) are the components of the balanced growth equation. In the theories of lower generality, B is biomass in g m^{-2}, W is individual body mass in g, T is mean temperature, P is production and C is fish catch, both in g yr^{-1}. Subscripts indicate if the units of mass are wet (w) or dry (d)

production may be predictable from size, but theories of respiration could be based on temperature and those for ingestion on food concentration, all operating under the general restrictions set by the laws of thermodynamics, but otherwise quite free to use different variables, analytical techniques, and theoretical structures.

If this material is to be taught, the links among the examples must derive from an explicit consideration of the qualities of good scientific practice. Students should learn about the nature of science, the place of creativity and criticism, the role of theory, and the purposes of observations and tests. Particular examples of success and failure should be discussed and a framework of interpretation provided.

A theoretical typology. One format with which to organize such a disparate set of ecological or biological theories invokes a typology of theories. For illustration, I have identified four basic types of successful theory, although there may be others and alternate typologies exist (e.g. Orians et al. 1986).

(1) Simple interpolative theories simply assume that a phenomenon measured at two or more points persists at intervening points. A common type of interpolative theory in ecology is the species distribution map. If a species is recorded at two sites we posit that it will be found at intermediate positions, provided physical-chemical conditions are similar. In fact, we often use the absence of a species as the first indication of subtle physical or chemical change.

(2) Limiting factor, mass balance and inter-conversion theories form a complex group of interrelated, but simple theories based largely on consistencies in the stoichiometry of living systems and the empirical observation that matter and energy are neither created nor destroyed in biological reactions. These theories are the basis for all the most important predictions that ecologists have made. For example, such theories allowed Vollenweider, Dillon, and Cornett to make some very quantitative predictions about the future of lakes (Chapter IX).

(3) Empirical holistic theories form the biggest and most diverse class of all. It is less a distinct set than it is one end of a spectrum of all theories. Such theories include predictions about the performance of an organism based on its size (Peters 1983), predictions about species number based on evapotranspiration (Currie and Paquin 1987, Currie 1991), predictions of litterfall based on latitude (Bray and Gorham 1964, Lonsdale 1988), and predictions of bioconcentration factor and effective lethal concentrations based on the relative solubilities of organic contaminants in water and an organic solvent (Verschueren 1983, Hermens 1986, McCarty 1987).

Ecologists frequently underestimate the value of empirical theories. Often we denigrate them as “black box theories” or “engineering”. At worst, we ignore them or believe they are not theories at all. This behaviour is self-defeating because if we were to look over the history of successful branches of science, we would discover that the most elegant analytical theories began their lives as humble empiricisms.

(4) Analytical theories lie at the other extreme of this spectrum. The difference between empirical, holistic theories and analytical theories is that the former merely predict, whereas the latter also give us the impression we know why the theories work. An analytical theory predicts and makes us feel at home by convincing us that we understand the system (Lehman 1986b). Analytical theories are usually, but not necessarily always, expressed in terms of the subsystems of the system. Sometimes it merely invokes fictitious state variables, such as gravity, magnetism or even animal magnetism. Most scientists aspire to produce such theories, but there is a time and place for analytical theories. The history of science shows that they follow empirical, holistic theories.

I see no gain in imposing my views on others, but I can urge that all of us who teach an approach to science do so explicitly. If our differences are exposed fairly and conscientiously, students would have a better grasp of both the strengths and weaknesses of science. Freed of popular misconceptions, they would be more confident in their ability to perform as well as their teachers, more willing to cast aside theories and constructs that have outlived their usefulness, and more prepared to accept the responsibility of creating new knowledge. They might even discover the real joy and freedom of research.

Graduate Education

One should not do science because it offers a socially acceptable career with adequate pay and interesting fringe benefits, but because something in one's nature compels one to do so. Such a student will find graduate school a reward in itself and the supervisor should ensure that this is possible.

Many scientists remember graduate school as a golden time when they had more intellectual freedom, more time to reflect, and fewer extraneous cares than at any other point in their lives. To preserve as much of this experience as possible, one must settle on a strategy for graduate study that allows students the freedom to do science, and is likely to offer them the chance to continue to do so after graduation.

The importance of role models. One way to develop theories about effective education is to look for pattern in the training of highly successful scientists. Galton (1875) provided one such pattern in discovering that future scientists often lost a parent. Another of Galton's discoveries is that leading scientists were usually trained by other leading scientists and that they regard that experience as critical to their own scientific development. This pattern has been repeatedly confirmed (Roe 1953, Merton 1968, Zuckerman 1977).

Ann Roe (1953) examined the experience of eminent American scientists from physics, biology, and the social sciences. There are many interesting aspects to that study, but I mention only the brief autobiographical sketches of family life and education given by each scientist. When reading these sketches, one recognizes a most interesting omission. Not one scientist commented on the type or quality of education they received, except for those who dismissed their undergraduate days as boring. However, all vividly remembered one scientist or teacher who had a strong impact on them and essentially revealed the meaning of science for them. Often, contact with this mentor was what started the eminent scientists on their successful careers.

Graduate education works because it is one of the last bastions of the apprentice system. The student learns by working with a master, and great masters tend to produce great students. If this hypothesis about eminent scientists is valid, the availability of at least one great teacher is critical to an effective education in science. We need teachers who inspire students so they will achieve this potential.

Many great scientists fit this model. Claude Bernard was diverted to a career in experimental medicine when François Magendie recognized his talent and chose Bernard to be his assistant. Antoine Lavoisier studied geology under Étienne Cruetard, a founder of the science, and chemistry with Guillaume Rouelle, famous throughout Europe for his classification of salts based on crystal structure. Johannes Kepler was started on his career by Michael Mastlin, a famous mathematician and astronomer. Darwin walked with Henslow. I have yet to find a great scientist who did not trace his beginning to another great scientist. The closest I have come to an exception was Carl Linnaeus whose inspiration came from Aristotle through a set of Aristotle's collected works given to him by his father on his sixth birthday. In ecology, we need only look at the success of Hutchinson's school at Yale (Edmondson 1971): their experience with that great master gave almost all of his students such ability and confidence that they were to define the science of ecology for a generation or more.

The phenomenon is well described by Helmholtz whose mentor, the great Johannes Müller, had influenced and inspired him to study physiology:

> When one comes in contact with a man of first rank, the entire scale of one's intellectual conception is modified for life; contact with such a man is perhaps the most interesting thing which life may have to offer.

Wise choices in graduate education. Graduate school provides both the credentials necessary for a life in science and the training needed to use those credentials. Once touched by the peculiar passion that drives scientists, one must go to graduate school. Selecting a school is an important step.

Since I am convinced that the most important element in the university is the great scientist who is an inspiring teacher, this must be a major determinant in choosing a graduate school. A single such teacher can make up for years of mediocre undergraduate instruction. And in the apprenticeship of graduate education, the presence of a great teacher becomes critical. Some fortunate students may have found this great teacher during their undergraduate years, so their choice should be clear. The others should strive to enter the graduate environment which is most likely to provide contacts with great scientists. One must try to work with the very best.

Although the very best masters are more likely to be found at the greatest institutions, the right one may be found at any university regardless of size. Institutional fame alone is a poor guide to graduate studies, because every university has its strengths and weaknesses, and because past glories may not signal present competence. One would do better to seek active laboratories, because there is ample evidence that the best labs train disproportionately more of the future leaders of the science (Zuckerman 1977).

One may also select among institutions and laboratories to find the intellectual leaders within one's chosen field, but the choice of teacher is more crucial than the choice of material. Thus if one must chose between a journeyman within one's precise field of interest and a master in some ancillary field, the latter is the wiser choice. Great scientists can train people to answer more than one question, but weak teachers may not even do that.

The scientist who influences the novitiate need not be the head of the laboratory. Indeed, the recognition that great scientists receive often proves to be a heavy burden, leaving them little time to interact with their associates. Much of the training in such laboratories may be done by younger researchers who are themselves destined for future greatness (Zuckerman 1977). Nevertheless, because great scientists often attract, train and work with other powerful scientists, larger laboratories and working groups are likely better choices than smaller isolated ones.

Finding the right laboratory is not easy. Since several applicants may compete for the best positions, the student should prepare for that competition throughout the undergraduate years: by learning about the field, by earning marks, and by winning fellowships. When the time comes to select a venue for graduate study, one might begin with a preliminary list of potential mentors, compiled from suggestions by instructors and fellow students, from readings and from lectures. Such a list should emphasize the approach of the prospective supervisor, not the material, because the approach captures the essence of the laboratory's science and usually endures longer. Since past scientific fame may not ensure adequate future mentorship, the student should research potential choices on the list thoroughly: read more of the laboratory's published work, correspond with possible supervisors, and discuss the possibilities with appropriate teachers in the undergraduate program. If possible, the prospective student should visit the lab, talk both with the potential supervisors and with their associates, tell the supervisor what is attractive in the laboratory's programme, try to determine if the potential supervisor provides a positive experience for his or her present associates, and find out if past associates have built on their experience in the lab to develop successful independent careers.

Researching potential supervisors takes more forethought, time and effort than most students are willing to commit. Indeed most are caught flat-footed by any number of deadlines. As a result, prepared students often stand out from the crowd, but it is a crowd that only the potential supervisor can see. Since the student cannot gauge the quality of competition, the worst thing the student can do is to decide against applying to the best laboratories because he or she feels unworthy. Science requires confidence.

There is now a tendency to hurry the student through graduate school, supposedly to increase the efficiency of education. I have little enthusiasm for that approach, because it cheats the student of the leisure needed to develop into an independent scientist. For similar reasons, prospective graduate students should not settle too quickly on a topic because the first topic may not allow exciting discoveries. Worse, it may immerse the student in stultifying drudgery. However, the student should not take this freedom as licence for sloth. Science is a demanding discipline and most scientists should expect to work 60 to 100 hours a week as they develop their scientific capacities, and for the rest of their lives. In compensation, the work is fun.

The student should try several avenues to isolate a research topic: thoughtfully considering one's own interests, perusing current "hot topics", searching for an original and valid approach, and using the expertise of the supervisor to vet and sort alternatives. In most cases, the supervisor will play a major role in selecting an appropriate topic, because such a selection normally requires more information and expertise than a beginner is likely to have. Eventually, a good student will surpass the mentor in that area of specialization, thereby wresting the problem away from the master and making it that of the student. This is an essential step because it shows that the student has the confidence required for scientific independence.

Finally, the student will leave the privileged atmosphere of graduate school and, usually after the respite of a post-doctoral fellowship, look for a job. A good job in science is the best guarantee available that one will preserve the freedom to express one's scientific ideas and skills. Such jobs have always been scarce. To get one, the student must, of course, be well-trained and do a piece of good research. The work must also be eye-catching, in the sense that other scientists perceive the work as contributing to an important problem. It is for this reason that I suggested the student look to hot topics. Ideally, the work should also use a novel methodology or approach because scientists appreciate such originality, but it must not be too new because some members of selection committees are likely too dull to appreciate real novelty.

Administrative Advice

To excel, a university must attract and keep people who can inspire a thirst for science among the students. In Canada, our record for attracting and keeping scientists of calibre is not good. Thomas Henry Huxley applied to the University of Toronto for a position in zoology, but despite letters of reference from Charles Darwin and other international scientists, Huxley was rejected in favour of a local boy. The successful candidate, who happened to be related to the provincial prime minister, was and remains totally unknown. Leopold Infeld, a collaborator of Albert Einstein, came to the University of Toronto for a while, but the university chose neither to build an institute for theoretical physics around him, nor to defend him when the local press attacked him as too leftist; he returned to his native Poland (Infeld 1978). Sir William Osler, who is still famous as an inspiring teacher, left McGill for Johns Hopkins and ultimately for Britain. McGill has graduated four Nobel laureates in science since World War II, but all achieved their eminence in the United States. Our one laureate, Sir Ernest Rutherford, was attracted to Montreal from New Zealand, and eventually left for greener pastures in England.

The brain-drain is not a particularly Canadian problem. Many smaller countries and institutions are similarly ineffective at retaining intellectual leaders. Why do we not attract great educators? And why can we not keep them when we have them? Perhaps we small players neither recognize nor want greatness. Many of our most promising individuals emigrate to places where their ambitions can find more scope. And if they had decided to stay home, we would interpret this as an indication of lesser stature. Since we do not recognize greatness, we strive for an egalitarian treatment of scientists and institutions which further insures that no individual or institution will rise above the others. We live in a self-imposed mediocrity.

The inability of smaller institutions to hold leaders is worsened by the advantage of great institutions in attracting such people. Merton (1968) has discussed this phenomenon as a part of what he called “the Matthew effect in

Science". In the new testament, Saint Matthew wrote, "To him who hath it shall be given in abundance: from him who hath not it shall be taken away." Great institutions attract great scholars, and so grow at the expense of smaller, less prestigious ones. Moreover, because these great scientists may inspire one another, the advantage of the great institution continues to grow, maintaining its preeminence and increasing its dominance.

If this is true, what can we do? I see only one answer. We must become more elitist. We can never hope to have great scientists in all departments at all universities. Let us therefore designate one or a few universities to become the Harvards or Oxfords of Canada, Sweden, Italy and Australia, or of Ohio, Ontario and Sicily. If we cannot designate whole universities as centres of excellence, then within universities, we might specify faculties or groups of departments for special treatment. If this is not possible, then let departments favour particular research and teaching groups, like limnologists, behaviourists, forest ecologists, and neuro-biologists. If even this is not possible, let us at least select the very best individuals among our scientific applicants. Too often, we select against the best scientist on the grounds that the teaching program or sub-disciplinary balance demands a different specialist, or that the best scientist may not be the most collegial colleague. This choice ensures mediocrity by sacrificing individual brilliance for the sake of academic bureaucrats who treasure the equanimity of undergraduate programs and departmental mix. Equanimity is almost always the antithesis of excellence.

An elitist choice would signal that we have accepted that we cannot teach all things to all students, and that the value of a university education does not depend on the number of facts or the breadth of coverage, but on the appreciation of ideas. In science, ideas are theories. Great theories, like other great ideas, are produced by inspired and dedicated individuals of great creative vision. If we wish to promote scientific education, we must encourage those few who can create powerful theories and, by example, train others to do so in the master-apprentice relationship. Our first priority must be to attract great individual scientists.

Once we have identified our favourites among universities, faculties, departments, research groups, and individuals, our next priority is to pour enough resources into them that we can keep the very best scientists in some small number of disciplines. We would then have somewhere to send the very best students — a place where they would have a good chance of encountering the odd brilliant scientist who might send them on that magical leap from the world of pedestrian research to great science.

XII The Questions of Relevance

> "The English ... surpass all other nations in snobbishness; our fastidious distaste for the applied sciences ... has played a large part in bringing England to the position she occupies in the world today."
>
> Sir Peter Medawar
> [*The Limits of Science* (1984)]

Previous chapters argue that contemplation of science should lead ecological researchers, and others, to profound changes in the way we do science. If that happened, we would be obliged to make consistent changes in other areas as well. For example the previous chapter discussed the possibility of changing the ways professors teach and students learn. This chapter instead focuses on the face which science turns to the public. That too must change, if we are to be honest with our public patrons and so keep their goodwill and support.

What Use is Science to Society?

Society has elected to support science. Politicians and bureaucrats think research is important. Every year, each industrialized country spends millions of dollars to pamper its scientists and researchers and to allow them to perform as well as they are able. There are several good reasons that this is so.

First, I can agree with Jacques Barzun (1964) that science is indeed a glorious entertainment. It is a tremendous substitute for material consumption to get us as happily as possible over that uncomfortable period between the cradle and the grave. Moreover, because science is such good entertainment, it completely occupies a whole class of technically competent, informed, thinking people who might otherwise make trouble because they tend to be socially difficult. In return, society gets some good from the expense in the vicarious pride that the country produces and supports good scientists, as well as good writers, singers and athletes.

The entertainment value of science cannot fully explain the generosity of society. After all, the arts, humanities, and religion offer many of the same advantages and somewhat more entertainment, yet they enjoy far less support. Society expects more from its scientists. It expects us to be useful, and we scientists encourage society to think so. To show that science merits support, we must show how useful it has proven to be.

There is really only one way that science is of special benefit to society. It generates theories that let us make predictions and so look into the unknown. These predictions help us choose courses of action that will lead to the results society desires. Science thus helps to achieve societal objectives, but it does not identify or judge these objectives. Many scientists believe they have the additional duty to direct society, but that duty should be shared among all citizens. Societal directions are set by policy makers who should represent the whole of society. The only distinguishing characteristic of scientists is their ability to produce theory.

Much of society is ignorant about the appropriate uses of science, and scientists too rarely recognise any limitations to those uses. Together, scientists and society have confounded one another with unrealistic claims and expectations. Their mutual uncertainty would be reduced if both sides were more aware of what science is, of how it differs from applied research and technology, and of what it can hope to achieve. This chapter shows that our jobs as biologists and ecologists would be much easier if we made explicit use of theory to define our tasks and capacities as scientists. It also suggests that the utility of ecology is harder to defend because we have not consistently made use of theory in the past.

Does science differ from applied research and technology? Science has the job of building and testing theories. For example, Einstein was definitely acting as a scientist when he developed the relation that

$$\text{Energy} = \text{Mass} \times \text{Velocity}^2 \tag{25}$$

A person engaged in science, a scientist, need not contribute directly to the solution of practical problems. The best the scientist can do in this respect is to become interested in a body of data about which society is concerned. For example, an ecologist concerned with the cycling of materials in ecosystems might elect to study the cycling of PCB, rather than that of sodium or carbon, because society is concerned about toxic materials in the environment. This selection of subject matter is not applied research, but merely a diversion of theoretical interests towards phenomena about which the society is concerned.

Applied research differs from science in that its purpose is not to build or to test theories, but to exploit potentially useful predictions from existing theories. The person who deduces from Eq. (25) that any transformation of matter resulting in a loss of mass would release an enormous amount of energy, and then searches for such a transformation in the hope of exploiting the energy released, is an applied researcher. It is this hope, the motivation of the research, which distinguishes applied from fundamental research.

Technology is the process of putting the results of applied research into practice as efficiently as possible. To follow my example, once applied researchers had identified uranium as having the best potential for the transformation of mass into energy and had investigated the general conditions under which energy release occurs, the technologists took over. They worked out effective methods of controlling the rate of transformation and of packaging the whole so it could be delivered to an appropriate site. Technology built the atomic bomb, and got a man on the moon.

The same person can do applied research, pure science and technology, but at different times. For example, an applied researcher who fails to achieve the desired ends may suspect that the fault lies with theory, and begin to test the theory whose predictions were to be exploited. To maintain my distinction between applied research and science, I claim that this applied researcher has become a pure scientist. The distinction is necessary to avoid working at cross-purposes.

A facile objection to this separation is that because one worker can do all three jobs, there is no reason to distinguish them. I disagree. To hold that no distinction exists between these activities is like saying that because one can eat at one time and talk at another, there is no reason to distinguish the process of eating from the process of talking. Although eating and talking are manifestations of a more general process called life, we still find it useful to distinguish between them. Similarly we can categorize the activities that constitute research, although we may not be able to categorize the individuals who do them.

A more difficult objection is the problem of what to call an activity that could be science, or applied research, or technology. For example, an individual might experiment with the fission of plutonium, not because he or she cared about bombs or domestic energy supply, but to test the theory represented in Eq. (25). In that case, the activities that were applied research or technology in my previous examples would be science. This might seem a reason to reject the categorization. I choose not to do so because the distinction helps focus attention on a most important aspect of research that is often ignored: the motivation for doing it.

Too much research is done for the same reason that a mountain is climbed ("because it is there"), and too little time is spent questioning the motives for doing so. We can ask why rational people have chosen to do something, and we should expect a cogent, meaningful answer. We need to know what goals are proposed for any particular piece of research so that we can try to determine the significance of the project and its likelihood of success. This knowledge would both help direct our research and protect us from the unrealistic demands of society, the overweening claims by scientists, and the ineffectiveness of undirected research.

Does Science Merit Support?

Up to this point, I have introduced three simple topics that receive too little attention from university scientists: the uses of science, the predictive aspect of theory and the differences among science, applied research and technology. I have done so because I feel we could be more effective as teachers and scientists. We can improve, but I also believe that we are unlikely to do so unless we give serious thought to the questions that serve as headings in this chapter.

My desire to improve is only partly altruistic. Society's attitude to the university scientist is changing. Our image has become tarnished and as a result, it is likely that our working conditions will become more austere. We could react to this by screaming at our tormenters, or we could become more useful and effective, thus earning a better image. I prefer the latter course.

How can we evaluate our science? Obviously any group of professionals likes to believe that its members are highly competent and without fault. Consequently, I must present evidence for my unflattering opinion of university science. I will not address the whole field but only a small part, biological limnology and, by extension, ecology. I will look at our strengths and weaknesses, and speculate on procedures we might adopt to make ourselves more effective.

Many of my views reflect personal experience with limnology in Canada, and could be dismissed as the major failings of a minor science in a minor country. To escape that fate, I must establish the relevance of the sample. When we consider the size of the Canadian population and the relative newness of science in Canada, the contribution of Canadian aquatic ecologists has been remarkable. For example, data for 1982 to 1992 compiled by the Institute for Scientific Information of Philadelphia ranks Canada second in number of citable publications and in number of citations in both aquatic sciences and ecology/environment. At the individual level, it is very reassuring and comforting to be a Canadian limnologist abroad. Almost everyone you meet expresses an interest in visiting Canadian limnological laboratories, and asks about the recent work of several colleagues. Canadian limnology is widely recognized and respected.

This reputation is well deserved. We owe it, in part, to the classic, great limnologists of the past such as A. Huntsman, J. R. Dymond, Ronald Hayes, Donald Rawson, Bill Ricker, Fred Fry and so on, as well as to imports, like Noel Hynes, Richard Vollenweider, and Dave Schindler. We can also be proud of the great federal laboratories, The Freshwater Institute and The Canada Centre for Inland Waters, that are in large part responsible for keeping our reputation alive. All in all, I am very proud to be a Canadian limnologist.

Although Canadians have reason to be pleased with our national accomplishments in limnology, we have no cause for smugness. Neither Canadian limnologists nor those of other nations nor ecologists in general have reason to be pleased when we evaluate our disciplines in relation to others.

Scientists are normally very careful not to evaluate their science relative to other sciences. Such evaluations are difficult to do, and potentially embarrassing. One tool in such comparisons is the analysis of patterns of citation because citation is one of the few quantitative measures of the impact of a given field, an individual or a publication. Although interpretations of these measures are disputed (Garfield 1985, Taubes 1993), I will begin with them, because I am a quantitative scientist and because alternative indices are even worse.

An assessment of the scientists. I began to evaluate limnology quite by chance while leafing through *Current Contents*, in which Eugene Garfield (1977a, b, c) had published a series of articles on the 250 most cited scientists. To hit the top of the pops, a scientist then had to receive at least 266 citations per year (this threshold would now be considerably higher). I was curious about where Evelyn Hutchinson would appear in this list so I looked him up. To my horror, I discovered he did not rate! Thinking that I might have chosen my top limnologist badly, I began to look for others — Thienemann, Naumann, Birge, Welch and so on. When I again failed, I went through the entire list looking for an ecologist. Not one had made it. A subsequent ranking for 1984 (Garfield 1986) does include a few ecologists, like MacArthur, May, and Schoener (McIntosh 1989), but no limnologists. What does this mean? What does it tell us about ecology in general and limnology in particular?

First I want to rule out the comforting interpretation that our peer group is too small to produce enough citations. The International Society of Limnology now has about 3000 members; at the time of Garfield's 1977 analysis, the figure was about 2500. If we consider terrestrial and marine ecologists, we will find at least as many more. Therefore, the minimum size of our group is 5000 scientists. If each member publishes only one paper every second year and if each paper has (on average) 20 citations, ecologists would have collectively generated 50 000 citations per year. In fact, there are more members, the members are more productive, and reference lists are larger (Peters 1989). We therefore generate quite enough citations to put a few ecologists on the first listing of most-cited scientists. We can rule out the hypothesis that our group is too small to produce superstars.

This argument does not falsify the hypotheses that large societies generate more citations or that their leaders are likely to score higher in such comparisons. In other words, the presence of one or more leading practitioners among Garfield's immortals is no proof that other sciences are strong. They undoubtedly share shortcomings with ecology, but that does not excuse our showing.

At the other extreme, I reject the hypothesis that ecology attracts less capable scientists and consequently that no ecologist is smart enough to become a superstar (I know some colleagues in cell and molecular biology who subscribe to this view). Many limnologists chose their field because they were interested in and good at physics, chemistry and biology, not because they were too stupid to become physicists or chemists. They found, in limnology, a discipline that would allow them to pursue their trans-disciplinary interests.

I have a third hypothesis. My hypothesis is that the state of our discipline makes it impossible for limnology or ecology in general to have superstars. The problem with ecology is that it is diffuse. It lacks focus. It isn't going anywhere. Ecology lacks the paradigmatic theories that identify exceptional scientists and their exceptional work.

An assessment of the science. Perhaps some readers are still in doubt about my meaning. If so, I will try to explain myself further by examining the characteristics of a superstar scientific paper. This information is available to us because Garfield (1977c) also listed the most highly cited papers written by each of his superstar scientists. When I looked over this list of 250 papers, I saw that they could be categorized into three main types: papers that describe new theories of moderate generality, papers that describe unexpected phenomena, and "methods" papers.

A new theory of moderate generality is a theory that makes very clear predictions about a moderately large body of phenomena. Darwin's theory would not do. It is too general, but a less general theory, like the theory of particulate inheritance, might count. These theories of intermediate generality help to link more general theories and concepts to theories of lower generality and to facts. Such theories suggest many new experimental tests or possible applications. All papers arising from these studies refer to the paper that described the new theory of moderate generality. One reason ecology lacks highly cited papers is that large numbers of ecologists do not agree about what construct of great generality needs to be linked to observation. Thus there is no place for exciting theories of moderate generality in ecology.

New unexpected phenomena excite great interest for one of two reasons. The first is that these observations are inconsistent with a widely accepted theory. If this is the case, many scientists immediately attempt to falsify the observations. If this fails, they will attempt to repeat the anomalous observations and to reconcile facts with theory. All of this work can generate many papers that refer back to the first discovery of the anomaly.

A second situation in which new unexpected phenomena are important is the situation that Thomas Kuhn (1962, 1970) described as a crisis. In science, a crisis exists when a paradigm has ceased to generate soluble problems. When this happens, leaders in the field converge on certain categories of anomalous observations. The paper that first directed them to these observations would be highly cited. The important common feature of both situations in which new phenomena are interesting is the existence of a generally accepted theory to identify the norm. The lack of such norms makes it hard to identify surprising observations in ecology.

The "methods" paper needs no definition. Everyone knows that the most highly cited papers are methods papers. One of the best known is the 1951 paper by Lowry and co-workers on protein measurement with the folin phenol reagent. This paper has been cited over 100000 times (to put this in perspective, the average paper is cited about 6 times). Fewer scientists recognize that such success is rare, that most methods papers are rejected or uncited, and that this is especially so in ecology (Jumars 1987). Good methods papers are hard to do.

The fact that ecologists do not produce famous methods papers is indicative. God knows we have as many methodological problems as any other group of scientists. For example, environmental toxicology has been held up for years by our inability to analyze toxicants accurately. In fact, we still lack acceptable methods for some commonly measured substances, like chlorophyll *a* or nitrogen. Turning the picture around, we discover that many of the methods we use have been developed by biochemists or chemists. For example, all of our popular methods for phosphorus analyses were developed by others and adopted by us. Why have no ecologists developed famous methods?

I think the answer is simple. It is very difficult to persist until a new method is perfected. Because thorough testing takes a great deal of time and effort, a good methods paper needs strong motivation. A large part of this motivation is provided by the recognition that the method is absolutely essential for scientific progress and the knowledge that one's peers need and will use the method. In short, when the whole community of scientists recognizes that certain measurements must be made, we know the methods are important, and we are willing to make the commitment needed to produce a strong paper about them. This recognition of important methods presupposes the direction provided by an overriding theory.

Thus in all three classes that I could identify in Garfield's list of famous works, writers and users were directed by a theory that identified what is important. I hypothesize that ecologists and limnologists do not agree about their paradigmatic theories and therefore have failed to produce famous papers and highly cited scientists.

Age of citation. We can test this hypothesis further by analyzing the age of material cited in different disciplines. If a field is flagging, old papers can be as valuable as new, so their appearance in the literature may be unheralded but their lifespan should be long. These comparisons should make some allowance for that spurious modernity which makes us cite the latest rediscovery of the wheel rather than the scientist who first did the work.

Where progress in science is rapid, worthwhile papers are discovered and used shortly after they are published. In such a discipline, papers also go out of date very rapidly. As an example, Fig. 34 compares citation patterns in ecology and biochemistry. It shows that biochemists cite propor-

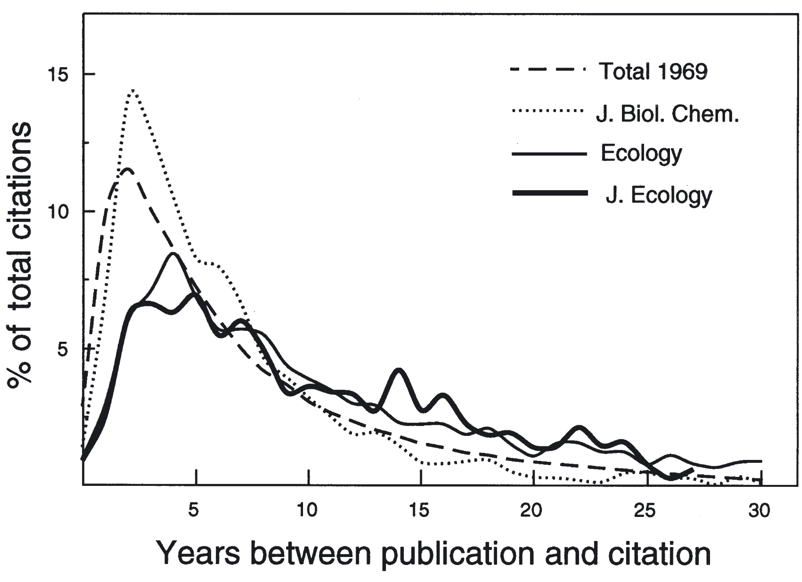

Fig. 34. The effects of age of papers, in all journals and in just ecological or biochemical journals, on the rates of citation to those papers

tionately more new papers, so the number of citations per year rises rapidly to peak at about 3 years, and then falls off. In ecology, the initial response is slower and less dramatic; citations rise to a low peak at about 5 years, and then relatively slowly decline. Comparisons among other journals yield similar data (Peters 1989, 1991a). This pattern suggests that ecologists do not immediately recognize exciting papers as important, or are not writing such papers.

Extent of application. In the past, some colleagues have thought this comparison of ecology and biochemistry unfair. They say that biochemistry differs from ecology because it has a dependent applied science, medicine. This additional audience for biochemistry leads to more rapid application and high citation rates. This objection actually gives additional support to my argument. Society needs an applied science of environmental management. The reason it does not have one is that we have failed to build the foundation of predictive theory that applied research and technology require. Therefore, I repeat that ecology moves slowly because it lacks paradigmatic theories which would attract citation, direct research and sustain applied research and technology.

How can ecology merit support? I have sought to describe a situation in science and tried to minimize the value judgements that arise from evaluation. To the extent that I succeeded in avoiding these judgements, I have acted like most other ecologists. We appear unconcerned with our failure to provide theory.

I find it sad that we do not care. Society is better disposed towards ecologists than to other academic scientists. The public accepts that we need powerful ecological science, applied ecological research and ecological technology. Society is prepared to pay dearly for such research. Regrettably, ecologists seem to have turned their backs on this opportunity to merit support. At least one learned ecological society, the American Society of Limnology and Oceanography, actually voted not to allow applied research papers space in their journal, *Limnology and Oceanography*. The Ecological Society of America has established an applied journal, *Ecological Applications*, but at this early stage much of the material appearing there seems as academic as that in their established journals, *Ecology* and *Ecological Monographs*. This has also been the fate of the British Ecological Society's *Journal of Applied Ecology*.

It seems I cannot help myself. Even when I try to change the topic, I still end up diagnosing the ecological disease. Ecological science lacks general theories; worse, ecologists do not recognize that deficiency or the theories of low generality that they do have. I must complete the metaphor by suggesting treatment, and that is how I will finish. The cure is simply to begin making theories and testing predictions. The first step in this cure is to ask ourselves questions about how successful we are as scientists:

(1) What do we want to know?
(2) What predictions do current theories make?
(3) How can we improve old theories?
(4) What research is likely to provide new theories?

I do not know how we will answer these questions. I suspect that the last two are unanswerable because theory improvement requires creative insight. However, I believe that the exercise of groping for answers will help give ecologists the directions we presently lack. We will then be in a position to earn the support of society, to return our patrons' investment many times over, and to fulfil our moral obligations to humanity and to nature.

XIII Funding Decisions

> "The course I propose for the discovery of sciences is such as leaves but little to the acuteness and strengths of wits, but places all wits and understandings nearly on a level."
>
> Francis Bacon
> [*Novum Organum* (1621)]

> "Quite ordinary people can be good at science."
>
> Sir Peter Medawar
> [*The Limits of Science* (1984)]

The search for funds, the writing of proposals and the evaluation of grant requests by our peers are major elements in the lives of most contemporary scientists. A clear grasp of what science is and what scientists can do is an indispensable aid in all those processes. This chapter therefore applies lessons from my contemplation of science to the various facets of grantsmanship. It identifies the legitimate expectations one can have of research proposals, discusses the gamble involved in trying to fund scientific creativity, and warns against some current practices in science. The chapter ends with an extended analysis of multi-disciplinary team research as an example of how the granting agencies' misconceptions about science can make science more difficult.

The Central Problem for Research Funding

Basically, a grant proposal promises to do a certain set of tasks in return for a specified sum of money. The problem for the proponent is to describe future research so that its promise is great. For the panel, the problem is to determine which of all the promises it reads are most likely to succeed.

One of the first discoveries one makes as a part of peer review is that ecologists have been largely untouched by the last three hundred years of philosophy: philosophers showed long ago that the applicants cannot possibly keep many of the promises their applications make. We all need a better grasp of what research can and cannot do.

Some applicants imply that theories can be produced when required, like rabbits from a magician's hat. They promise that if given enough funds, they will make predictions about phenomena of immediate interest to society and resolve long-standing questions in science. The continual barrage of promises raises unjustifiable expectations in the public, administrators and legislators who need useful answers from scientists.

Other applicants seem to subscribe to the old belief that theories are produced by a logical process based on data collection, that theories can be verified by further observations, and that after sufficient verification, they will be accepted as true natural laws. This set of beliefs assumes that if we make the correct observations carefully and thoroughly, the facts will logically and inevitably lead us to discover true theory. Consequently, applicants believe that if they can promise to make new observations correctly, then they will also be able to derive, from these observations, a new theory that would generate predictions needed by society. David Hume, building on the earlier work of Locke, Berkeley and others, showed in the middle of the 18th century that this ancient belief is false.

We now know (to the extent that we can know anything) that a body of specific facts can never lead logically to more general statements, that logic cannot lead us to discover a new theory. Medawar (1984) called this idea the law of conservation of information: "No process of logical reasoning — no mere act of mind or computer-programmable operation can enlarge the information content of the axioms and premises or observations from which it proceeds." Instead, any body of facts can give rise to an infinite series of different theories (Chapter I). The competing theories must subsequently be winnowed and selected by scientific tests.

Scientific theories are a product of an inspired human mind via a process we neither understand nor control. We cannot promise to be inspired, and for that reason, scientists cannot design a project that is sure to produce a theory. Since no one can promise to be inspired, grant reviewers must be suspicious of any proposal built around an attempt to create a theory. Yet any granting panel finds application after application that proposes to do just this. Sometimes these proposals even merit funding.

Reasonable expectations from research. Scientists cannot promise to create a theory, but they can undertake other aspects of research where the product is fairly certain. Most of these are premised on the prior existence of some theory, because scientists use accepted theories as paradigms to direct their research effort. In the absence of theory, ecologists lack direction to do anything, and research flounders. For example, I believe that the current drifting of ecology reflects the non-existence of the theories ecologists want and their unwillingness to recognize the theories they have. The goal of this section is to show how theory structures research and research proposals, and its motive is to further stress the need for theory in everything scientists do.

Theory testing. If a theory is any good, it specifies certain observations as more likely to be observed under given conditions, and others as improbable. Our grant proposals can promise to test these predictions. A scientist can make this promise because the test merely involves gathering data specified in the theory. In this case, the reviewer can expect a clear exposition of the theory, the logical derivation of deductions from that theory, a statement of the observations that will be made, specification of what observations would be inconsistent with the theory, a description of the methods that will be used to make them, and a statement of the accuracy with which they will be made. If one or more of the specified, improbable events occurs in a series of tests, we are likely to reject the theory. If a predicted event occurs, our faith in that theory becomes stronger than our faith in competing theories. Theory testing is one scientific activity from which we can expect results.

Since I have repeatedly charged that ecological theories are flawed, unpredictive, unrecognized or non-existent, theory testing may seem irrelevant to ecology. This need not be so. All that is required is that the proponents elaborate the theory themselves before approaching the granting agency. In other words, we must think about what we are going to do before we do it. This is not a new paradigm for ecological research, because theory creation has always been an individual effort, but it does require that the proponent describe the theoretical prototype and render it interesting to the granting panel. It also requires that the panel and agency recognize the importance of funding research that is based on theory, even when the community cannot agree which theories constitute its paradigms.

Applied research. The preceding chapter defined applied research as a search for the potentially useful predictions of existing scientific theories. Scientists can justifiably propose to do an applied research project because, as I have defined it, applied research does not commit us to the production of new theory. Instead applied research tests existing theory within the limited framework of application to socially interesting problems. Neither are we committed to succeed if the existing theory is wrong.

Technology. Chapter XII also defined technology as the process of extracting maximal benefits from the successes of applied research. This definition does not preclude the possibility of technological advance on its own nor does it deny that at times science has developed in the wake of technological advance. However, I am concerned with designing projects in ecology and in that field, I believe technological projects will largely exploit the results of applied research. This again is suitable material for a project, because we do not have to invent new theories to succeed in technology. We merely have to find the best ways of applying those that already exist.

Surveillance monitoring. Monitoring involves the routine measurement of a set of predetermined variables. In surveillance monitoring, the variables to be measured are selected because they give a sensitive measure of the state of the system at minimum cost. This process of assessment should not be confused with research monitoring whose purpose is to discover relationships among the monitored variables, and so to develop new patterns and generalities.

Programs of surveillance monitoring require theory, but are not intended to test those theories. They involve simple fact-gathering and can therefore promise to deliver specified results (tables of measured values) within a specified time. These facts are empty by themselves, but the collection may be useful, because these facts may be used as "predictors" or "independent variables" in existing theories.

For example, mussel-watch programmes to detect phytotoxins in commercial mussels (*Mytilus edulis*) are a form of surveillance monitoring. In Canada, when ambient levels of toxin in commercial mussels reach the critical value of 20 $\mu g\ l^{-1}$, potentially contaminated shellfish are kept from market (Novaczek et al. 1992). Surveillance monitoring is needed because no accepted theory predicts phytotoxin concentration. The programme is still derived from theory, because only a theory can associate a given toxin level in shellfish with the poisoning of human consumers. Nevertheless, the monitoring programme is a form of technology not a test of theory, because we do not wait to see if the poisoning would actually occur. In other words, the theory is not tested, it simply directs sampling.

Surveillance monitoring is normally undertaken by consulting firms or government agencies, not by scientists. If possible, a programme monitors "primary variables", those that are of greatest interest to the society. For example, in eutrophication monitoring, primary variables may be greenness of the water, fish yield, water taste and odour. Since the primary variables are not always easy to measure — greenness varies in space and time, fish catch is influenced by human whims and accidents, taste and odour are hard to quantify — many monitoring programmes focus on "secondary variables". Secondary variables are related to the primary variables by theory, but are more easily measured ("simplifying secondary variables": e.g. Secchi disc depth), vary less ("integrating secondary variables": e.g. total phosphorus concentration, hypolimnetic oxygen content) or warn us that the primary variables that characterize the system are likely to change ("causal secondary variables”: e.g. the number of permits issued for logging or building in the catchment). There is also place for “confounding variables”, like temperature or solar radiation, that might obscure trends in the primary and secondary variables.

Monitoring programmes begin with a crucial decision about what should be measured, and any proposal for surveillance monitoring must include a reasoned defense of the variables selected. Since the only acceptable defense for surveillance is that the variables function in a theory to tell us something about the primary variables of interest, proposals for surveillance monitoring must specify the relevant theories.

Since ecology recognizes few relevant theories, many programmes of surveillance monitoring have not been well defined. As a result, they end in indefensibly large collections of almost whimsically selected variables. For example, I was once involved in developing a strategy to monitor eutrophication in the Great Lakes. As part of this process, three authoritative lists of potential variables were developed: one from the OECD eutrophication monitoring programme, one from G. Fred Lee, and one from Jack Vallentyne. These lists (Table 18, overleaf) each identify between 9 and 27 essential variables, and together include a total of 38 characteristics. The types of variables considered essential also differed. OECD listed a series of anions and cations, whereas Lee and Vallentyne ignored them all. Only Lee considered the various forms of phosphorus and nitrogen to be essential, and only Vallentyne recommended any measurements involving benthos or sediments. One may conclude that different authorities used different criteria to compile their lists, but these criteria were not made explicit.

The clearest implication of the discordance among the lists in Table 18 is that the more opinions sought, the more variables will be considered essential. Surveillance monitoring risks a thoughtless accretion of variables, and this is especially likely if the programme is developed by a committee. The only protection for the proponent and for the reviewer is to insist that all monitored variables be tied explicitly and tightly to theory.

How to gamble with research funds. Avenues of research that confidently promise scientific advance are premised on the existence of theory. For me, such ecological research is exciting because such a programme must contain a rare treasure, testable ecological theory. In contrast, research that is not premised on theory is almost indefensible.

Because ecology seems to lack theory, but obviously abounds with important fundamental and applied problems, scientists often propose to create new theory to address those problems. Any such proposal is a gamble, and if the reviewers and the agency administrators decide to fund such a proposal, they are gambling with research funds. The question I address in this section con-

Table 18. Variables thought to be essential (***) or desirable (*) measurements in a programme to monitor eutrophication of lakes, according to three authorities in the early to mid-1970's

	OECD	Lee	Vallentyne
Physical variables			
Temperature	***	***	
Conductivity	***	***	
Water colour	***		
Turbidity	*	*	
Secchi disc		***	***
Solar radiation	***		
Chemical variables			
pH	***	***	
Dissolved O_2	***	***	*
Total P	***	***	
Soluble P		***	
Soluble reactive P		***	
Total N	***		
Nitrate		***	
Ammonia		***	
Organic N		***	
SiO_2	***	***	
Alkalinity	***	***	
Acidity	***		
Ca	***		
Mg	***		
Na	***		
K	***		
SO_4	***		
Cl	***		
Total Fe	***		
H_2S	***		
Trace elements	*		
Nutrient load			***
Biological variables			
Chlorophyll *a*	***	***	***
Particulate organic C	***		
Primary production	***		
Algal dominants	***		***
Algal genera	*	***	
Zooplankton counts	*	***	
Benthic invertebrates			***
Sediment cores for:			
Pollen			***
Diatoms			***
Invertebrates			***

cerns the odds of the gamble. We know that a new theory cannot be guaranteed, but we can shorten the odds in its favour.

Empirical theory. When no brilliant insights are available, one way to shorten the odds against theoretical success is to develop the simplest kind of theory. These are empirical, interpolative or correlative theories, and are based on the identification, analysis and description of naturally occurring patterns in phenomena of interest: identify the variable of interest, describe the distribution of its values, and perhaps, explain some of this variation statistically by reference to other variables. This has been the universal path to theory in other sciences and is the one which granting agencies should preferentially support.

If the identification of appropriate dependent or independent variables seems a challenge, there are ways to identify likely possibilities. For example, one can test the applicability of an existing theory beyond established limits. We might extrapolate a regression beyond the data base on which it was built, as Dillon and Rigler (1974a) developed a general phosphorus-chlorophyll regression by applying Sakamoto's (1966) relation to non-Japanese lakes. Or we might attempt to adapt a theory built for one type of system to another type, as Smith et al. (1984) showed that phosphorus-chlorophyll response models developed for temperate lakes also apply in the sub-Arctic.

Another way to increase the likelihood of success in theory-building is to exploit possible homologies to existing theories. For example, one can be reasonably confident that most physiological rates will be affected by body size (Peters 1983, Calder 1984), so as yet uncorrelated autecological processes, like the rate of uptake of organic contaminants or the time to die from exposure to heavy metals, are likely to be predictable from body size. Because the effects of size are so conservative (Peters 1983, Calder 1984) we can even hypothesize that the exponents will be 0.75 for individual rates of uptake and 0.25 for physiological times. The homology can be less close: the widespread occurrence of resource limitation suggests that successful theories to predict biomass might well use resource level as a predictor (Peters 1991a); similarly, Keddy (1989) posits, on the basis of a small series of comparisons, that competitive relations will be most easily predicted by differences in competitor size.

The characteristic of all these relations and patterns is that they can be elaborated as concrete, testable theories with only a small amount of thought. Pattern identification is sufficiently easy that a rudimentary theory can be expected as part of the grant proposal, perhaps based on preliminary results or literature survey. If ecologists were satisfied with simple patterns as theories, we would recognize that our science already includes a vast corpus of theory and potential theory. If we recognized these relations for what they are, we would soon be led to theory-testing, the soundest basis for research proposals.

Research monitoring. At times, scientists may propose surveillance monitoring, but they are usually interested in more than simply gathering facts. They may believe that the facts will provide inspiration for a new theory; or they may want to make other measurements that involve little expense over and above the cost of surveillance. Scientists often wish to collect facts that were not previously known because they have a gut feeling those facts will be important, yet the only way they can afford to play their hunch is under the guise of surveillance monitoring. Such a proposal should be seriously considered, because the end result can be a more efficient use of research funds, but the lure of economy should not obscure the fact that this type of work promises to create theory. Research monitoring must be treated with the scepticism that risky research deserves.

Explanatory theory. There are also ways to increase the odds against creating theory. The most difficult thing a scientist can do is to develop a new explanatory theory, and the more general the theory the harder the task. Regrettably, the majority of ecologists would not be satisfied by seeking patterns in nature. They yearn to develop general, explanatory theories, and by trying to do so, they make their tasks vastly more difficult.

Because the demands of creating general explanatory theory are great, such theories are exceptionally rare. The few people who succeeded are revered as geniuses, like Newton, Einstein, Mendel and Darwin. Perhaps it is significant that in these particular cases, no proposal was written and the work was not publicly funded. Indeed, proposals to develop theories of high generality rarely come to granting agencies, and when they do, they are usually not funded. The gamble is too large and the pay-off too uncertain.

Science benefits immensely from genius, but researchers of such quality are too rare to be the basis of science policy. Heroes are not models for the common-or-garden variety of research proposal. Administrators since Francis Bacon (Eiseley 1973) have recognized that science policy must be designed for the best of the common scientists. The agencies hope to recognize and pamper genius if it appears, but they cannot found a policy premised on the existence of genius. Perhaps the best we can expect is enough funding for our leading scientists that the select few will find both the freedom and ability to create in this heroic sense.

Some realities of ecological research. Effective research can be designed to test an existing theory, to collect data so a theory may be applied, or to use existing theory in applied research and technology. All of these projects are premised on the existence of theory. We must also accept that, although no project can be designed to produce a new theory, we must find ways to fund scientists in the hope that some will succeed in creating a theory anyway. However, much of what grant applicants propose does not fit any of these research strategies.

Many scientists try to show how good existing theories are, and their proposals are therefore designed to corroborate, not test. These researchers are doing normal science (Kuhn 1962, 1970). Some ecological proposals adopt a similar strategy, even in the absence of theories. They focus on a topic that interests some sub-component of ecology (the 1991 index issue of *The American Naturalist* suggests these topics might include, among others, altruism, sex ratios, density dependence, food web connectivity, patch selection, polygyny, and philopatry) and strive to interpret associated phenomena in terms of the concepts and theories of their sub-subdiscipline. This methodology recalls Aristotle's search for circles in nature. Most such work is usually confirmatory and therefore serves to entrench ideas in the sub-subdiscipline. Such studies are among the least worthy of support. They strive to defend the status quo, rather than to improve the science.

The Dream of Multi-Disciplinary Environmental Science

Granting agencies have a necessarily close relation to the scientists they support. As a result, the proponents' misconceptions about the nature of ecology reappear among reviewers and agency representatives. However, because the agencies are so powerful in shaping science, the misconceptions of their agents can be particularly dangerous. Given that science continues to flourish, such agencies more or less succeed in their mandate, but whether this success is because of their interference or in spite of it is usually hard to judge.

Sometimes, agency initiatives are misplaced. One example of the latter is the decision to encourage multi-disciplinary research in environmental science. This initiative reveals a profound failure to appreciate the nature of science. Yet similar initiatives have been made by most agencies around the world.

The advantages of team research. I intend to criticize the emphasis on scientific research by multi-disciplinary teams as counter-productive in ecology, so let me begin by stressing that I am not criticizing team research in general, teams of researchers, or multi-disciplinary approaches to applied research and technology.

There are many projects for which teams are essential, and even more for which teams have proven useful and effective. Teams of researchers provide an economy of scale; two researchers may need no more spectrophotometers, scintillation counters, or chromatographs than one. Sympathetic colleagues provide support in ways ranging from helping to move the furniture to tempering a personal crisis in one member of the group. Such colleagues, working on more-or-less related fields, represent informal teams and are invaluable as sources of ideas, criticism, and information. I believe too that we should promote collegial teams so they become centres of excellence, not because team research is better than individual research or because teams are more productive than individuals (they are not; Cohen 1991), but because teams provide a context within which individual scientists are more likely to flourish (Chapter XI). It is appropriate to encourage research teams, provided this encouragement does not discourage the single researchers who have always been the source of most of the new ideas in science.

More coordinated teams are necessary when a single scientist is unable to test the predictions of existing theories, perhaps because the tests require too many data collected over too short an interval or too vast a scale. Such problems must be addressed by team research, but the teams need not be multidisciplinary. Indeed, the need for teams of workers who are interested in addressing the same problem would seem more likely to arise in single disciplines with strong central theories. Such theories will attract people to test the theory the group holds in common. Under this scenario, the requirement for team research is generated by the science. A funding agency should have policies in place to accommodate team research proposals as they arise, but this is very different from the current inclination to impose team research on sciences which are not ready for them.

Multi-disciplinary teams have repeatedly demonstrated their utility in applied research and technology. The Manhattan project and NASA are among the best examples. In those cases, the scientific problems were largely solved when the team was formed, but immense challenges remained in application and technology. The basic problem was to construct a mechanism along established principles that could perform a single well-specified job. Multi-disciplinary teams function well in attacking such questions. The mechanism can be reduced to its parts, farmed out among different experts for solution, and the many parts eventually assembled as the whole machine. The machine is then tested to see if the assemblage works. If some parts fail, they can be redeveloped by the appropriate teams. In summary, the success of multi-disciplinary projects demonstrates the advantages of the guiding theoretical structure in mature sciences, of the greater financial efficiency and camaraderie in teams of researchers, and of a specified goal in applied research.

The problems of multi-disciplinary research in ecology. I think it is fair to say that, although scientists need to be continually reminded of their shortcomings, some of us ecologists have been bitterly aware of ours for decades. We have tried to remedy the problem. Our most common response was probably to ask for more money, but another common response was to form multi-disciplinary teams to attack the problem.

Before I begin to tell my tale I must carefully define the type of ecological question that I am addressing. There are many types of ecological research, and I am discussing only one, the hardest and the most important. When we really run into trouble and where we have had the poorest record of success is in trying to forecast the effects of human disturbance on any ecosystem. The question we almost always fail to answer is "What will happen if...?" A good example of this type of question is the request for an impact statement: What will happen to the organisms in a given stream if a dam is built across it? or What will happen if a factory discharges its wastes into the stream?

Ecologists hailed the multi-disciplinary approach as a panacea for such questions. Now we have had enough experience to ask if it has lived up to expectation. I suggest that the multi-disciplinary approach has not been as successful as we hoped and that there are two reasons for its failure. First, these questions ask us to predict in areas where we lack explicit theory, and second they require that we use theories from many different scientific disciplines. Neither difficulty is addressed well by research teams.

Our failure to foresee environmental problems. I have said that we have proven unsuccessful at ecological forecasting, but I should explain myself. What I mean is that none of our major environmental problems was predicted. Instead of warning society that a problem would develop, ecologists have always had to tell society that a problem has developed. Here are a few examples.

(1) The eutrophication of our inland waters was documented, not predicted. Many of our lakes had already turned green at the surface and anaerobic at the bottom long before we decided whether phosphorus, nitrogen or carbon was the element limiting production in lakes.

(2) We condoned the use of DDT to control insect pests without predicting its bio-accumulation and bio-concentration, or its harmful effects on non-target species. We discovered the danger of DDT only when it had already driven several species towards extinction.

(3) We did not predict the accumulation of contaminants, like mercury or PCB's, in freshwater fishes. We discovered it only after contaminants had concentrated to dangerous levels.

(4) While ecologists in Canada were studying the problem of acidification near the nickel smelters at Sudbury, Ontario, just as they had a generation before at the Trail smelter in British Columbia, acid precipitation from coal-

fuelled generating plants all over eastern North America was quietly acidifying thousands of lakes from New York and Ontario through Québec to New Brunswick.

In each of these examples, ecologists performed a useful service to society, because we discovered the problem. However, in every case we failed to predict the problem before it arose. Since predictions arise from theories, we could only forecast such problems if we had a theory of ecosystem response. If no such theories exist, the most important task for concerned ecologists must be the creation of pertinent theories.

The scientific activity for which team research is least appropriate is the creation of new theory. This step depends on inspiration, and inspiration occurs inside a single human mind. A team cannot undertake to create a new theory. Indeed, since teams often act like committees, they may discourage creativity and new directions in research, by striving for consensus. Until ecology has theories that are general enough to interest many researchers, team research in ecology will largely be premature.

A false solution. The second reason that environmental forecasts are difficult is that the required general theory will almost always derive from existing theories of lesser generality from several scientific disciplines. The general theory can then be called multi-disciplinary. The flaw in our approach to such problems is that we assumed that the development of such theories required multi-disciplinary teams of uni-disciplinary individuals. The multi-disciplinary approach to ecology failed, as I think it had to fail, because that central assumption was erroneous.

We have very good reasons for thinking that progress in environmental science will be slow if we work within the boundaries of the traditional disciplines. Environmental problems never attended university, and therefore do not respect the conventional compartmentalization of scientific knowledge. For example, to predict the distribution and effects of air-borne contaminants, we probably need knowledge from chemical engineering, meteorology, atmospheric physics, phase, surface and inorganic chemistry, botany, soil science, hydrology, limnology, biochemistry, ecology and so on. Our mistake arises when we extend this argument to scientists and argue that to solve multi-disciplinary problems, we must assemble multi-disciplinary teams. That response was and is counter-productive.

Since we need new theories, we must depend on the individual scientist, and since the problems transcend conventional disciplines, we need individual scientists whose training and interests are similarly unconstrained. What we really need to solve such problems is a new breed of scientists, single "trans-disciplinary" creators whose breadth is such that they can cross traditional disciplinary boundaries.

The time-honoured solution. We have failed to produce predictive theories, and the institution of multi-disciplinary research teams has contributed to this failure. What is the alternative? To find this alternative, and to discover the flaw in the multi-disciplinary approach, I suggest you examine very carefully the history of the branch of science that you know best. When you do this, you will discover that major scientific progress has always taken place along a very well-defined pathway:

(1) Identify the class of systems under study.
(2) Observe the behaviour of these systems intact.
(3) Discover pattern and quantify it as empirical theory.
(4) Study the system components, probably by mechanistic dissection.
(5) Replace empirical theory with explanatory theory.

The important point for this discussion is that if successful sciences studied isolated components of their system at all, they did so only after they had achieved a theory. Successful scientists discover the regularities of their system before they try to explain them. Reductionist methods are used only in step 4 where they provide inspiration for step 5.

I should digress momentarily to say that although I may appear to be taking a hard line, I am actually middle-of-the-road. There are very strong arguments leading to the conclusion that it is never appropriate to study isolated subsystems (Peters 1991a), unless it is the behaviour of isolated subsystems that we want to predict. I went into these arguments in Chapter VII, but here I have taken a weaker position that is justified on historical grounds only.

What strategy is appropriate to ecology? Earlier I gave examples of our inability to predict environmental problems. We discovered them after the fact. This suggests to me that environmental science is at a very early stage. It has not yet produced an adequate set of empirical theories. If my conclusion is correct, we should concentrate our efforts at steps 1 and 2 in the sequence. We should attempt to define and classify the systems about which we need predictions. When this is done, we should study the behaviour of these systems. Perhaps then, we will produce the empirical patterns and theories required for further scientific advance.

Where does the multi-disciplinary approach lead? With these guidelines in mind let us now think about the multi-disciplinary team, and ask ourselves how it will approach multi-disciplinary problems. Experience shows that the multi-disciplinary group quickly decides to dissect the system and to study its fragments by the techniques appropriate to each discipline. For the physicist or chemist, this is the approach to which they have been conditioned. They come from advanced disciplines that are replete with highly explanatory theories. In these disciplines, the tradition of dissecting the system into smaller and smaller fragments is well established. They succeed to the extent that commonly held, general theories keep the whole enterprise together.

The ecologist in the team could be expected to act differently because general theories in ecology are almost non-existent. However, as I have argued previously, most ecologists reject the lessons of history. They have decided that because their systems are more complex than those studied by other sciences, ecologists must reverse the normal process of science. They begin at step 4. They are methodological reductionists, looking for an explanatory theory before they have discovered the regularities that need to be explained.

Because the members of the multi-disciplinary team tend to reductionism so does the team. In the extreme case, each member engages in reductionist studies aimed at furthering development of his or her discipline rather than in developing new theories for ecology.

This is the flaw in the multi-disciplinary approach.

Where do we go from here? Since I cannot end on this depressing note, I will suggest very briefly that there is a viable alternative to the multi-disciplinary approach. To develop an alternative, I think we must first accept that ecology and limnology are disciplines in their own right. They depend on theories of chemistry, physics and biology, but they are not merely an aggregation of these. Because the ecological sciences must predict about a different class of systems, their problems are different from the problems of the chemist, physicist and biologist.

Ecological solutions require a trans-disciplinary generation of scientists. We must learn to use the theories of the traditional academic disciplines as tools and to stop making their theories the object of our research. In addition, we must learn how to train new scientists as ecologists or environmentalists. They must realize that they are not physicists or biologists who were not fortunate enough to get a job in real science. They are scientists with primary allegiance to a different natural system. In other words, they must be trained to see their speciality as a science in its own right, not just as an applied appendage of some “real” science.

XIV Darwin and Evolutionary Science

"The amount of assumption and reasoning in a vicious circle involved in these [current evolutionary theories] renders it certain that none of them can long survive."

Sir William Dawson
[*Modern Ideas of Evolution* (1890)]

In this chapter, I want to show how an appreciation of science can help to interpret the history of our discipline, and conversely, how a knowledge of our history can help us to understand our science. I will begin by describing how Darwin's observations on the Galapagos may have allowed him to falsify competing theories of the origin of the species and so to develop his own theory based on that experience. My idea may be wrong, but I find that it makes Darwin and the Galapagos more interesting and vital than no idea at all. Having given Darwin some of his due as a scientist, I will then examine some critics of Darwin's theory to see if they are equally robust. The purpose of the exercise is to show that a grasp of the nature of science can clarify the context of our work.

Like other biologists, I have always admired Charles Darwin. I admire him because he dedicated decades of his life to an articulated series of studies involving different methods and organisms, all directed to the development of a coherent vision of the living world, because his experimental work was carefully considered and carefully done, because he saw further than the rest of us (Ghiselin 1969) and because he succeeded in science without abandoning either his family or his community. Nevertheless, I am dismayed because he is rarely treated with the respect and dignity that a scientist of his stature has earned.

Darwin is either deified by his followers or vilified by his foes. Both extremes are inappropriate. Darwin was one of the greatest scientists of all time, and his ideas should be treated accordingly. We do him greatest honour when we treat his ideas as instances of contemporary science, open to test, rejection and revision. If we elevate his writings to the level of sacred texts, we do him and his science as much insult as those who reject his views as inconsistent with a literal reading of the Bible. Science needs no dogma.

Darwin on the Galapagos

Biologists all know that while visiting this tiny archipelago over 150 years ago, Darwin made the observations that sent him reluctantly and inevitably along a path he had known about but previously avoided. The result of his subsequent labours was one of the few theoretical revolutions that biology has ever experienced. It was a revolution that changed our world view dramatically and irreversibly. The effects spread like a chain reaction, first through biology by precipitating new lines of research in comparative anatomy, comparative embryology, population genetics, etc. Subsequently, history, economics, ethics, metaphysics, sociology and even art and poetry were changed beyond recognition by new attitudes engendered by the theory of evolution by natural selection. All this started on Darwin's trip to the Galapagos!

The observations Darwin made must have been remarkable. But what were they? After asking yourself, ask some colleagues to see if they know what observations he made. If you and your colleagues are as well informed as I was when I first asked this question, the answers will be disappointing: "Didn't he observe finches with different beaks adapted to different foods?", or, "He saw the results of finches and turtles evolving to adapt themselves to new environments." Although such answers seem satisfactory on first inspection, a little thought shows us that they are not. If Darwin merely saw that the body parts of different animals were well suited to a function and to the habits of those animals he saw nothing new. No one in his time, or before, expected a lion to live on grass or a cow to be a carnivore. To tell us that Darwin saw the results of evolution through natural selection on the Galapagos is to phrase the answer in terms that were meaningless before his theory existed and to imply that the results of natural selection were not to be seen elsewhere in the world.

If our standard answers are unsatisfactory, where can we go to find better ones? Years of conditioning as students and teachers will probably send us to introductory biology texts. Here we will find more disappointment. By and large the texts give answers just like ours, although more detailed and accompanied by attractive illustrations. At least our own ignorance has been explained. The answer to my question was unknown when the text-books from which we learned our biology were written.

Why, then, were these answers either forgotten or undiscovered? The first reason I suggest is that we mostly subscribe to the old-fashioned "truth theory of science": all current theories are true, all discarded theories are false. And because of this we shy away from serious discussion of rejected theories. Consequently we were not taught, are not really interested in, and do not teach rejected theories or the reasons theories were rejected. Therefore the observations that led to the rejection of a theory are not significant to us. In this particular case however, there is another source of our difficulty and that is that Darwin never said what observations influenced him while on the Galapagos. All he gave were some pretty broad hints in his diary from the voyage of the 'Beagle'.

Because I believe the events leading up to the rejection of a theory are important in helping us to understand our science I will try to interpret Darwin's hints. To begin, we must know what theory or theories existed in Darwin's time. The old biblical theory of creation at a single time and place had been long abandoned, and two alternatives were competing for dominance. One, proposed by Lamarck, said that God created life with a built-in drive towards perfection. This force alone caused slow evolution, but the process was accelerated and often diverted by the environment. Thus, similar environments would produce similar species. The competing theory was proposed by Georges Cuvier, and Charles Darwin encountered a modified version of this theory in Lyell's geology text which he read during the voyage. This theory explained the known facts about fossils and animal distribution by postulating different centres and times of creation. It did not allow for production of new species by slow evolutionary change.

Now let us consider the Galapagos in the light of these two conflicting theories that formed Darwin's world view. He saw a group of islands that were obviously of volcanic origin and, unlike South America, obviously very recent because the lava streams showed no signs of erosion. He saw birds and plants that were peculiar to the islands, but similar to species he had seen in South America. Even more surprisingly, the species were unlike anything he had seen on the Cape Verde islands near Africa, despite the similar climates and geologies of the two archipelagoes.

Can we explain these facts in the light of Lyell's or Lamarck's theories? According to Lyell, the organisms of the Galapagos, being endemic, must have been created there. Since South America is ancient and the Galapagos were recent, they must have been populated by two separate acts of creation widely separated in time. If so, why would the Author of Nature, who creates species to suit the conditions they will encounter, create species for the Galapagos on the South American rather than the Cape Verde plan? The facts just do not make sense in relation to the theory and to our image of the Creator. Then let us follow Lamarck and see what he would predict if the Galapagos had been populated by migrants from South America that subsequently evolved to suit the conditions they found on the Galapagos. This is where the finches become relevant, because Darwin had seen one, and only one, species of finch living under incredibly diverse conditions all along the west coast of South America. Clearly this must have been the species that first colonized the Galapagos where it gave rise to eleven different species. But if species evolved to adapt to the conditions they encounter, why was there one species in South America and eleven in the climatically and geologically uniform Galapagos? Surely Lamarck's theory would have predicted just the opposite!

Now that we know the theories, we can see that the facts of the Galapagos seemed to contradict them. Of course, the facts did not force Darwin to postulate his theory, but they did send him on a quest that led eventually to his theory. How his thinking was led to ideas about natural selection is quite a different story that has nothing to do with the Galapagos. In fact, because that involved a creative step it may have no rational explanation at all, whereas the rejection of existing theories on the evidence is simply good science by a great scientist.

Critics of Darwin

McGill University, where I am writing these notes, is well known in evolutionary circles as one of the last outposts of anti-evolutionary thinking. The famous anti-Darwinist that gave us this reputation was William Dawson, principal of McGill from 1855 to 1897.

Dawson was a Nova Scotian who studied geology at the University of Edinburgh where he put up with the dull lectures much more willingly than Darwin. On return to Canada he began to publish geological articles and in 1855, his first book, *Acadian Geology*, was published. The McGill University Dawson took over that year was very different from the one where I work. It had 16 professors, but 15 of them were only on staff part-time. Dawson played a large part in making the university financially secure and building its early reputation. Sir William Dawson obviously did not find the job of establishing McGill very challenging because while doing this, he also delivered approximately 20 lectures a week on a variety of subjects, published a series of geological papers and books, and as a sideline, presumably to fill in his spare time, he tried to demolish Darwin's theory of evolution. And that explains how William Dawson wormed his way into this section of my book, which is not about Darwin, but about a cacophony of critics. I intend to examine the evolution of anti-evolutionists.

The first school: early emotionals. As I see it, there are four schools of anti-Darwinists. Dawson was a holotype of the first of these: the early emotionals. This group of Darwin's critics are easily recognized by their similarity to those Anglo-Saxon tourists who believe that everyone in the world can understand English provided it is spoken in a sufficiently loud voice. The early emotionals shouted their opposition rather than learning the language of their opponents.

The early emotionals were characterized by a clear idea of the way in which human beings should behave. They saw in Darwinism a dreadful new religion that would make us deviate even farther from the ideal behaviour. What Dawson opposed was the idea of a process that was not entirely and continually guided by a divine intelligence.

> If the universe is causeless and a product of fortuitous variation and selection, and if there is no design or final cause apparent in it, it becomes literally the enthronement of unreason, and can have no claims to the veneration or regard of an intelligent being. If man is merely an accidentally improved descendant of apes, his intuitions and decisions as to things unseen must be valueless and unfounded. Hence it is a lamentable fact that the greater part of evolutionist men of science openly discard all religious belief, and teach this unbelief to the multitude who cannot understand the process by which it is arrived at, but who readily appreciate the immoral results to which it leads in the struggle for existence or the stretching after material advantages. It is true that there may be a theistic form of evolution, but let it be observed that this is essentially distinct from Darwinism or Neo-Lamarckianism. It postulates a Creator, and regards the development of the universe as the development of His plans by secondary causes of His own institution. It necessarily admits design and final cause.
>
> (Dawson 1890)

Dawson tries to convert us, largely by emotional attacks like this, to show that the theory of evolution will have a short life and is already dying. Lest I be unfair to Dawson, let me acknowledge that he also had some scientific objections. He recognized, for example, that no case of transformation of species had been observed, that the theory did not account for the origin of sex, and that a mechanism was required to produce variance, but the only one postulated, inheritance of acquired characteristics, had been falsified by August Weisman. However the stronger element in Dawson's anti-Darwinism is the appeal to emotion.

Dawson was not a solitary representative of this school. He had some unusual allies, one of the most surprising being the dogmatic atheist George Bernard Shaw. Shaw hated evolution. He, like Dawson, had a vision of what the human race should be, and he saw evolutionary theory as something that opposed his lifelong battle to cure all of the social and intellectual sickness of mankind.

Shaw attacked Darwin on a number of occasions, the most vicious being in the preface to *Man and Superman* (1931).

> I really do not wish to be abusive; but when I think of these poor dullards, with their precarious hold of just that corner of evolution that a black-beetle can understand — with their retinue of twopenny-halfpenny Torquemadas wallowing in the infamies of the vivisector's laboratory, and solemnly offering us as epoch-making discoveries their demonstrations that dogs get weaker and die if you give them no food; that intense pain makes mice sweat; and that if you cut off a dog's leg the three-legged dog will have a four-legged puppy, I ask myself what spell has fallen on intelligent and humane men that they allow themselves to be imposed on by this rabble of dolts, blackguards, imposters, quacks, liars, and, worst of all, credulous conscientious fools. Better a thousand times Moses and Spurgeon [a then famous preacher] back again. After all, you cannot understand Moses without imagination nor Spurgeon without metaphysics; but you can be a thorough-going Neo-Darwinian without imagination, metaphysics, poetry, conscience, or decency. For "Natural Selection" has no moral significance: it deals with that part of evolution which has no purpose, no intelligence, and might more appropriately be called accidental selection, or better still, Unnatural Selection, since nothing is more unnatural than an accident. If it could be proved that the whole universe had been produced by such Selection, only fools and rascals could bear to live.

In the preface to *Back to Methuselah*, Shaw (1921) provided his longest attempt to discredit evolutionary theory. Here we see why Shaw hated it so much.

> There is a hideous fatalism about it, a ghastly and damnable reduction of beauty and intelligence, of strength and purpose, of honour and aspiration.

Shaw believed that the theory of evolution reduced human virtues to chance events. And what is wrong with chance events? Shaw says that if they rule us:

> What hope is there then of human improvement? According to the Neo-Darwinists [and] to the mechanists no hope whatever, because improvement can come only through some senseless accident, which must ... be presently wiped out by some other equally senseless accident.

Shaw also rustled up the odd scientific argument, but his main thrust was emotional. He ridiculed evolutionists and tried to defeat them by demonstrating his intellectual superiority.

Biologists withstood the attack. The early emotional school is now virtually dead. As expounded by fundamentalist Christians, it still serves a role in allowing novices in evolutionary theory a chance to fight against a weak foe, and so sharpen their intellectual teeth. If this opposition is often a match for us, it is a measure of the over-confidence scientists put in their positions and a warning about the need for thought and preparation of even a clear-cut case.

The second school: directional deists. The directional deists constitute a more formidable and organized opposition to Darwin than the early emotionals. This is because they not only bring a wider range of scientific objections to bear on Darwinian theory, but also because they are more constructive. They do not just destroy Darwinian theory. They provide an alternative.

This is essentially a French school of thought, derived from Lamarck's early theory. Lamarck postulated that when God created the earliest single-celled creatures, He built into them a directive force that influenced the direction of evolution. Thus evolution according to Lamarck is not a random, directionless process. There may be random elements in it caused by unusual interactions of a species with its environment, but the mainstream of evolution inexorably flowed towards a god-like creature: *Homo sapiens*. The three best-known directional deists are, in order of appearance, Henri Bergson, Pierre Lecomte de Noüy and Pierre Teilhard de Chardin.

The first of the three is particularly interesting. Bergson (1911) disliked evolution, not for its own sake, but because he thought it supported determinism. He wanted to believe that human beings have free choice. He disliked Darwinian evolution because he disliked deterministic philosophy and deterministic science. Bergson developed a whole battery of probabilistic arguments to show that the selection of random mutations was simply not powerful enough to cause the evolution of highly complex structures. He postulated the existence of an *élan vitale* that would drive evolution towards improvement.

The eye particularly fascinated Bergson. He argued that so complex and perfect a structure as the eye could not evolve by accumulation of chance mutations, because any mutation would make it less effective. Take this in conjunction with the fact that the eye and brain must evolve simultaneously and we are straining credulity. Finally, when we consider that similar eyes of great perfection evolved independently in vertebrates and in the scallop (*Pecten*), we realize the eye could not possibly have arisen by Neo-Darwinian evolution.

Bergson's criticism implies that the eye must be perfectly and fully formed if it is to function. But this is contrary to observation. Comparative anatomy provides us with a series of photo-receptors ranging from simple light sensitive cells to the complexities of a falcon's eye, all of which are functional and useful to their possessors. Similarly, we ought not be surprised that evolution in different lines should converge to one of a few solutions to the same physical problems: light sensitivity.

Bergson produced a series of impressive arguments of this type but they all had the same weakness. They were founded on totally non-quantitative statistics. Bergson was a master of the "logically-black-is-white-slide' (Flew 1975, Peters 1991a) whereby improbable becomes highly improbable and ultimately impossible.

Lecomte du Noüy (1947), a biochemist, made his contribution by overcoming this weakness of qualitative argument. He worked on the origin of life and demonstrated — to his own satisfaction — that for a single protein molecule to have originated by chance, within the lifespan of our universe, we would have needed a universe entirely made of amino acids, 10^{19} light years in diameter. He also developed an argument from the second law of thermodynamics to the effect that because the universe tends to disorder, evolution to greater order is impossible.

Both of du Noüy's objections now seem easy to dismiss. Arguments about the probability of an observed event depend on the null model one has in mind; whether an event seems probable or not depends on the selected model. We need only posit rules for the assembly and duration of amino acids to make the events that are improbable to du Noüy probable to an evolutionist, and there is now experimental evidence that the latter position is more correct. Similarly, no one is any longer puzzled by local increases in complexity in parts of an open system like the biosphere: the solar system is tending to greater entropy and the biosphere simply slows this flux temporarily. Biological complexity is an eddy in the heat death of the universe.

Finally, Teilhard de Chardin (1955, 1959) does not attack the old, but creates anew. For Bergson's *élan vitale*, he substitutes a universal mind-substance that has God-given tendency to coalesce. Evolution is proceeding to "point Omega" when all the mind in the universe will coalesce in perfect unity with the mind of God. Needless to say, we have not reached point Omega yet, but it does provide a goal for the universe, and that is apparently a bodily need for this school of critics. They are vitalists who introduce an unobservable into science and thereby make the universe more understandable, but no more predictable.

The third school: cataclysmic creationists. The catastrophists have a long honourable lineage that can be traced back to Buffon and Cuvier. Their argument is that there has not been enough time for Darwinian evolution to produce the vast array of highly perfected species we see on earth. To speed up the process, they postulate a series of cataclysmic events that eliminated most existing species, followed by either a new supernatural act of creation or a sudden evolutionary spurt.

The most esteemed of the cataclysmic creationists was Louis Agassiz. Agassiz, like Dawson, was a geologist and a powerful academic. He is best known as an advocate of the theory of the ice age and as a teacher at Harvard University.

Agassiz argued until he died that the facts falsified evolutionary theory and fitted special creation. He believed that God had created four distinct groups of animals at the beginning: chordates, molluscs, articulates and vertebrates. Agassiz (1859) held that these four groups have no anatomical similarities and thus offer no evidence of evolutionary connections. And as God creates new species, he always follows one of these four basic plans. Since the four coexist everywhere, the effect of environment on animals must be negligible.

A more recent cataclysmic creationist is Immanuel Velikovsky. He is distinct from all other cataclysmic creationists in that God is missing from his scheme. Velikovsky's cataclysms were produced by natural events. Briefly, he believed that planetary near-collisions so dislocated the earth that the conditions of life on earth changed dramatically and instantaneously (Chapter III). These changes caused mass extinctions, but instead of postulating supernatural acts of creation, Velikovsky postulated that the great heat and intense radiation associated with his cataclysms would cause multiple mutations and instantaneous formation of new species. Unfortunately, Velikovsky's genetic ideas are presented so summarily that it is not clear how these new species arise.

Although they differ greatly in matters of detail, the catastrophists agree on one point: they reject uniformitarianism, and hold that we cannot explain the facts of life unless we postulate the existence of unobserved phenomena such as world-wide cataclysmic events. This school has perhaps gained new respectability in the last decade or so, because paleontologists are increasingly willing to entertain the idea of catastrophes and variable evolutionary rates. However, contemporary ideas about catastrophes require no fundamental change on the part of the scientific community and have been incorporated into evolutionary thought relatively easily. They differ from their predecessors in using the full scope of geological time and so need no recourse to special creation or novel causes of evolutionary change.

The fourth school: Popperian purists. The last group of critics of evolutionary theory are a strangely schizophrenic lot because they do not reject evolutionary theory. Neither do they try to replace it with another theory. Deep in their hearts they believe in evolutionary theory as if it were a truth.

Let me describe these Popperian purists to you. Their name comes from their prophet: Sir Karl Popper, a philosopher of science. He is largely responsible for convincing us that we cannot verify a theory; we can only falsify it. Thus Popper holds that science progresses by discovering mistakes and correcting them, not by establishing truths. Scientists do this by testing the predictions of their theories. It is a corollary of this view that theories are rated not by their truth value, but by the richness of their predictions. A good theory makes many predictions about different categories of facts and consequently offers us many opportunities to falsify it. A poor theory makes predictions about a small body of facts. If a statement makes no predictions, it is not a theory at all.

To look at Popper's arguments another way, what a scientific theory really tells us is that, given present circumstances and knowledge, one or more specifiable states will not be observed. The best theory rules out all but one future observation. It is easily falsified. The worst theory rules out no future state; so whatever happens is consistent with the theory. Nothing can falsify such a bad theory.

I can illustrate these differences with a simple example. The theory that "on April 1, the sun rose at 7:06 AM south-east of Montreal" is a good theory. The theory that "the sun rose on April 1" is less good. And the theory that "either the sun rose sometime in an unspecified direction from somewhere, or it did not" is such a bad theory that it is no theory at all. The Popperian purist judges a theory only by its value as a predictive tool. I have purposely set this example in the past to stress that the theory predicts an unknown state, not simply a future state. And I have chosen this familiar example to stress that the knowledge we gain is personal knowledge, not just the realization that someone else knows the answer. Alternatively one may say that the future which a theory predicts is the future state of our knowledge.

Not all Popperian purists are anti-evolutionists. Those who are believe that the theory of natural selection is no theory at all because it makes no predictions that we can falsify. Most are not so extreme. They are like the agnostic who is desperate to believe, but argues against the existence of God in the hope that someone will provide the conclusive evidence that She exists. They argue against the theory of evolution by natural selection, but hope that their argument will one day attract an evolutionist who can conclusively demonstrate that the theory makes falsifiable predictions. This is my position.

I claim to be a Popperian purist, but I am very close to agnosticism. My childhood conditioning and undergraduate training were so effective that in the innermost, animal reaches of my brain, where there is no science, there is the knowledge that the theory of evolution by natural selection is true. Unfortunately, I cannot show this to be so.

Two other biological schools. There are other kinds of biologists. Biological historicists see science as a narrative describing the sequence of causal events that preceded any observation, and the true chronicle of events that preceded the present on earth. They are fascinated by evolution, but are more interested in explaining past observations than predicting new ones. If they acknowledge the importance of prediction at all, it is to justify the explanation they have already developed.

A sixth group of biologists I will call the heurists. They see science as a way to inspire themselves to create more theories or to realize a unity with nature that they call understanding. For example, many Darwinians and Neo-Darwinians try to re-trace the thoughts of their name-sake. They hope that this vicarious recreation of Darwin's mind will inspire them to similar understanding and creativity. If heurists accept that prediction is important, it is because they see prediction as a useful way of warranting their understanding. If their understanding is sound, it should lead to predictive success, but whether that prediction helps us gain control over our lives is incidental.

Conclusions

What is the message of this re-examination of old arguments and observations? In part, it serves to remind the reader of a tradition of anti-Darwinism that dates back to the last century, and to suggest that not all of this resistance is rooted in fundamentalist dogma. There are alternative ways of viewing science. A university program in biology should offer a wide assortment of historicists, heurists, and Popperian Purists. The student would then have the opportunity to sample all points of view, and come out of the system behaving more like a scientist than like a Pavlovian dog. I hope these students, better trained and more aware than I was, will think more about the nature of science than I did, and so avoid the slavish conditioning that still restricts my thought.

XV Is The Future Grim?

> "A man's reach should exceed his grasp, else
> what's a heaven for?"
>
> Robert Browning
> [*Andrea del Sarto* (1855)]

For most university biologists, science remains a glorious entertainment. For them, calls to change or to rethink the foundations of research seem unnecessary. After all, they can pursue their profession in the same way as their predecessors, earn a decent wage, enjoy the respect of their peers, and sometimes make a contribution towards the sum of human happiness. Most of us want little more.

This chapter suggests that, pleasant as a life in science may have been, those who imagine it will not change are living in a fool's paradise. I believe that society feels the time has come to change the university. If university scientists were to think about science, we too would see that a change is in store. If professors do not lead the way in this process, society may force us to accept changes that are both more onerous and less productive.

Any imposed change threatens our ideals as professors. These are to master the current ideas of humanity, to contribute our own ideas to this precious store, and to disseminate both. There is little else that justifies our place in society. Indeed, because ideas are the most lasting of human accomplishments, there may be nothing else that matters in life, but ideas. University staff are therefore in a rarely privileged position. We are the pampered guardians of the intellectual traditions of humanity.

The best ideas in science are theories. Thus our efforts as university scientists are directed to the assessment of existing theories and the production of new ones. As idealists, we should encourage changes that favour theory, but inflexibly oppose any change that makes theorizing more difficult. Any changes to the university should be intended to produce, in our lives and in the lives of our graduate students, the conditions that are most conducive to theory-making and theory-testing.

The Gilt Age of University Research

After World War II, an awe-struck society held an unrealistically exaggerated view of the collective prowess of its scientists. Science, particularly the pure science of the universities, was touted as a panacea. University scientists were consulted on all important matters, quoted in the press, invited to advise governments, and raised up in the social hierarchy. During this period, we discovered a social conscience. Staff lectured to schools, associations and politicians. We joined extra-mural committees and spent time consulting with industry or working on government commissions.

The postwar enthusiasm for universities convinced us of our greatness. It convinced us that we could be all things to all people and that in us alone lay the power and knowledge to save the world. We would solve practical problems, teach everything to the new generations and preach to the community at large. We would discover truth, and our success would demonstrate the superiority of intellect over materialism. These beliefs made every two-bit department aspire to greatness.

Not only were we wooed rapidly into accepting society's inflated opinion of universities, but we also convinced ourselves that these remarkable powers would, if provided with the proper nourishment and exercise, continue to grow. Young turks dismissed the aging scholars in cluttered labs as irrelevant. They talked not of a science they loved, but of developing excellence, importing eminence, capturing the very best of the young Ph.D.'s, and building inter-disciplinary teams. We ridiculed the short-sighted granting agencies that did no more than keep us salivating with slow infusions of thin gruel, and were encouraged to seek new, more generous sources. We pressured the library for our share of new journals and symposia volumes, and the university for new buildings and research facilities. At one time, we even put six graduate students in the space designed for three.

Meanwhile, growth of the university and the egocentricity of its staff caused committees to proliferate and administrative duties to become more onerous. Within my department alone over twenty committees flourished. I could go on to recount our forays into big science and our discovery of multi-disciplinary institutes, but these stories are familiar. We had the money and time to do more and more, and we did. All these extra duties left little time for reading. To keep up with science we became world travellers, attending scientific gatherings at up to three exotic places a year.

The Gathering Challenge to University Science

Adulation, like power, corrupts. Our particular form of corruption was that we came to believe what the newspapers said about us. We could do anything provided we had enough money. The money came (we could and did say even that was not enough), the years passed, but we did not produce the promised successes. Our disillusioned bride realized our failure first and now we too suspect the truth. We had not fully recognized our limitations.

The postwar honeymoon of the university and the public was primarily due to the widespread belief that a university degree was the surest key to the good life for society and personal success for the individual. Student activism, devaluation of the degree designation by mass education, and then economic realities destroyed that faith; and a more realistic evaluation of the material value of university degrees has decreased teaching allocations. A second problem for university science is a growing suspicion that much of the work scientists define as important is actually irrelevant and that useful scientific output per dollar may be unrelated to the dollars per scientist. Governments have already reacted to these changes by reducing support for universities.

I doubt that our modern troubles arose simply because society sometimes wavers in its support for science. Sometimes, society adopts new patterns. I think the latter is happening now. Society has permanently changed its attitude to universities, and that changing temper of society will inevitably change the conditions of university science. The new trend is not a local Canadian problem. It permeates the United States, Britain, Germany and other nations because it reflects a fundamental limitation of resources. As new patterns form in society, some old institutions suffer. I fear the university is due for a little suffering.

We should expect our budgets to become still less generous. Science has grown exponentially since the 17th century. Its doubling time is about 10 to 15 years, twice as fast as the economy and three or four times faster than the population of North America and Europe (Chapter I; Price 1986). This can only be a temporary situation. Eventually, the growth rate of science must decrease until it comes into line with the economy and the population. Although we cannot predict the final share of society's resources and personnel that science can expect, this decrease must make itself felt sometime within the next 100 years. By then, extrapolation of historical rates of growth show that science would be as large as the economy and that the population of scientists would exceed the number of people (Price 1986). This Malthusian argument against the continuing unrestricted growth of science, compounded by the disillusionment of society with university science, leads me to suppose that the financial pinch in which we now find ourselves is no temporary correction. It is a permanent change.

Since we can expect further belt-tightening, 'Science Policy' will continue to evolve in its present direction. We ought to expect more economic restraint, not a return to opulence. Tighter control over research monies means these monies will be redirected from universities to government agencies where costs and research can be better controlled. Even more emphasis will be placed on contract work, industrial and government partnerships, and on group research into subjects of direct interest to government agencies. There will be less call for independent theory-making, and pure research by university staff will be further downgraded. Graduate students, who now perform the bulk of university research, will be less in demand and many of those who do enter graduate school will work on applied research, not science. If this scenario is even approximately correct, the attitudes we have fostered over the last 50 years may have to be abolished.

University Responses

We professors must respond to government and societal penny-pinching. But how? Should we spend more time in public relations, shouting our praises? Should we lobby for a larger share of the tax revenues? Should we try to convince the appropriate agencies that because our particular university is better than others, it needs a bigger share of the budget for post-secondary education?

Before we spring to the accustomed defensive position of every privileged minority, we should ask whether or not this reduction in status and financial support really will decrease our ability to do good science. I think it could, but only if we respond inappropriately. I also think it has given us the opportunity to re-evaluate ourselves and to do better science.

I had six years experience with big science while directing the Char Lake Project which was but a trivial part of the massive International Biological Program. This experience convinced me that big money makes administrators of scientists and produces data but not ideas. I believe that big science restricts, rather than expands, our mental horizons. In our university role, we should exercise our talents to produce ideas, not harassed executives.

An inappropriate response to shrinking budgets will simply dissipate our energies striving for funds to maintain our research budgets and defending our own area in frantic turf wars with other researchers. If I thought that spirited defense of our present position would succeed and that success would help us achieve our ideals, I would counsel battle. But we would not succeed. Battles must sometimes be fought, but one should always avoid a battle when the outcome will be disastrous. There is no gain for us in a protracted defense of the big science we have come to practice.

Even if we fought and won a momentary respite, I am uncertain that a return to fat budgets and more-of-the-same would achieve our ideals. The universities could perhaps find a new functional role for themselves that would justify a bigger share of the pie, but our concern is to protect our old role, the preservation and development of ideas, not to acquire new duties. And in any case, the Malthusian restriction, that we cannot indefinitely grow faster than our resources, would make itself felt again in short order.

My colleagues and I already spend our days and nights racing to keep up to our image of what a scientist should be. We cannot fight harder, indeed most of us have already compromised ourselves by trying to do too much. Deep down, we know we are frauds (Medawar 1990). University scientists are simply normal men and women doing our best to keep our heads above the flood of duties, demands and interests that only a superman could do well, but afraid to admit that we can only do them badly. Perhaps we will offer a secret sigh of relief if society takes away our Captain Marvel cloaks and forces us to consider where we go from here.

The cure I recommend involves no genius, no technological breakthroughs, nor any other mythical unicorn horn. It is simply the ecological solution that we must learn to live with less: less waste, less heat, less inefficiency and less ineffectiveness, but not with fewer ideals or fewer ideas. We should seek out any change that will lower our aspirations until they come within shouting range of our abilities. I simply recommend that we return to our ideals.

A Policy for the Future: Closing the Aspiration Gap

There is now so large a gap between what we can do and what we are expected to do that a sense of frustration and impotency is inevitable. A gap may be essential, but a chasm is counter-productive. I suggest that we determine what it is we must do and try to find the most efficient way to achieve those ends. To do so, we must sacrifice many of the trappings we have accumulated in the last generation, but we need not compromise our effectiveness in learning, teaching and developing theory. All of my recommendations are therefore intended to produce more uninterrupted time for thought and research without spoiling our teaching efforts.

Undergraduate teaching. The equilibrium between teaching and research is unstable, so there can be no optimum balance between these two critical activities of a university professor. Nevertheless, we must recognize that we are paid to teach, and that everything else is largely self-imposed. In keeping with our loss of prestige, we can expect society to stress the importance of undergraduate teaching. Since there will be no decrease in student numbers, no increase in staff, and continued demands for good teaching, we must make our teaching much more efficient and effective.

Equalize teaching loads. Assuming that a happy teacher is a better teacher, we should equalize teaching loads. This will make teachers happy because the greatest source of friction in most departments is the perceived inequality of the commitments of various colleagues to the burden of undergraduate instruction. The reassignment of teaching loads must be done without reference to outside duties, to the number of pages of print we produce annually, or to the number of graduate students we train. The workload should be evenly distributed. This will protect those who enter the system in the future from being pushed into too much teaching, but it will also help to close the aspiration gap by impressing us with the fact that we are here as teachers and we should not be rewarded for other activities by having our teaching load reduced.

Abolish tenure. It is a corollary of the central role of teaching in university life that we should be judged as teachers and that useless teachers should be dismissed. This freedom can only be achieved if we abolish tenured positions. I see no virtue in cut-throat competition, so some alternatives to throwing our colleagues into the street must be found. Perhaps those who fail as teachers too late in life to find another job could be transferred to administrative posts.

Tenure is widely applauded as a bastion protecting those whose views challenge authority. Thus, the abolition of tenure is abhorred because it would leave the most precious members of the community open to arbitrary dismissal. The protection of deadwood is seen as the cost of academic freedom. This defense seems disingenuous: professors with unpopular views have never been well defended by tenure, because university and state administrations have too often buckled to public pressure. Tenure really protects incompetence.

The end of tenure will impress on us the fact that we are ordinary mortals, not above judgement. It will also make it easier for new staff to become good teachers, because they will justifiably devote more time to preparation for teaching. Neither will they have to do research in desperate haste to achieve the number of publications demanded by tenure committees. They can do it because they enjoy it.

Reduce course offerings. The equalization of teaching loads could stifle research, unless we are careful to contain the total teaching burden. Therefore I recommend that we reduce the number of course offerings by pooling specialized courses and allowing students more freedom of choice among courses and subject matter. This reduction would be facilitated by eliminating labs from many courses, and limiting the number of lecture hours, thus giving students more time for independent work.

We should also eliminate all courses with less than 10 to 30 students. The cut-off is arbitrary but a minimum class-size acknowledges that small courses waste money and professorial time. If offered at all, they should be offered only every other or every third year. Small, specialized courses are in demand by staff who see in them the opportunity to study their own speciality in even more detail and to teach an easy subject. They are defended as a device to attract graduate students, but obviously this is not so. If it were, enrolments would be larger.

Reduce teaching burdens. To make our work as efficient as possible, we should eliminate or at least limit the mind-numbing chores that seem so much a part of university teaching. We should exploit the multi-media approach, the computer and any other approach or device that will eliminate repetition of lectures and hand-marking of anything over 100 identical examinations in a week or two by one professor. Our objective should be to make teaching large classes an enjoyable job.

Graduate training. Graduate education is also one of our primary duties. I have de-emphasized it in my considerations because graduate education will be less important in the university science of the future. Decreased budgets, increased emphasis on undergraduate education and the de-emphasis of independent research will relieve us of the obligation we once felt to increase our graduate training programme. Indeed, a slower rate of growth of science will mean that our graduate training programmes will have to be curtailed. Professors will therefore have more time and will be able to do the work themselves.

To encourage this curtailment, we should institute a policy that will protect us from our own inability to refuse good applicants. Even good graduates cost money and thus distract professors from research by sending them out looking for more or bigger research grants. Weak students do this, and also demand even more professorial time in training.

Scholarship. Scholarship is what we modestly call “our own work”. My schemes are intended to make it possible for us to do and enjoy our own work in the coming university environment. We must find ways to avoid the busy work that cuts us off from research.

For example, the telephone is probably the single greatest obstruction to scholarship and meaningful intercourse amongst staff. I would remove all telephones from professors’ offices, although I would not prohibit graduate students or staff from renting their own. Fax machines and E-mail are similarly invasive.

The mobility of big science also robs us of the calm we need to think and to develop theory by bringing us colleagues and visiting lecturers who themselves dedicate days of their time to deliver an hour's lecture. Too often, that lecture is appreciated by only a tiny fraction of the audience. The rest are there only to hold up the side, or as a courtesy to the visitor. This is clearly inefficient. All visiting lecturers and seminars should be aimed at undergraduates first and graduates second, since students more frequently are the people with the time to listen to and the minds to learn from visitors.

Inter-disciplinary institutes are also devices to sabotage meaningful research. They are based on a flawed model of our needs and abilities (Chapter XIII) and they lock the individual into the narrow confines of his or her speciality as one element in a systems approach (Chapter VIII). If one wishes to develop one's own ideas in science, one must not start such institutes or participate in their programmes.

Staff members should be actively discouraged from seeking large research grants. They might, for example, be asked to justify their proposals in terms of their ideals to the department staff. Large research grants increase the output of data, but spending money is such a time-consuming occupation that it can reduce the quality of research. The danger will increase in the future because the evolving science policy will mean that when we get large grants, we will be required to conduct research programs designed more by others than by ourselves. All of this is obviously anathema to our ideals as professors.

Administration. Administration presents a problem for which I have no solution. At the departmental level, we have some control over the amount of administrative busy-work we impose on ourselves, but we have none over the university as a whole. Thus, university committees and commissions will continue to propagate regardless of our attitude toward them. Furthermore, we will be expected to serve on them.

My limited experience with these activities is that they waste a great deal of time. They are unnecessarily protracted by aspiring administrators who cannot bear the thought of disappearing back into the obscurity of their own office, whereas any professor worthy of the name should be eager to return to the lab or office to pursue his or her ideas. Although we cannot escape the feeling of obligation to contribute our minimal share towards the running of the university, it would probably function just as well if we were to opt out.

Perhaps there is nothing we can do about this impediment to teaching and scholarship, but we should disabuse ourselves of the belief that active participation in university affairs is a virtue. Certainly, administrative duties should be irrelevant to advancement and job security at the university.

Two reservations. What I have tried to say is that for almost half a century, we have been obsessed with a chimera: we have tried to achieve better science with grantsmanship instead of scholarship. I have made entirely reasonable suggestions like these in the past and been surprised that they were not universally accepted. My listeners instead suggested that such changes could undermine science by setting such low goals that researchers would cease to strive for new ideas and become apathetic towards science. We would return to a tweedy and unproductive past. From these objections, I can only infer that my cloudy literary style can obscure the dazzling brilliance of my ideas. Therefore, I will end with a brief rebuttal of those suggestions.

A formula for apathy? There is a widespread belief that because we have an animal need to strive, it would be undesirable for us to reach our ideals. This fear is now particularly acute, because apathy is the disease of the age. It is not my position that we should stop striving. That would merely aggravate the situation and produce more apathy. The modesty of my proposals could inadvertently discourage some scientists and prevent them from trying to improve, but that is not my intent.

Unlike Browning's Andrea del Sarto, I believe it is more frustrating to attempt the impossible than to set our goals so low that we can actually reach some of them. If we actually did achieve our modest goals, we would not be finished as scientists. Success would stimulate, not inhibit us.

The goals of a scientist are like those of the exhausted traveller. It is not the end of the journey, but the next tree or stone that remains the goal. This is the view of science propagated by 20th century philosophers like Sir Karl Popper and historians of science like T. S. Kuhn (Chapter III). We never reach an ultimate truth. We merely continue to elaborate and change our ideas as we progress, not to a lasting goal, but farther and farther away from our primitive, fumbling beginnings. Thus I think we can be both realistic and idealistic. By combining the two, we will stimulate not inhibit scientific excitement.

A step back? For some, my suggestions represent a step back to some lower rung of the evolutionary ladder of science, but that applies only for some unessential aspects of research. I am looking back or down only if it is retrogressive to emphasize doing science rather than chasing research dollars. For a generation, university scientists aspired to greatness, and almost destroyed themselves. Individuals competed, unified departments fragmented, and some of us discovered that university life was no longer pleasant. In this sense, I hope my solutions are retrogressive.

I want to escape what the modern university has become. However, I am not prepared to return to mindless, unchallenging research that grubs for new facts or defends favourite theories from scientific scrutiny. The opportunity that social change offers us is not a return to the trifling puzzles of the past, but the chance to consider what we have done, what we are doing, and what we should do. If we can escape from the trap of our own self-image, we can begin to contemplate science.

Conclusion

Big science and societal power have caused professors to lose track of their ideals and goals. In doing so, they have almost destroyed the university as an intellectual retreat. When I begin to hear more staff members whistling in the corridors or humming in their labs, I will be content that we have come into a happier equilibrium with reality. Under these conditions we will not only be able to do more effective research, but we will also discharge our duty to society. We will pass on the tradition that intellectual activity is more exciting than material consumption. We will have learned to contemplate science.

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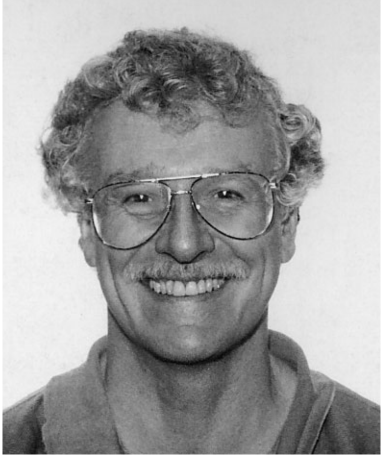
About the Author and the Book

Professor Robert H. Peters is the winner of the ECOLOGY INSTITUTE PRIZE 1991 in limnetic ecology. Born in 1946 in Toronto, Canada, he obtained his Ph.D. in 1972 from the University of Toronto under the supervision of Frank H. Rigler, a major figure in limnology, who died much too early, leaving behind a host of important work and thought. In his EE book, Peters presents highlights of Rigler's unpublished notes and ideas and combines them masterfully with his own accomplishments and expertise.



Robert H. Peters

Chaired by Professor Jürgen Overbeck (Max-Planck-Institut für Limnologie, Plön, Germany) the ECI Jury selected Rob Peters for his work on phosphorus cycling in lakes, which provides examples of excellent research and illuminates important insights into the measurement and availability of phosphorus in aquatic systems.

This book reaches far into the realms of science history, philosophy and methodology, the significance of science for society, and the research and teaching in universities. It documents that ecologists have collected impressive amounts of observations and facts, but that they have failed to sufficiently identify and formulate theories which go beyond the facts — theories that can be tested and that can predict.

About the Ecology Institute (ECI)*

The international ECI is a not-for-profit organization of research ecologists. Director and scientific staff — 52 marine, terrestrial and limnetic ecologists of outstanding professional reputation — strive to honor excellence in ecological research; to further the exchange among marine, terrestrial and limnetic ecologists; to promote advancement in environmental sciences; and to bridge the gap between ecological science and its application for the benefit of nature and society.

In order to approach these goals the ECI annually sets out two international prizes, the ECI and IRPE (International Recognition of Professional Excellence) Prize, and it supports — via the Otto Kinne Foundation (OKF) — promising young environmental scientists in Eastern European countries by providing financial assistance for professional travel, scientific equipment or published information. Each ECI Prize Laureate is requested to author a book taking into account ECI's aims. The book is published in the series "Excellence in Ecology" and made available worldwide at cost price; a considerable number of books are donated to libraries in Third-World countries. In this way leading ecologists are offered the possibility of disseminating their personal views on current ecological issues and of serving the general public who depend acutely on definitive ecological knowledge for planning our present and future.

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