EXCELLENCE IN ECOLOGY

7

O. Kinne, Editor

David H. Cushing

Towards A Science of Recruitment in Fish Populations

Published 1996 by
Ecology Institute, D-21385 Oldendorf/Luhe
Germany

EXCELLENCE IN ECOLOGY

OTTO KINNE
Editor

7

David H. Cushing

TOWARDS A SCIENCE OF RECRUITMENT IN FISH POPULATIONS

Introduction (Otto Kinne)

David H. Cushing: A Laudatio
(John D. Costlow)

7

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

David H. Cushing

198 Yarmouth Rd.
Lowestoft
Suffolk NR32 4AB
United Kingdom

ISSN 0932-2205

Printed in Germany
Typesetting by Ecology Institute, Oldendorf
Printing and bookbinding by Westholsteinische Verlagsdruckerei Boyens & Co., Heide
Printed on acid-free paper

Contents

Introduction

Otto Kinne

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

This introduction addresses essential messages of David Cushing's book. It then refers to the aims, activities and awards of the Ecology Institute, and lists ECI prize winners and OKF Fellows. Finally it presents the names of the 1996 ECI staff, and OKF trustees.

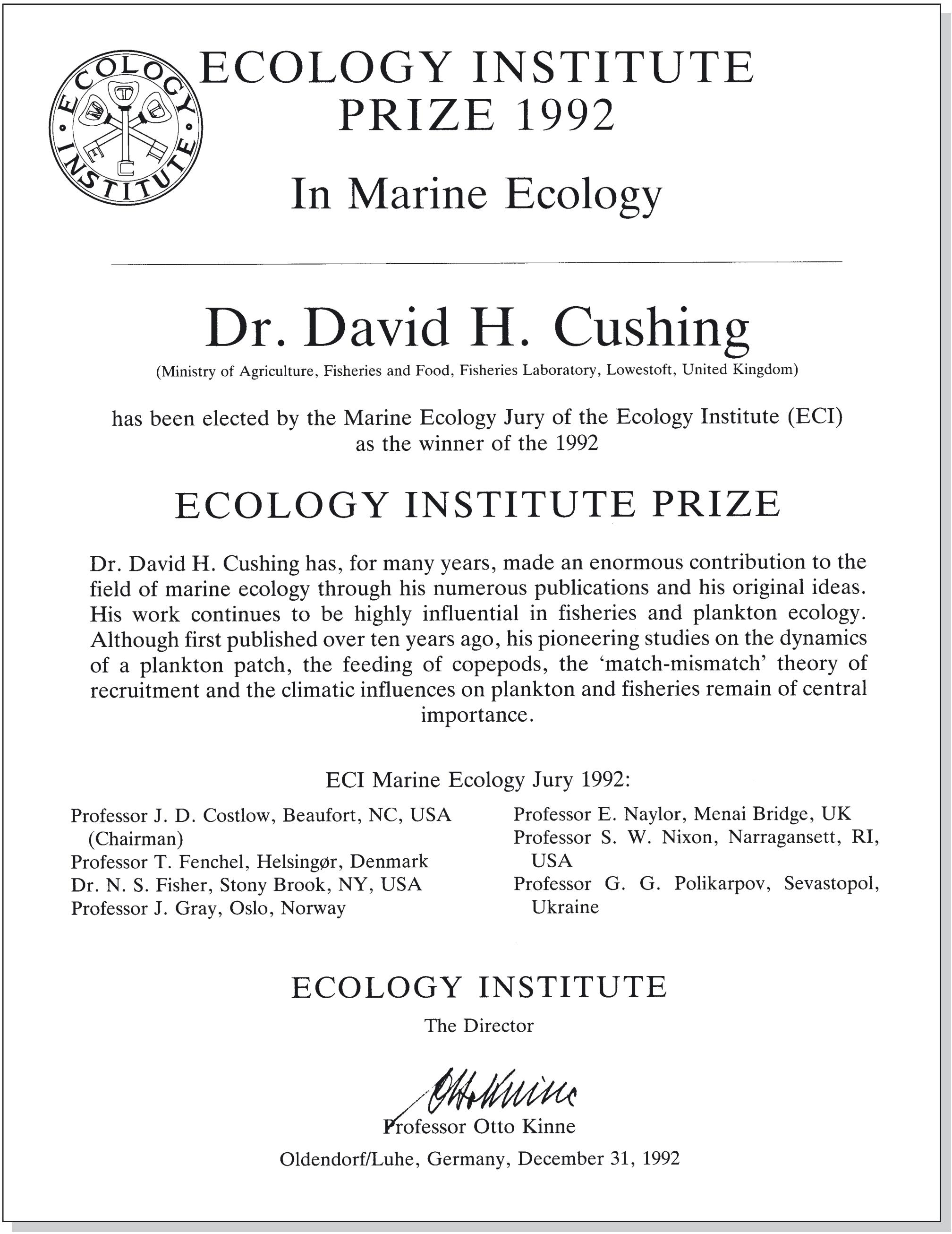
About this book

Knowledge on stock recruitment is the backbone of fisheries research and the basic prerequisite for sustaining the fishing industry. In this Excellence in Ecology book, David H. Cushing presents and weighs essential information on the conditions, known or hypothetical, that determine reproduction, growth and abundance of commercially valuable fish populations in oceans and coastal waters. He takes a close look at the history of fisheries and considers in detail environmental and human influences on fish production, and the autecological rules and dynamics of recruitment processes. Cushing's intimate knowledge and solid expertise allow him to outline fascinating details on the birth of a new science—the science of recruitment—and to draft guidelines for developing that science in the years to come.

David H. Cushing has dedicated most of his life, more than half a century, to fisheries research. No wonder, then, that his book comprises a unique wealth and diversity of information. To a considerable extent, he has produced this information himself. The reader is presented with facts, thoughts and conclusions that have ripened over a long period of time.

Human involvement with reproductive events in commercially exploited fish populations has ancient and multiple roots. These reach far into fields outside of scientific research. In fact, the total body of information available is enormous. But even more enormous is the complex web of interacting factors involved and the size of the space in which all this happens: the seas and coastal waters which cover some two-thirds of the earth's surface. Large sums of money, much ship space and numerous highly trained people are required for conducting modern ocean-wide fisheries investigations.

Not surprisingly then, David Cushing concludes that we still do not know enough about the essential ecological phenomena of fish recruitment. And



ECOLOGY INSTITUTE PRIZE 1992

In Marine Ecology

Dr. David H. Cushing

(Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, United Kingdom)

has been elected by the Marine Ecology Jury of the Ecology Institute (ECI)
as the winner of the 1992

ECOLOGY INSTITUTE PRIZE

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.

ECI Marine Ecology Jury 1992:

Professor J. D. Costlow, Beaufort, NC, USA (Chairman)
Professor T. Fenchel, Helsingør, Denmark
Dr. N. S. Fisher, Stony Brook, NY, USA
Professor J. Gray, Oslo, Norway
Professor E. Naylor, Menai Bridge, UK
Professor S. W. Nixon, Narragansett, RI, USA
Professor G. G. Polikarpov, Sevastopol, Ukraine

ECOLOGY INSTITUTE

The Director

Professor Otto Kinne

Oldendorf/Luhe, Germany, December 31, 1992

Ecology Institute Prize 1992 in the field of marine ecology. Reproduction of the prize awarding document that our means for evaluating specific situations, for predicting future developments, or for formulating detailed measures of protection and control remain, more often than not, inadequate. However, things are beginning to change: “Many have considered the study of the Stock Recruitment Relationship a dead end, but it is now starting to yield information” (p. 140).

Most fish populations are heavily exploited, often overexploited. Whatever is left is very vulnerable to impacts—natural or human-made. This is especially so if early offspring are overfished. Hence there is a great need for stricter fishing rules, protection and control. However, fishermen resist such interference with their business. They must make a profit to survive and they face increasing equipment costs and growing competition. Here, in the conflict between ecological and economical needs, lies the crux of it all.

What can be done? True management of the vast areas of oceans and coastal waters is impossible. Besides, our oceans are more than production areas for human food and utilities. We must strive to accomplish three things: Reduction of the overall human impact on the seas. Enlargement and deepening of our knowledge on fish ecology, especially on larval stages. Enforcement of international cooperation in research, protection, politics and economics.

About the Ecology Institute

The international Ecology Institute (ECI) was founded in 1984. It is a non-governmental institution, sponsored by Inter-Research Science Publisher. ECI’s aims and activities have been described in detail in Excellence in Ecology Book 3 (Gene E. Likens, *The Ecosystem Approach: Its Use and Abuse*, 1992). In part, the ECI strives to achieve its aims by setting out awards to honor outstanding scientists: the ECI Prize and the IRPE Prize. The Institute also supports postgraduates in eastern European countries via the Otto Kinne Foundation (OKF).

ECI and IRPE Prizes. The ECI Prize honors the sustained high performance of outstanding research ecologists. It is 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.

The IRPE (International Recognition of Professional Excellence) Prize honors a young (not more than 40 years of age) research ecologists who has published uniquely independent and/or challenging papers representing an important scientific breakthrough and/or who must work under particularly difficult conditions.

OKF. The Otto Kinne Foundation supports promising postgraduates in environmental sciences in eastern European countries—especially in the fields of ecology, microbiology, disease studies, and climate research. The foundation aids individuals—without distinction of race, religion, nationality, or sex—by providing financial assistance for research, for professional travel, and/or for acquiring scientific equipment or published scientific information. Details are available from 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.

EE Books. Excellence in Ecology books are authored by the winners of the ECI Prize. In these books, the laureates are offered the possibility of publishing their personal views on the state of the art in their fields of expertise and of bringing 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.

EE books are made available at cost price.* A large number are donated to libraries in Third-World countries.

Nominations. 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 (in 1996: Prof. I. Hanski, Dept of Zoology, P. Rautatiekatu 13, FIN-00100 Helsinki, Finland; fax +358 191 1917492) 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.

---

*For details see information at end of book. Please address orders for EE books to:
Inter-Research, Nordbünte 23, D-21385 Oldendorf/Luhe, Germany
Tel: (+49) (0) 4132 7127; Fax: (+49) (0) 4132 8883; E-mail: books@int-res.com;
Internet: http://www.int-res.com

Nominations for OKF Fellows, addressed to Dr. J. Lom (address given above) and accompanied by a letter of support as well as a brief documentation of the nominee's performance, are invited from scientists worldwide and especially from ECI members and members of the Editorial Staffs of the four international Inter-Research journals.

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)

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)

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: The Ecosystem Approach: Its Use and Abuse. (Published 1992)

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: Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective. (Published 1994)

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: The Globalization of Ecological Thought. (In preparation)

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: Science and Limnology. (Published 1995.) 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: Towards a Science of Recruitment in Fish Populations. (Published 1996)

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. (In preparation)

Colin S. Reynolds (Ambleside, UK), ECI Prize winner 1994 in limnetic ecology.
Quotation of the Jury (Chairman: William D. Williams, Adelaide, Australia)
The research of Dr. Colin S. Reynolds in algology has several components interfacing with other biological disciplines, and, indeed, other sciences. He has pursued his research in depth and great detail and yet been able to relate and apply findings to holistic analysis of ecosystem function. Thus, his contributions to our understanding of the dynamic controls and responses of planktonic algae have provided new insight into several controversial areas of ecology. Dr. Reynolds' ideas have also been widely applied in the water industry to reduce the impact of algal growth in reservoirs. His conversion of these ideas into mathematical models has resulted in a vastly increased application of his knowledge to the benefit of society.
Book 9: Planktonic Vegetation: A Model of Ecosystem Processes. (In press)

Ramon Margalef (Barcelona, Spain), ECI Prize winner 1995 in marine ecology.
Quotation of the Jury (Chairman: Ernest Naylor, Menai Bridge, UK)
Ramon Margalef is generally acknowledged to be the most prominent marine ecologist that Spain has produced. He has excelled in the study of unicellular algae, developing the paradigm of phytoplankton organization when previously such organisms were considered to be in unstructured suspension. He also pioneered the use of multidimensional statistical analyses in wider studies of marine plankton. The contributions which he has made to theoretical ecology have brought him particularly high international prestige, and have made him one of the most frequently quoted contemporary ecologists. As one reviewer of his work has noted, "Margalef's ideas have provoked thought, an enviable encomium for any scientist".
Book 10: Our Biosphere. (In press)

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.

Stephen J. Hawkins (Centre of Environmental Sciences, University of Southampton, United Kingdom), IRPE Prize winner 1995 in marine ecology.
Quotation of the Jury (Chairman: Ernest Naylor, Menai Bridge, UK)
At the start of his research career Stephen Hawkins resisted pressures to work on topics for which funding was known to be available, preferring to develop his own ideas and to be judged on those. It was a brave stance when trying to formulate a Ph.D. programme in a harsh financial climate, but he was successful and began imaginative field experiments on rocky shore communities to test his ideas on species/area concepts and on the temporal basis of mosaic distributions. He followed these with detailed studies of intertidal gastropods as models for ideas on niche theory and competition. The outcome of his work has been to generate important new insights into quantitative sampling techniques and environmental impact assessments of rocky shore communities.

OKF Fellows

Alexei Essenin (Yesenin), 1994
Institute of Evolutionary Morphology and Ecology of Animals of Russian Academy of Sciences, Laboratory of Bioindication, 33 Leninsky prospekt, Moscow 117071, Russia
Supported project: *Metal accumulation patterns of terrestrial invertebrates*

Vojtech Novotny, 1994
Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic
Supported project: *Ecological research on insect groups in a Papua New Guinea rainforest*

Inna M. Sokolova, 1995
White Sea Biological Station, Zoological Institute of the Academy of Science of Russia, Universitetskaya nab., 1, St. Petersburg 199034, Russia
Supported project: *Influence of salinity on marine bivalve populations*

Andrej V. Grischenko, 1995
Faculty of Biology and Soil Sciences, St. Petersburg State University, 16 Linia, 29, St. Petersburg 199178, Russia
Supported project: *Ecology of intertidal bryozoans of the Commodore Islands shelf region*

Ferenc Baska, 1995
Veterinary Medical Research Institute, Hungarian Academy of Sciences, POB 18, 1581 Budapest, Hungary
Supported project: *Identification of fish coccidia and myxosporea using MAb and PCR techniques*

Ecology Institute Staff 1996 (in brackets: year of appointment)*

Director and Founder: Professor O. Kinne, D-21385 Oldendorf/Luhe, Germany

Marine Ecology

Prof. F. Azam, La Jolla, CA, USA (1985)
Prof. S. W. Chisholm, Cambridge, MA, USA (1993)
Prof. J. D. Costlow, Beaufort, NC, USA
Dr. D. H. Cushing, Lowestoft, UK (1993)
Prof. T. Fenchel, Helsingør, Denmark (1985)
Dr. N. S. Fisher, Stony Brook, NY, USA (1985)
Prof. J. Gray, Oslo, Norway (1984)
Prof. B.-O. Jansson, Stockholm, Sweden (1989)
Prof. V. Kasyanov, Vladivostok, Russia (1993)
Prof. E. Naylor, Menai Bridge, UK (1984)
Prof. S. W. Nixon, Narragansett, RI, USA (1989)
Prof. W. Nultsch, Hamburg, Germany (1994)
Prof. R. T. Paine, Seattle, WA, USA (1990)
Dr. T. Platt, Dartmouth, NS, Canada (1984)
Acad. Prof. G. G. Polikarpov, Sevastopol, Ukraine (1985)
Dr. T. S. S. Rao, Bambolim, India (1985)
Prof. V. Smetacek, Bremerhaven, Germany (1993)
Prof. B. L. Wu, Qingdao, China (1993)
Acad. Prof. A. Zhirmunsky, Vladivostok, Russia (1988)

Terrestrial Ecology

Prof. T. N. Ananthakrishnan, Madras, India (1984)
Prof. F. S. Chapin, III, Berkeley, CA, USA (1986)
Prof. J. Ehleringer, Salt Lake City, UT, USA (1986)
Dr. P. R. Ehrlich, Stanford, CA, USA (1994)
Prof. M. Gadgil, Bangalore, India (1985)
Prof. G. Glazel, Vienna, Austria (1995)
Prof. I. Hanski, Helsinki, Finland (1993)
Prof. J. L. Harper, Penmaenmawr, UK (1986)
Prof. E. Kuno, Kyoto, Japan (1986)
Prof. A. Macfadyen, Coleraine, UK (1985)
Prof. A. P. Møller, Copenhagen, Denmark (1995)
Prof. H. A. Mooney, Stanford, CA, USA (1991)
Dr. M. Shachak, Sede Boker, Israel (1989)
Acad. Prof. V. E. Sokolov, Moscow, Russia (1986)
Prof. Sir R. Southwood, Oxford, UK (1986)
Prof. E. O. Wilson, Cambridge, MA, USA (1988)

---

*Following their receipt of the ECI prize, laureates are invited to join the institute's staff

Limnetic ecology

Prof. N. V. Aladin, St. Petersburg, Russia (1994)
Prof. H.-J. Elster, Konstanz, Germany (1996)
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)
Prof. R. Margalef, Barcelona, Spain (1986)
Prof. J. Overbeck, Plön, Germany (1984)
Prof. T. J. Pandian, Madurai, India (1985)
Dr. E. Pattée, Villeurbanne, France (1987)
Prof. R. H. Peters, Montreal, PQ, Canada (1992)
Prof. E. Pieczyñska, Warsaw, Poland (1993)
Dr. C. S. Reynolds, Ambleside, UK (1995)
Prof. J. G. Tundisi, São Paulo, Brazil (1990)
Dr. D. Uhlmann, Dresden, Germany (1989)
Prof. W. Wieser, Innsbruck, Austria (1987)
Prof. W. D. Williams, Adelaide, Australia (1986)

OKF Trustees 1996

David H. Cushing: Recipient of the Ecology Institute Prize 1992 in Marine Ecology. A Laudatio

J. D. Costlow

201 Ann Street, Beaufort, North Carolina 28516, USA

As we approach the end of the 20th century, it is rare to find a scientist, in the field of marine sciences or any of the related fields of natural sciences, whose contributions in research have not only spanned half of this century but who has evolved a primary field of interest with equal attention to the basic sciences and the applied sciences. The recipient of the ECI Prize in Marine Ecology 1992 has achieved these goals in a manner which has brought him recognition by the scientific community throughout the world, as evidenced by his nomination for the Award from colleagues in several countries.

Dr. David H. Cushing, Fellow of the Royal Society, was born in Alnwick, in Northumberland, England. He began his education at the Duke's School, Alnwick, and continued prior to the Second World War at the Royal Grammar School, Newcastle upon Tyne. His university career at Balliol College, Oxford, was interrupted by a tour of duty with the Royal Artillery and with the 1st Bn Royal Fusiliers after which he returned to Oxford to complete his studies. Immediately thereafter, Dr. Cushing joined the staff of the Fisheries Laboratory, Lowestoft, Suffolk, England, of the Ministry of Agriculture, Fisheries and Food, where he remained for all of his scientific career, becoming head of the Biology Section in 1965 and Deputy Director in 1974. He has served on numerous advisory groups and been a long-time member of the International Council for the Exploration of the Seas (ICES). His contributions have been recognized by his colleagues, both in England and abroad: election to the Royal Society, Rosenstiel Medal in Oceanographic Science from the University of Miami, Medal of Albert 1st of Monaco from the Institut d'Oceanographie of Paris, and the Award of Excellence from the American Fisheries Society. In addition to an impressive record of publications, he has been much sought as speaker and lecturer in public circles as well as in universities in England, North America, and the Orient.

Since 1993, Dr. Cushing has been a member of the scientific staff of the international Ecology Institute, Oldendorf/Luhe, Germany. He has served on the Editorial Board of 'Marine Ecology Progress Series' for many years.

Cushing's published work has focused primarily on a variety of fields relating to fisheries although many of his papers are concerned with basic oceanographic concepts. Rather than confining his research to an ever narrowing examination of one topic, his publications have continued to provide new information within three general areas of marine science: fisheries, ecology, and oceanographic processes associated with these, including studies which, from the very beginning, provided guidance and direction in the use of modern technology in fisheries.

A review of his publications since his first in 1951 reveals continued interest in the central theme of marine fisheries, although on occasion he expanded this area to include fresh-water fisheries. Within the area of marine fisheries, his primary interest has continued to be in species living in the North Sea. However, even in this major theme, he has periodically made valuable contributions to our understanding of species found in the North Atlantic and the waters adjacent to South Africa, India, and Indonesia. Problems of recruitment, factors affecting abundance, overfishing, diet, predation, migration, and approaches to estimating stocks have all attracted his attention. Many of his observations and conclusions are now considered basic to the study and management of marine fisheries. Within the realm of fisheries management, as it has evolved to encompass state, national, and international commissions and multi-national organizations, his publications and advice have come to be highly regarded not only by the scientific community but also by those in the political realms responsible for development of policy and its implementation.

It is indeed remarkable to review the publications of Dr. Cushing in a number of areas of marine science which, while relating to fisheries biology, comprise significant contributions to our basic understanding of ocean processes. In 1951 he published on vertical migration of planktonic crustaceans, an area which stimulated further research and resulted in a number of papers on plankton populations, phytoplankton, grazing, trophic chains, and eventually, a basic hypothesis on the phenomenon of patchiness in marine waters. As early as the beginning of the '70s, he considered the impact of climate on fisheries with observations on the effect of large-scale temperature changes which are timely to the more recent concerns over global warming.

Presumably from his early interest in plankton and vertical migration Dr. Cushing developed a lasting fascination for the use of modern techniques and instrumentation wherever it might contribute to a better understanding of a specific function or oceanic process. Early in his scientific career he demonstrated the practical use of acoustical techniques, initially in a general application but evolving to more specific applications relating to estimates of populations, catches, and aspects of vertical migration. His interest in possible application of modern approaches expanded to include the use of radioisotopes in studies on phytoplankton and studies utilizing the Coulter Counter in determinations of productivity in the marine environment. Cushing's contributions, in contrast to those of many scientists examining aspects of the world's oceans, were not restricted to theory. He bridged not only the realms of science and policy but also translated some of his and his colleagues' findings to the real world of commercial fisheries.

Although his interests over half a century continued to revolve around marine fisheries, his breadth of interest is evidenced by the occasional excursions into topics which he found challenging. Thus, interspersed within his publications are those dealing with 'Kipling and the White Seal', observations on the central gyres of the Pacific, the flow of energy in marine ecosystems of the continental shelves, and a consideration of the impact of El Niño on the Peruvian anchoveta.

It is indeed significant and highly appropriate that Dr. David H. Cushing should be the winner of the ECI Prize 1992, based on his significant contributions to science and his nomination by peers from several countries. He has, for many years, made an enormous contribution to the field of marine ecology and his published work will undoubtedly continue to be highly regarded and influential in the studies of fisheries and marine plankton.

Preface

I joined the Fisheries Laboratory in Lowestoft (UK) nearly 50 years ago. During my service I spent more than a thousand days at sea and worked in all oceans except the Antarctic. In the early salad days Michael Graham was the Director of the laboratory. For one cruise in the Herring season he let me have three ships at once. Later, I asked him for 2 ships for 3 months and in 10 minutes, I got them.

In April 1955 I became responsible for research on the East Anglian herring fishery and in the autumn of that year the fishery started to fail. In 1964, the collapse was attributed to recruitment overfishing and in 1967 the last drifter sailed from Lowestoft and the fishery, recorded since the seventh century, was over.

I continued to work intermittently on the Stock Recruitment Relationship. We now know that the only way in which the problem will be solved is in the examination of the dynamics of life in the larval stages. The research is needed and, without it, management will remain self defeating. Paymasters will learn this, if slowly, so slowly.

Lowestoft, UK, January 1996 D. H. Cushing

I HISTORY OF THE FISHERIES

The commercial harvesting of fish for human consumption, the fisheries, has appeared and disappeared all through the long stride of history. Fish stocks respond to environmental change by changes in the magnitude of recruitment, the youngest age group in the stock. The 1904 year class of the Norwegian spring spawning herring *Clupea harengus* is famous not only for being traced in age for many years, but also for its abundance. It was the first year class of the Norwegian herring period of the twentieth century. Fish stocks respond to environmental conditions that change all the time in ways that are, more often than not, unexpected. For example, the Scanian fishery off southern Sweden, which formed the basis of the Hanseatic League, endured for some centuries and then vanished, never to return. The changes recorded give the lie to the idea that a stock is insulated from its environment to yield steady catches for very long periods.

Recruitment can be estimated by present methods. Some records extend back for up to 7 decades. There is, however, little understanding of the mechanisms by which the magnitudes of recruitment are generated. The study of recruitment, in spite of considerable advances, has remained a science in its infancy.

The Long History of the Fisheries

Men have caught fish from the earliest times. Hooks, barbed harpoon heads and gorges have been found in palaeolithic remains (for example at Kesslerloch in Sweden; Rau 1884); bones of freshwater fishes, in the valleys of the Dordogne and the Vézère in France. Pictures of marine fishes on reindeer horn have been recovered. The Danish middens have yielded bone hooks, floats made of bark, grapnels for recovering lines, flax nets and stone sinkers. The fishes recorded on the artifacts of history can be readily recognized today. Radcliffe (1921) provides evidence of fisheries and fishermen from the classics. Fishermen were portrayed on the vase of Phylakopi. On this vase, a Nile perch *Lates niloticus* features clearly. Fishing methods are depicted on a Roman mosaic at Sousse in Tunisia. Anglers were illustrated on Egyptian tiles in 2000 B.C. From Egypt stems a picture of 7 fishermen hauling a seine from a boat in the Nile. Fig. 1 shows a mosaic from Pompeii with fishes most of which we can recognize. Aristotle, who may have lived by the sea, looked at the scales of fish and saw that they thickened and enlarged with age. Of *Murex*, he wrote that it “lived for about six years and the yearly increase is indicated by a distinct interval in the spiral convolutions of the shell”. Today, fisheries biologists estimate age in days or years by the rings on scales or otoliths, earstones used by the fish for balancing.

There is a broad record of fish and fisheries from the classics. The fullest account is given in the Halieutica of Oppian, who listed more than 40 species and many varieties of gear, cast nets, draw nets, drag nets, seines and “a crooked trawl”. Oppian described the capture of a whale (probably a pilot whale) with thick ropes and a large hook; the line had bladders attached in

Fig. 1. Mosaic from Pompeii (now in the Naples Museum, Italy) depicting animals to be seen on Roman fish markets (after Radcliffe 1921), e.g. octopus, mullet, squid, dogfish, conger eel, anchovy and ray

order to bring the whale to the surface where it was attacked by tridents and axes. Oppian also wrote that the hunting of dolphins was immoral and noted that they chased the fish towards the tridents of fishermen.

According to D'Arcy Thompson (1937) turbot *Scophthalmus maximus* was caught off Ravenna, Italy; sturgeon *Acipenser oxyrhynchus* off Rhodes. Bonito *Sarda sarda* was best at Istanbul and eels *Anguilla anguilla* were numerous where the River Mincio runs into Lake Garda. Tuna were sighted by *speculatori* on tall masts. Swordfish *Xiphias gladius* were taken off Scilla in Calabria where they are still caught today with boats with similar tall masts. Bluefin tuna *Thunnus thynnus* were taken at many points on their migratory routes in the Mediterranean where the madragues are sited at the present time. Mackerel *Scomber scombrus* were caught with hooks baited with a gull's feather, much as they are taken off Cornwall today. Fishermen in classical times had developed gears very similar to those used today, even if ours are bigger and more complicated; the Greeks and Romans ate the same fish as we do and shared our preferences (Cushing 1988a).

A significant treatise was published by Duhamel du Monceau (1769) on the coastal fisheries of France. He illustrated the gears in use, for example, a cast net (Fig. 2a), a lift net from a scaffold to catch shrimps, prawns and crayfish (Fig. 2b), a drift net for herring, sardine and mackerel (Fig. 2c), a shore seine hauled by horses (Fig. 2d) and a trawl (Fig. 2e), both of which were used to catch demersal or bottom living fish. Such are also the main methods of capture today.

Today we use Danish seines on the sea bed for demersal fish, purse seines with power blocks and sonar to catch herring in the open ocean, capelin, sardines and anchovies and various other species. Drift nets up to 80 km in length are used for salmon in the North Pacific, but on a large scale their use has ceased because they are very labour intensive. Trawls are used to catch demersal fish on the sea bed and pelagic fish in midwater. They can be very large. In general, the gears and the vessels have become larger and more complex. For example, the ships that catch soles in the southern North Sea use 3 or 4 thousand horse power to drag heavy trawls armed with many rows of tickler chains to stir the fish from the sea bed, where small simple trawlers were used 40 years ago. The fisheries described by Duhamel du Monceau (1769) were small and coastal, and the stocks were almost certainly lightly exploited. The industrialization of fisheries started on the eastern seaboard of the United States in the eighties of the last century and in the North Sea in the nineties. The process continued throughout the present century with the Russian and Japanese fishermen covering the world ocean. The result is that most areas are heavily fished or overexploited. In Chapter V a brief account is given of the overexploitation of fish stocks throughout the world ocean.

Some fisheries last only for a decade or so, or for a few centuries. Others have persisted for as long as records have endured. The Scanian fishery for herring (as noted earlier) was centred on the towns of Skanør, Falsterbø and Dragør in southern Sweden. It flourished between August and November each year between the eleventh and sixteenth centuries after which it disappeared, never to return. The Hanseatic merchants came to the Scanian ports to buy herring. The fish were caught with drift net or set net from open boats with crews of 3 to 7 and they could carry as much as 12 lasts (or about 29 tonnes). On landing the fish were gutted, roused in salt and packed in barrels for export. The salt was found in the region. Indeed, many of the early herring fisheries were based on places where salt was available. The record of catches is sporadic. In 1368, 160 vessels from Lübeck, Germany, landed 4250 tonnes. And in 1463, about 50 000 tonnes were taken by 501 vessels. The fishery varied greatly in time, with good yields in the second half of the thirteenth century and in the first 30 years of the fourteenth century. In 1527, the sea in the Sound was filled with herring and some were caught at the surface with shovels. The Hanseatic merchants carried the salted herring to Venice and to the northern cities from Amsterdam to Moscow. The herring

Fig. 2 (above and on subsequent pages). Coastal fisheries of France in the 18th century (after Duhamel du Monceau 1769). (a) Cast net was the first packaged food to sustain people in the northern winter. Towards the end of the sixteenth century the herring left Scania "on account of the people" (Cushing 1988a).

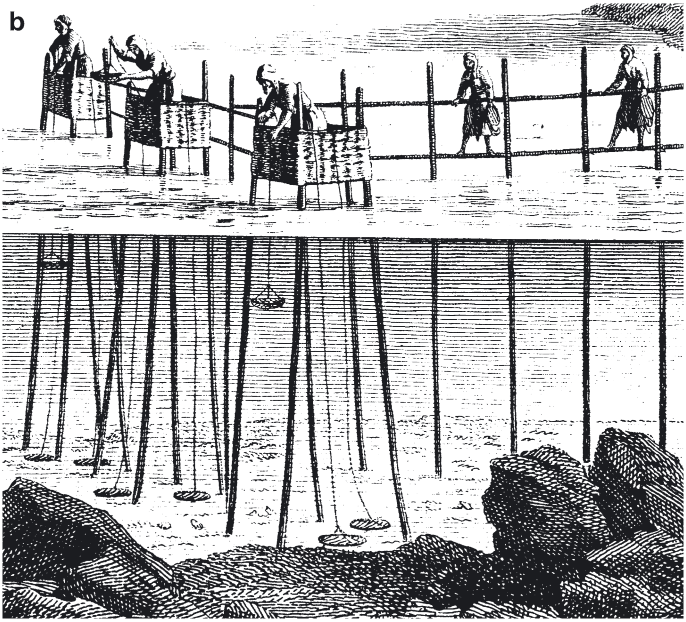


Fig. 2, continued. (b) Lift nets worked from a scaffold. (c) Drifter with its nets that drive with the tide for herring, sardines or mackerel

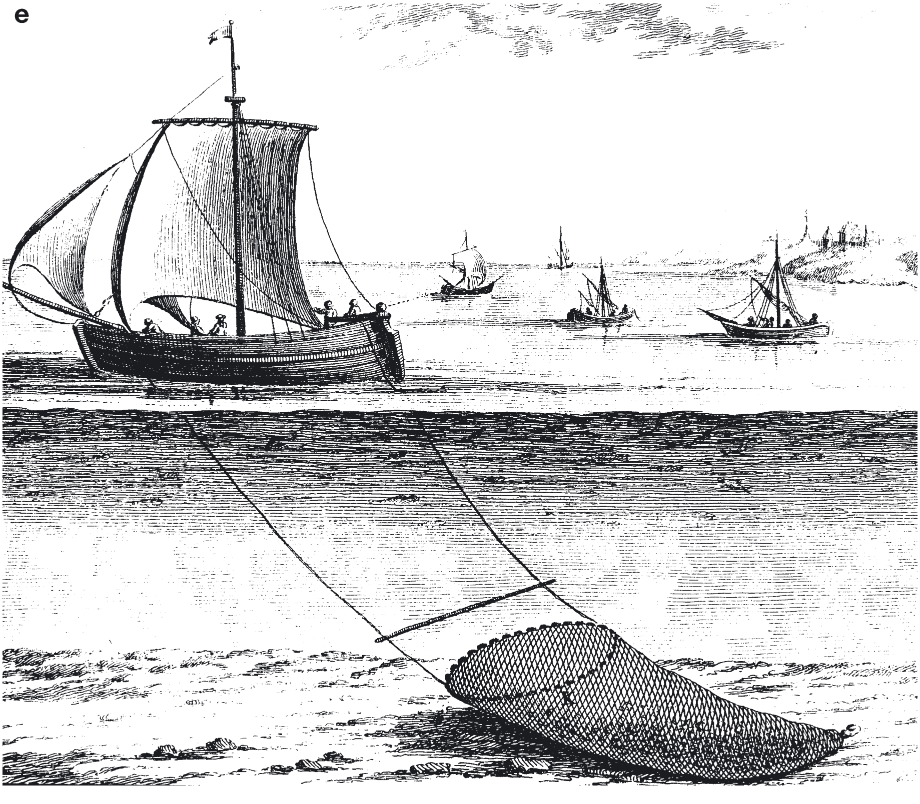


Fig. 2, continued. (d) Shore seine hauled by horses. (e) A trawl

A herring fishery flourished between October and March on the northern side of the Firth of Forth in Scotland between 1794 and 1805 and catches were taken by fast sailing vessels to London. This must have been a response to increased abundance for a decade in a small and very local fishery. Another herring fishery was worked from Wick in the far north of Scotland between the last quarter of the eighteenth century and the first quarter of the nineteenth century; in 1789, a hundred boats were working out of Wick and they landed about 1250 tonnes. Such an event has not recurred in that region. Transient herring fisheries occurred in Loch Fyne, off the rivers Dee, Tay and the Tweed in Scotland. Such were the records of transient herring fisheries which must have reflected differences in recruitment in local stocks which can be recognized today (Mitchell 1864). It might be thought that such events were ordered by economics. Fish are for sale, but I have the strong impression that an increment in abundance precedes exploitation and sale.

Halibut *Hippoglossus hippoglossus* were caught on George's Bank off New England for a few decades up to 1850, "the year when the halibut gave out". Mackerel and menhaden *Brevoortia tyrannus* were caught in summer between Cape Hatteras and the Gulf of St. Lawrence; the mackerel migrated north between the Chesapeake and Nantucket about 30 to 80 km offshore (Brown Goode et al. 1884). The fleets were based in Maine and Massachusetts, USA, particularly from Provincetown and Gloucester. The mackerel boats were swift and could carry 20 to 60 tonnes. The fish were caught by hook and line until 1860 when the purse seine was introduced; it probably originated in the region north of Cape Cod in about 1860. Fig. 3 shows the catches of mackerel by the citizens of Massachusetts in barrels from 1804 to 1881 (100 000 barrels are about 12 500 tonnes). The schooners worked in spring off the Chesapeake and moved north during the summer to the Gulf of Maine. The market for mackerel was for fresh and canned fish. The menhaden was reduced to oil and guano. During the decade 1873 to 1882, the first steamers appeared and they carried the dories from which the purse seine was worked. The oil was used mainly for currying leather in the Far West. Catches of mackerel were very variable in time; in recent decades much heavier catches were again made in the region of the Gulf of Maine.

Ljungman (1882) and Boeck (1871) traced back for some hundreds of years the alternation between the catches from the Norwegian spring spawning herring stock and those from the Swedish one for autumn spawning herring. The Norwegian period tended to occur at the start of each century. The best evidence is given by Devold (1963) where the alternation from 1760 to 1960 is recorded between the Bohuslån fishery on the west coast of Sweden and the fishery off the west coast of Norway (Fig. 4). There is some overlap between the last Swedish period and the recent Norwegian one, but we should recall that the latter really started with the strong 1904 year class which persisted for many years in the fishery after it appeared in 1910 onwards. Devold (1963), following Boeck (1871), showed that towards the end of the Norwegian period the stock tended to move northward, as it did in the fifties and sixties of the present century. Höglund (1972) examined the vertebrae from the oil pits on the skerries off the Bohuslån coast and showed that the Bohuslån fishery exploited North Sea herring. A resurgence of the Bohuslån fishery might have been expected in recent decades, but the North Sea stock has been heavily exploited, indeed reduced so much by recruitment overfishing that catches were banned from 1977 to 1982.

Variability and Management

The fisheries briefly described so far were very variable, characterized by their presence or absence in time or by dramatic changes in abundance. Indeed some—like the Norwegian herring—reappeared at the start of each century, but others vanished, never to recur. But, some fisheries have persisted for very long periods. The first record of the cod *Gadus morhua* fishery in the Vestfjord in northern Norway dates from the twelfth century and catches there have persisted since. But changes in abundance do take place.

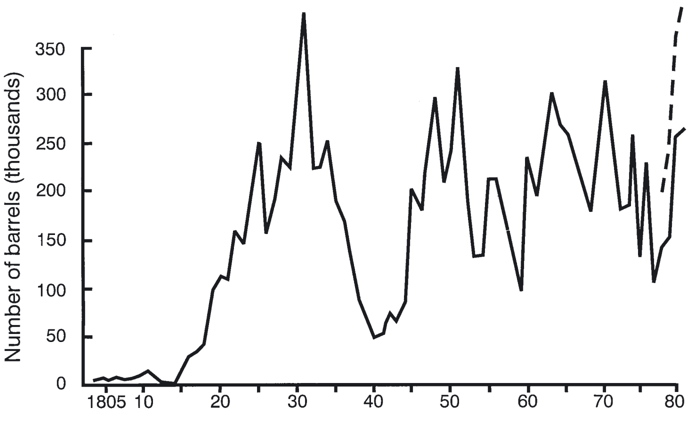


Fig. 3. Catches of mackerel by the citizens of Massachusetts, USA, between 1804 and 1881. Solid line: barrels of pickled mackerel; broken line: total quantities expressed in barrels. (After Brown Goode et al. 1884)

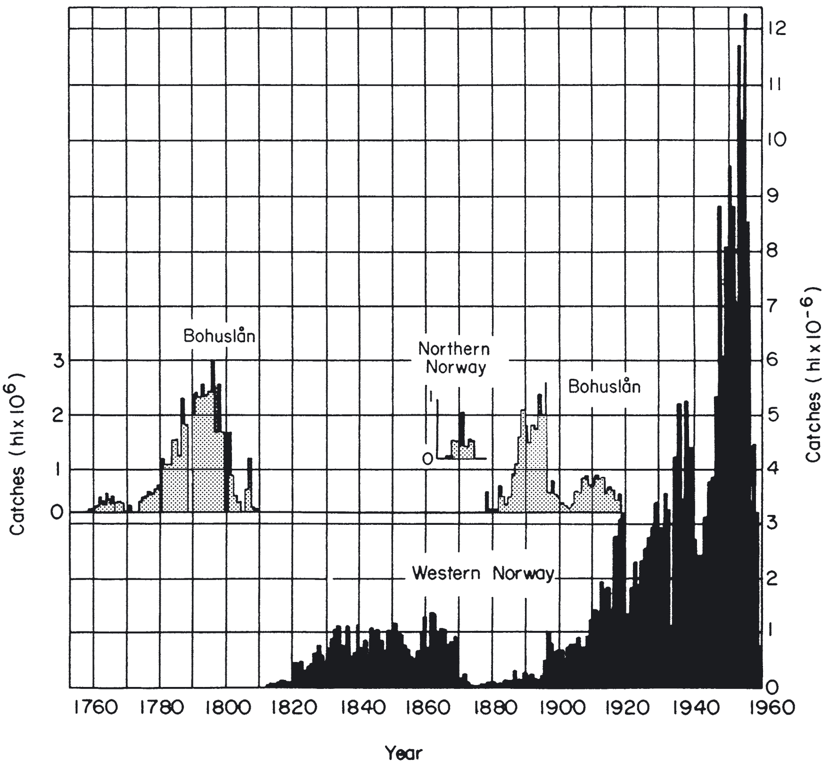


Fig. 4. Alternation of catches of herring in the Swedish Bohuslån and Norwegian spring fisheries from 1760 to 1960. (After Devold 1963)

Fig. 5a shows the catches of cod in the Vestfjord from 1885 to 1958 where most of the Arcto-Norwegian cod spawn in spring. In Fig. 5b are displayed the catches per unit of effort in that fishery from 1921 to 1977. The observations in both figures are fitted by a compound curve derived by Ottestad (1969, 1986) based on climatic factors which will be described in the next chapter. The catches declined by a factor of 2 to 3 in the last 5 years of the nineteenth century, and they remained low until about 1925 or so when they increased by the same factor. Between 1925 and 1929 the cod appeared on the Svalbard Shelf, where they were exploited as immature and mature fish by a large international fleet until 1977, when the Norwegian Exclusive Economic Zone (EEZ) was extended to 200 miles (some international fishing was subsequently permitted but the number of vessels was low). The cod were absent from the Svalbard Shelf for nearly 30 years. The changes illustrated must indicate considerable differences in stock over long periods of time. Cod were caught off West Greenland between the twenties and forties of the nineteenth century, but were absent there until the second decade of the present century.

A second persistent fishery is that for cod on the Grand Bank from 1531 to the present day. For centuries it was a transatlantic fishery based on ports in England, Spain and Portugal, but predominantly in France, and the demand was again based on the need for winter protein, particularly in the Catholic countries. The cod were salted and sun dried. The fish were caught by hand lines from dories working from the carriers anchored in the fjords of Newfoundland.

With intermittent observations, estimates are available of the number of vessels from France and England visiting Newfoundland between about 1580 and 1750. With a rough estimate of the average catch of about 200 tonnes per vessel, it is likely that up to about 250000 tonnes were caught each year. Fig. 6 shows an estimate of catches on the Grand and Western Banks (with some minor catches from George's Bank) from 1750 to 1930. The rise in catches occurred when the fishery became industrialized, as steam (and later, diesel) trawlers worked on the edge of the Bank. After the Second World War, with bigger and more numerous vessels with larger trawls, catches increased considerably. In recent years, the stock of Northern cod, which spawns between Labrador and the northern Grand Bank, has declined sharply (see Chapter IV).

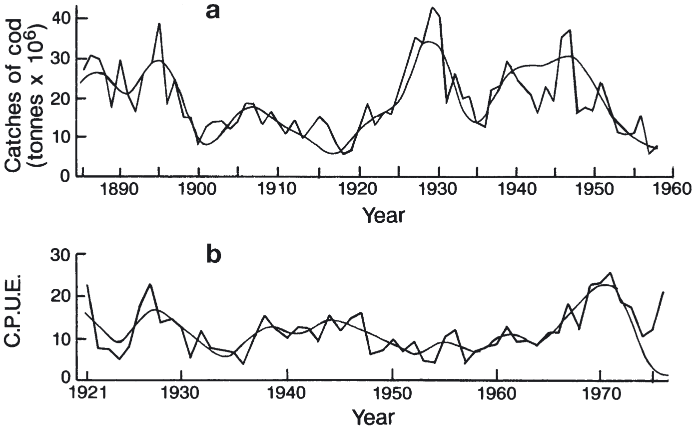


Fig. 5. Cod and climate. (a) Catches of cod in the Vestfjord from 1885 to 1958; (b) catches per unit of effort of cod in the Vestfjord from 1927 to 1977. Curves were fitted by a compound function of 4 periods based on the widths of the annual rings on pine trees on the southern side of the Vestfjord in northern Norway. Cod spawn in the fjord. (After Ottestad 1969, 1986)

A third persistent fishery was the East Anglian fishery for herring, the first record of which dates from 647, when Felix I, bishop of the East Angles, built the church of St Benet "to pray for the health and success of the fishermen that come to Yarmouth in the herring season" (Mitchell 1864). Records of the fishery were noted in each century, from the eleventh. It was always an international fishery. For example, between 1331 and 1360, there were 40 English boats and 200 to 400 foreign vessels. In 1597, there were 220 vessels, and a thousand fishermen spread their nets on Yarmouth denes; up to 125 000 tonnes were landed in many countries in northern Europe. In 1751, Dutch and French boats landed 22 000 tonnes. Such events were recorded as exceptional, indicating some marked variation in the stock (Cushing 1988a). In general, the catches ranged from about 5000 tonnes up to 125 000 tonnes and in 1913, 313 000 tonnes were landed at the ports of Yarmouth and Lowestoft on the East Anglian shore, for export to Germany and eastern Europe. The fish had always been caught with drift nets, each about a mile and a half in length. In 1950, more than a hundred of the largest trawlers then extant assembled on the herring spawning grounds between the Sandettié and Ruytingen banks in the chops of the Channel. The spawning grounds were of limited extent (1 km by 200 m; Bolster and Bridger 1957) and the sticky eggs were laid on patches of gravel. The fishery looked like a naval battle, with the large trawlers working in parallel lines up to 2 cables (1 cable = $^1\!/_{10}$ nautical mile, or about 185 m) from each other. This most

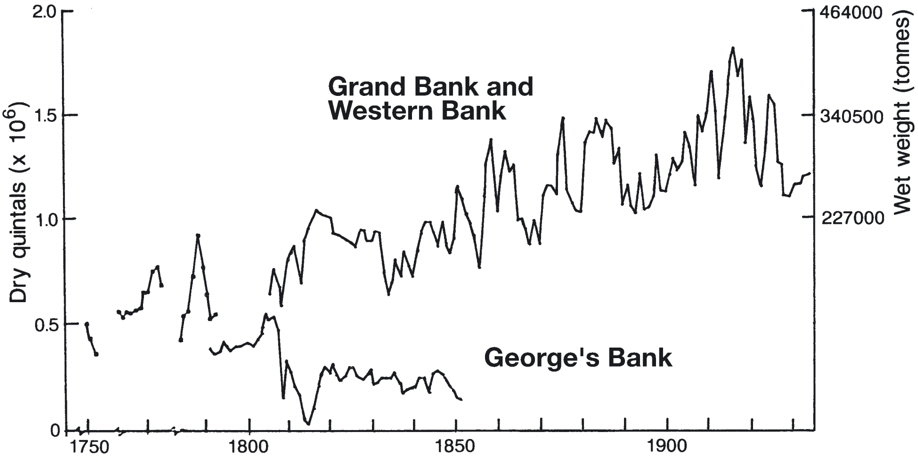


Fig. 6. Catches of cod off Newfoundland from 1750 to 1935 and on George's Bank. (After Cushing 1988a)

intense fishery lasted for about a decade, and the old East Anglian herring fishery collapsed due to recruitment overfishing. Some fisheries have persisted for centuries and have varied much in abundance. Others have lasted for a few decades or even for 3 or 4 centuries before they vanished. Stocks have been exploited and have suffered changes in abundance. From this brief history of the early fisheries, some appeared for relatively short periods, 1 or 2 decades. Others lasted for some centuries only to disappear, never to return.

Some fisheries persisted for very long periods, within which there were obvious changes of abundance, such as in the Arcto-Norwegian cod or in the alternation between the Norwegian and Swedish fisheries for herring. There may have been changes in abundance in the cod stocks on the Grand Bank or in the East Anglian herring stock, but the observations are not frequent enough to show them, although periods of abundance could be suspected. Some of the changes must have been modified by the numbers of trawlers or the price of fish, but each of these is the consequence of profound changes in abundance driven by sharp rises or falls in recruitment.

The overwhelming impression from the history is that fisheries appear and disappear and that the great stocks experience considerable fluctuations in abundance. This is the substance of Hjort's papers (1914, 1926) who wrote that the prime problem of fisheries science was to describe and understand the nature of such fluctuations. However, the causes of differences in recruitment from year to year remain unknown and unexplored. Good estimates of recruitment emerge from the present methods of stock assessment (described below), but their variation has not been examined on a broad scale.

The stocks of fish are reduced by fishing. Michael Graham (1943) referred to the Report of the Select Committee of the House of Commons (UK) in 1893 to investigate the state of the stocks in the North Sea. At this time, the fleets were being industrialized as the sailing smacks were being replaced by steam trawlers and the beam trawl was being superseded by the more flexible otter trawl. From the questions and answers in the Report, Graham noted that the catch per vessel decreased in weight each year, but that the total yield did not decrease because the smacks fished further afield at greater cost and that the average size of the fish decreased as the number of vessels increased. Such are the classic signs of the effect of heavy fishing.

Fishing effort is defined as number of vessels, or as number of vessels weighted by their power, the force that causes death by fishing. As the numbers of vessels rose, the catch per unit of effort, the stock density, diminished and the profits of the fishermen declined. Graham expounded the Great Law of Fishing: “Fisheries that are unlimited become unprofitable.” He was much influenced by the recovery of the Pacific halibut in catch per unit of effort after the fishing effort had been restrained in 1929/30. The reason for the collapse of profit is that the stocks are common property which belong to nobody, which is “the Tragedy of the Commons” (Hardin 1968). As illustration, Hardin wrote of grazers living off a common pasture; the grazers competed with each other and they bought more animals, resulting in overgrazing and bankruptcy. Because the fishermen must compete with each other, each works harder to obtain a larger share of the stock and that stock is reduced further. The only way to solve the problem is to restrain the fishing effort by international agreement if needed. So fish stocks have to be managed.

The first international instrument to manage a marine resource was the North Pacific Fur Seal Convention established in 1911. Catches of the fur seals on and around the Pribilof Islands in the North Pacific were regulated by agreement between Canada and the United States. The International Halibut Commission was founded in 1923 and on the basis of scientific advice given by it, a treaty was signed between the United States and Canada to limit the fishing effort exerted on the stock. Many other organizations followed them, distributed across the world ocean, subsumed finally in the de facto Law of the Sea in 1977. The object of the Law of the Sea Conference was to extend the jurisdiction of the coastal state to 200 miles, the Exclusive Economic Zone (EEZ). The intention was really to exclude foreign fishermen like the British from Icelandic waters, but it might also have provided an escape from the Tragedy of the Commons. As will be shown in Chapter V this did not happen, although in Iceland, New Zealand and in the Falkland Islands some success has been achieved.

The first makers of Fisheries Science were Petersen (1894), Garstang (1900), Russell (1931), Hjort et al. (1933), Thompson (1937) and Graham (1935). They formulated the problem and proposed the first solutions. After the Second World War, the science was placed on firm ground by Schaefer (1954), Ricker (1944, 1954) and Beverton and Holt (1957). In Schaefer’s surplus production model, the inverse linear dependence of catch per unit of effort was raised by effort to give a parabola of yield in weight on effort. Thence, Ricker’s phrase “maximum sustained yield” found its application in international treaties. In the model of Beverton and Holt, yield was estimated as a function of growth and mortality by age and it was adapted to control the demersal stocks of the North Sea by mesh regulation; they expressed their model as “yield per recruit”, by which the variation due to differences in recruitment from year to year is avoided.

Before the Second World War the plaice stock suffered from heavy overfishing. Beverton and Holt showed that the fishing mortality then amounted to 0.73. The maximum yield per recruit was at about one third of that value. Rather than put two thirds of the fishermen out of work, they demonstrated the same result could be obtained by increasing the mesh size in the codends of the trawls. Gulland (1965a) was able to show that, as a result of mesh regulation, the plaice stock recovered to the degree expected by the yield per recruit formulation. The dependence of recruitment on parent stock was described by Ricker (1954) and by Beverton and Holt (1957).

Fish have annual rings on their scales (Dahl 1907, Lea 1927) and otoliths (Hickling 1931, Rollefsen 1934). In temperate waters and high latitudes they are clear enough to yield good estimates of age, but in tropical seas they tend to be less reliable. Outside the tropics good estimates of growth and mortality are readily available. In tropical waters today, length measurements are often used for this purpose. Brothers et al. (1976) discovered that there are daily rings on the otoliths of the Pacific hake *Merluccius productus* and the northern anchovy *Engraulis mordax*. Hence the growth rates and death rates of the larval fish can be determined and are now widely used for that purpose. As will be shown below this has great importance to the study of how fish populations regulate themselves.

Today the effects of exploitation can be estimated readily by the common methods of fisheries research. The fish populations are studied in the following way.

$$N_1 = N_0 \exp(-Z)$$

where N_0 is the number at the start of the year; N_1 is the number at the end of the year; Z is the instantaneous coefficient of total mortality.

$$Z = F + M$$

where F is the instantaneous coefficient of fishing mortality; M is the instantaneous coefficient of natural mortality.

The number of deaths during the year is

$$N_0 - N_1 = N_0 - N_0 \exp(-Z) = N_0[1 - \exp(-Z)].$$

F/Z is the proportion of deaths due to fishing. Then the catch in numbers by the end of the year is

$$C = (F/Z)N_0[1 - \exp(-Z)].$$

The exploitation rate $E = (F/Z)[1 - \exp(-Z)]$. If F/Z is high, $E \approx F/Z$.

After λ years in the year class or cohort,

$$N_\lambda = N_0 \exp(-Z\lambda)$$

and the catch in numbers of the cohort is

$$C = (F/Z)N_0[1 - \exp(-Z\lambda)].$$

If there are λ years in the cohort, there are also λ age groups in the stock in any one year. Then the annual catch in numbers of all age groups in the year is given by the same equation. N_0 is the number at the start of the first year of exploitation of the cohort or year class. It is usually called Recruitment, R, and thus $C = (F/Z)\,R\,[1 - \exp(-Z\lambda)]$.

The average stock is $R\,[1 - \exp(-Z\lambda)]/Z = \bar{N}$ and $C = F\bar{N}$. Then

$$C/R = (F/Z)[1 - \exp(-Z\lambda)]$$

where C/R is catch per recruit (in numbers), an important parameter in which the natural variation of recruitment is avoided; as will be shown below, it is usually expressed in weight as yield per recruit.

$$F = qf$$

where f is the fishing intensity, or number of vessels of standard power per unit area; q is the catchability coefficient. Then

$$C/F = C/qf = R[1 - \exp(-Z\lambda)]/Z.$$

So, under ideal conditions, the catch per unit effort is a proper index of stock. But, amongst shoaling species at least, $q = aN^{-b}$ (Pope and Garrod 1975); in that case catch per unit of effort is no longer a simple index of stock, which limits the use of surplus production models.

Virtual population analysis was developed by Gulland (1965b) in the following way:

$$C_t = F_t N_t = (F_t/Z_t) N_t [1 - \exp(-Z_t)]$$

in the year t. $N_{t+1} = N_t \exp(-Z_t)$, so

$$C_t/N_{t+1} = (F_t/Z_t)[1 - \exp(-Z_t)]/\exp(-Z_t)$$

The problem is to find F_t. Let $Y = \exp(-Z_t)(C_t/N_{t+1}) - (F_t/Z_t)[1 - \exp(-Z_t)]$. With an iterative method find F_t for $Y = 0$ (Anonymous 1994).

An important point is that the ratio C_t/N_{t+1} is that of the catch at the end of the year t to the stock at the beginning of the $(t+1)$th year, that is at the same time. In the year class or cohort there are n equations with $(n+2)$ unknowns. A notional value of M is used and F is guessed (or estimated) for the oldest age group in the cohort.

$N_{t+1} = (C_{t+1}Z_{t+1})/\{F_{t+1}[1 - \exp(-Z_{t+1})]\}$ from the estimates of M_{t+1} and F_{t+1}. Then, given C_t, M_t and N_{t+1}, determine F_t and then N_t. As the calculations proceed backwards to the younger and more abundant age groups the error of estimation is reduced, so if there are enough age groups in the cohort the younger and abundant ones are well estimated.

The result of such analyses is a matrix of fishing mortality by age on years. The same material yields another matrix of stock by age on years. With weights at age a further matrix of biomass by age and year may be derived. Quotas (or Total Allowable Catches) can be estimated by extending the calculations into the next year. This is the mechanism by which present controls of fishing are established. Natural mortality may be poorly estimated, fishing mortality may change with age and errors in age determination may be propagated along the cohort in age. So independent estimates of stock are needed, such as groundfish surveys, egg surveys and acoustic surveys. Stock in weight is estimated by raising stock in numbers by weight at age. Then estimates of yield per recruit in weight can be easily derived. For our present purposes the time series of recruitment are as well estimated as is possible. One of the important aspects of virtual population analysis is that it is based on the equation $C = F\bar{N}$ and the catches per unit effort are not used in that calculation. In this sense, virtual population analysis has an advantage over production models because catches per unit effort can vary with abundance. But virtual population analysis needs age determinations or length measurements. As will be shown below, catches per unit effort are used in the "tuning" methods where the catches per unit effort of research vessels are used as standards.

The estimation of quotas or Total Allowable Catches (TACs) is not as simple as it might appear. The initial errors in the older age groups are reduced as estimates converge towards the true abundances, after about 5 years (Pope 1972). In the matrix of fishing mortality (or numbers) by age and year there is a sector of the latest age groups in which the calculations have not converged. This sector is the one needed to estimate quotas. The problem is solved by "tuning" or "calibration" methods which really depend on research vessel surveys, the catchabilities of which should remain the same from year to year or assuming that the catchability of commercial fleets has remained the same. Forty years ago stock assessment depended upon market samples only, but today fuller samples are needed. Research vessel surveys are needed to fill the gaps and also to provide a base of constant catchability.

The problem is to estimate the catchabilities, *q*, of both the commercial fleets and the research vessels. There are many ways of doing this, and one used frequently is that of Laurec and Shepherd (1983) (see Pope and Shepherd 1985). At each age and in each year, ln *q* is calculated, each weighted by the ratio of variance in *q* by the research vessel to that of the commercial fleet(s). Then, at each age an average of (ln *q*) is calculated for a short period (but at least 5 years) and in the final year $F = \exp(\text{average } \ln q) \times (\text{average effort})$. The terminal fishing mortality (that for the oldest age in the last year) is a fixed multiple of the younger age groups weighted for selectivity. It is essentially ln *q* weighted by the ratio of catch at age in the fleet(s) to that from the research vessels allocated to each item in the age and year matrix.

The fishermen become progressively more efficient, so *q* tends to increase with time. Devices are used to obviate such trends. The important point is that *q* is assumed constant because research vessel surveys are used. ADAPT (Gavaris 1988) is another method by which fishing mortalities for ages in the last year are used with catchability coefficients to relate numbers to the survey data. Differences between the observed and survey values are minimized non-linearly. Extended Survival Analysis (Anonymous 1994a) is based on an estimate of abundance (in a year and at an age) from cumulative survivals, the terminal population (survival to the end of the year) and sums of catches. The same principles are used as in the Laurec-Shepherd method to estimate catchability, but the terminal *F* can be estimated with an error.

This is a rude simplification of somewhat complex procedures, some statistical like ADAPT, and some not, like Laurec-Shepherd. Their justification is that TACs can be produced in which the managers can put their trust. In moderately exploited stocks which do not vary too much in abundance the result is successful. In heavily exploited stocks, where the variability of recruitment drives differences in TACs from year to year, the procedure demands high skill in the management of uncertainty.

The origin of Gulland's method lies in papers by Jones (1961, 1964) and Murphy (1965). Pope (1972) published a simplification called cohort analysis. Sometimes the more general term "sequential population analysis" is used. This is a somewhat simplified account of the most successful procedure used today in fisheries research. There is an extensive literature on the methods, particularly in the Methods Working Group of the International

Council for the Exploration of the Sea. My interest is limited to the estimation of recruitment, *R*.

There are 2 forms of overexploitation, growth overfishing and recruitment overfishing. Many demersal fish grow by an order of magnitude during their adult lives and if they are caught before they have put on enough weight, the best and most profitable yields are not obtained. The problem of growth overfishing was solved by Beverton and Holt (1957). With estimates of growth and mortality derived from the age distributions they formulated the yield per recruit as a function of fishing mortality. The fishing mortality in the North Sea plaice in the 1930s was 0.73. To obtain the maximal yield per recruit, fishing mortality would have to be reduced by a factor of 3, which meant that two thirds of the fishermen would lose their livelihoods. The solution was obtained by increasing the mesh sizes in the trawls, allowing the little fish to escape and put on weight before they were caught again. In the 1950s, improved yields were obtained by increasing the mesh sizes of the trawls in the North Sea, an application of yield per recruit theory. However, because it was a mixed fishery, the solution was not quite as simple.

The other form of heavy exploitation, recruitment overfishing, occurs when the stock declines so far that the recruitment itself is reduced. The only way of solving this problem at the present time is strictly to ban catches until the stock recovers. Recruitment overfishing cannot be diagnosed from the traditional Stock Recruitment Relationship, because when a decline in recruitment is recognized it may be too late to prevent that form of overfishing. But, as described below, the real trouble is the confusion between the effects of fishing and the advent of poor year classes from environmental causes. This means that recruitment overfishing can be mitigated by banning catches, but we can never be sure that the ban will be effective. The purpose of this EE book is to propose that fisheries science will never be secure until we understand how recruitment is generated.

Fig. 7 shows 2 Ricker Stock Recruitment Relationships with ln Recruitment varying, first by a factor of 10 (Fig. 7a) and secondly by a factor of 3 (Fig. 7b), in a one year class stock. In each, a succession of 3 poor year classes is shown at 2 standard deviations below the geometric mean. With the high variability, stock was reduced by a factor of 5 and by a factor of 2 with the low variability. The one year class stock is heavily exploited. So, under these conditions, the stock with a highly variable recruitment is more vulnerable to recruitment overfishing. A succession of 3 poor year classes is perhaps not very common (see Chapter III), but the recruitment in some stocks is more variable than shown in Fig. 7 (Cushing 1988b).

A number of devices have been invented to prevent recruitment overfishing. An early device was published by Ricker (1958), the limiting or maximal rate of exploitation, that at which stock is reduced to zero, $1 - \exp(-P_r/P_m)$, where P_r is stock at replacement and P_m is that at which maximal recruitment is produced. In Cushing (1971) I used this device to show that in the Californian sardine the maximal rate of exploitation had been exceeded between 1945 and 1950 and that there was circumstantial evidence of high exploitation in the stocks of Japanese sardine, Atlanto-Scandian herring and the Hokkaido herring. The device is useful in such historical studies and perhaps as a rate that should not be exceeded. Nearly all the more recent devices require up to 2 decades of observations. One of the better methods is F_{med}, illustrated in Fig. 8 for the George's Bank haddock (Sissenwine and Shepherd 1989). Fig. 8a shows the Stock Recruitment Relationship and the 3 "replacement" lines represent *Recruit per Stock.* The inverse *Stock per Recruit* is plotted as a function of fishing mortality in Fig. 8b, together with the yield per recruit curve (Fig. 8c). The *Recruit per Stock* is led by the dotted line to its inverse, *Stock per Recruit*, and thence to fishing mortality. So the replacement line on Fig. 8a is labelled $F = 0.5$. If

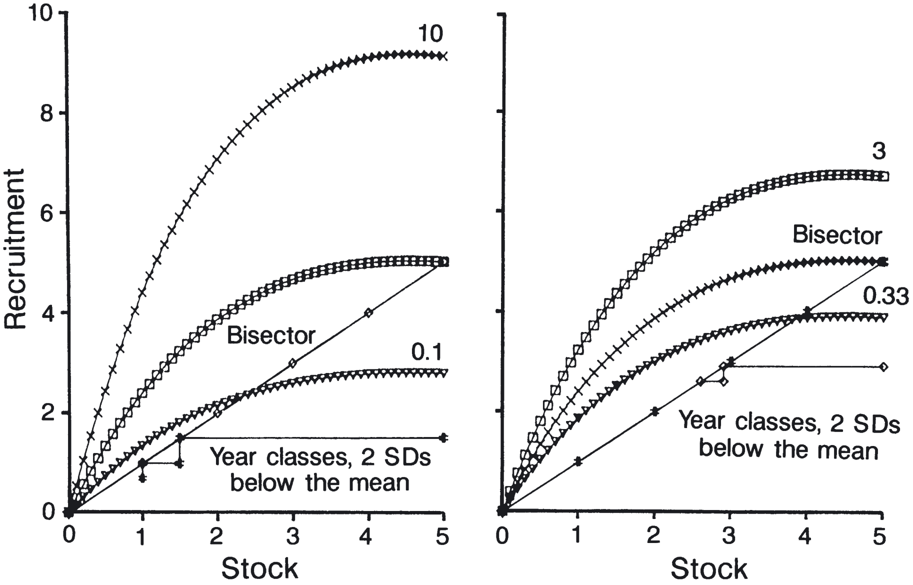


Fig. 7. Ricker Stick Recruitment Relationships. Three poor year classes. Recruitment in a 1 year class stock varies (a) by a factor of 10 and (b) by a factor of 3. The poor year classes lie at 2 standard deviations below the geometric means of Ricker curves ($a = 3$, $b = 0.22$). (After Cushing 1988b)

$F > F_{\text{med}}$ (= 0.5), there is danger of recruitment overfishing. If $F < F_{\text{med}}$ the stock should be secure from recruitment overfishing.

If the 3 poor year classes appear in sequence, F_{med} is reduced a little. If recruitment varied by a factor of 10, the common case, stock would be reduced by a factor of 5 in the 3 years and recruitment overfishing would have taken place. The use of F_{med} requires that recruitment overfishing is produced by too much fishing, which is the simple and straightforward definition. Three poor year classes appeared when the stock of the Peruvian anchoveta *Engraulis ringens* collapsed. It is quite possible that some of the dramatic collapses of fish stocks could have taken place because of environmental influence when fishing mortality was high. Some might consider it perverse to describe the condition as recruitment overfishing. The single year class indicates high fishing mortality and recruitment fails. It cannot be distinguished from recruitment overfishing *sensu strictu* and would have to be treated as such.

Four herring stocks have suffered from recruitment overfishing, the British Columbian herring, the Icelandic summer spawning herring, the Downs herring and the North Sea herring, all of which recovered after a

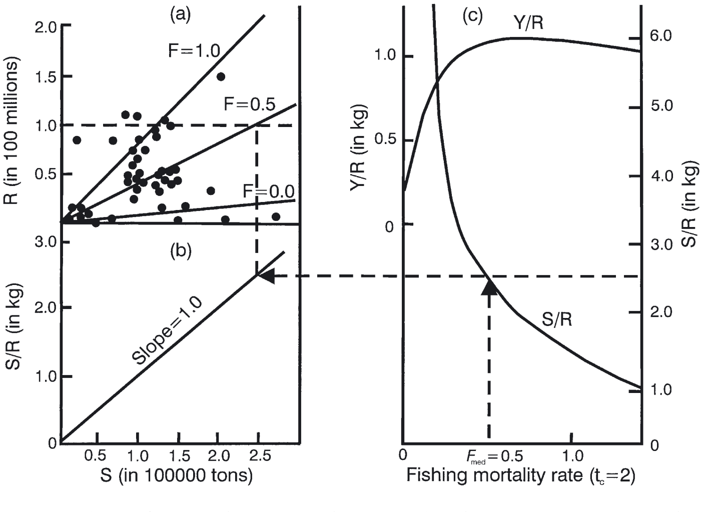


Fig. 8. (a) F_{med}: value of Recruits/Spawning Stock Biomass (R/S) at which half the observations in the Stock Recruitment Relationship lie above the line and half below (for George's Bank haddock). (b) The inverse, S/R, plotted on S. (c) Yield per recruit (Y/R) and S/R, plotted on fishing mortality, *F*. The dotted line links R/S to S/R which defines *F*. As *F* increases, so does R/S and the chance of recruitment overfishing increases. But at F_{med}, the chance of recruitment overfishing, due to fishing alone, is low. t_c = age at first capture. (After Sissenwine and Shepherd 1989)

period during which catches were banned. The Iceland spring spawning stock did not recover. It is likely that the Californian sardine *Sardinops sagax* did so also (but it cannot be shown because recovery did not take place after a ban on catches); the stock recovered subsequently after 2 or 3 decades. The Peruvian anchoveta stock has recovered very recently after a lapse of more than 20 years. Perhaps the regime shift was generated by fishing. It is possible that other herring stocks in the North Atlantic suffered from recruitment overfishing, but there is no evidence. In recent years, the cod stocks in the North Atlantic have tended to decline with poor recruiting year classes and although environmental changes have been postulated, none has been shown. Catches of the Northern cod off Labrador and on the Grand Bank were banned in 1992 (see Chapter IV).

I have shown above how variable were the fish stocks and how irregular were the presences or absences of the catches through the centuries. Chapter II describes how much of this variability is linked to the long-term changes in the climate. Chapter III gives a brief account of our limited knowledge of the mechanisms of recruitment. Fishermen would like to take steady catches, as for example from the plaice stock of the Southern North Sea. This stock lives in a rather special tidal environment where production continues for some months, and it occurs at about the same time each year. Hence the recruitment does not vary very much (if we exclude the high year classes which arose in the cold winters).

The outstanding question is why the study of recruitment, of the fluctuations in stock, has not received the attention it deserves. Long ago, Hjort (1914, 1926) called attention to the fluctuations of the stocks in time, which are in fact the differences in recruitment from year to year. Much research on recruitment has taken place, but it is of a particular nature. It is primarily correlative and because recruitment varies with climatic factors the correlations must be expected to fail. This in itself is discouraging, but the examination of the failing correlations should be pursued until the cause of failure is understood.

The second reason for the failure to study the fluctuations is that indices of recruitment are fed into the assessment procedures in order to proceed to estimates of TACs. In the North Sea such indices are obtained from the international surveys. But they are no more than numbers with an error attached. We need to understand how such numbers were generated.

There is a third reason for not studying the fluctuations: the Stock Recruitment Relationships are not trusted because of the variability of recruitment. Some fisheries scientists say that “there is no Stock Recruitment Relationship” by which they mean that recruitment is not reduced at low stock. This is quite right, but they may not realize how quickly recruitment overfishing can take place despite the events of the past 3 decades.

The real reason, of course, is the cost of research into recruitment. It is usually assumed that the only way in which the research can be carried out is with research vessels for long periods. People have thought that such costs are not worth bearing if recruitment overfishing occurs only from time to time, despite the loss of jobs by the fishermen. This attitude takes no account of the fact that stocks may be expected to change their abundance every few decades. This alone should encourage us to bear the costs. However, in Chapter V, it will be shown that the use of research vessels can be limited.

II CLIMATE AND FISHERIES

Chapter I has recorded anecdotal evidence of the appearance and disappearance of fisheries down the ages, which derives from the great variations in recruitment. Chapter II presents information which displays more fully the link between such events and changes in the climate. First, an account is given of the northerly extensions in range of a number of subtropical animals in the dramatic decade between 1925 and 1935. Then, evidence is presented of the real effect of climatic change on the stocks. From an analysis of 5 pelagic stocks—Pacific mackerel, Pacific sardine, Northern anchovy, Peruvian anchoveta and North Sea herring—it is shown that the larvae reduce the stock of their food organisms. They depend upon them and on the conditions that govern the production of their food. If that is the case their mortality might be density dependent. The account will be restricted to some events since the 1920s in the North Atlantic, all of which are related and which have depended on the extensive and long-term changes in the ocean and atmosphere, primarily the long-term development and collapse of the Greenland High. The driving event was the change in global atmospheric temperature from 1870 onwards which peaked about 1945, manifest in the events of the dramatic decade cited above. The following phenomena will be described: the profound changes in the western English Channel termed "Russell cycle", the concurrent rise and fall of the West Greenland cod fishery, the reduction in recruitment to 13 "deep water" stocks under the passage of the Great Slug or Great Salinity Anomaly of the Seventies, the decline of phytoplankton and zooplankton in the North Sea by the 1970s and their recovery in the 1980s and, lastly, the gadoid outburst in the North Sea in the 1960s and 1970s and early 1980s.

Faunal Movements and the Recent Period of Warming

All animals respond to climatic changes by changing their numbers and by changing their distributional range, or both. During the recent period of warming in the Northeast Atlantic between the 1920s and the 1950s, broad changes took place in the northerly movements, particularly in the dramatic decade 1925 to 1935. At this time when the Greenland High was developing, a period of cyclonicity in winter and early spring started across the North Atlantic (see Fig. 13d). With low pressure there at this season, one would expect southerly winds in the Northeast Atlantic and so subtropical animals were carried north. On the west coast of France, the turtle *Dermotochelys coriacea*, the trigger fish *Balistes* sp. and the medusa *Callianthus ruber* appeared between 1930 and 1932. The saury pike *Scomberesox saurus* was found in 1932 off the Isle of Man and in the North Sea. Albacores *Thunnus alalunga* were seen off the west coast of Scotland and off Fair Isle. The swordfish, twaite shad *Alosa finta*, dragonet *Callionymus maculata* and pollack *Pollachius pollachius* appeared off Iceland for the first time and many other fishes became more abundant there. Redfish *Sebastes marinus*, catfish *Anarrichas lupus*, Greenland halibut *Rheinhardtius hippoglossoides* and the ca'ing whale *Globicephala balaena* were numerous off East Greenland in the 1930s. Off West Greenland, salmon *Salmo salar* and the craspedote medusa *Halopsis ocellata* appeared at the end of the 1920s; redfish and haddock *Melanogrammus aeglefinus* appeared there in 1925 and 1929 respectively, and both cod and haddock returned to the Barents Sea towards the end of the 1920s (Cushing 1982). The appearance of these southern animals off the British Isles between 1925 and 1935 suggests that the cyclonicity was becoming more intense (see Fig. 13d).

Blacker (1957, 1965) recorded the presence or absence of conspicuous benthic animals on the Svalbard Shelf in 2 periods, 1878–1931 and 1949–1956. Atlantic species—*Lithodes maia*, *Hippasterias phrygiana*, *Geodia barretti* and *Sabina sarsi*—were found in 100 to 200 m as far north as Bear Island in the first period. In the second, they had migrated as far north as Prince Charles' Foreland on the northwest coast of Spitzbergen. Nesis (1960) charted a similar movement of benthic animals on the Murman coast of Arctic Russia. A similar northerly movement occurred in the dramatic decade off the west coast of North America (Walford 1931, Hubbs 1948) but that may well have been associated with an El Niño event. A most interesting change was the spread of the southern barnacle *Chthalamus stellatus* around the British Isles in the 1920s and 1930s replacing the northern *Balanus perforatus*, particularly in the western English Channel as far east as St. Alban's Head near Swanage. Between 1960 and 1962 *Balanus* started to return (Southward 1967). Such are a few examples of great extensions in range that occurred between 1925 and 1935. The increase in southerly winds in winter and spring, associated with the rise in cyclonicity, carried the subtropical animals to the north. The Atlantic current off Norway intensified and carried the benthic larvae further north in the Barents Sea. The most interesting point is that low-pressure winds carried animals to Iceland and the southerly wind in the Denmark Strait might well have intensified the Irminger Current, carrying them to West Greenland.

Evidence of Climate Effects

An early demonstration of the link between fish catches and climate change was given by Ottestad (1969, 1986) (Fig. 5 on p. 10). Erlandsson (1936) examined the widths of the annual rings on pines and spruce in northern Sweden and northern Finland. The data were smoothed by moving means of threes and subjected to Fourier analysis. Ording (1940/41) extended the observations to trees on the southern edge of the Vestfjord, where the Arcto-Norwegian cod spawn. Ottestad constructed a compound curve with 4 periods, 11, 17.5, 23 and 57 years each of which has an astronomical basis. The first is the sunspot period, the second the nodal tide, the third the double sunspot cycle and the fourth perhaps the Gleissberg cycle. Fig. 5a shows the fit of this curve to catches of cod in the Vestfjord between 1885 and 1959, lagged by 7 years to correct for the age of recruitment to the adult stock. Fig. 5b shows the relationship in catches per unit effort in the Vestfjord between 1921 and 1968. While trees and cod live in different environments, the common denominators are light intensity (or at the sea surface: irradiance) and temperature, both linked to wind strength and cloudiness. All these are factors that govern primary production and thence food for fish larvae. This implies that the main processes that determine recruitment occur at a relatively early stage in the life history of the cod.

There has been a long history of the study of putative links between recruitment and climatic factors. Long ago, relationships were established with temperature and/or salinity, merely because the observations were available. Recently, the variables examined have become more complex with some promising results. These will be discussed in Chapter III.

Two studies in the last decade or so have established that recruitment is, indeed, modified by climatic factors. Shepherd et al. (1984) examined the recruitments to 18 stocks in the Northeast Atlantic between 1962 and 1976. They made a principal component analysis of ln Recruitments by regions: the first 2 eigenvectors were significant, which means that variation is common within regions. A second principal component analysis was made on Sea Surface Temperatures in February, March and April in the North Sea and off the west coast of Scotland. Three components were significantly correlated with those estimated from the recruitments, accounting for 84% of the variance. The first component was related to temperature and the second to the rise in temperature from February to April. The first component of Sea Surface Temperature is significantly correlated with that of recruitment. The link between the 2 sets of principal components expresses the fact that the recruitments to the stocks between regions depend on differences in temperature from year to year and differences in its rate of increase. Most of the fish species were spring spawners and temperature may be a proxy for those processes that govern the time of onset of the spring outburst when food for the larvae is produced. Hence the variation in year-class strength is properly linked to changes each year in the physical environment.

Table 1a shows the correlation between the first principal component of ln Recruitments and the 3 principal components of Sea Surface Temperature, T_1, T_2 and T_3; Table 1b shows the correlation between the recruitments of 9 stocks and the 3 principal components of Sea Surface Temperature.

Some of the correlations in Table 1 are positive, some are negative. This means that different species have selected different facets of the physical environment in the changes from year to year. In the Northeast Pacific, Hollowed et al. (1987) studied recruitments to 59 stocks of 28 species in 5 regions (Bering Sea, Gulf of Alaska, Canada, Washington/Oregon, California). Expressed as deviations from 5-year running medians, the year classes were grouped in quartiles and the extremes lay in the upper and lower ones. Within regions, year classes were positively correlated, but between them they were not. However, extreme year classes were common to the 5

Table 1. (a) Correlations between the first principal component (PC) of ln Recruitments and the 3 principal components of Sea Surface Temperature (T_1, T_2 and T_3). (b) Correlations of ln Recruitments to 9 stocks and the 3 principal components of Sea Surface Temperature. (After Shepherd et al. 1984)

	T_1	T_2	T_3
(a) First PC of Recruitment vs 3 PCs of Sea Surface Temp.			
	–0.80	–0.33	–0.23
(b) Recruitments vs the 3 PCs of Sea Surface Temp.			
Sole	–0.45	0.35	0.25
Plaice	–0.55	0.45	–0.26
Cod	–0.65	–0.26	0.25
Haddock	0.60	0.13	–0.26
Whiting	0.43	0.17	–0.13
Whiting, West Scotland	0.65	0.07	–0.24
Saithe	0.64	0.06	0.13
Saithe, West Scotland	–0.06	–0.19	–0.13
Herring	–0.56	–0.14	–0.26

regions. Hence there are processes that are distinct for the extreme and for the normal year classes. Fig. 9 shows the proportions of strong and weak recruitments from 1951 to 1982 (Hollowed and Wooster 1992). The El Niño of 1958/59 reduced the year classes as the Kelvin wave travelled north along the shelf break. Again the high year classes of 1960–63 occurred at a time when changes took place in the waters around the British Isles. The studies by Shepherd et al. and by Hollowed et al. come to the same conclusions: elements of recruitment are common within regions but not usually between them. The size of such regions is roughly that of the ordinary depression or anticyclone. This suggests that differences in recruitment might originate in differences in wind strength and direction.

The 3 studies are of some value in demonstrating the importance of climatic factors in determining the magnitude of recruitment. The early work of Ottestad suggested that the cod recruitment in the Vestfjord was linked to some common factors that modify the growth of pine trees in the same region, which must be wind strength and irradiance. The study by Shepherd et al. established relationships between recruitment and temperature in the waters around the British Isles; temperature might well be a proxy for other factors, for example, wind strength and irradiance. Hollowed et al. showed that the distribution of strong and weak year classes was common within regions but not between them. Such is the evidence that recruitment depends on climatic factors, particularly those that might affect larval rather than juvenile lives.

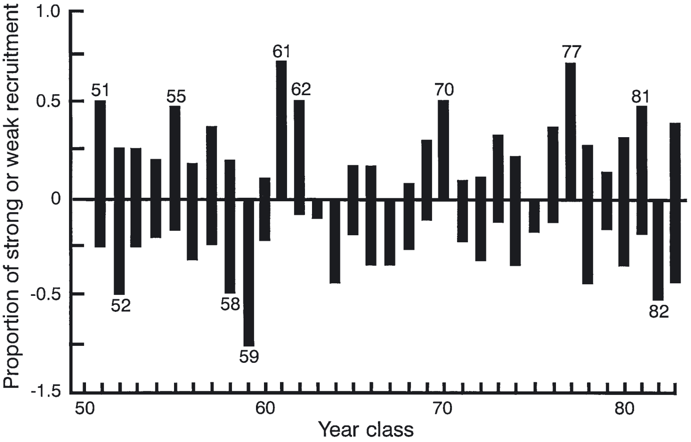
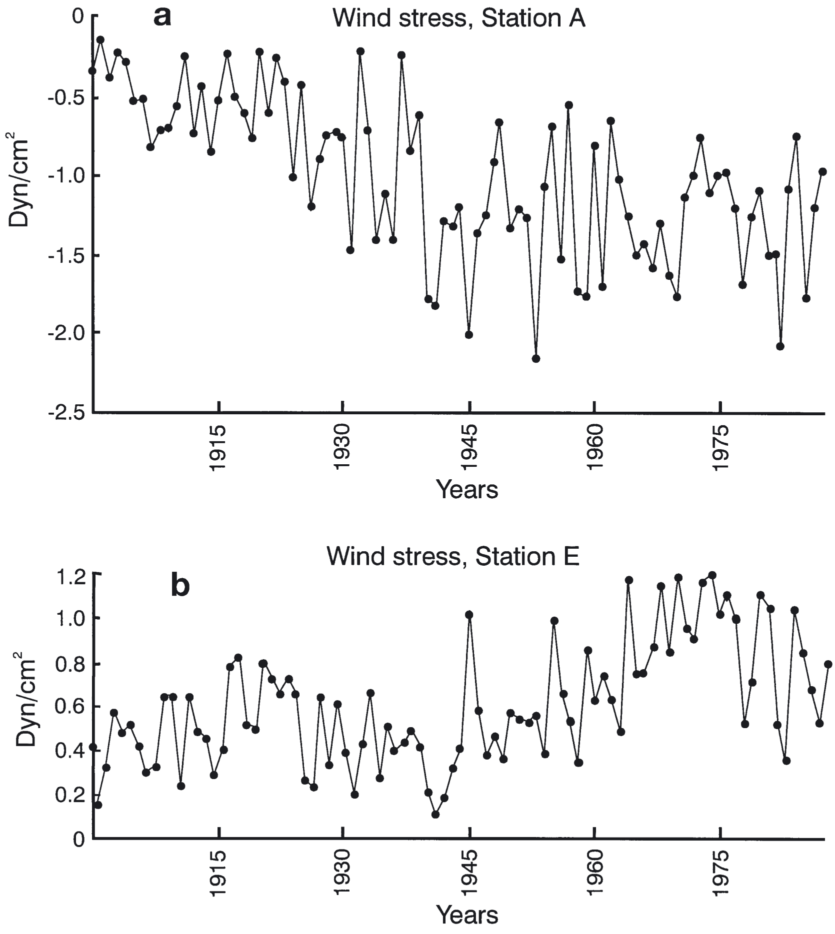


Fig. 9. Proportions of strong and weak recruitments from 1951 to 1982 in the Pacific Northwest. (After Hollowed and Wooster 1992)

Responses of Five Pelagic Stocks to Climate Changes

The responses of pelagic stocks to climate changes have been pronounced, with some fisheries appearing and disappearing over the centuries. Here we shall examine 5 fish stocks: Pacific mackerel, Pacific sardine, Northern anchovy, Peruvian anchoveta and North Sea herring.

Fig. 10 illustrates changes in alongshore winds in dynes cm^{-2} in the Alaska gyral and off the coast of California from 1899 to 1988 (Xie and Hsieh 1991). There are 2 parts to this remarkable time series: (1) the slow increase in wind stress from the 1930s onward at Station A which remained high through to 1988; (2) the small increase in wind strength off



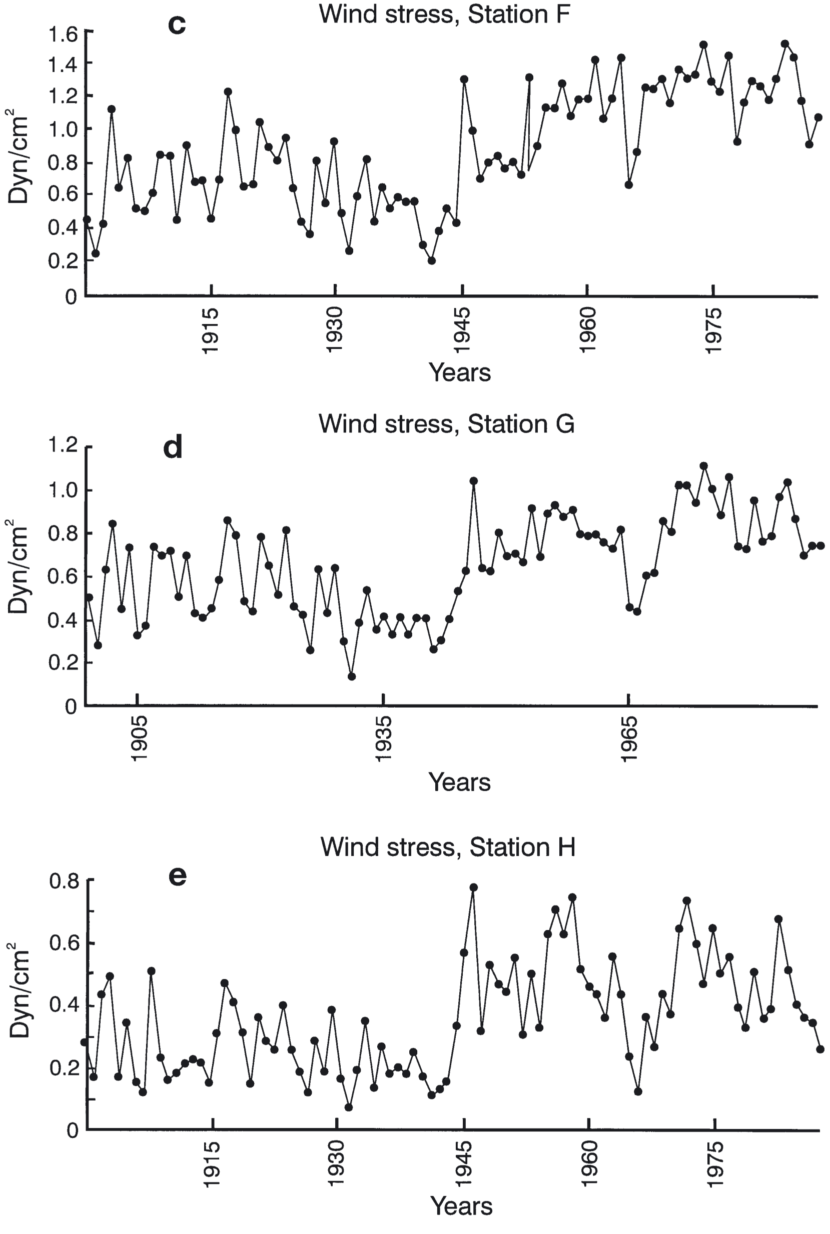


Fig. 10 (facing page and above). Changes in alongshore winds on the west coast of North America from 1899 to 1988. (a) Wind Station A in the north of the Alaska gyral; (b) Station E just north of Cape Mendocino; (c) Station F off San Diego; (d) Station G half way down the peninsula of Baja California; (e) Station H at the southern end of that peninsula. (After Xie and Hsieh 1991)

Table 2. Correlations of recruitment, R (transformed as ln $R+1$)—and for the Northern anchovy, of ln Residuals from the Stock Recruitment Relationship—on wind stress. (After Cushing 1995a)

Wind station	Pacific mackerel	Pacific sardine	Northern anchovy
E	–0.28	–0.56***	0.06
F	–0.39*	–0.74***	0.35
G	–0.53***	–0.72***	0.53**
H	–0.47***	–0.64***	0.36

$^*p < 0.05$, $^{**}p < 0.02$, $^{***}p < 0.01$

the coast of California and Baja California in the 1920s, followed by a decline and then, in the late 1940s, by a sharp increase that subsequently remained high (although it declined somewhat north of Cape Mendocino in the 1980s).

Table 2 shows correlations of recruitment R (transformed as ln $R+1$) or ln Residuals from the Stock Recruitment Relationship for 3 Pacific stocks (Pacific mackerel, Pacific sardine, Northern anchovy) on wind stress in dynes cm^{-2} at Stations E, F, G and H (Xie and Hsieh 1991). Wind stress is used as proxy for food in the upwelling areas (the possibility of offshore transport is discussed below).

Some of these relationships have been described before (see, for example, Parrish and MacCall 1978 on Pacific mackerel). ln Recruitments and ln Residuals were normally distributed and Lowess fits were near linear.

For Pacific mackerel the following relationship was calculated:

$$R = a\,\mathrm{SSB}^{b}\,\mathrm{Wind}^{c}$$

where R is ln $(R+1)$; SSB is Spawning Stock Biomass in tonnes; Wind is wind stress in dynes cm^{-2}; a, b, and c are constants. The following ANOVA was calculated ($r^2 = 0.38$):

	Coefficient	Standard error	*t* (2-tail)	p
Constant	3.260	0.769	4.239	0.000
SSB	0.293	0.178	1.648	0.109
Wind	–0.849	0.353	2.406	0.022

The coefficient of SSB is not significant, so the simple negative regression of recruitment on wind may stand.

For Pacific sardine the ANOVA was ($r^2 = 0.86$):

	Coefficient	Standard error	*t* (2-tail)	p
Constant	2.307	0.769	3.715	0.001
SSB	0.880	0.107	3.715	0.001
Wind	–0.216	0.314	–0.909	0.329

The coefficient of wind stress is not significant and dependence of recruitment on SSB (which is near linear) predominates.

For the northern anchovy the ANOVA was ($r^2 = 0.45$):

	Coefficient	Standard error	*t* (2-tail)	p
Constant	–4.861	2.033	2.391	0.026
SSB	0.760	0.312	2.437	0.024
Wind	1.536	0.591	2.598	0.017

Both the coefficients of SSB and of wind are significant. Perhaps as the wind stress increased, so did the recruitment.

It has been suggested (Bailey 1981, Sinclair et al. 1989) that the negative dependence of recruitment on wind stress was the result of offshore drift by Ekman transport. However, the eggs and larvae of the Pacific mackerel are distributed in abundance up to 500 km offshore whereas the boundary to coastal upwelling lies about 50 km from the coast. So the argument that the negative regression is the result of offshore transport falls. Eggs and larvae of Pacific sardine and Northern anchovy were also distributed up to 500 km offshore. The real point is that the dependence of recruitment on wind stress may be positive or negative, independently of the offshore transport.

Fig. 11a shows the trend in upwelling winds off Peru which increased from 1953 to 1984. From the early 1970s the rate of upwelling increased in this area. As upwelling winds increased, zooplankton declined (Fig. 11b). The recruitment to the anchoveta stock (October to December) was correlated positively with the abundance of zooplankton (Fig. 11c). As the zooplankton declined during the period of increased upwelling, this may have contributed to the collapse of the anchoveta stock in 1971–73; the stock was heavily fished at this time. With stronger upwelling, the quantity of the zooplankton declined and with it the recruitment to the anchoveta stock. The concatenation of physical and biological events shows how the three poor year classes that reduced the stock of Peruvian anchoveta might have been generated.

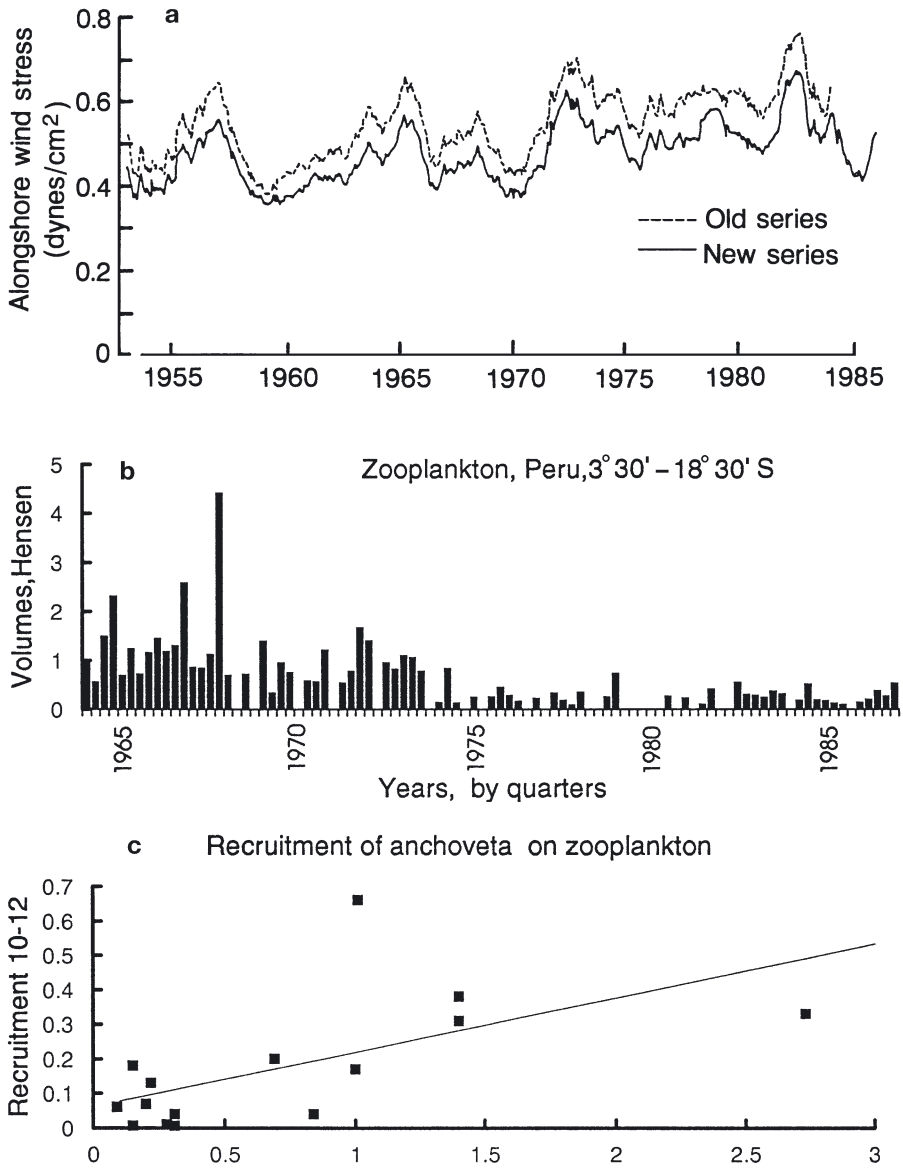


Fig. 11. Upwelling off Peru. (a) Rising trend of upwelling from 1953 to 1984 after which it tends to decline (after Bakun and Mendelssohn 1989). (b) Decline in zooplankton from 1964 to 1987 (after Carrasco and Lozano 1989); values in wet weight (g) taken by a Hensen net. (c) Relationship between recruitment to the anchoveta stock in October to December (10–12) off Peru and zooplankton in that month (after Cushing 1995)

The North Sea herring flourished in the 1950s and early 1960s, but it collapsed in the early 1970s after a period of heavy purse seine fishing. After a ban on catches from 1977 to 1982, the stock recovered. Presumably it had suffered recruitment overfishing. Hardy (1924) had shown that larval herring in the North Sea depended on the presence of *Pseudocalanu*s. Table 3 shows the relationship of ln Residuals from the Stock Recruitment Relationship of North Sea herring upon ln *Para/Pseudocalanus* from the Continuous Plankton Recorder Network in areas B2 (northwestern North Sea) and C2 (west central North Sea) from 1948 to 1991 (data with the permission of the Director of the Sir Alister Hardy Foundation for Ocean Science).

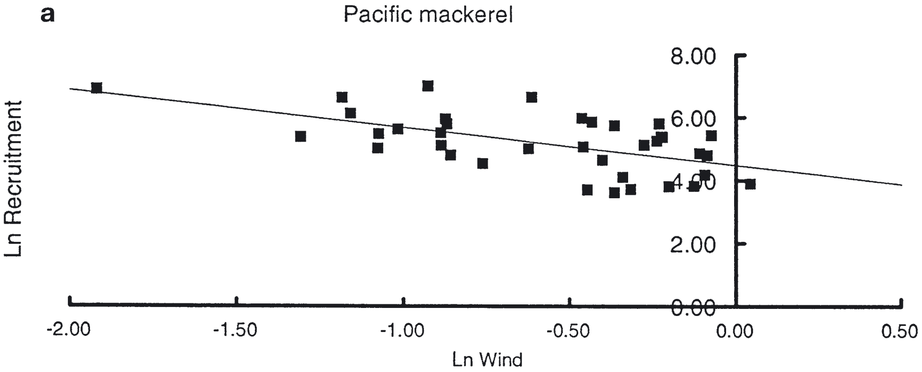
There are 2 remarkable points about Table 3. The first is that the important relationships are negative, as in the Pacific mackerel. The second is that they were established 3 to 6 months after hatching, when the larvae were approaching metamorphosis. In other words, if recruitment is determined during the larval stage it is the later stages which are important. Perhaps North Sea herring depend not only on the autumn outburst but also on the outburst in the following spring. They subsist on *Pseudocalanus* throughout the winter, when it eats detritus.

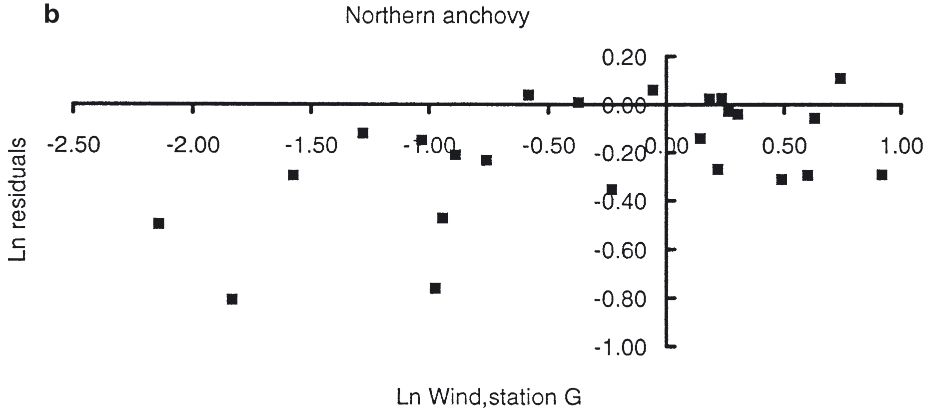
Fig. 12a shows the negative regressions of ln Recruitment on wind stress for the Pacific mackerel and Fig. 12b shows the positive one of the ln Residuals from the Stock Recruitment Relationship of the Northern anchovy on

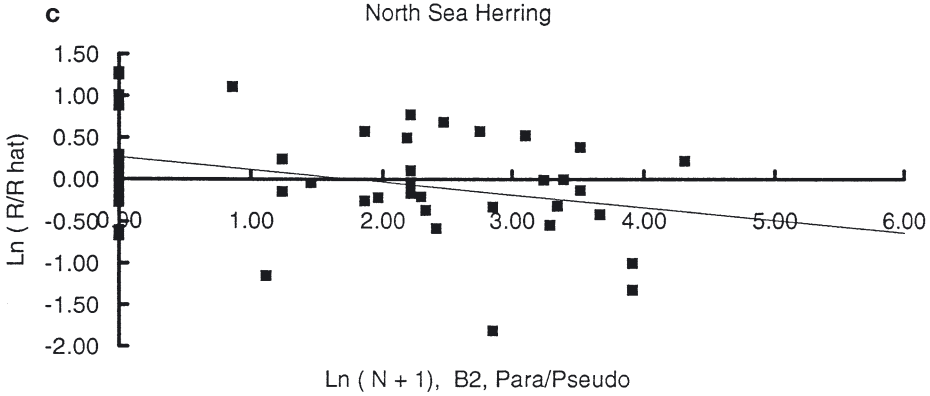
Table 3. Dependence of ln Residuals from the Stock Recruitment Relationship of North Sea herring on ln *Para/Pseudocalanus* in areas B2 (northwestern North Sea) and C2 (west central North Sea). (After Cushing 1995a)

	B2	C2
September	0.02	–0.06
October	0.14	–0.04
November	–0.33*	–0.11
December	–0.36*	–0.12
January	–0.04	–0.31*
February	–0.33*	–0.37**
March	–0.26	–0.48***
April	–0.08	–0.38**
May	–0.17	–0.33**
June	–0.11	–0.25

*$p < 0.05$, **$p < 0.02$, ***$p < 0.01$


a
Pacific mackerel
Ln Recruitment
8.00
6.00
4.00
2.00
0.00
-2.00
-1.50
-1.00
-0.50
0.00
0.50
Ln Wind


b
Northern anchovy
Ln residuals
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-1.00
-2.50
-2.00
-1.50
-1.00
-0.50
0.00
0.50
1.00
Ln Wind,station G


c
North Sea Herring
Ln (R/R hat)
1.50
1.00
0.50
0.00
-0.50
-1.00
-1.50
-2.00
0.00
1.00
2.00
3.00
4.00
5.00
6.00
Ln (N + 1), B2, Para/Pseudo

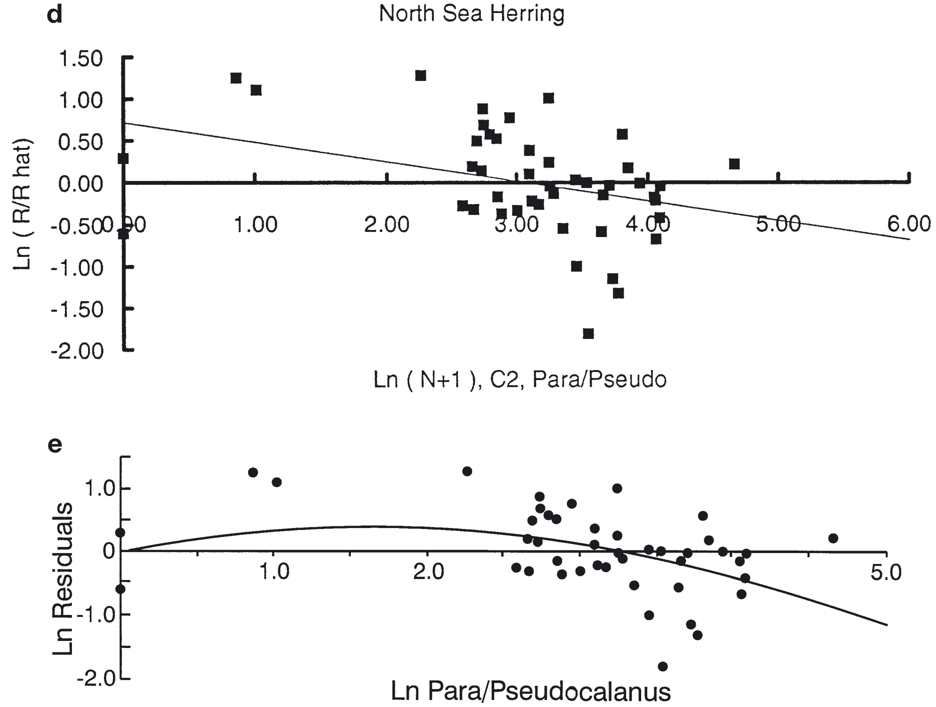


Fig. 12 (facing page and above). Relationships of Recruitment (ln R+1) or ln Residuals from the Stock Recruitment Relationship on wind stress or zooplankton. (a) ln (R+1) of Pacific mackerel on wind stress at Wind Station G; (b) ln Residuals from the Stock Recruitment Relationship of Northern anchovy on wind stress at Wind Station G; (c) ln Residuals from the Stock Recruitment Relationship of the North Sea herring on ln *Para/Pseudocalanus* in the Continuous Plankton Recorder Network area B2 (northwestern North Sea) in December; (d) ln Residuals from the Stock Recruitment Relationship of the North Sea herring on ln *Para/Pseudocalanus* in the Continuous Plankton Recorder Network area C2 (the west central North Sea) in March, 6 months after spawning; (e) eye-fitted relationship of ln Residuals from the Stock Recruitment Relationship of North Sea herring on ln *Para/Pseudocalanus* in the Continuous Plankton Recorder Network area C2 (the west central North Sea). (After Cushing 1995a)

wind stress. The figure also reveals the negative regressions of ln Residuals from the Stock Recruitment Relationship of North Sea herring on ln *Para/Pseudocalanus* for the areas B2 and C2 in the western North Sea (Fig. 12c, d). North Sea Herring spawn in the western North Sea and their larvae are drifted towards the German and Danish coasts and the Skagerrak. The question again arises whether the negative regressions for the herring are the consequence of the drift away from the western North Sea. The relationship of ln Residuals on ln *Para/Pseudocalanus* remains negative and significant when all areas of the North Sea are used, B2, C2, B1 and C1 (that is all areas of the North Sea north of the Dogger Bank), so the possibility that the negative regression stems from the drift to the east does not arise.

There are 2 negative regressions on food, 1 negative one on wind stress and 1 positive one on wind stress. Cushing (1995a) lists 9 such regressions, some positive, some negative. The simplest explanation of this phenomenon is that there is a predator/prey relationship in which the fish larvae can sometimes reduce the numbers of their food organisms. Then one would expect a positive relationship between predator and prey when the prey numbers are high and a negative one when they are low, relative to the numbers of predators. This is analogous to the production of fish as a function of the stock, which Schaefer (1954) expressed as a parabola with a maximum at half stock. Fig. 12e illustrates a relationship of ln Residuals from the Stock Recruitment Relationship of the North Sea herring on ln *Para/Pseudocalanus* in the Plankton Recorder area C2 in March. The curve through zero is eye fitted. If this relationship is true, then not only are positive and negative regressions to be expected, but also the lack of any relationship at all.

There are 2 conclusions from this brief survey (Cushing 1995a): (1) recruitment is at least partly determined during the larval stage as a function of the food available and just before metamorphosis; (2) if recruitment depends on food for the larvae it must also depend on the conditions of food production expressed, for example (and only as an example), in the Sverdrup mechanism. This is the real basis for the extraordinary link, long known, between climate and fisheries.

In an earlier section links were demonstrated between recruitment and climatic factors, particularly those which might affect larval or late-larval stages. In this section a complex relationship has been proposed between recruitment and food for larvae. If the Sverdrup mechanism is at the root of the process, then the time of onset of the spring outburst in temperate or high-latitude waters (or its analogue in upwelling areas) is of some importance. It has some bearing on the validity of the match/mismatch hypothesis (Cushing 1990).

The general relationship between recruitment, stock and ln *Para/Pseudocalanus* is dominated by the stock component. However, there is a negative relationship between ln Recruitment and ln *Para/Pseudocalanus* perhaps generated in the 1950s and early 1960s when North Sea herring were particularly abundant, and perhaps the herring larvae reduced the stocks of their food. It is tempting to suggest that the delay in production during the 1970s reduced the quantities of *Para/Pseudocalanus* at that time and may have played a part in the decline of the herring recruitment in the 1970s. Such a thesis cannot be developed with the methods used above because our analyses are spread over long time series that include the events of one decade or another. The variability of the Stock Recruitment Relationship is high enough to prevent further analysis by the present simple methods.

The Climate of the North Atlantic

The changes in global atmospheric temperature from 1860 to the present day are shown in Fig. 13a in which a warm epoch lasted from the 1920s to the early 1960s to be succeeded by a cool one (Schlesinger and Ramankutty 1994). All the events described above derive from this major long-term change. In the North Atlantic, a number of long-term changes have been recorded. Fig. 13b shows the time series of the North Atlantic Oscillation

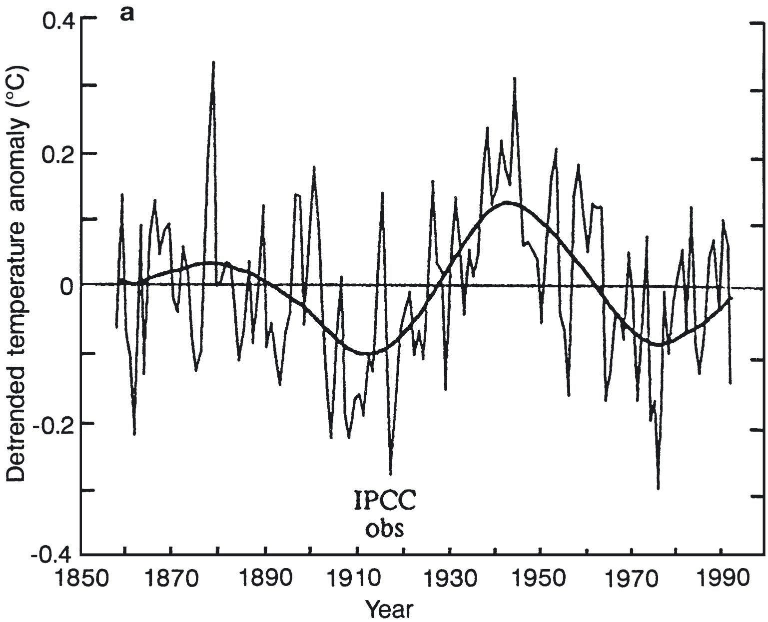


Fig. 13 (above and on subsequent pages). Climate change in the North Atlantic. (a) Changes in global atmospheric temperature from 1860 to 1991 from the Intergovernmental Panel on Climate Change (IPCC) (after Schlesinger and Ramankutty 1994)

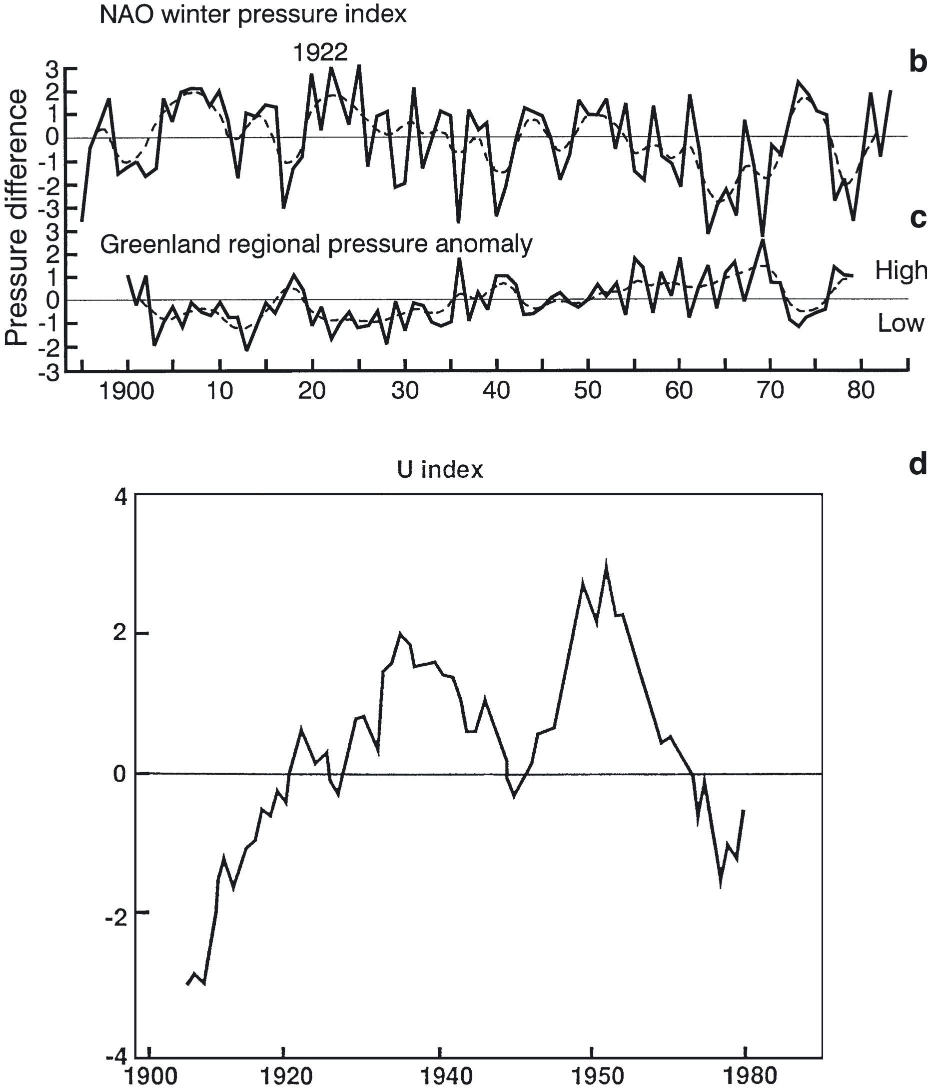
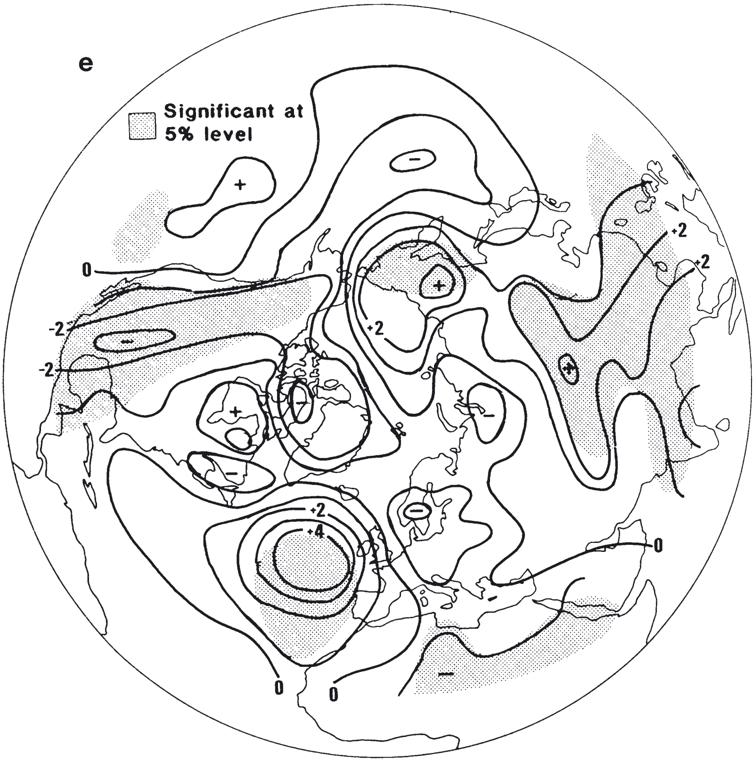
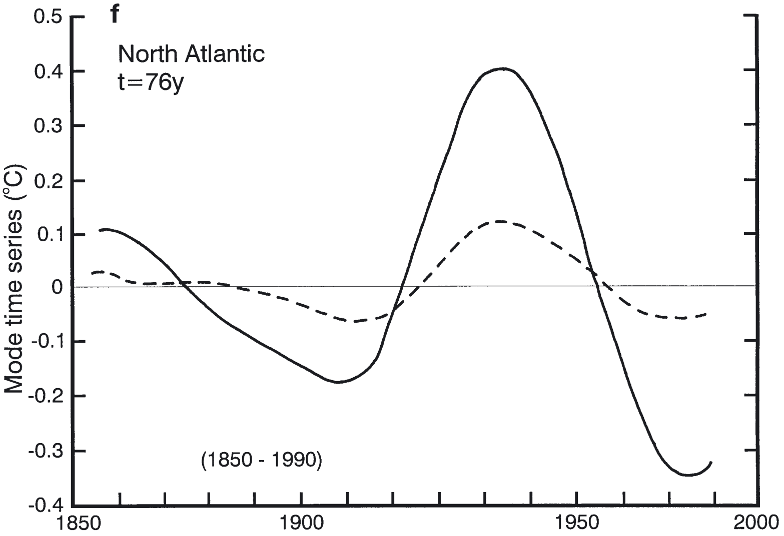


Fig. 13, continued. (b) North Atlantic Oscillation, the normalized winter pressure difference between Punta Delgado in the Azores and Akureyri in Iceland (after Rogers 1984); Rogers believed that the system peaked in 1922; (c) Greenland winter mean pressure anomaly between 1900 and 1979 (after Rogers 1984); (d) index of cyclonicity, the 15-year running means of the difference between the winter zonal component (at 30°–40° N, 20°–40° W and 50°–60° N, 20°–40° W) (after Kushnir 1994); (e) ridge of pressure difference in March and April in the Northeast Atlantic between the 1950s and the 1970s (after Dickson et al. 1988a); (f) the curve derived by Schlesinger and Ramankutty for the North Atlantic only


e
▨ Significant at 5% level
+
−
0
-2
-2
−
+
+2
+
−
+
−
+
−
+2
+2
+2
+4
−
0
−
0
0


f
North Atlantic
t=76y
Mode time series (°C)
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
(1850 - 1990)
1850
1900
1950
2000

from 1895 to 1983 (Rogers 1984), which is the mean normalized winter pressure difference between Punta Delgado in the Azores and Akureyri in Iceland. It indicates changes in the mid-latitude westerlies; in general, it weakened from 1925 onward to a minimum in the 1960s. Fig. 13c illustrates the Greenland winter mean pressure anomaly between 1900 and 1979 (Rogers 1984). It shows how the Greenland High developed slowly from the mid-1930s to a peak between 1955 and 1970, after which it collapsed; the build-up corresponds very roughly to the increase in the wind stress at Stn A in the north of the Alaska gyral (Fig. 10a). The lines on both Fig. 13a and Fig. 13b show the data smoothed by a low pass filter. The North Atlantic Oscillation tended to decrease as the Greenland High became more prominent. Fig. 13d shows the 15-year running means of the difference between the wintertime zonal component at 30°–40° N, 20°–40° W and 50°–60° N, 20°–40° W; positive values indicate a cyclonic circulation (Kushnir 1994). So the central North Atlantic was dominated by it between 1920–25 and 1970. Fig. 13e displays the ridge of pressure difference between the 1950s and the 1970s in March and April in the Northeast Atlantic; as a consequence, the northerly wind in spring increased in the North Sea. At the same time the incidence of gales rose in the western North Sea, but not in the east (Dickson et al. 1988a). The Greenland High had collapsed in the 1970s. The existence of the Greenland High and the cyclonicity in the North Atlantic are really distinct parts of the same phenomenon and the increase in northerly wind over the British Isles between the 1950s and the 1970s was a consequence of the collapse of the system.

The 4 events—cyclonic circulation in winter in the North Atlantic, Greenland High, North Atlantic Oscillation and ridge of pressure difference—all stem from the succession of a warm epoch by a cool one. Dickson and Namias (1976) examined the weather and climate along the eastern seaboard of the southeastern United States. They found that the maintenance of the Greenland High depended upon changes in the baroclinic field along that seaboard, themselves probably stemming from changes in the heat budget of the North Pacific.

The 3 indices yield different views of the same phenomenon. The index of cyclonicity starting in 1925 betrays the existence of low pressure in winter and early spring across the North Atlantic. So the westerlies portrayed in the North Atlantic Oscillation declined a little from 1925 onward. The index of cyclonicity declined towards the end of the 1960s. The Greenland High started in the 1930s and persisted to the end of the 1960s. The Greenland High might be the proximate cause, with the low pressure further south being the consequence. Then, when the Greenland High collapsed at the end of the 1960s the pressure difference ridge in the Northeast Atlantic became established.

Schlesinger and Ramankutty (1994) analyzed the material from the atmospheric changes in temperature in the North Atlantic (Fig. 13a) and extracted a period of 76 years (Fig. 13f), which is twice that of Kushnir's cyclonicity index. Such a period did not exist in the Indian Ocean or the South Pacific. They suggested that the cause lay in the ocean-atmosphere system. When we consider the herring and pilchard periods in the western English Channel as part of the extended Russell cycle (see below), it will be suggested that such a periodicity is not unlike that of Schlesinger and Ramankutty.

Records of fisheries and biological oceanography do not extend very far back in time, the earliest reliable material dating from the 1920s, although there are earlier records of catches. The 5 phenomena described above are facets of the long-term secular change in temperature. Five distinct effects on fisheries, ecosystem or the plankton will be described below, all of which are rooted in the changes described in earlier paragraphs. They are the Russell cycle (the changes in the ecosystem of the western English Channel), the rise and fall of the West Greenland cod fishery, the effects on recruitment of the passage of the Great Slug or the Great Salinity Anomaly of the Seventies, the decline and recovery of phytoplankton and zooplankton in the North Sea and lastly the gadoid outburst in the North Sea.

Russell Cycle

Sir Frederick Russell and Dr Alan Southward sampled the larger zooplankton, including fish larvae, at Station E1, south of the Eddystone Lighthouse in the western English Channel, from 1924 to 1988; they intended to sample the system once a week, but this was not always achieved. The main signal was the reduction in winter phosphorus in 1930/1 by nearly 30% and its recovery by nearly the same factor between 1968 and 1971 (Russell et al. 1971, Southward and Boalch 1994) (Fig. 14); a partial recovery took place in the mid 1950s (see below). In October 1965 Sir Frederick recorded the presence of *Pelagia noctiluca*, a scyphomedusan with ephyra larvae; for him, this signalled a return to the conditions of the 1920s. Indeed, changes in the ecosystem that had taken place between 1925 and 1935 were reversed between 1965 and 1979. The Russell cycle is approximately the half period of that observed by Schlesinger and Ramankutty (1994).

There were 5 changes in the ecosystem: in winter phosphorus, numbers of fish larvae, quantities of the macroplankton (including *Calanus*), presence or absence of the northwest indicator *Sagitta elegans* or the southwest indicator *Sagitta setosa*, and presence or absence of a large pilchard population.

The Plymouth herring population started to decline with the 1926 year class and by 1938 the fishery had ceased. Macroplankton declined by a factor of 4 in 1930/1. In 1935 large numbers of pilchard eggs were caught at Station E1 (which implies that a good year class had hatched 3 or 4 years before). Summer-spawned larvae (excluding the clupeids) declined after 1931 and spring-spawned ones after 1935. In 1965, the numbers of fish larvae increased by 1 order of magnitude. In autumn 1970, the amount of macroplankton rose by a factor of 4, and in the same year *Sagitta elegans* replaced *Sagitta setosa*, but the numbers did not reach those of the 1920s until 1978. Southward (1963) showed that the medusa *Aglantha digitalis*, the polychaete *Tomopteris helgolandica*, the mollusc *Spiratella retroversa* and the euphausiid *Meganyctiphanes norvegica* all disappeared after 1931. They were replaced by the southwesterly animals *Euchaeta hebe*s, *Liriope tetraphylla* and the euphausiid *Nyctiphanes simplex*. The change from the northwest to the southwest indicators led Sir Frederick Russell to believe that it was of advective origin. These events are illustrated in Fig. 15.

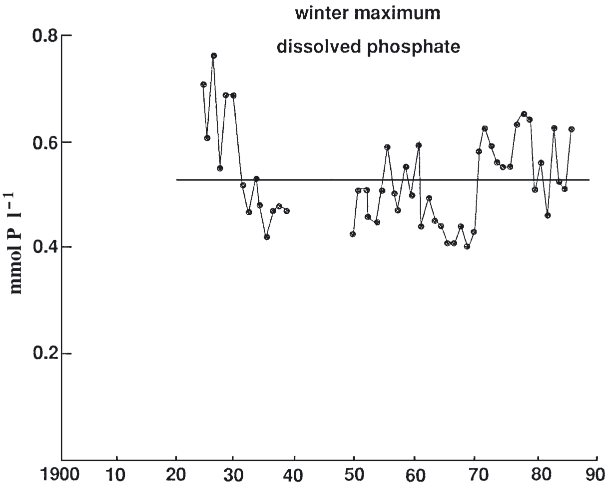


Fig. 14. Changes in winter phosphorus at Station E1 in the western English Channel between 1924 and 1988. (After Southward and Boalch 1994)

Southward et al. (1975) found a secular trend in warming in sea surface temperatures at Station E1 between 1924 and 1972 which peaked in 1945, so the pilchard period was a warm one. They found positive correlations of both catches of hake and summer numbers of pilchard eggs with temperature, but autumn numbers of pilchard eggs were inversely related to temperature (see also Southward et al. 1975). Southward and Boalch (1994) documented that towards the end of the pilchard period, the warm one, the stock retreated to the west and spawned later in the year. From old records of the pilchard fishery in Cornwall they demonstrated that catches of herring and pilchard alternated from the late sixteenth century and suggested that the alternation expressed long-term secular changes in temperature, as noted above.

Cushing (1961) believed that herring and pilchard populations competed with each other. Catches per unit of effort of the recruiting herring year classes were positively related to the winter phosphorus 1 year after they were hatched, but numbers of pilchard eggs depended inversely on the winter phosphorus 6 months after they were hatched. So herring hatched in winter appeared to be inversely related to pilchards hatched in the following summer—linked by the quantity of winter phosphorus in succeeding relationships. The recruitments to the herring populations declined from 1926 to 1930 and subsequently. The rise in numbers of pilchard eggs was not recorded until 1935 but it is possible that the decrement in phosphorus represented an increment in 6-month-old pilchards. The question arises whether waters with low phosphorus values could be found elsewhere in the North

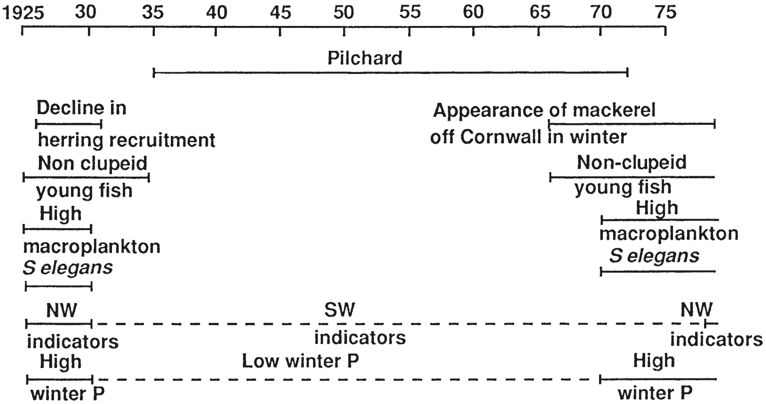


Fig. 15. Changes in the ecosystem of the western English Channel at Station E1 between 1924 and 1978, showing the Russell cycle. (After Cushing 1982)

Atlantic. Winter phosphorus values of about 0.7 mmol P l^{-1} were found in the Faroe Shetland Channel, in the North Irish Sea, in the North Atlantic (at 55° to 58° N) and in the Rockall Channel (Johnstone and Jones 1965, Ellett and Martin 1973). The low values characteristic of the western Channel and the region south of Ireland in the pilchard period (Southward 1962) are not found elsewhere and are probably not due to advection.

The changes in the ecosystem in the western English Channel were profound, involving herring, pilchards, spring- and summer-spawned larvae, macroplankton and *Calanus*, an array of indicator species and shell gravel molluscs. There is, of course, no information on the driving force of the ecosystem, such as primary production (save in the late 1970s and 1980s). The 3 possible explanations for the changes—advection, alternation of warm and cool periods, and competition—may well all be true. During the period of cyclonicity in the North Atlantic the average wind would have blown from the southwest and from the northwest during the cool periods before and after. The recent half period between 1925–35 and 1966–78 was a warm epoch of pilchards with southwesterly indicator species. It has recurred at intervals since the late sixteenth century. The northwesterly indicators characteristic of the herring period, the cool period, were observed before 1930–31 and after 1965–71 (in fact, mackerel replaced herring).

From the evidence there is an alternation of warm and cool epochs with a period of about 76 years. The warm pilchard time is characterized by cyclonicity across the North Atlantic, low winter phosphorus and a particular arrangement of the marine ecosystem there. When the index of cyclonicity fell sharply in the mid 1950s the winter phosphorus rose. It appears that the ecosystem responds to changes in the atmosphere. If the period really exists, there is the possibility that the next switch can be predicted and then the whole ecosystem in the western English Channel can be re-examined.

The changes in the western English Channel under the name of the Russell cycle are characteristic of regime shifts which have been recognized throughout the world ocean (Steele 1985). The most prominent is that between sardine and anchovy in the upwelling systems and off Japan (perhaps the coastal boundary of the Kuroshio should be regarded as an analogue of a major upwelling system). Off Japan, sardines flourished from the early 1920s to the early 1940s and they recovered in the early 1970s. In the intervening years between the late 1940s and the 1970s the anchovies predominated. Similar switches occurred off South America, in the Benguela Current and off California. They were observed in detail for nearly 2000 years in the scales recovered from anoxic deposits off California (Soutar and Isaacs 1974, Smith and Moser 1988, Baumgartner et al. 1992). Each regime appears to last about 30 to 40 years, which is roughly that observed in the Russell cycle. The regime shifts (Steele in press) in the western English Channel occurred at the start and at the end of the period of cyclonicity in the North Atlantic. Analogous atmospheric events may occur in the upwelling areas like the sharp increase in wind stress off California in the early 1950s (Fig. 10).

West Greenland Cod Stock

Dickson et al. (1994) recorded the presence of cod on the offshore banks off West Greenland in the twenties and forties of the nineteenth century. They were absent from those banks in the late nineteenth century and in the first decade of the present one. Between 1912 and 1923, small catches were made, 20 to 680 tonnes. Between 1925 and 1930, catches rose to about 60 000 tonnes. Good year classes occurred in 1922, 1924, 1926, 1934, 1936, 1942 and 1945 and the last good ones were hatched in 1956, 1961 and 1963 (Cushing 1982). Fig. 16 shows the Sea Surface Temperature Anomalies off West Greenland between 1876 and 1970. The Greenland High implies easterly winds across the Denmark Strait and relatively warm southerly winds along the west coast of Greenland. Between 1876 and 1920 the water off

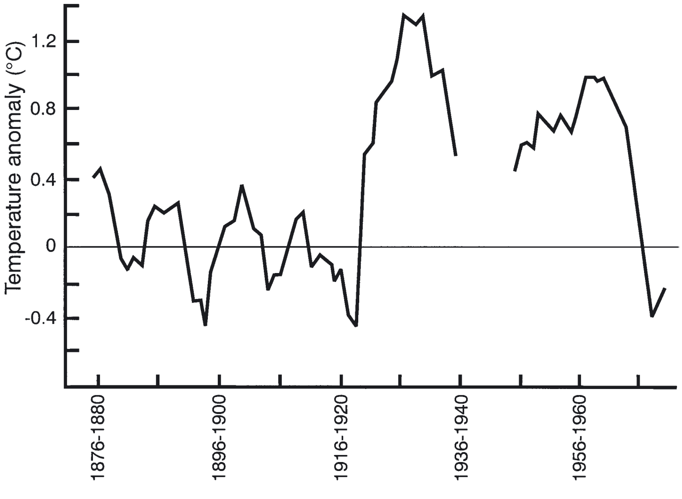


Fig. 16. Sea Surface Temperature Anomalies off West Greenland, 1876 to 1970. (After Høvgard and Buch 1990)

West Greenland was cold, perhaps too cold for the cod. The warm period on the banks persisted from the early 1920s to the late 1960s, and this was the period of the fishery from which very large quantities of fish were taken, worth more than US $12 billion at present day prices.

The West Greenland cod stock probably originated in the drift of larvae and juveniles from Iceland in the Irminger Current, which streams from Iceland towards Greenland where it mixes with the southbound East Greenland current as both round Cape Farewell, the southernmost point of Greenland. Fig. 17 illustrates (1) the lack of any larval drift in 1903–06 (Schmidt 1909); (2) the presence of larvae and juveniles across the Denmark Strait in 1963 during the Norwestlant expedition (Hansen 1968). A remarkable tagging experiment, carried out between 1924 and 1936 by Tåning (1937) and subsequently by Hansen (1954), showed that 8-year-old mature cod migrated from West Greenland to Iceland to spawn, particularly in the years 1931–36; few Icelandic mature fish reached West Greenland to spawn. At that time mature cod were also spawning at West Greenland; the proportion of tagged West Greenland fish fell between 1945 and 1969. Schopka (1991) showed that from 1953 onwards 700 000 tonnes of 8-year-old cod of the 1945 year class were caught at Iceland. However, in later years, the migration from West Greenland was less intense. There has, however, been a continuous input from West Greenland to Iceland of mature cod up to the present day particularly of the 1973 and 1984 year classes (Shepherd and Pope 1993).

The West Greenland cod fishery owes its existence to the Greenland High, when easterly winds blow across the Denmark Strait and southerly winds blow north along the west coast of Greenland; the Greenland High persisted from 1935 to the late 1960s, the period of the cod fishery. Fig. 18 shows (1) the change in mean winter sea level pressure and surface winds between 1890–1914 (a cold period) and 1925–1939 (a warm period); (2) the change between 1970–84 (cold) and 1950–64 (warm). In both cases there is an increase in easterly winds across the Denmark Strait and a deepening of low pressure in the central North Atlantic. Thus as the temperature rose in the late 1920s, the easterly winds increased across the Denmark Strait, presumably carrying the larvae and juveniles in the Irminger Current from Iceland to Greenland. As the temperature fell, there was a southerly wind over the Denmark Strait denying transport across it to Greenland (Fig. 19).

Most remarkably, the period of the West Greenland fishery (Fig. 20) is that of the Russell cycle starting in the early 1920s and ending in the late 1960s. Further, the period of relatively warm water at West Greenland also

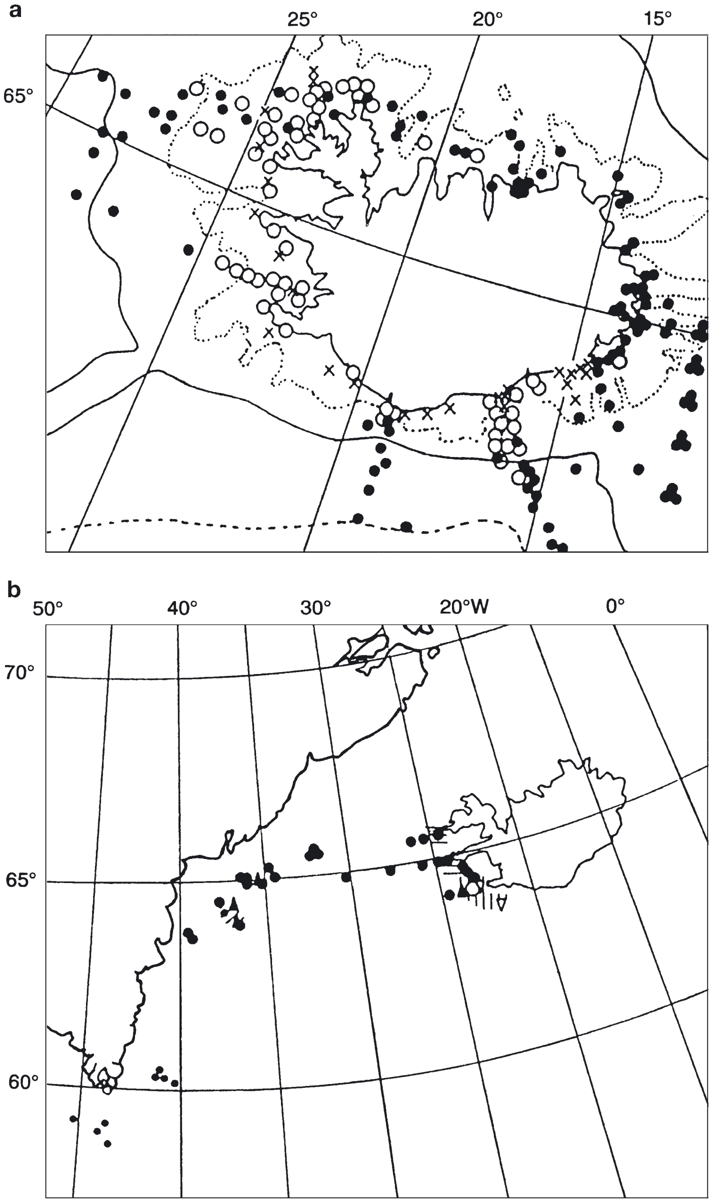


Fig. 17. Passage of eggs and larvae across the Denmark Strait. (a) Lack of larval drift in the first decade of the century (after Schmidt 1909); (b) presence of larvae and juveniles across the Denmark Strait in 1963 (after Hansen 1968). In (a), open circles represent presence of pelagic larvae; full circles, samples with no larvae; and crosses, eggs. In (b) the symbols represent presence of cod eggs and larvae at different levels of abundance, and short hatch lines indicate spanning grounds

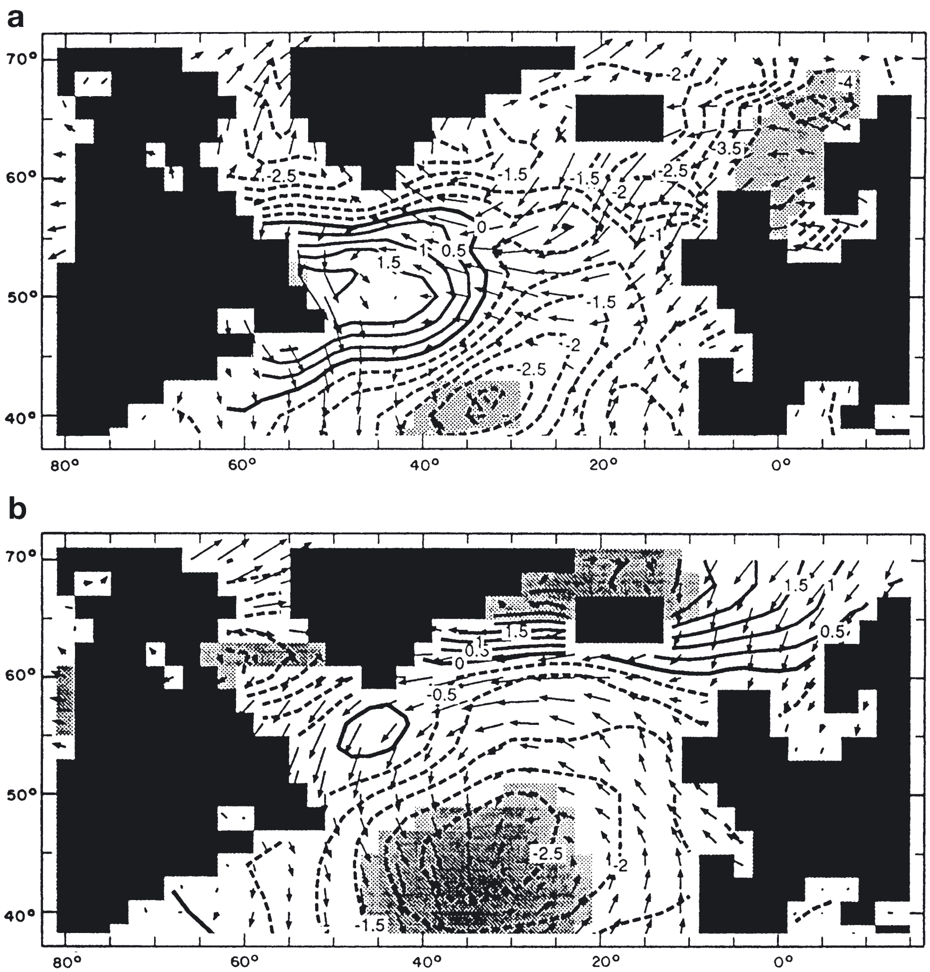


Fig. 18. Generation of easterly winds across the Denmark Strait. (a) Change in mean winter sea level pressure and surface winds between 1890–1914 (a cold period) and 1925–1939 (a warm period). (b) Change between 1970–1984 (a cold period) and 1950–1964 (a warm period). (After Dickson and Brander 1993)

Fig. 20. The period of the West Greenland cod fishery (catches are indicated by the line). Appearance of haddock (which do not spawn off Greenland) off West Greenland is also shown (indicated by the bars). (After Dickson and Brander 1993)

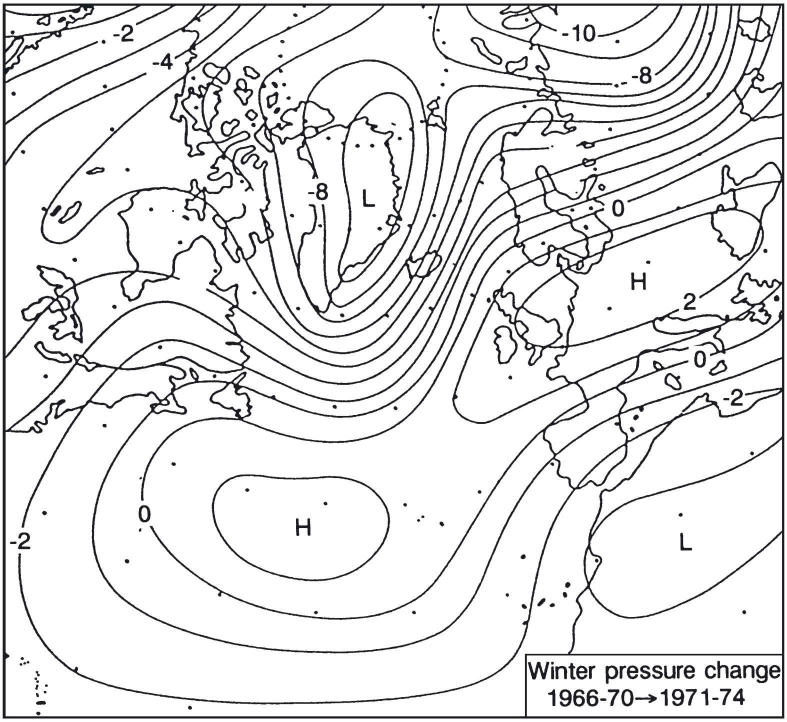
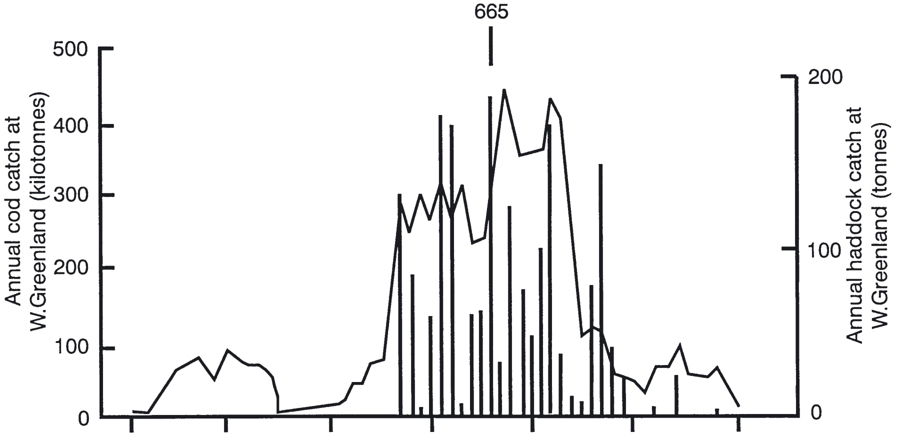


Fig. 19. Pressure difference distribution over Greenland between 1966–70 and 1971–74 showing a southerly wind in the Denmark Strait and a northerly wind over West Greenland. Pressure differences are given in mb. (After Cushing and Dickson 1976)



started in the late 1920s (Fig. 16). Dickson and Brander (1993) showed that during the period of the West Greenland cod fishery, haddock appeared, which do not spawn there, providing evidence of transport. In itself, this is evidence of a high over Greenland. Kushnir's (1994) index of cyclonicity is positive for the period of the Russell cycle (1925–30 to 1965–70) (Figs. 14 & 15) and it also implies the existence of the Greenland High to the north. But as shown in Fig. 13c the Greenland High anomaly did not develop until 1935 and the fishery did not really expand until the 1942 and 1945 year classes appeared. If the Russell cycle is an expression of alternating herring/pilchard or cool/warm periods, then it might be possible that such an alternation exists elsewhere, for example, off Greenland.

The rise and collapse of the West Greenland cod stock was a most dramatic event, studied scientifically from an early stage (1924). The colonization of the offshore banks at West Greenland was the result of atmospheric and oceanic events as described above. But some of the mature West Greenland cod find their way back to Iceland, presumably in the Irminger Current (against the current or in a counter current). From West Greenland, cod larvae are drifted across the Davis Strait to Labrador. This means that certain year classes of the Northern cod on the Grand Bank are augmented from West Greenland (Dickson and Brander 1993).

The stock of West Greenland cod is a unit in the sense that it is managed consistently with distinct vital parameters. But physical links are maintained as larvae and juveniles are carried to Labrador and as mature fish are returned to Iceland. Hence the 3 spawning groups suffer admixture to some degree which may depend on oceanic and atmospheric events. Of course the condition may well be an extreme one because the offshore banks are at some periods inhospitable to cod.

Great Salinity Anomaly of the Seventies

Towards the end of its life, the Greenland High changed its shape becoming reduced to a region over East Greenland, and northerly winds blew along the eastern coast of Greenland from 1965 to 1971. The East Greenland Current became a polar stream carrying ice. Then as the surface salinities fell below 34.7 ppm, density declined, convection was suppressed and ice formed even more readily. The result of these processes was the formation of a large mass of cool water down to about 500 m which took 7 years to pass through the waters north of Iceland (Dickson et al. 1988b).

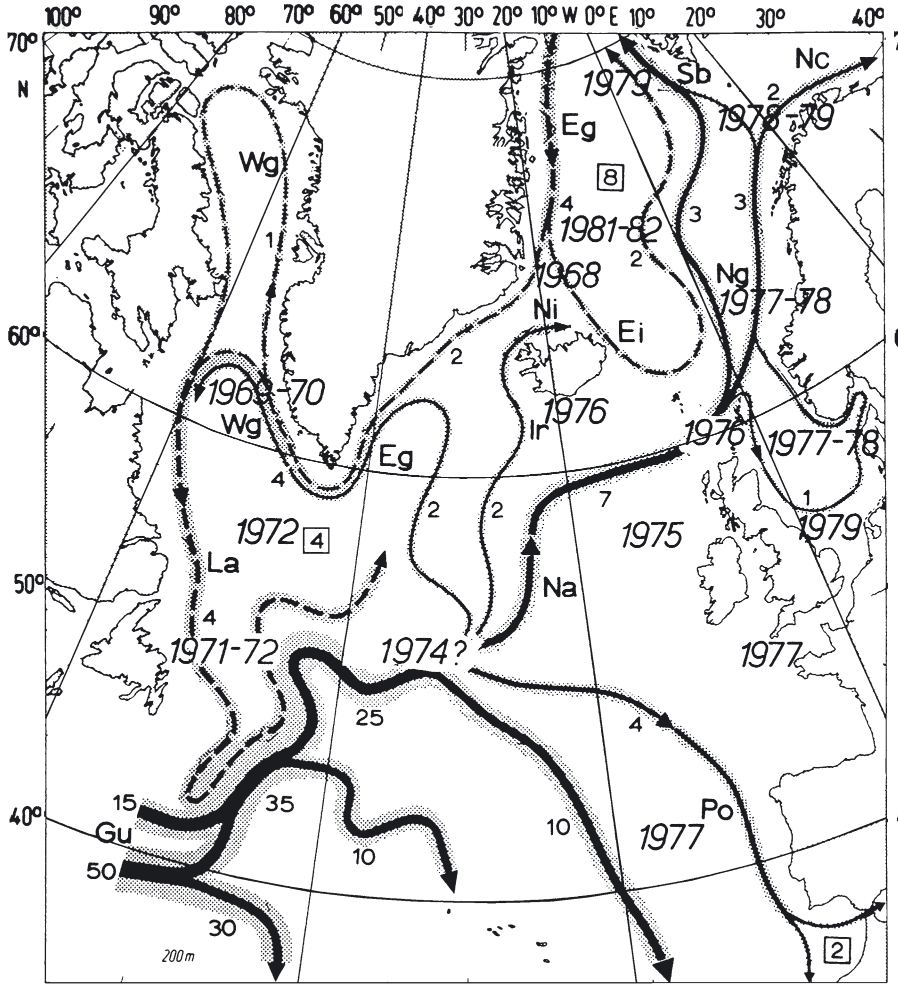


Fig. 21. Passage of the Great Slug (the Great Salinity Anomaly of the Seventies) across the North Atlantic as shown by the years at the positions at which it was recorded. The small numbers represent transports in Sverdrups; currents are abbreviated as: Eg, East Greenland; Ei, East Iceland; Ir, Irminger; La, Labrador; Na, North Atlantic Drift; Nc, North Cape; Po, Portuguese; Sb, Spitsbergen. (After Dickson et al. 1988b)

The Great Slug moved from Iceland to West Greenland, across the Davis Strait to Labrador, to the edge of the Grand Bank, across the Atlantic to the Rockall Channel, the Faroe Shetland Channel and to the Barents Sea. The passage lasted 14 years and the mass of water retained its identity (Fig. 21).

At the start, north of Iceland, the Slug was 2 to 4°C cooler than might be expected and a difference was maintained throughout its passage, the difference being about 2°C when it reached the Barents Sea. Such cooler water would take longer to stratify and production might thence be delayed. North of Iceland primary productivity was reduced by nearly a factor of 4 (Thoradottir 1977) and zooplankton by a factor of 3 (Astthorsson et al. 1983). On the Grand Bank phytoplankton, copepods and euphausiids were reduced by a factor of 3 in 1972 when the Great Slug passed by. Thus, there is a little evidence that production was reduced.

The recruitments to 15 deep-water fish stocks were examined. The magnitudes of those in the years of the passage of the Great Slug were tested against the rest with a Wilcoxon rank test and 13 were significantly lower. Table 4 shows the results. The anomalous years were defined from the information in Dickson et al. (1988b).

Eleven out of fifteen recruitments were significantly less than those of the non-Slug years. The same exercise was not carried out on stocks in the shal-

Table 4. During the years of the passage of the Great Slug the recruitments to a number of fish stocks were reduced, as tested by a Wilcoxon rank test comparing the anomalous years with the rest. ns: not significant. (After Cushing 1988c)

Stock	Anomalous years	No. of year classes	p
Iceland summer herring	1965–71	36	0.01
Iceland spring herring	1962–71	45	0.01
East Greenland cod	1965–71	13	0.05
West Greenland cod	1969–72	15	0.01
N Grand Bank cod	1971–73	20	ns
S Grand Bank cod	1971–73	22	0.05
West Scotland saithe	1974–78	16	0.01
North Sea saithe	1975–77	18	0.05
Faroe saithe	1975–77	18	0.01
Faroe plateau cod	1975–77	18	ns
Faroe plateau haddock	1975–77	18	ns
NE Arctic saithe	1978–81	19	ns
NE Arctic cod	1978–81	21	0.01
NE Arctic cod, 0-group	1978–81	15	ns
NE Arctic haddock	1978–81	22	0.01
NE Arctic haddock, 0-group	1978–81	16	ns
Blue whiting	1978–81	6	0.01

low seas, for example the North Sea, because the effect of the Great Slug was perhaps modified by the shallow water or by the tides. Production was reduced north of Iceland and on the Grand Bank during the passage of the Great Slug and it is possible that the cooler water inhibited the onset of stratification. We cannot show that the reduction in recruitment was the consequence of delayed production but there is as yet no other explanation for the reduced recruitment to all those stocks affected by the passage of the Great Slug (Cushing 1988c).

It remains extraordinary that the recruitments to some "deep-water" stocks were reduced during the passage of the Great Slug. One of the points that did not emerge from Table 4 is that the reduction of recruitment, if significant, was also considerable. The puzzle is that the recruitments were always reduced. The only information available is that the water was much cooler. If recruitment varies with the time of onset of the production cycle, recruitment would be expected to be high or low. If however the production cycle was delayed considerably, recruitment would expected to be low.

Chapter I considered that 3 poor year classes in succession might cause recruitment overfishing. In each of the 15 stocks listed in Table 4, such sequences did occur. The Iceland summer spawning herring suffered from recruitment overfishing (Jakobsson 1985) and the stock of the Iceland spring spawners disappeared.

Zooplankton in the North Sea

Fig. 13e shows the difference in sea level pressure in spring in the northern hemisphere between the 1950s and the 1970s. In that period of 20 or 30 years a ridge of pressure difference developed and the northerly wind increased in the North Sea and the Northeast Atlantic in spring; so did the incidence of gales in the west central North Sea (but not in the east) (Dickson et al. 1988 a). During this period, *Para/Pseudocalanus* (from the Continuous Plankton Recorder Network) in the North Sea as a whole declined by a factor of 5 (Glover 1979).

The decline of the phytoplankton (from 1957 to 1980) and of the zooplankton (from the late 1950s to 1980) in the North Sea and the Northeast Atlantic had been well documented in the Plankton Recorder Network. The causes were not known but in the early 1980s both the animal and plant communities started to recover which ruled out any effect of pollution. Fig. 22 illustrates seasonal changes of 12 spring phytoplankton species in the west

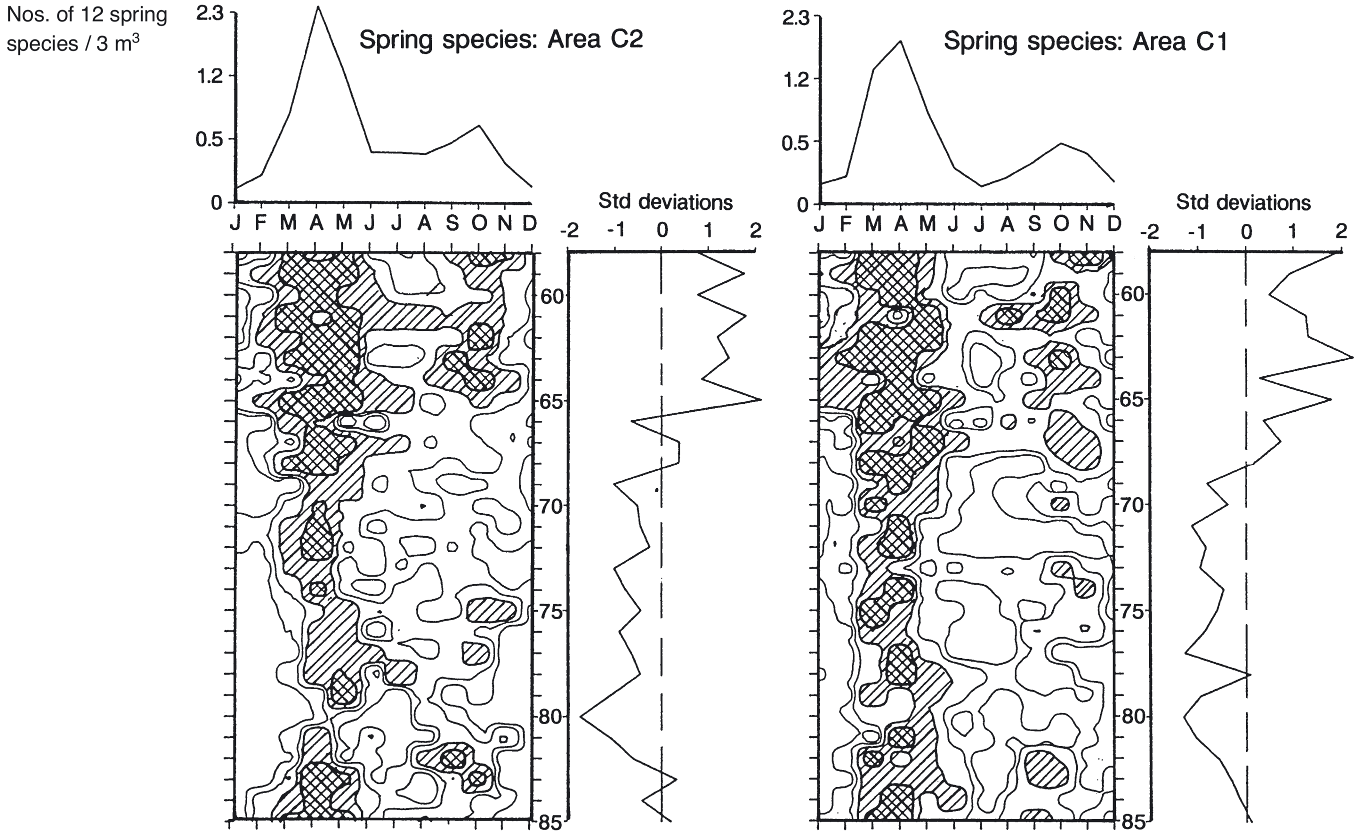


Fig. 22. Seasonal changes of 12 spring phytoplankton species in the west central North Sea (C2) and the east central North Sea (C1) between 1958 and 1985. Mean seasonal distributions are shown at the top of each figure; mean annual distributions, along the side of each figure. (After Dickson et al. 1988a)

central and east central North Sea between 1958 and 1985. The average seasonal picture is shown at the top of each area representation and the average trend in time is displayed along the side of each area diagram. In both regions, abundance (as greenness) declined to the 1970s after which it recovered to some degree. But in the west central North Sea production was delayed in the 1970s by about a month although the time of the spring outburst had returned to its earlier state by 1983–85.

Hardy (1924) showed that the larval herring ate predominantly *Pseudocalanus*. So it is not surprising that the recruitment to the Downs stock of herring in the southern North Sea depends positively on the quantity of *Para/Pseudocalanus* (Cushing 1992). In the northern and central North Sea, the ln Residuals from the Stock Recruitment Relationship are inversely related to ln *Para/Pseudocalanus* in each of the areas of the North Sea (Fig. 12c and d illustrate those for areas B2 and C2 in the western North Sea); in the 2 areas shown there is no trend in time of *Para/Pseudocalanus*. This suggests that the numbers of *Para/Pseudocalanus* are reduced by the herring, presumably in the larval stage.

There are 2 processes at work: reduction in numbers of *Para/Pseudocalanus* first by herring larvae which eat them, and second by the delay in production in the 1970s under the increase in northerly winds. The stock of herring suffered from recruitment overfishing in the late 1960s and early 1970s. It remains hard to separate the 2 forms of change because they occurred at different times. The multiple regression of Recruitment on Stock and ln *Para/Pseudocalanus* is dominated by the Stock Recruitment Relationship. There is a negative relationship of ln Recruitment and ln *Para/Pseudocalanus* perhaps generated in the 1950s and early 1960s when the North Sea Herring was particularly abundant and the herring larvae may have reduced the abundance of their food. The delay in production in the 1970s probably reduced the quantities of *Para/Pseudocalanus* at that time and this could have played a part in the decline in herring recruitment in the 1970s. But recruitment overfishing took place.

Gadoid Outburst

In the North Sea the 1962 year class of haddock was 25 times larger than the average from 1918 to 1961 (Jones and Hislop 1978). Subsequently the recruitments of 5 gadoid species—cod, haddock, whiting, saithe and perhaps Norway pout—increased by a factor of between 4 and 5 by the late 1960s

(Cushing 1980). Fig. 23 shows the increase in cod catches during the 1960s, 1970s and 1980s as compared with earlier years in the century. This was an event of considerable importance to the fishermen of the North Sea and the reasons for it are sometimes difficult to disentangle. Many believed that the collapse of herring and mackerel stocks in the North Sea at about that time was linked in some way to the gadoid outburst, perhaps by relaxed predation by herring and mackerel larvae on the cod larvae. But the 1962 year class of haddock was hatched at a time when the North Sea herring was more abundant than at any time since the early 1920s, with the strong 1956 and 1960 year classes.

Jones (1973) thought that cod and haddock larvae fed on the nauplii and copepodites of *Calanus* and indeed that the cohorts of cod larvae and their food grew up together, providing much opportunity for match or mismatch of larval production to that of their food. Cushing (1982) noticed a correlation between cod recruitments and *Calanus* in the northeastern North Sea between 1962 and 1977; the presentation of age distributions of stock by virtual population analysis started in 1962. From the Continuous Plankton Recorder Network, I compared the seasonal distribution of *Calanus* in the northeastern North Sea for the periods 1949–61 and 1962–78 and found that the peak of seasonal distribution had been delayed by a month. Brander (1992) later showed that juvenile cod are most abundant in that region of the North Sea; the northeastern North Sea was the region where *Calanus* had

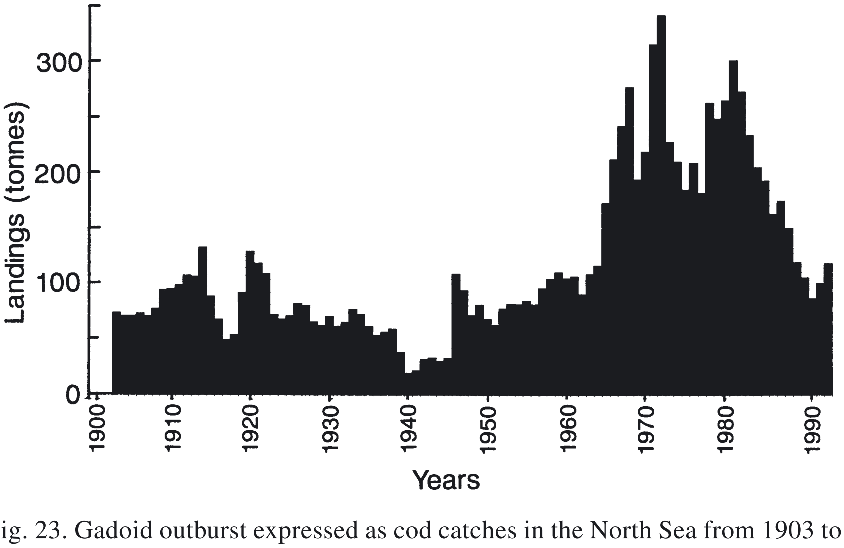


Fig. 23. Gadoid outburst expressed as cod catches in the North Sea from 1903 to 1993. (After Daan et al. 1994)

remained abundant from 1948 onward (Cushing 1982). An index of delay in months after the spawning date in March was used, i.e. April, May and June, and the cod recruitment was significantly related to the delay in *Calanus* production. According to Cushing (1984) the delay period was extended to July and a multiple regression calculated of *Calanus* abundance, delay and March temperature for the period 1954 to 1978.

Dickson et al. (1988a) described the delay in the production of plankton in the western North Sea in the 1970s as compared with the 1950s (see previous section). Hence the delay in production obvious by the 1970s in the western North Sea started to occur a little earlier further north. Indeed, a recent summary of the phytoplankton colour index in area B1 in the northeastern North Sea from 1949 to 1992 shows that the spring peak of phytoplankton colour there was delayed by about a month from 1962 onward and this condition remained until 1990 (Anonymous 1994).

Brander (1992) recalculated the regression of cod recruitment on delay from 1962 to 1988 for the *Calanus* of the northeast quadrant of the North Sea and found that it no longer existed. Further, my 1984 regression from 1954 to 1988 also failed. I then returned to the original one with delays up to June (Cushing 1982) and not to July because in July the little cod might have started to feed on young fish; the regression remained for the periods 1955–70 to 1955–74 ($r^2 = 0.38$, $p < 0.01$) after which the correlation coefficients were low. Hence the original view that the origin of the gadoid outburst may have depended upon the delay in the production of *Calanus* in the North Sea has been reinforced and I shall return to this point when I discuss the match/mismatch hypothesis in a later chapter. But, in common with most correlations of recruitment with climatic factors the relationship failed and the proximate reason is not known. The general reason however is that the science of recruitment does not exist. I shall return to this problem in Chapter V in the description of the decline of the North Sea cod stock. In particular with a much longer time series from 1903 to 1993, it appears that the stock of whiting did not rise in the early 1960s as part of the gadoid outburst (despite the evidence to the contrary at the time).

The question arises in 1995 whether the gadoid outburst is over. The recruitments to cod, haddock and whiting were all less from 1985 to 1994 than they were in the earlier years. That for the saithe remained about average. For the North Sea haddock, the gadoid outburst comprised 3 large year classes only, the last being in 1974. Recent cod year classes with one exception (1991) have all been poor, from 1986 onward (Anonymous 1994a). Recruitment to the saithe stock has not declined. The gadoid outburst started with a bang but it appears to be ending at different rates in different species.

The North Sea herring stock has recovered during the middle 1980s and the question will be asked whether the rising stock of herring has reduced the numbers of larval cod. The North Sea herring stock collapsed in the late 1960s after the gadoid outburst started (Cushing 1984) and its recovery occurred as gadoid recruitments declined at different rates. What is needed is a multispecies analysis which includes the larval fish as well as the juveniles.

A Broader View

There are many links, real and supposed, between recruitment and climatic factors, but the small group described above is associated with one phenomenon. the build-up and collapse of the Greenland High between the mid 1920s and the late 1960s. The effects were considerable, in scientific understanding and in reward to the fishermen, US $15.5 billion at present-day prices from the West Greenland cod fishery and the gadoid outburst in the North Sea. In the Russell cycle dramatic changes were distributed through many parts of the ecosystem. The mechanism of change remains unknown; when the cycle recurs it might be investigated more fully. The signals to be expected are well known and the first is likely to be the appearance of southwesterly indicator species followed by changes in other parts of the ecosystem. The decisive change will be the reduction in winter phosphorus from ca 0.70 mmol 1^{-1} to ca 0.50 mmol 1^{-1} about 5 years after the appearance of the southwesterly indicators.

The most valuable events were the rise of the West Greenland cod stock (tied in time and in atmospheric structure to the Russell cycle) in the last warm period and the gadoid outburst, which took place when the last cool epoch started (in the terminology of the Russell cycle). In 1962, when the large haddock year class appeared in the North Sea to start the gadoid outburst, the southern barnacle *Chthalamus stellatus* started to retreat westward in the English Channel, giving way to the northern barnacle *Balanus perforatus*.

As the Greenland High was ending its career, northerly winds generated the Great Slug off East Greenland and it started its 14-year passage across the North Atlantic. It was much colder than the surrounding seas and the recruitments to 13 “deep water” stocks were reduced; it would take much longer to heat the cooler water, much longer to stratify the water column, and would delay the production of food and perhaps reduce recruitment. North of

Iceland and on the Grand Bank the production levels of both phytoplankton and zooplankton were considerably reduced, by factors of 3 to 4. This alone suggests that the thesis of delayed production is a reasonable one to account for the reduced recruitments, which would then demand that the production of fish larvae had moved from a matched condition to a mismatched one (Chapter III).

The most extraordinary point is that the recruitments to stocks across all the North Atlantic were modified by a single long-term event, the passage of the Great Slug. The arguments of Shepherd et al. (1984) that climatic factors affect recruitment receives astonishing confirmation from the broad array of factors following the development and collapse of the Greenland High.

The decline in zooplankton in the North Sea between the 1950s and the 1970s and its subsequent partial recovery in the 1980s was almost certainly a consequence of the increase in northerly winds in spring across the North Sea and of the incidence of gales in the western half of that sea. As a result, production was reduced and delayed in spring to advance again and to increase in the middle 1980s. We know now that the production cycle in the northeastern North Sea was also delayed by a month or so from 1962 to 1990. Hence, the delay in the production of *Calanus* there by a month or so from 1962 onward was not unexpected. Then, this delay might well have generated the gadoid outburst as the production of gadoid larvae became matched to the production of their food in the western North Sea and in the northeastern North Sea. Such a thesis requires that the long period from 1903 to 1962 was one of mismatched production of cod larvae to that of their food (Fig. 23).

The account given so far is limited to the consequences of the development of the Greenland High because they were so widespread and of such great economic importance. But fisheries have been affected by climatic factors in many other parts of the world with equally dramatic economic effects. A particular example is El Niño, the warm current that appears off Peru at Christmas time every 3 to 7 years or so. The first signal of its arrival is the appearance of hungry guanay birds in the streets of Guayaquil in Ecuador because the warm current has less food despite the fact that the upwelling winds continue to blow. El Niño originates in the stack-up of water in the western Pacific under the stress of the trade winds. When the mass collapses, the water is carried eastwards in the Equatorial countercurrent in the form of a Kelvin wave; this is a gravity wave with a wavelength of thousands of km. Water crosses the Pacific in about 3 months. The eastern tropical Pacific is flooded with warm water and the thermocline is pressed deeper in the water column. It floods to the south off Peru and starves the ecosystem there. The stock of anchoveta collapsed in 1971–73 (these are the 3 very poor year classes that might have generated recruitment overfishing during the El Niño of 1972–73); the proximate cause remains unknown but a long-term one was the competition between the fishermen and the guanay birds. During the 3 El Niños of the late 1950s and the 1960s, the stock of guanay birds was reduced in 3 stages as fishing increased (Cushing 1982). As indicated above the reduction of the zooplankton in 3 stages may well have played a critical part, as shown above in Fig. 11c (p. 32).

When the Kelvin wave reaches the continental shelf of the Americas it turns not only south but also to the north as it travels as a trapped coastal wave at the shelf break. A notable event in the 1958–59 El Niño was the invasion of the waters of southern California by the pelagic crab *Pleuroncodes planipes* amongst other southern animals (Longhurst 1967). Year classes of the Pacific mackerel were higher in years of southern and El Niño influence (Sinclair et al. 1989). But the wave travels much further north and from time to time the year classes of the herring are enhanced during the El Niño years off British Columbia (Mysak et al. 1982).

El Niño is a transpacific phenomenon. The warm water in the eastern tropical Pacific changes the wind stress across the ocean, which in turn trips the Kelvin wave that travels in the Equatorial countercurrent. This led to the suggestion that the system was a coupled oscillator. It varies in intensity and every 40 years or so it is strong and there are droughts in Australia, heavy rains in Chile, storms in California and storms in the southeast United States (Cushing 1982).

Another series of events took place as anchovy tended to succeed sardine in the major upwelling regions of the world ocean, as referred to above. The Japanese sardine collapsed in the late 1930s and early 1940s to recover in the early 1970s. The Californian sardine collapsed in the late 1940s as the upwelling winds increased there and was succeeded by the northern anchovy. Then, in the 1980s, the sardine tended to return. Anchovies flourished off Peru until 1971 and were replaced to some degree by sardines. In the last 2 years the anchovies have returned. Off Japan the anchovies flourished in the 1950s and 1960s to be replaced by sardines in the early 1970s. A very large fishery developed for sardines in the 1970s off Chile. In a somehat rough manner the sardine flourished in warm periods and anchovies in the cool ones (Cushing 1995a).

Off Japan the sardines flourished from the 1920s and early 1930s, to be followed by anchovies between 1950 and 1970 and then to return from 1972 onward. Off California, sardines were caught in quantities from 1920 and then the stock collapsed in the late 1940s in a period of increased upwelling. They were succeeded by anchovies in the 1960s and 1970s in an epoch of stronger upwelling. Similar changes occurred in the Benguela Current and, of course, off Peru as described above. Kawasaki (1983) made a diagram of the catches of pelagic stocks across the Pacific which showed that 3 sardine stocks appeared to fluctuate contemporaneously, sardines off California, Japan and Chile to be followed by anchovies off Japan and California (Fig. 24). Sardines returned to both Japan and California at about the same time in the early 1970s and very large catches started to be taken off Chile at that time.

In rather general terms, sardines live in warm periods of weak upwelling and anchovies in cool ones of strong upwelling. Dickson et al. (1988a) noticed that sardine larvae grew quickly and anchovy larvae slowly; hence the sardines really need weak but persistent upwelling (like that off a cape) whereas the anchovies can tolerate the stresses of strong upwelling which may be intermittent. In the western English Channel, herring flourished in the cool periods and pilchards in the warm ones. In the upwelling areas anchovies thrived in the cool periods and sardines in the warm ones.

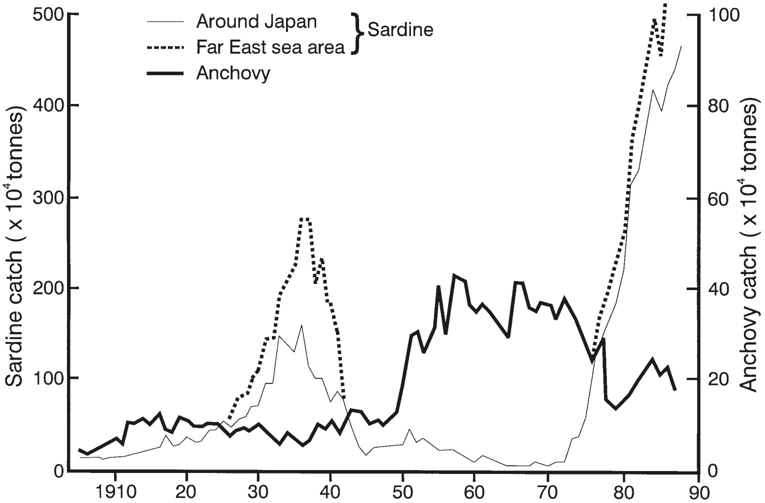


Fig. 24. Regime shift off Japan. The thin line shows sardine catches around Japan; the dotted line, sardine catches in the Far East sea area; the thick line, anchovy catches. (After Kondo 1988)

The alternations between herring and pilchard (or sardine) and between anchovy and sardine are now called regime shifts (Steele in press). Herring predominated in the western English Channel during cool periods and pilchards in the warm ones. In the upwelling areas and off Japan, the anchovies probably flourish in cool times (for example, off California when the upwelling wind increased in the 1950s). Steele (1985) noticed that noise in the sea was red, which means that low frequency events, or long wave events (like the red light in the visible spectrum), were to be expected. They reside in the ocean/atmosphere system of the form described by Schlesinger and Ramankutty (1994). Further, the periodicity differs between oceans. Hence, we would not expect the herring/pilchard exchange in the North Atlantic to fit that of the anchovies and sardines in the North Pacific very closely.

Another point made by Steele (in press) is that the total production in the ecosystem is more or less the same from year to year (Jones and Henderson 1988a for the North Sea; Cohen et al. 1980 for George's Bank). If this is true then the shift takes place within the fishy part of the ecosystem. As noted above, larval anchovies off California may tolerate a strong upwelling wind whereas the sardines need a weaker wind system.

Some complete records of catches go back for a century or more and those of stock (or stock density) extend back for some decades. Few such series show no changes in time. Hence it need not surprise us that they are attributed to climate changes. The real surprise is that as time passes by the links between recruitment, or its proxies, and climatic factors tend to harden.

The relationships described above are all the result of climate changes. In the sea, the prime physical factors are heat, irradiance and wind stress. There are, of course, minor actors on that stage, but these three take the major parts. The great changes in the global air temperature portrayed in Fig. 13a result in differences in cloudiness, in Sea Surface Temperature and in the time of stratification from year to year and from decade to decade. They are all remote causes and we need to establish the links between them and the biological processes that govern recruitment.

Let us re-examine the phenomena. The rise and collapse of the West Greenland cod stock was attributed to changes in wind direction associated with the location of the Greenland High, easterly winds across the Denmark Strait and southerly winds along the coast of West Greenland, but the detailed mechanisms remain quite unknown.

The extensive changes indicated by the Russell cycle were perhaps remotely caused by changes in wind direction, by temperature (both possibly effects of a single remote cause in the atmospheric distributions in the North

Atlantic) and by competition. But the causes of the changes in recruitment to the herring and pilchard stocks have not been revealed. The same is true of the other components of the ecosystem in the western English Channel.

The recruitments to 13 “deep water” stocks were reduced in the passage of the Great Slug or the Great Salinity Anomaly of the Seventies. It was suggested that production was delayed and shreds of evidence were produced to show that stocks of phytoplankton and zooplankton were indeed reduced. The mechanisms by which recruitment to any of the 13 stocks was generated, let alone reduced, are not known at all.

A real delay, as opposed to a putative one, occurred in the western North Sea under northerly winds and gales and, as a consequence, both phytoplankton and zooplankton between the 1950s and the 1970s were reduced. Both components of the ecosystem recovered in the 1980s. Fig. 12e shows the relationship between the ln Residuals (from the Stock Recruitment Relationship of the North Sea herring stock) on ln *Para/Pseudocalanus* in the west central North Sea. This relationship implies that the larval herring can reduce the quantities of their food which can generate density dependent mortality. This raises the possibility that the origin of the magnitude of recruitment might be understood, but that must be in the future.

The seasonal delay in production of *Calanus* from the early 1960s onwards may have generated the gadoid outburst which was of some value to the fishermen. It has recently been shown that the production of the algal stock was delayed in the northeast North Sea in 1962, to be advanced again in 1991. There are perhaps hints at the mechanism but it has not been revealed. Perhaps there will be an opportunity to mount such a project to study it properly if the gadoid outburst recurs.

One of the great mysteries of fisheries science is the failure of recruitment to the stock of the Peruvian anchoveta in the years 1971–73. El Niño flooded the waters off Peru in the summers of 1972 and 1973 and primary production was low. But recruitment had first failed in 1971. Hypotheses have been proposed, for example, that the stock had failed to mature and produce enough eggs. Had there been a science of recruitment such questions might have been answered.

The Kawasaki diagram displays changes in 7 major pelagic stocks in the Pacific. Much of the discussion of the problems stems from the apparent alternation between sardine and anchovy. There may be differences in the larval growth rates of the 2 species, but the argument is no more than speculative. As with the other examples cited there is no evidence of the mechanism.

The evidence for a link between recruitment and climatic factors is persuasive, but in the end circumstantial. The changes in the fisheries are dramatic and demand explanation. An immense amount of work has been done on the associative and correlative relationships between the two. But a deeper understanding is needed before the science of recruitment is established.

There are 2 forms of evidence on the relationship between climatic factors and recruitment. The first is in the general and large-scale events like El Niño and the apparent alternation between anchovy and sardine (or herring and pilchard). The second is the array of events in the North Atlantic all of which stemmed from the long existence of the Greenland High and its collapse. Both forms of evidence are dramatic and demand explanation. The only way in which such explanation can emerge is by examining the growth and mortality of fish larvae and early juveniles in the science of recruitment.

III A SIMPLE VIEW OF RECRUITMENT

In Chapter II, evidence was provided and discussed of climate effects on fish stocks. Cod catches in the Vestfjord were linked for nearly a century to differences in the growth rates of tree rings in the same region. The climatic factors common to both events were heat input, light intensity and wind stress. These affect productive processes in the sea including the production of food for larval fish. The lives of juveniles are remote from such productive processes. Control processes also occur in the juvenile stages; this will be described in Chapter IV.

A recruiting year class suffers mortality throughout early life and responds to differences in the environment by growth in the months after hatching. The unexploited stock usually comprises many year classes (10 in herring and perhaps 20 or more in plaice). Hence the quantity of eggs produced represents the average of a number of year classes. The fish population of many ages samples the varying environment with each of the recruiting year classes and it represents a running mean of the annual samples of recruitment.

The first problem in determining the magnitude of recruitment is to find out when in the life history that magnitude is established. For a long time it appeared insoluble, but in the last 2 or 3 years, part of the solution has started to appear. The main processes are generated between the ages of the late larvae and of the early juveniles. A second problem is how to express the lack of food. The word “starvation” has often been used, but it does not express the meaning I need. The growth rate, G, may be less than the maximal, $G_{\max}$; the fraction $G/G_{\max}$ expresses a continuum of feeding from poor to rich, whereas “starvation” means no food at all. A brief review will be given of the field studies in so far as they apply, followed by an account of predation. Arguments on the match/mismatch hypothesis are rehearsed to be followed by a model of match which might be considered as the forerunner of a science of recruitment.

When Is the Magnitude of Recruitment Determined?

The age at which recruitment is determined is not properly known. The magnitude of recruitment is not fully established until the age at which the recruits join the adult stock. However, as Ricker (1954) pointed out, growth rates and mortality rates are highest during the larval stages and perhaps the processes which determine recruitment magnitude start then. This magnitude cannot usually be estimated from the numbers of eggs or early larvae. But numbers at recruitment can sometimes be estimated 2 to 6 months after hatching. This implies that the age of determination lies between that of the late larvae and that of early 0-group fishes.

Bückmann (1942) used a Petersen Young Fish Trawl to capture herring larvae near metamorphosis up to 40 mm in length. The trawl was not really a quantitative gear, but later methods of capture did not take the larger herring larvae at all, until quite recently. Morse (1989) and Somerton and Kobayashi (1989) showed that the traditional gears are not very efficient at catching larger fish larvae. Fig. 25 illustrates the nature of the problem in the capture of the nehu *Engrasicholina purpurea* with a 1 m net. A demonstration of poor sampling was given by Brander and Thompson (1989) who sampled herring larvae with 3 gears, pump, Mocness net and the Longhurst-Hardy sampler, and expressed their results as night/day ratios for each gear. The night/day ratio for herring larvae of 24 mm length was >3 and, of course, would have been very much larger for larvae of 40 mm, near metamorphosis, as caught by Bückmann. Thus the late larvae have sometimes been poorly sampled.

It is not surprising then that links between numbers of larvae (which must often have been early ones) and recruitment have not been established. Sissenwine et al. (1984), Smith (1985), Wooster and Bailey (1989)

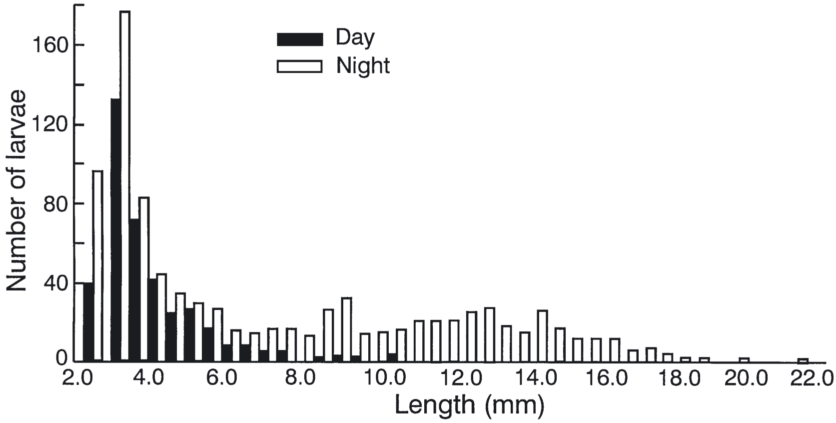


Fig. 25. Length distribution of nehu *Engrasicholina purpurea* (a Hawaiian anchovy) as sampled with a 1 m net (335 µm mesh) during the day and at night. (After Somerton and Koyabashi 1989)

and Taggart and Frank (1990) all make this point. The conclusion is that the numbers of early larvae, as caught by some contemporary gears, do not predict recruitment because the processes that determine it are not complete.

It has been known for a long time that the numbers of juveniles just after metamorphosis provide a reasonable index of the recruitment to come, and indeed such estimates are used regularly in standard assessment practice. What is less well known is that the late larvae may also provide that index. Simple relationships have been documented, for example, by Burd and Parnell (1971) for herring larvae, MacCall (1979) for Pacific sardine larvae, and Leggett et al. (1984) for capelin larvae off Newfoundland and by Crecco and Savoy (1987) for larvae of the American shad *Alosa sapidissimma*. Parmanne and Sjøblom (1984, 1987) sampled herring larvae with a Gulf V net at 7 stations in 4 areas off the coast of Finland every week between May and August from 1974 to 1986. The numbers of larvae were correlated with the ensuing recruitment in 3 areas and at different lengths of larvae (Table 5).

Thus, recruitment can be forecast from the numbers of herring larvae at the age of about 2 months. Van der Veer (1986) found a correlation between the numbers of late plaice larvae entering the Wadden Sea in northern Holland and the subsequent recruitment. For the Arcto-Norwegian cod, Bjørke and Sundby (1987) found that the numbers of early juveniles (just after metamorphosis, at the age of about 2 months) were correlated with the numbers of 0-groups, themselves correlated with the numbers of recruits. Thus, the age by which recruitment is in the main determined can be as short as 2 or 3 months.

Table 5. Correlation of numbers of herring larvae in June and subsequent recruitment off Finland. (After Parmanne and Sjøblom 1987)

Length	Area		
	29	30	32
<10 mm	0.714**	0.492**	0.209
>10 mm	0.649*	0.464*	0.828**
>15 mm	0.632*	0.240*	0.792**

*$p < 0.05$, **$p < 0.01$

The estimation of density-dependent mortality is a little difficult and might be derived from $N_{t+1} = a N_t^{-b}$, where N_t and N_{t+1} are numbers at successive times t and $t+1$, b is a coefficient of density dependent mortality (<1.0) and a is the intercept. The intercept in logs is a conventional estimate which on the scale of N_t may mislead. There are 2 ways out of the dilemma. The first is that used by Bradford (1992) who replaced the intercept with a random variable. He examined the numbers and mortalities of eggs, larvae and juveniles of 97 stocks. Fig. 26 displays the coefficients of determination of the relation between the numbers of eggs, first feeding larvae, 10-day-old

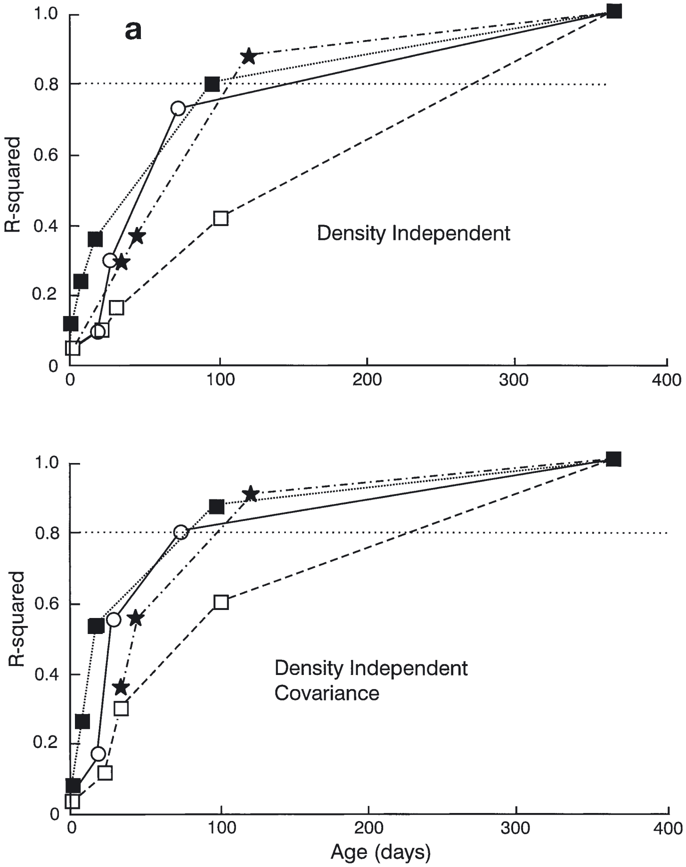
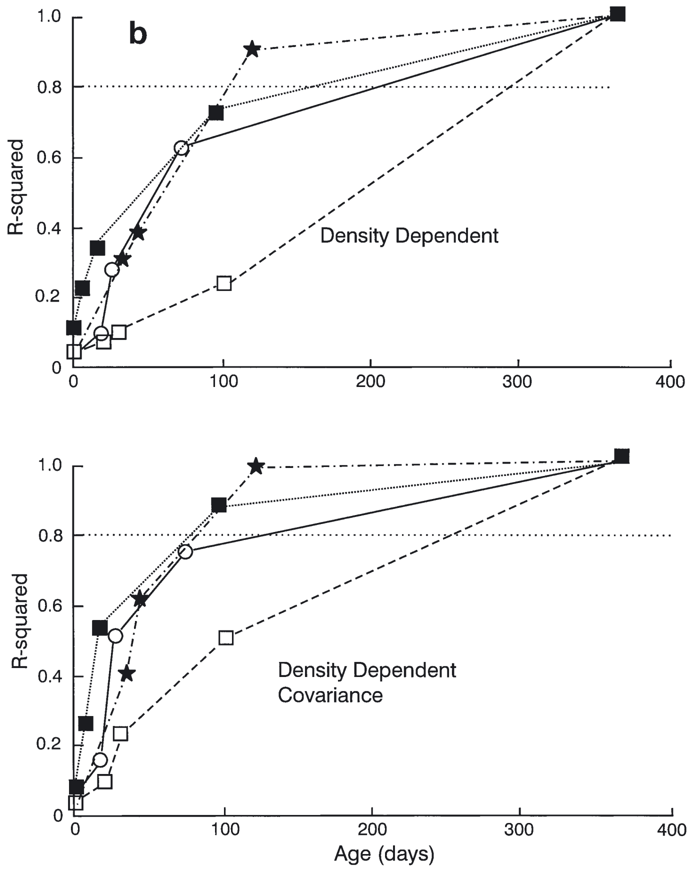


Fig. 26 (above and facing page). Coefficients of determination of the relationship between ln Numbers of eggs, first feeding larvae, 10-day-old larvae and metamorphs and ln recruitment: (a) with density-independent mortality ($b = 1.0$); (b) with density-dependent mortality ($b = 0.7$). (After Bradford 1992) larvae, metamorphs and the magnitude of recruitment, (a) for density-independent mortality (*b* = 1), and (b) for density-dependent mortality (*b* = 0.7). For cod, anchovy, plaice and herring, the correlations between recruitment and metamorphosing larvae are relatively high. This is the first decisive evidence that the magnitude of recruitment is in the main determined by the age of metamorphosis and this implies that the major processes take place during the late larval stages.

The second way out of the dilemma was used by Myers and Cadigan (1993) who removed the intercept from their subsequent analysis. With 14 juvenile demersal stocks in the Northeast and Northwest Atlantic they showed that the density dependent coefficient was <1.0. This means that juvenile mortality was density dependent. They assume that the random variability approximated the density-independent mortality and showed that



it was low, much less than the variation in recruitment. Therefore the density-dependent component was greater than the recruitment variability and so the major source of differences in recruitment from year to year lay in the prejuvenile stage, i.e the larval stages. Myers and Cadigan believe that the magnitude of recruitment is determined during the larval stage and that it is modified by density-dependent mortality in the juvenile stage. I shall return to this point in Chapter IV. All that need be noted here is that the Stock Recruitment Relationship demands relatively high density-dependent mortality (Shepherd and Cushing 1980).

The conclusion is that the numbers of early larvae cannot be used to predict recruitment. It has been known for a long time that the numbers of juveniles can form reasonable forecasts of recruitment, and indeed they are used in the normal practices of stock assessment. From the work of Bradford and of Myers and Cadigan the magnitude of recruitment is determined from the numbers of late larvae and of metamorphosing animals.

Lack of Food

Hjort (1914, 1926) proposed that recruitment was determined during the period of first feeding when the early larvae are learning to feed. According to Hunter (1972), the Northern anchovy, which grows rather slowly during its larval life, took up to 30 days to learn to feed properly. Such processes in the laboratory have been summarized by Miller et al. (1990). May (1974), Leggett (1986) and Anderson (1988) believed that the hypothesis was not viable. Taggart and Leggett (1987a) found no link between the mortality of early capelin larvae and their food. The work of Bradford (1992) and of Myers and Cadigan (1993) indicates that late larvae and metamorphs are the stages at which recruitment is determined. This rules out Hjort's hypothesis.

Leggett (1986) and Blaxter (1988) noted that the minimal food densities needed to support growth in the laboratory were higher than those in the field. This point was pursued by Mackenzie et al. (1990), who took into account effects of weight and temperature and suggested that the rates of encounter might be greater in the wild than in the laboratory. Rothschild and Osborn (1988) introduced the idea that encounter rates were higher under turbulent conditions (Yamazaki and Osborn 1988). This was shown to be true experimentally by Costello et al. (1990) using Strickler's technique of cinematographic observation, and in the field by Sundby and Fossum

(1990). Sundby et al. (1994) extended their study at sea at a range of wind stresses. Their method was to plot feeding ratio (nauplii/gut) on density of nauplii in the sea. In Fig. 27, their adaptation of the Ivlev equation is plotted on the density of nauplii in the sea at different wind speeds, U. This shows how contact rate increases with turbulence, based on much data at sea. Mackenzie and Leggett (1991) developed a model in which the dissipation of turbulent kinetic energy was expressed as a function of depth and wind speed. They suggested that the contact rates at low densities might be underestimated by an order of magnitude. In 1994, Mackenzie et al. produced evidence that the probability of capture declines with turbulence and then, combining this effect with the probability of encounter, found that ingestion is a dome shaped function of turbulence. With a method of transformation, Cury and Roy (1989) demonstrated that recruitment to some pelagic stocks in the upwelling areas formed a dome shaped curve as a function of wind stress, the dome peaking roughly at that stress at which turbulence begins.

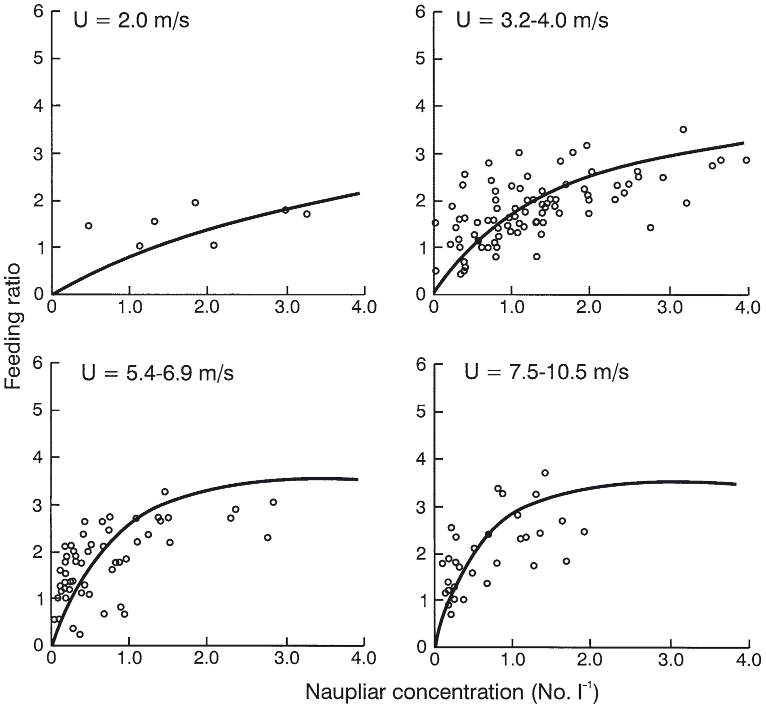


Fig. 27. Nauplii of *Calanus finmarchicus* per gut of cod larvae as a function of density of nauplii at 4 levels of wind stress, U. (After Sundby et al. 1994)

The development of this study originated in the expectation that turbulence must affect feeding and in the observation that the fish larvae could not grow fully on the food quantities observed in the sea. The negative relationship shown in Fig. 12 of ln Recruitment or ln Residuals from the Stock Recruitment Relationship on wind stress or food density suggests that the latter is affected by the numbers of fish larvae. This may be the direct effect of turbulence on the probability of capture, or merely the reduction in the numbers of food organisms by the fish larvae. These 2 possibilities cannot be distinguished. However, the reduction in ln Recruitment or the ln Residuals appears to be more than might be expected from the effects of turbulence estimated from the laboratory experiments. In both cases, we conclude that food was of considerable importance in the determination of the magnitude of recruitment.

Pepin and Myers (1991) examined the variation in recruitment for a large number of stocks with respect to some variates of egg and larval life. They showed that the standard deviation of recruitment was not related to egg diameter or to larval length at hatching. It was correlated instead with the increment of length during larval life ($r = 0.59$); the residuals did not depend on egg size, length at hatching or length at metamorphosis. Hence, differences in larval growth (and thence food) are important in the generation of recruitment.

An important event in the history of larval studies was the rediscovery of the microzooplankton and their density in the sea by Beers and Stewart (1971) in the California Current. Many of the little animals had long ago been identified and described by Lohmann (1908). Berner (1959) had shown that the larval anchovy needed mainly food particles of 60 to 80 µm in the microzooplankton. Then Lasker et al. (1970) successfully reared the larvae of the Northern anchovy fed on the dinoflagellate *Gymnodinium splendens*, which is in the size range required (Hunter and Thomas 1974). But they also found that even moderate larval growth needed densities of the dinoflagellate greater than those found at sea by Beers and Stewart. They implied that the difference might be more than that to be expected from normal patchiness.

At sea, Lasker (1975) found a layer of *Gymnodinium splendens* between Malibu and San Onofre off California. The layer was broken by a storm and Lasker concluded that the larval anchovies needed stable layers to survive, provided that the food was *G. splendens* and not *Chaetoceros*, which they did not like. He examined the anchovy year classes from 1962 to 1977 and the best was hatched in a year of stable seas. But the worst was also hatched in stable seas, when the predominant organism was *Gonyaulax polyedra* which is not eaten by the larval anchovy (Scura and Jerde 1977). Such evidence led Lasker (1981) to formulate his stable ocean hypothesis which stated that the larval anchovy needed a stable sea to provide enough food of the right size in order to survive.

Peterman and Bradford (1987) devised an index of stability (or calmness), 4 days of wind speed <10 m s^{-1}, that is, a little less than that needed to generate turbulent mixing. Larval mortality rates between the ages of 5 and 19 days were plotted on the number of calm periods per month (or Lasker events, as they were named), yielding an inverse relationship (Fig. 28). Thus, larval Northern anchovy survive better in stable waters with enough food. The reduction in mortality was considerable, being halved with a doubling of the number of calm periods per month. Cury and Roy (1989) described an inverse relationship of Lasker events on turbulence (expressed as the cube of the wind speed). Peterman et al. (1988) reconsidered the material and found that the numbers of anchovy larvae, at about 9 mm in length (Owen et al. 1989), were not related to the numbers of 1-year-old recruits. Such larvae may be fairly well sampled but they are still much smaller than the metamorphosed ones, for the later larvae >9 mm in length were not sampled. Butler (1991) found no relationship between the mortality of sardine larvae (as opposed to that of the anchovy larvae) and the number of calm periods off California. The anchovy larvae grow slowly and tolerate strong upwelling in turbulent waters, whereas the sardines grow quickly where the upwelling is weak and the turbulence low

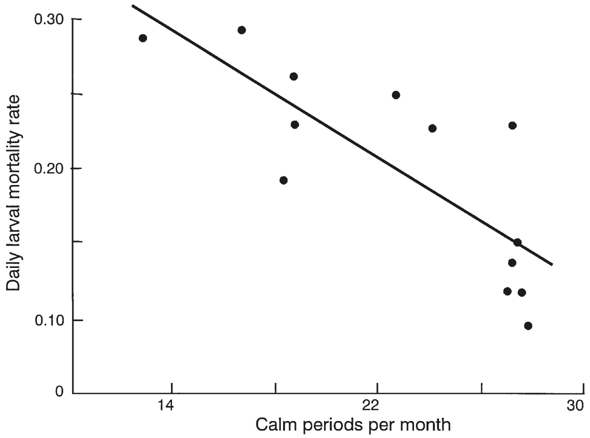


Fig. 28. Northern anchovy. Larval mortality as a function of number of Lasker events (number of 4 day periods of wind speeds <10 m s^{-1}, i.e less than that needed to generate turbulent mixing). (After Peterman and Bradford 1987)

(Dickson et al. 1988a). Perhaps this is a sufficient explanation of the different responses of the 2 species. In recent years, the stable ocean hypothesis has been criticized, but the late larvae were possibly not well sampled and the criticisms are not well based. Lasker's work was of great importance, based on the proposition that recruitment may depend on the availability of food for the larvae.

Templeman (1948) had suggested that the onshore winds were essential for good survival of capelin, which lay their eggs in the sediments in summer, as the spring tide ebbs on the beaches of Newfoundland. This was shown decisively by Frank and Leggett (1981a, b) as they dissected the processes stage by stage. Frank and Leggett (1982) compared the times of hatching on the beach with those in the laboratory (using water from the beach) and the larvae hatched on the beach and in the laboratory at the same time, presumably an effect of temperature. The onshore winds disturb the beach sediments and the larvae emerge into water that is relatively warm. It is rich in zooplankton and has few predators (Frank and Leggett 1982). When the wind blows offshore, the cool upwelled water has no zooplankton but many predators, and the larvae remain in the sediments. On the other hand, in the St. Lawrence estuary capelin larvae emerged at dusk and at dawn. This behaviour was confirmed in the laboratory (Fortier et al. 1987).

Leggett et al. (1984) summarized the extensive investigation in a simple relationship. Spawning dates varied from year to year and so did the dates of hatching. They expressed this as follows:

$$Yc = 16.1 - 0.19\,(\text{onshore wind}) + 0.19\,(\text{tempsum})$$

where Yc is year class strength in numbers; onshore wind is measured in m s^{-1}; and tempsum is the sum of degree days in the top 20 m of the sea between July and December (Fig. 29). Hence a good year class depended on onshore winds from the northeast and the larvae emerged into the warmer water with few predators and lots of food. By spectral analysis Taggart and Leggett (1987a, b) found the average period of onshore winds to be 5.3 days. According to Frank and Leggett (1984) capelin eggs were eaten by the adult American plaice *Pseudopleuronectes americanus*, and the larvae were often eaten by jellyfish (de La Fontaine and Leggett 1988). This pervasive analysis depended entirely on the proposition that recruitment depends on the food available to the larvae.

Arcto-Norwegian cod spawn in the thermocline in the Vestfjord in northern Norway. The cod larvae feed on the younger stages of *Calanus finmarchicus* Gunnerus. Fig. 30 shows the inverse relationship between the

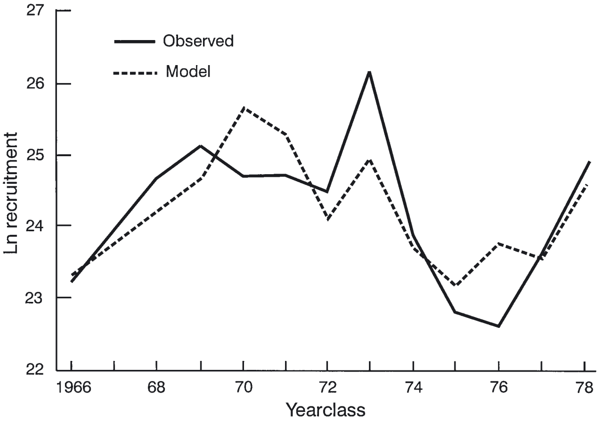


Fig. 29. Capelin. Relationship between year class strength, onshore winds (off Newfoundland) and tempsum between July and December. Tempsum is the number of degree days in the top 20 m of the water column. (After Leggett et al. 1984)

date of peak abundance of copepodite stage 1 of *Calanus finmarchicus* and temperature between April 1st and May 24th (Ellertsen et al. 1987). If the cod larvae survive best on the numbers of stage 1 *Calanus*, it follows that their survival varies from year to year as a function of temperature; recruitment has been shown to be a rough function of temperature (Ellertsen et al. 1987).

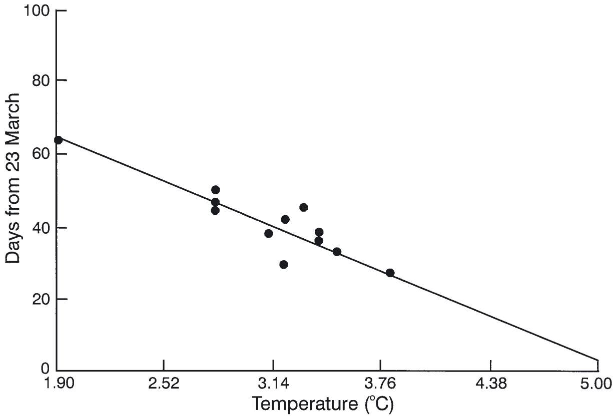


Fig. 30. Stage 1 *Calanus* copepodites. Inverse relationship between date of peak abundance and temperature between April 1st and May 24th. (After Ellertsen et al. 1987)

Comparing 4 year classes (1982, 1983, 1984, 1985), the following relationship was established:

	Dry weight at 6 mm length	Temperature (°C)	Peak Julian Day of abundance of stage 1 *Calanus*
1982	98.75	2.10	149
1984	107.35	3.08	123
1985	120.00	3.50	114
1983	146.33	3.60	109

As temperature increases, the peak date of abundance of stage 1 *Calanus* copepodites occurs earlier and the dry weight of the larvae at 6 mm length is greater. In fact, there is an inverse relationship between dry weight of larvae and the peak date of *Calanus* stage 1 production. This implies that variation in the time of onset of production of *Calanus* stage 1 is linked to the growth rate of the larvae.

Fig. 31 displays the percentage production in time of cod eggs, of first feeding larvae for 6 year classes (1960, 1980, 1981, 1983, 1984, 1985) and of nauplii, the primary food of cod larvae. The figure also shows the level of 5 nauplii l^{-1}, at which the cod larvae are adequately fed (Sundby and

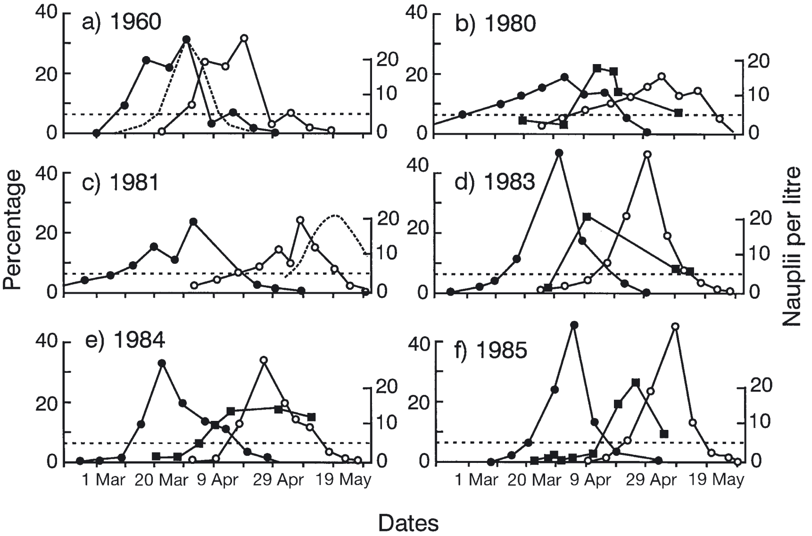


Fig. 31. Percentage production of cod eggs (●), of first feeding larvae (○) and of *Calanus* nauplii (■) in time for 6 year classes, 1960, 1980, 1981, 1983, 1984, 1985. The level of 5 nauplii l^{-1} is that at which the larvae are well fed. (After Ellertsen et al. 1989)

Fossum 1990). Year classes of 1960, 1980 and 1981 were poor ones and the production of larvae was mismatched to that of their food. Those of 1983, 1984 and 1985 were good and the production of larvae was matched to that of their food and indeed the 1983 year class was a strong one and from the table given above the 1983 year class appeared to survive the early stages well. Thus there are 2 groups of year classes—mismatched ones, that are poor, and matched ones, that are strong.

Gislason et al. (1994) investigated production on the cod spawning ground south west of Iceland in the years 1990–92:

	1990	1991	1992
Chlorophyll *a*	Late May	Early May	Late May
Calanus	May	April	May
Fish eggs	End of May	Early May	Early May

This information suggests that *Calanus* spawns at the early stages of chlorophyll or on early stratification and that perhaps the cod spawn when they feed on the spawning *Calanus.*

In spring, the overwintering adults of *Calanus finmarchicus* rise from 600 m in the Atlantic and are transported by currents, the West Spitsbergen to the Svalbard shelf, and the North Cape to the banks off northern Norway. The time of onset of the spring outburst may well vary as shown in Fig. 30, because the dependence on temperature may reflect the physical changes that determine that time. Then the cod larvae may survive best when the production of *Calanus* nauplii is matched to that of the cod larvae.

From the work described above it is quite clear that differences in food from year to year and the consequent differences in growth during larval life play an important part in the generation of recruitment. There are, of course, more distant causes, like changes in wind direction in Bryant's Cove, storms over Lasker's Lake, or input of *Calanus* onto the shelf in the Norwegian Sea in Solemdal's Parish. The effect of turbulence on the feeding process has been well established in laboratory studies, in model studies and in the sea; it may well be at the root of a dome shaped relationship on indices of upwelling. The larvae in the sea are probably short of food and grow at less than the maximal rate. Hjort's original hypothesis can now be discarded. But the work of Lasker, Leggett and Solemdal confirms that the generation of recruitment may depend to some degree on lack of food for the larvae.

Field Studies

In the past there have been many, many attempts to correlate recruitment with environmental factors, single or multiple, physical or biological. Such approaches require an environment which remains constant during the time series. The correlative approach has often failed, probably because the environment changed during the period of examination. Hence the problem is to find a mechanism by which the fish population can adapt to the changing environment, for example by modifying the growth rates and mortality rates of the larvae and the early juveniles as the cohort develops.

The earliest full study of larval mortality was made by Sette (1943) on the 1932 year class of the Atlantic mackerel between Cape Hatteras and the Gulf of Maine. Metre nets were used for the first seven cruises and 2 m stramin nets for the two subsequent ones when the larvae were bigger, so the larvae were probably well sampled up to a length of 20 mm (say 60 days old). Sette followed the modes of log length in time and so derived an estimate of age. Fig. 32 displays the decline in log numbers as a function of age (and of length). The average mortality is about 10% d^{-1}, but between 9 and 11 mm length (at an age of about 40 days) it is much higher, up to 35–40% d^{-1}. This is presumably the period at which the larvae grow fins and start to shoal, the age of metamorphosis. The increased mortality during a period when the zooplankton was low was perhaps the crucial event in the history of the 1932 year class, which was a poor one.

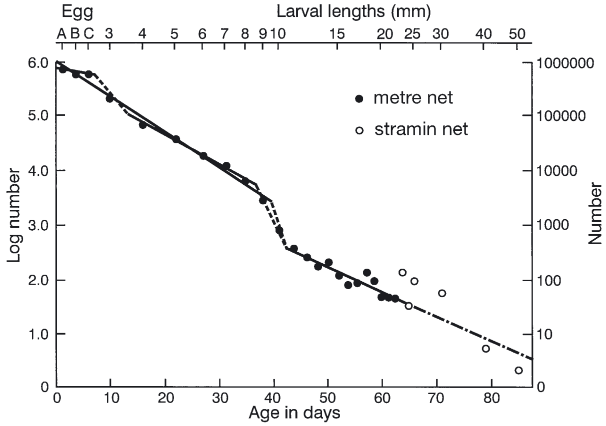


Fig. 32. Atlantic mackerel. Decline in log Numbers of larvae as a function of length and cage. (After Sette 1943)

Beverton and Iles (1992a, b) made a comprehensive study of all the work done on the mortality of 0-group (and older juveniles) flatfishes in European waters. Together with the estimates of larval mortality they constructed a life table (Fig. 33) for the first year showing a decline in mortality rate with age. The overall decline in mortality is only to be expected because that at the age of recruitment is really that of the adult stock. In recent years studies in the North Sea of the gut contents of demersal fish have revealed the same form of decline in mortality with age for the juvenile fishes (Pope and Macer 1991).

Another study of egg and larval mortality was carried out by Harding et al. (1978) on plaice in the Southern Bight of the North Sea. The larvae metamorphose at 11 to 12 mm length and are caught quantitatively. Brander and Thompson (1989) show that such larvae are sampled well by the gears then in use. Successive cruises were made over the spawning grounds between December and the following May. With the numbers of eggs or larvae on each cruise, the production of each morphological stage in time was estimated as a function of temperature. Then the ratio of successive productions in successive stages provided an estimate of mortality; this procedure requires that predation is assumed to be constant during the period of examination, which may not be true (MacKendrick 1926). Fig. 34 shows the egg and larval mortalities for the years 1962, 1968, 1969 and 1971. In general, larval mortality tends to be less than that of the eggs. This is to be expected as the larvae grow through the predatory fields of larger but fewer predators. This is the main generalization that emerges from the life table of the plaice

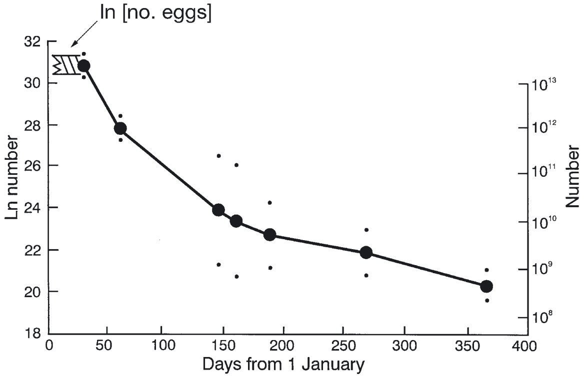


Fig. 33. Southern North Sea plaice. Life table from spawning to the end of the first year of life. ln Number ± SD. (After Beverton and Iles 1992a)

shown in Fig. 33. An interesting point is that the coefficient of variation of the abundance of eggs in 1962 was 50% and that of the larvae was 35% (Harding and Talbot 1973). Variability declined with diminishing mortality rate.

The most remarkable point is the difference between the 1969 year class and the other three, a difference of more than 2 orders of magnitude in the numbers of late larvae. But the 1969 year class as it recruited was merely average, presumably because the excessive numbers of larval plaice were eaten by shrimps as they settled (van der Veer 1986). The mortality of the late larvae was much less than that of the early ones, which implies that predation was much reduced on the later animals.

The larval mortality of the Pacific sardine and the Northern anchovy was estimated by Butler (1991). With the daily rings on the otoliths, larval ages were back-calculated from the growth rates. Then, mortality rates were estimated using a Pareto hazard function. The mortality rates of both species from 1951 to 1967 are shown in Fig. 35a; Fig. 35b displays the dependence of sardine mortality on anchovy biomass. At this time the anchovy stock was increasing at the same time as the rate of upwelling increased. At 2 years of age the sardine recruitment was not correlated with larval mortality rate, but was correlated inversely with anchovy biomass and with the combined biomasses of sardine, anchovy and mackerel, the total pelagic biomass.

Physical oceanographers can now model the loss of particles on the larval drift from spawning ground to nursery ground. With a three-dimensional model of George's Bank and its environs, Lough et al. (1994) were able to estimate losses of particles from the Bank and their retention on it.

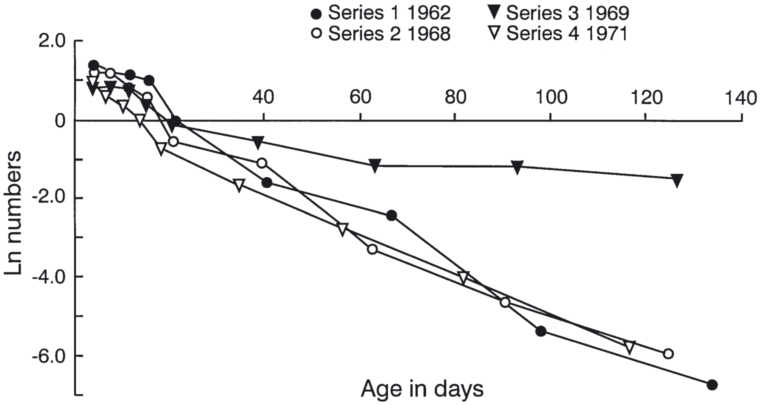


Fig. 34. Plaice. Loss in numbers of eggs and larvae in the Southern Bight of the North Sea for the year classes 1962, 1968, 1969 and 1971. (After Harding et al. 1978)

Fig. 36a shows how some particles are blown out over the ocean and how the remainder end up on the nursery ground on the southwestern corner of the Bank. Up to June 1st, the percentage losses ranged from 30 to 80% from a February release, and from 30 to 60% from a March release. From a spawning distribution and from estimates of wind stress across the region, de Young and Davidson (1994) with a two-dimensional model estimated retention on the shelf in the Labrador Current; they found a weak correlation between recruitment and retention, perhaps because the larvae left the

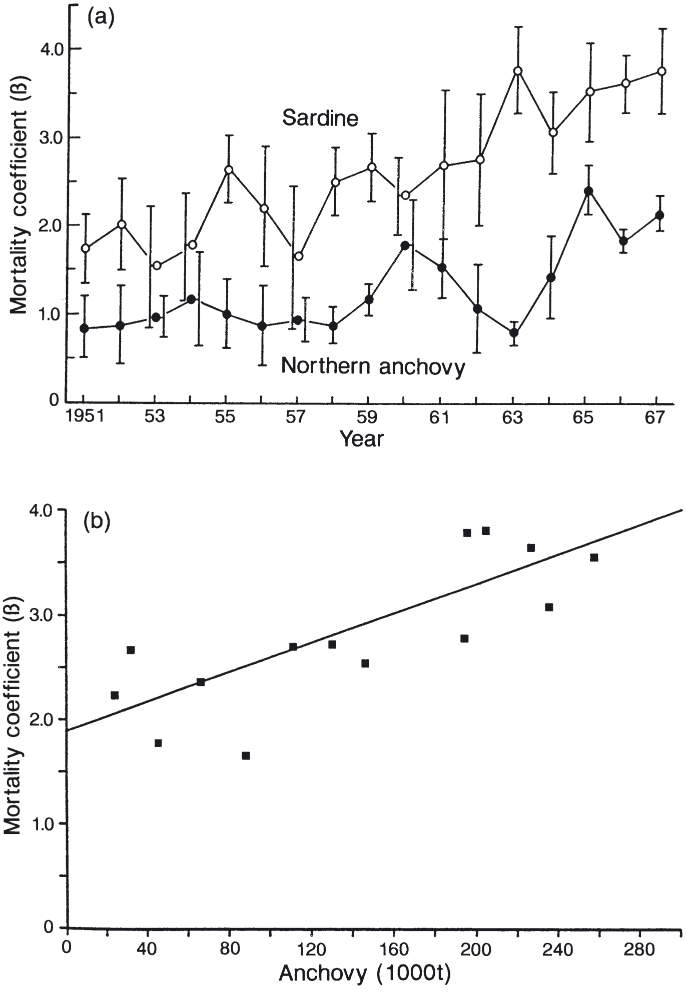


Fig. 35. (a) Mortality rates of larvae of Pacific sardine and Northern anchovy; (b) relationship between the sardine mortality and anchovy biomass (after Butler 1991)

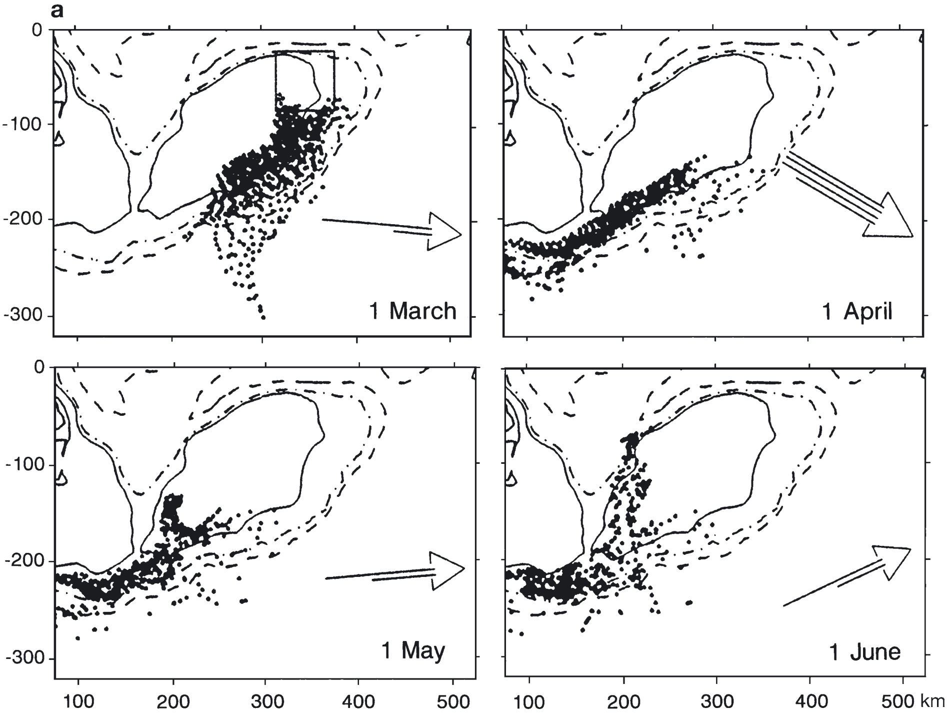


Fig. 36 (above and on facing page). Physical loss of cod larvae from larval drift. (a) Larval loss from George's Bank (after Lough et al. 1994). The arrows indicate the wind vector; each full line represents a stress of 0.04 Pa

current to move up onto the Grand Bank itself. In their 1994 paper, Davidson and de Young showed that the particles from the spawning ground of the Northern cod on the shelf break (Wroblewski et al. 1995) in the Labrador Current were drifted onto the Grand Bank itself where the juveniles live (Fig. 36b). Adlandsvik and Sundby (1994), with an adaptation of the Princeton Ocean model, developed a Lagrangian approach to the flow of particles from the Lofoten spawning grounds of the Arcto-Norwegian cod (Fig. 36c). They showed clear separation from the West Spitsbergen and North Cape currents for different wind stresses and demonstrated that advective losses could be estimated. The important part of their work is to estimate the losses and to establish the true mortality. It is unlikely that recruitment is determined only by the losses during the larval drift, because simple correlations of recruitment on wind stress would have survived.

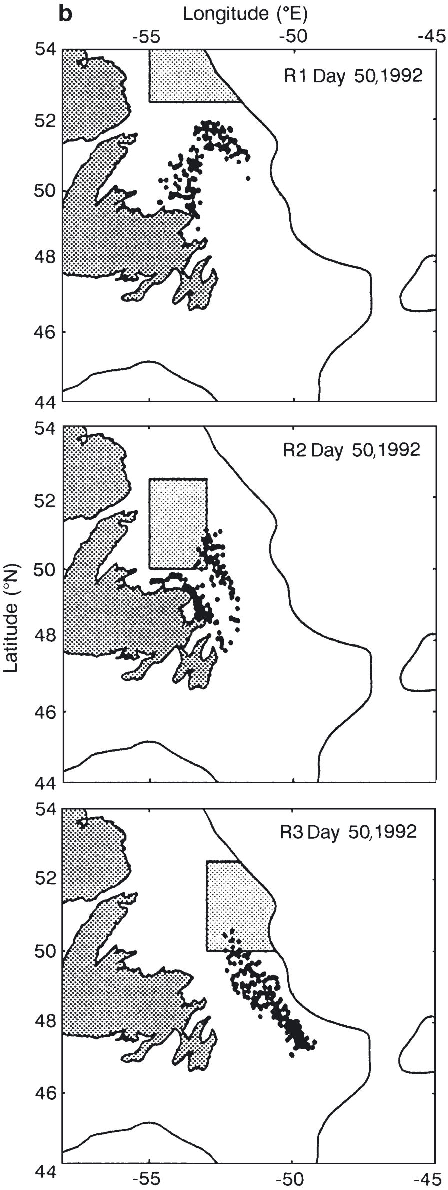
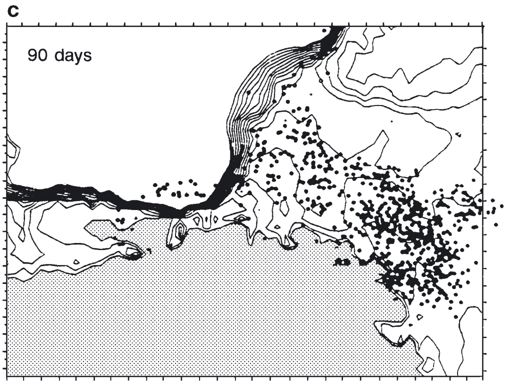


Fig. 36, continued. (b) Larval loss from 3 regions on the Labrador Shelf, R_1, R_2 and R_3 (after Davidson and de Young 1994). (c) Larval loss from the Atlantic current into the Barents Sea (after Adlandsvik and Sundby 1994)

There is an important distinction between the term "retention" and the phrase "larval drift" in that the first is included in the second; for example, the larval drift will include the behavioural changes that take place when plaice larvae move deeper as they migrate across the Southern Bight of the North Sea, or as larvae of the Northern cod leave the deeper water in the Labrador Current and move up onto the Grand Bank.

Predation

Bailey and Houde (1989) classified the invertebrates and fishes as ambush or cruising predators. They reviewed the relationship of both cruising speed and burst speed to length from estimates in the literature and how the larvae respond to attack as a function of length. They described in detail the problems of estimating predation at sea, identification and in-



gestion. Mesocosm studies revealed that larvae survive well with low food, and that very fit larvae remain susceptible to predation. Further, after metamorphosis early juveniles may themselves chase fish larvae.

Predation comprises 3 parts: encounter, attack and capture. Fuiman and Magurran (1994) have described the defences against predation. Within this system is a point of primitive foraging theory, that one should take the biggest cream bun at least cost. In the processes of *encounter*, transparency protects early larvae for a short time but they become vulnerable as they become more conspicuous. A video camera was used to record predation by yearling herring on herring larvae and numbers of larvae responding and numbers escaping were recorded, as were the predator's errors and numbers caught. All were recorded as a function of length and expressed as simple or more complex regressions. Litvak and Leggett (1992) exposed capelin larvae of different sizes (from large and small eggs) to sticklebacks which took the larger larvae because they were no longer transparent. Predators are often more attracted to prey that move than to those that do not.

In *attack*, the predator relies on motion detection. Larvae may be detected at a range of about 10 cm by vibrations in the otoliths of the predator and at shorter ranges (say 2 cm) with the neuromasts of the lateral line. Shoaling starts at metamorphosis when the little fish grow fins and this may confuse the predator. The schools are maintained by communication with the lateral line (Gray and Denton 1991).

Many small larvae do not respond to a predator's attack and errors in attack are relatively rare. But the larvae do dodge attacks by medusae. Startle responses are evoked from larvae by an acoustic stimulus at 100 Hz. Further, herring larvae do not respond to a predator's attack until the rods in the retina have developed. They do not really respond to the attacks until they reach a length of about 26 mm.

The gross vulnerability (V) to a predator is the product of the probabilities of encounter (P_E), attack (P_A) and capture (P_C). The probability of encounter was formulated by Gerritsen and Strickler (1977) and developed by Rothschild and Osborn (1988) and their successors in the study of turbulence (see above). The essential terms are the encounter radius of the predator, the escape radius of the prey and their relative attack and escape speeds. Fig. 37 shows the changes in vulnerability with length as yearling herring chase herring larvae. The latter become more vulnerable at first as they enter the sphere of influence of the predator, and as they get bigger, between 20 and 30 mm, they tend to evade predation by one means or another. Such distributions can be constructed readily from experimental studies in mesocosms.

There are 2 parts to the estimation of predation at sea. The first is the identification of the predator(s) from the gut contents of potential attackers. The second is the allocation of mortality by the proportions in the guts. Then mortality must be well estimated, for example by ratios of production of larvae at successive stages. This method is expensive, as indicated above, because research vessels have to be maintained at sea for 4 to 5 months. A second method samples the larvae at a time predicted by the rate of development at temperature; this is much less expensive and potentially provides more information (Harding and Talbot 1973). A third possible method is based on the estimation of instantaneous rates of production and may be relatively cheap (Hunter 1972). At the same time it is desirable to catch all the potential predators, from jellyfish and copepods to fishes, which requires an array of sampling equipment. From this very brief statement of the problem, it is obvious that cheaper methods of sampling are needed before predatory mortality can be properly estimated.

The estimation of predatory mortality at sea should be linked to the quasi-theoretical structure displayed in Fig. 38. It might be possible to make a model of predation based on a series of predatory fields or spheres of influence as illustrated. This demands experimental work at sea and work in mesocosms. If it were successful a limited number of cruises might be needed to calibrate the course of mortality in time.

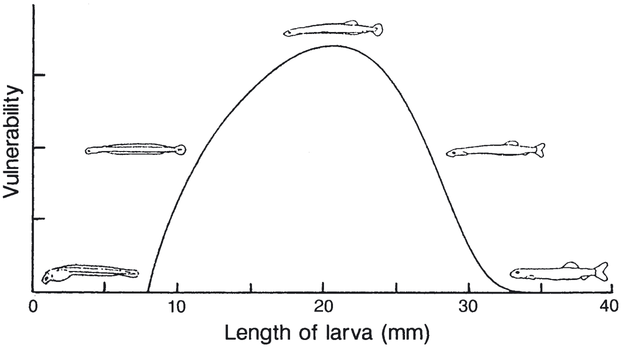


Fig. 37. Change in herring larval vulnerability with length. (After Fuiman and Magurran 1994)

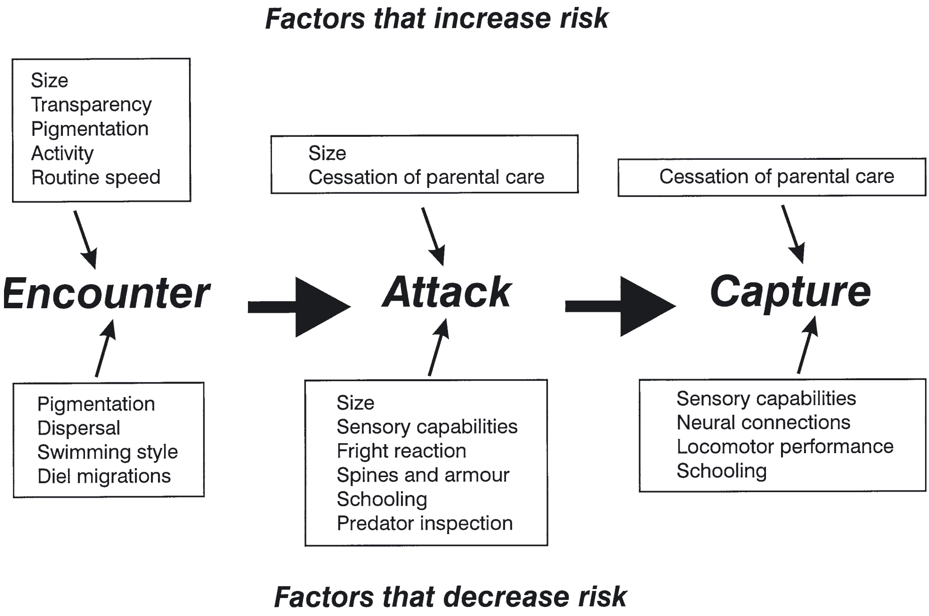


Fig. 38. Structure of predation. (After Fuiman and Magurran 1994)

Variability of Recruitment

To illustrate the variability of recruitment, I have used data from 9 stocks for which there are about 3 decades of observations at least (Myers et al. 1990); 3 cod stocks, the Arcto-Norwegian, Iceland and Northern cod; 3 flatfish stocks, North Sea sole, North Sea plaice and the Pacific halibut; 2 herring stocks, the Downs stock in the southern North Sea and the North Sea herring; and the Skeena stock of Sockeye salmon. In each time series recruitment is displayed with the geometric mean and 1 standard deviation.

The 36-year time series of recruitment to the Iceland cod stock shows 2 poor year classes and 4 good ones; the strongest year class is about twice the mean (Fig. 39a). Until the late 1980s when recruitment was reduced somewhat, variability was low (the ratio of the standard deviation to the geometric mean ranged from 0.7 to 1.45). In the Arcto-Norwegian cod (Fig. 39b), the general variation was also low (0.5 to 2.0), but there were 3 strong year classes, each about 4 times greater than the mean; further there were 3 poor year classes during the time series of 38 years. Perhaps in another few

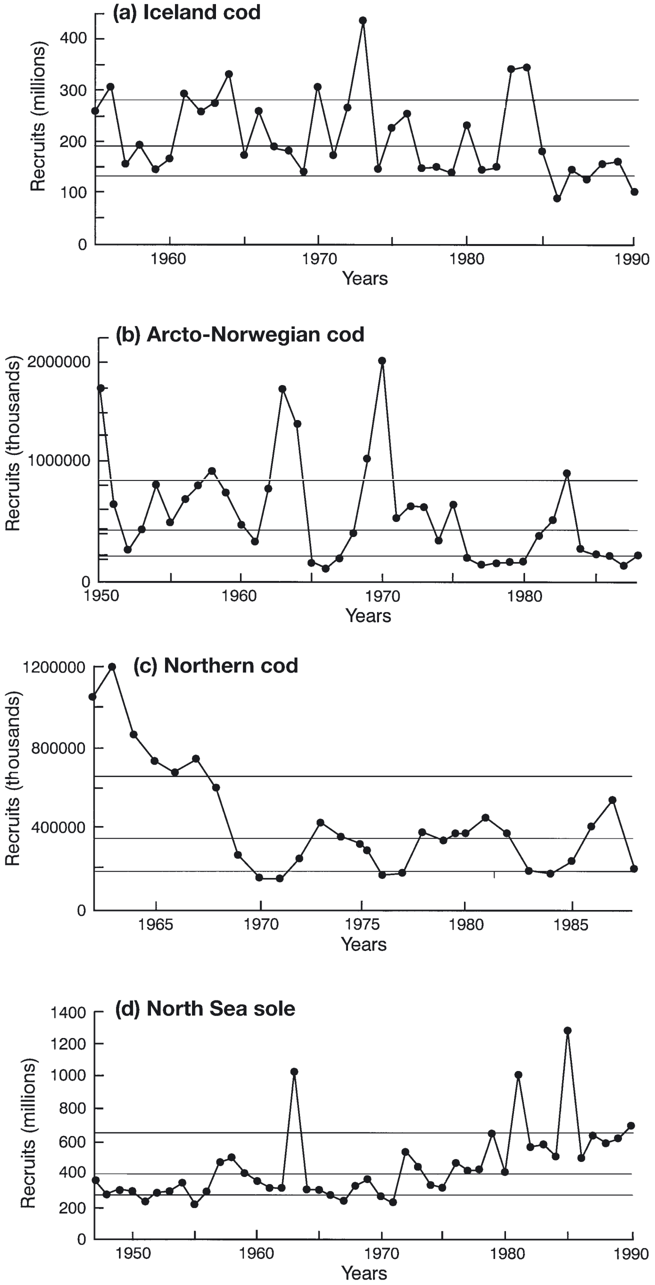


Fig. 39 (above and on subsequent pages). Variability of recruitment. (a) Iceland cod; (b) Arcto-Norwegian cod; (c) Northern cod; (d) North Sea sole

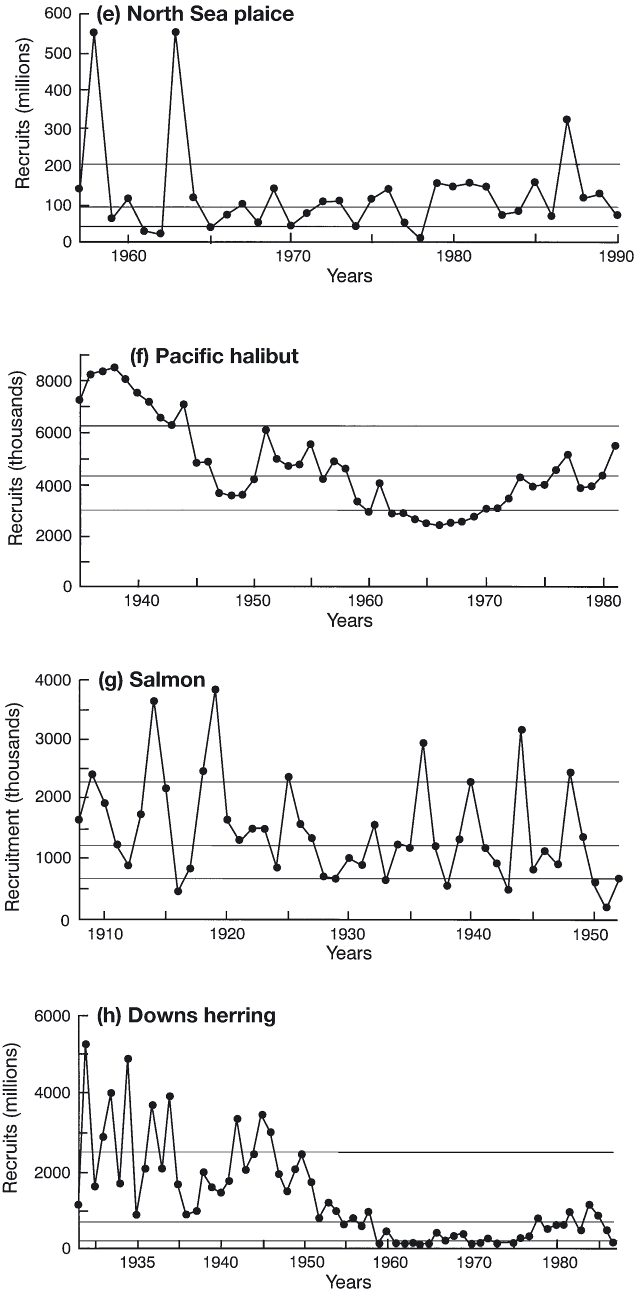


Fig. 39, continued. (e) North Sea plaice; (f) Pacific halibut; (g) Skeena sockeye salmon; (h) Downs stock of herring

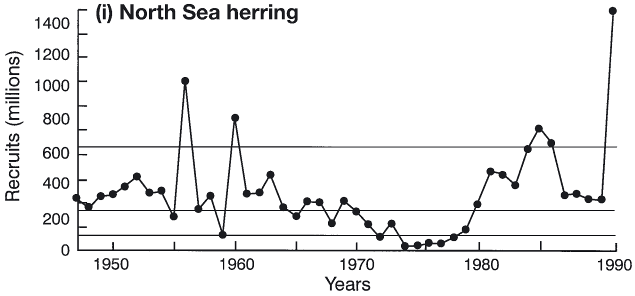


Fig. 39, continued. (i) North Sea herring. (After Cushing 1995b)

decades a periodicity will emerge from such material. The Northern cod (of of the Labrador Current and the Grand Bank) has only been sampled in this presentation for 28 years (Fig. 39c) but recruitment has declined from recruitment overfishing (Chapter IV).

In the North Sea sole between 1957 and 1990, there were 3 strong year classes, 2 of which were more than 5 times larger than the mean (Fig. 39d). There are very few poor year classes and there is a tendency for the general level of recruitment to rise with time. In Fig. 39e is illustrated the recruitments to the stock of North Sea plaice between 1957 and 1990. There are very few poor year classes and 3 strong ones, 2 to 3 times larger than the mean, but there is an upward trend in recruitment from the late 1960s. In the Pacific halibut (Fig. 39f), from 1935 to 1982, there has been a downward trend and a partial recovery, the nature of which has not yet been described.

In the stock of the Skeena sockeye salmon (Fig. 39g) between 1908 and 1952, there were 4 strong year classes and 2 poor ones; the strong were 3 to 4 times larger than the mean. Both the Downs stock of herring and the North Sea stock of herring (Fig. 39h and i) suffered recruitment overfishing and so recruitments were reduced after which they recovered. I have distinguished the Downs stock from the North Sea stock because the former is distinct (Cushing and Bridger 1964, Cushing 1992). The North Sea catches included those of the Downs stock but during most of the period the proportion of Downs catches was very low. In the North Sea herring there were 4 strong year classes, 3 to 6 times larger than the mean. In both herring stocks the series of poor year classes are the result of recruitment overfishing.

If we examine the 5 stocks that did not suffer recruitment overfishing (or trend sharply during the period as in the Pacific halibut), the strong year classes appear as follows:

Arcto-Norwegian cod	3 in 38 years
Iceland cod	4 in 36 years
North Sea sole	3 in 33 years
North Sea Plaice	3 in 43 years
Skeena sockeye salmon	4 in 44 years

This is a small sample but there is some evidence that a strong year class appears about once a decade. This is a remarkable point and it may even suggest that the emergence of such strong year classes is part of the strategy of survival. The distributions of recruitment are logarithmic, for which a variety of reasons may be cited. Some outstanding year classes are much larger then the upper standard deviation, which suggests that once in each decade the conditions of growth and mortality must be optimal.

Match/Mismatch Hypothesis

The match/mismatch hypothesis has attracted attention and some criticism. I defended it in detail in Cushing (1990). If the magnitude of recruitment is established at the late larval stage and among the metamorphs, the match/mismatch hypothesis depends really upon the survival of larvae where and when food is abundant. If larvae in the open sea are not as well fed as expected from the maximal growth rate, the survival must depend on differences in food available to larvae from year to year. This is no more than a statement of the match/mismatch hypothesis.

I have returned to the early evidence in some detail because there appears to be a real difference betweeen the Northeast and the Northwest Atlantic, which is worth investigating. Further, much of the evidence lies in papers published a long time ago. Cushing (1966) described the climatic changes that had occurred in British waters from the 1930s to the 1960s. The natural changes in the western English Channel were described as were those in the growth and recruitment of the North Sea herring, both of which appeared to be linked to the system of production. I wrote: "If fish spawned at the same time each year, then variations in *timing*, *amplitude* and *spread* of the productive cycle would have profound effects on the subsequent recruitment to the adult stock. It is not known whether the mortality of larval fish is due to food lack or to predation, but variations in the productive cycle could alter either."

During the 1950s and early 1960s we surveyed the herring spawning grounds between the North Foreland and the Sandettié Bank in the Southern Bight of the North Sea and had learned from echo surveys that the herring appeared there in the first week of November. The late Professor Jenne Zijlstra used to say that the same was true of the herring stocks that spawn around the Dogger Bank.

Cushing (1967) showed that spring and autumn herring spawned just before a production cycle occurred in the North Sea; the evidence for winter spawners was weak, perhaps because the winter *Pseudocalanus* (on which the larval herring feed) is an omnivorous feeder outside the period of the spring or autumn outburst. In Chapter II it was shown that the ln Residuals from the Stock Recruitment Relationship were inversely related to the quantities of ln *Para-/Pseudocalanus* in the spring months, particularly in March. Perhaps the autumn spawners depend on the autumn outburst (prominent in the North Sea) to survive and on the subsequent spring outburst to determine the magnitude of their recruitment. It was also shown that facets of the biology of the herring (growth, egg size and fecundity) were related to depth of water and to variability in the timing of the production cycle (Cushing 1967). For example, winter spawners hatched in shallow water with low variation in the time of onset of the production cycle and spring spawners in deeper water with high variation in the time of onset. Today, with more information, we know that the variation in recruitment of the winter spawners, like the Downs stock, is very much less than that of the Norwegian spring spawners (Cushing 1995b).

Cushing (1969) showed that the idea of a fixed time of spawning in temperate fishes could be sustained. For example, the production of plaice eggs in the Southern Bight of the North Sea had been estimated in 8 years between 1911 and 1950 and a measure of the peak date of spawning in any one year could easily be made. The later cruises in 1962, 1963, 1969 and 1971 were not used because they started later in January to sample the larvae and not the eggs. There was no trend in time between years and so the distributions could be combined to give a mean peak date of spawning (January 19) with a standard deviation of about a week.

Runnstrøm (1941) made a detailed study of herring spawning off the Norwegian coast with grab samples for eggs on the seabed every day during February and March on 14 known spawning grounds for up to 7 years. There were trends in mean date for 3 grounds, but the standard deviations of date were still low, a week or less (including the material with a trend in the mean date of spawning) and of course the standard error of that date was very low. Greater changes in spawning time on a broader scale have been recorded for the Norwegian spring spawning herring (e.g. Devold 1963), presumably due to loss or abandonment of grounds, perhaps temporary on a longer time scale.

For the Fraser River sockeye, detailed descriptions of spawning were given in the Annual Reports of the International Salmon Commission for 51 sites and for 17 years. The time series were displayed in my paper and only in one was there a trend in time. The standard deviations in the mean date of peak spawning was of the order of 5 days. It will be recalled that the sockeye spawns in autumn and that the alevins hatch in the following spring and the fry emerge from the gravel a few weeks later.

For the Arcto-Norwegian cod I used records of catches in the Vestfjord in northern Norway, covering 13 to 15 weeks each year between 1894 and 1958. The dates of peak catch were variable and a 10 day moving mean was fitted to the data, but the range of trend was low, less than 10 days. The standard deviation of the mean peak date of catch, including the trend, was 4 days. Since my analysis, Ellertsen et al. (1987) showed that the peak date of spawning was 14 days later than that of peak catch. With evidence of maturation, Pedersen (1984) found that for 7 years the peak date of maturation was remarkably constant.

The peak date of spawning on Georges Bank was inversely related to temperature, but this was not true on Brown's Bank (Page and Frank 1989). According to Hutchings and Myers (1994), the date of cod spawning on the Grand Bank varied in response to temperature. The fixed time of spawning suggests dependence on photoperiod, but this may be overlain by temperature. Temperature may be proxy for other climatic events, cool water indicating late date of spawning. If the dependence of date of spawning is inversely related to temperature, delayed spawning in cooler water is an advantage, because production cycles are also then delayed as stratification is delayed. Hutchings and Myers (1994) established that spawning periods increase with age. The stocks examined in Cushing (1969) were in the main lightly exploited. Is it possible that the difference between the cod stocks in the Northwest Atlantic in recent years and the Northeast Atlantic some decades ago is really a difference in the degree of exploitation?

The older fish tend to spawn first and then, as the stock is exploited, the mean date of spawning occurs later. Part of the stock will comprise recruits, the arrival of which may depend on temperature. The Norwegian herring, sockeye salmon and Arcto-Norwegian cod were not exploited very heavily when the samples used were taken. The plaice stock in the southern North Sea was fished heavily in the 1920s and 1930s but in the late 1940s and 1950s when the egg samples were taken the stock was fished more lightly. In recent years the stocks of cod on George's Bank and on the Grand Bank were fished harder than in earlier years.

As described above, recent work has suggested that the major processes by which the magnitude of recruitment is determined occur between the stages of late larvae to early juveniles, including the metamorphs. This means that the magnitude of recruitment is vulnerable to climatic factors. The second point to have emerged in recent years is that the masters of larval science have established that the little animals suffer much from lack of food and that therefore their growth rates are often less than the maximal. Hence, provided that the predators do not aggregate on their prey, the mortality generated by adventitious predators must increase with low growth rates, the Ricker-Foerster thesis. If these statements are true, the magnitude of recruitment is determined by differences in growth and mortality during larval life. The match/mismatch hypothesis states no more than this and in general terms has been established. But the use of the hypothesis has not been pursued.

The first reason for the lack of use is that the growth and mortality of larvae from hatching to recruitment have not been examined. A paper entitled "Had I but world enough and time..." (Cushing 1985) suggested that these parameters be measured from hatching to recruitment. It has not been done because, with traditional methods, it would be very expensive. The variation in recruitment is very low as compared with the loss in numbers from spawning to recruitment. Large cod may lay millions of eggs but the recruitment varies by factors of 10 to 30, which implies continuous and close control. But it is the differences within that range which drive the changes in the fish stocks.

The second reason for lack of use is that belief is suspended for a variety of very good reasons. The most important is that the short argument set out above is not very well known. Another is that the control may be close and continuous, but its remainder, the recruitment, is sometimes considered to be randomly distributed. All this means is that we need not be interested in the differences on which that distribution is based. Of course there are errors of all sorts in the distribution of recruitment but as described above there is ample evidence that recruitment does depend on specified climatic factors. There are a number of suggestions that fishes release their eggs into a rising production cycle or upwelling system (as sardines spawn off a cape where upwelling must occur). Such signals provide some evidence that fish larvae depend on food to grow and perhaps to defy mortality. But we now know that independently.

There are 2 or 3 events that might provide evidence that the match/mismatch hypothesis is worth pursuing. The study of the gadoid outburst, as a response to climatic factors, was discussed in Chapter II and it was concluded that the idea that the initiation of the gadoid outburst was linked to the delay in the production of *Calanus* became once more valid. As noted in the previous chapter, the delay was in fact observed in the northeastern North Sea from 1962 to 1992. Cushing (1984) published a multiple regression of cod recruitment on delay of production, on *Calanus* production and on temperature in March when the cod spawn ($r^2 = 0.75$). The negative relationship of cod recruitment on the abundance of *Calanus* might have been the result of predation by cod larvae on *Calanus*. The only way in which progress could be made on this problem would be to create models of secondary production and of the generation of recruitment.

A second event was the evolution of the year classes of the Arcto-Norwegian cod as described above. For 4 years there was an inverse relationship between the dry weights of larvae at 6 mm length and the peak date of abundance of stage 1 *Calanus* (taken from the dependence of peak date on temperature). In other words: the earlier the peak date of *Calanus* production the greater the dry weight for the 4 year classes. This suggests that in the warm years the production of cod larvae is matched to that of their food and in cool ones it is not.

Mertz and Myers (1994) extended the study of the match/mismatch thesis. Let the degree of mismatch be t_0 and when $t_0 = 0$, larval production is fully matched to that of their food; σ is the half width of the distribution of larval production in time and δ that of the production of larval food in time. With a larval mortality rate of about 10% d^{-1}, a theoretical development led to $\Delta F/F \approx -t_0^2/(\delta^2 + \sigma^2)$, where $\Delta F/F$ is the relative change in food, F, analogous to a coefficient of variation. Then it is related inversely to the degree of mismatch, t_0. Fig. 40 shows the inverse relationship between the coefficient of variation of recruitment and the standard deviation of the spawning distribution ($r = -0.68$, $p = 0.02$). If the width of the spawning window is linked to the relative change in food, fish stocks can reduce the variation in recruitment by spawning over a protracted period.

Myers and Cadigan (1993) showed that part of the juvenile mortality is density dependent and they believe that the major processes which determine the magnitude of recruitment occur during the late larval stages to be modified later by density dependent mortality. Mertz and Myers (1994) suggested that the relative changes in cumulative mortality approximated the relative change in food (if escape depends on length and weight depends on food, mortality may depend on $F^{1/3}$). Then they would expect an inverse relationship between the coefficient of variation of prejuvenile numbers and the standard deviation of the spawning window. The match/mismatch hypothesis has been advanced. The new piece is the idea that fish stocks reduce the variation in recruitment (and that of the precruit mortality) by spawning over a protracted period. This is a direct consequence of the hypothesis, not formulated before.

A Model of Match

At the Fisheries Ecology 111 meeting in Miami (Florida, USA) in 1982, a view was expressed that the fish larvae could not affect the quantities of gross zooplankton. But the needs of fish larvae are much more specific. Haddock (and cod) larvae feed on the nauplii and early copepodite stages of *Calanus finmarchicus* (Marak 1974) and Jones (1973) suggested that the larval cohort grew up alongside a cohort of their food. This is really an extension of the match/mismatch hypothesis and the idea was pursued by Jones and Henderson (1988) and by Nival et al. (1988). Cushing (1983) tried to answer the question raised in Miami and showed, from field and laboratory work by Laurence (1982) on haddock larvae, that the larvae might reduce the numbers of nauplii and copepodite stages of *Calanus* by up to 2–3% d^{-1}, which is fairly considerable when expressed cumulatively for 40 days.

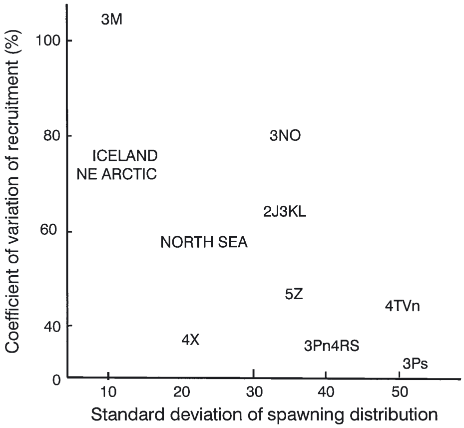


Fig. 40. Inverse relationship between the coefficient of variation of recruitment and the standard deviation of the spawning distribution ($r^2 = 0.68$; $p = 0.02$). The codes refer to ICNAF divisions in the NW Atlantic. (After Mertz and Myers 1994)

An extension of the argument appears in Cushing and Horwood (1994) in which a cohort of haddock larvae grows with a cohort of *Calanus* in a matched condition so that the smallest larvae feed on nauplii and then larvae and food organisms grow together. Mismatch was not pursued at this stage. The first step was to estimate the volume searched by 1 larva:

$$V = \frac{2}{3}\pi\,\delta^2 a\, l$$

where V is the volume searched by 1 larva in ml s^{-1}; δ is a search radius in body lengths; a is a constant of swimming speed ($1\ s^{-1}$); l is body length in cm. According to Blaxter and Staines (1971), the larva searches about ⅔ of a circle ahead.

Fish larvae are visual feeders so they search for about 12 hours per day in the temperate spring.

Let $A = (2/3)\,\pi\,\delta^2\,a \times 3600 \times 12$ or $0.076 \times 10^6\ l^2\ d^{-1}$, for $\delta = 0.075\ l$ and $a = 1.5$. Then $V = A\ l$ (in ml d^{-1}).

The weight/length relationship of the larval haddock is

$$W = 0.044\, l^{4.476}$$

where W is dry weight in μg and l is length in mm (Laurence 1982); or

$$l = 0.2009\, W^{0.2234}$$

where l is length in cm.

Then $V = 0.076 \times 10^6 \times 0.2009\, W^{0.2234} = 0.0154\, W^{0.2234}\ m^3\ d^{-1}$. The next step is to establish the volume searched by a number of larvae, N, but first the growth rates and mortality rates of the larvae have to be described. The larva grows:

$$W_{t+1} = W_t \exp(G)$$

where W_t is the weight of a larva at time t; W_{t+1} is the weight of a larva at time t+1; G is the instantaneous growth rate from t to t+1. The larvae die:

$$M_t = \frac{M_{\max}}{1 + bt}$$

where M_t is the instantaneous mortality rate of the larvae at time t; $M_{\max}$ is the instantaneous mortality rate of the eggs at time $t = 0$; b is a constant of units t^{-1}. This expression allows mortality rates to diminish in time; it was developed for the plaice of the Southern Bight of the North Sea (see Cushing

1995b) and was adapted to the haddock larvae on George's Bank (Laurence 1982). Then

$$N_{t+1} = N_t \exp(-M_t)$$

where N_t is the number of larvae at time t; N_{t+1} is the number of larvae at time t+1. The volume searched by N larvae m^{-3}, P_t (= $N_t V_t$), at time t+1 is $P_t = N_t\, 0.0154\, W_t^{0.2234}$, which implies that search volumes do not overlap.

The number of food organisms declines:

$$F_{t+1} = F_t(1 - P_t)$$

where F_t is the number of food organisms m^{-3} at time t; F_{t+1} is the number of food organisms at time t+1.

Food organisms grow:

$$w_{t+1} = w_t \exp(g)$$

where w_t is the weight of a food organism at time t; w_{t+1} is the weight of a food organism at time t+1; g is the instantaneous growth rate of the food organism assumed constant with time.

The daily ration of the fish larva, R, in numbers of food organisms, is given by:

$$R_t = \frac{\Delta W_t + K\, W_t^n}{(1-\alpha)\,\beta\, w_t}$$

where ΔW_t is the increase in weight of the fish larva during day t; K and n are metabolic constants; α is the fraction of food lost in metabolism; β is a digestive coefficient: $\beta = \beta_{\max}\,[1 - m \exp(-j(W - 70))]$, where m and j are constants.

A maximal growth rate $G_{\max} = 0.12$ where $R_{\max}$ is the number of food organisms eaten. Then if $R_t > R_{\max}$, $R_t = R_{\max}$. $R_{\max}$ implies a $P_{\max}$, and $F_{t+1} = F_t(1 - P_{\max})$. R_t is calculated as $R_t = P_t F_t / N_t$.

The model is run from P_t, F_{t+1}, R_t, ΔW_t, W_{t+1}, G_t, w_{t+1}, N_{t+1} and M_t. If $G_t > 0.12$, G_t is set at 0.12 and W, $R_{\max}$ and $P_{\max}$ are recalculated. A list of constants is given in the original publication.

Metamorphosis in the pleuronectids is very obvious and so the age of metamorphosis can be determined in the laboratory. Chambers and Leggett (1987) did this for 18 populations of winter flounder *Pseudopleuronectes americanus* fed ad libitum. Length and age at metamorphosis were, of course, correlated, but the age of metamorphosis ranged from 44 to 71 days. Because growth rates and rates of development were correlated, the slow growing larvae metamorphosed later, presumably because they were defeated in the competition for food. At a maximal rate of growth, metamorphosis is reached in 40 days and the model was run at first for 60 days.

The growth of the haddock larvae is illustrated in Fig. 41 at different levels of food organisms between 1000 and 10 000 m^{-3} for periods up to 60 days; the very slow growth rates are perhaps unrealistic. In Figs. 41 to 48, the initial number of larvae is 1 m^{-3} and $b = 0.005$. Fig. 42 shows the dependence of average growth rate on the number of food organisms; the growth rate is that averaged to the age of metamorphosis. Fig. 43 displays the relationship between the cumulative mortality to the age of metamorphosis and the number of food organisms; there are 2 constraints: (1) the maximal growth rate at high food levels; (2) the limit to cumulative mortality at the age of metamorphosis at 60 days. These 2 constraints are clear in Fig. 44 which shows the relationship of cumulative mortality on average growth rate. In Fig. 45 is shown the relationship between the numbers of larvae surviving to metamorphosis and the number of food organisms; this is an estimate of recruitment at metamorphosis. The same parameter is plotted on initial numbers of larvae at different levels of numbers of food organisms in Fig. 46. This figure looks like a Stock Recruitment Relationship, but it is not, because the events illustrated are limited to larval life and because the idea behind it is limited to the Ricker-Foerster thesis.

Fig. 47 depicts the dependence of cumulative mortality (summed to the age of metamorphosis) upon the initial numbers of larvae (0.1 to 7.5 m^{-3}) at different levels of food organisms (2000 to 10 000 m^{-3}). About one third of

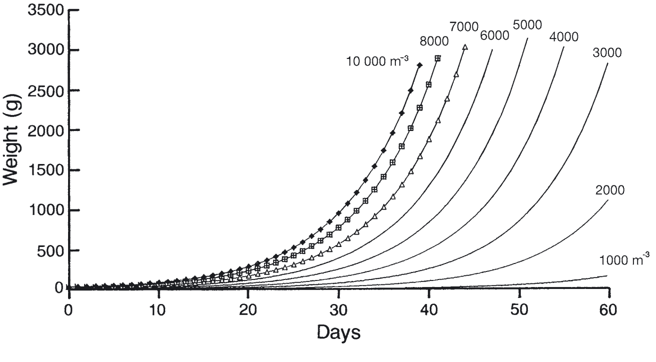


Fig. 41. Haddock. Growth of larvae at different levels of food (1000 to 10 000 m^{-3}). (After Cushing and Horwood 1994)

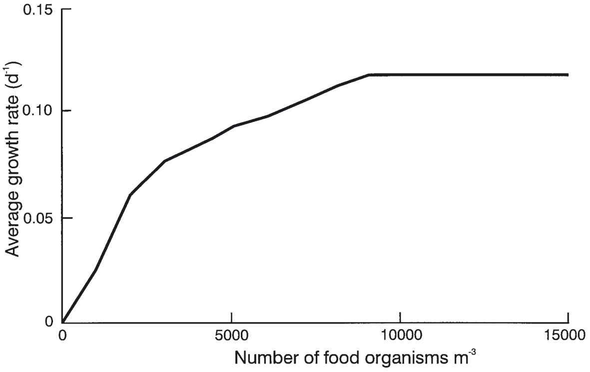


Fig. 42. Relationship between average growth rate (averaged to the age of metamorphosis) and number of food organisms. (After Cushing and Horwood 1994)

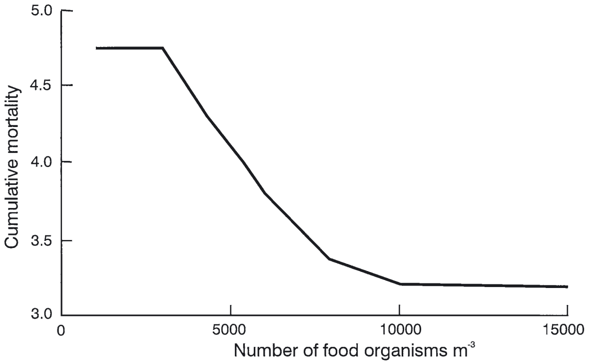


Fig. 43. Relationship between cumulative mortality (to the age of metamorphosis) and number of food organisms. (After Cushing and Horwood 1994)

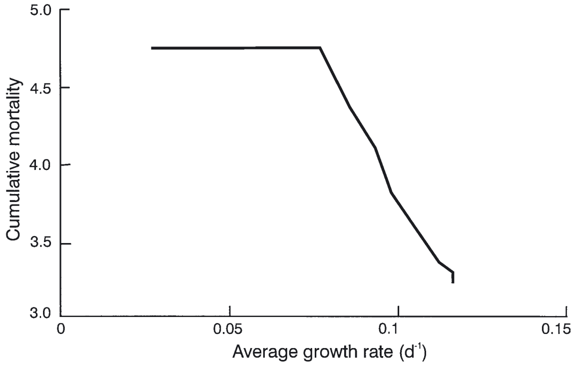


Fig. 44. Relationship between cumulative mortality (to metamorphosis) and average growth rate. (After Cushing and Horwood 1994)

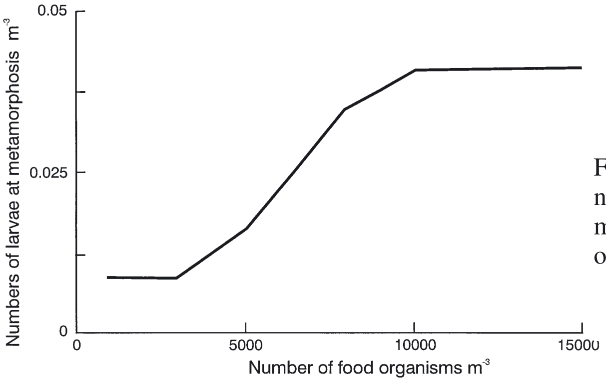


Fig. 45. Relationship between numbers of larvae surviving to metamorphosis and the number of food organisms. (After Cushing and Horwood 1994)

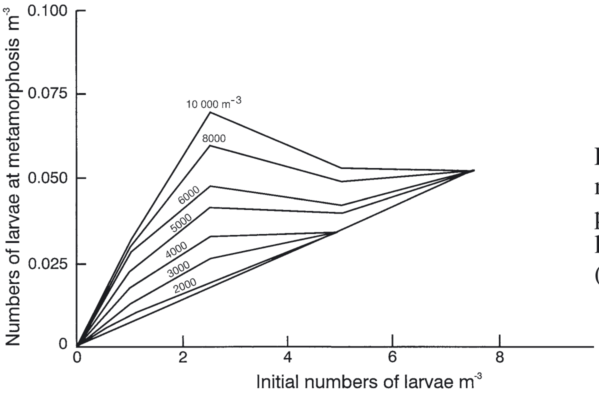


Fig. 46. Relationship between numbers of larvae at metamorphosis and initial numbers of larvae at different levels of food (1000 to 10 000 m^{-3}). (After Cushing and Horwood 1994)

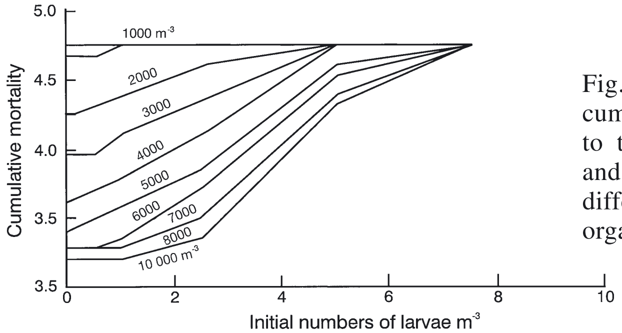


Fig. 47. Relation between cumulative mortality (summed to the age of metamorphosis) and initial numbers of larvae, at different numbers of food organisms. (After Cushing and Horwood 1994)

this mortality is density dependent and is apparently greater at high levels of food. This was a surprising result, partly because the proportion of density dependent mortality is higher than expected and partly because, at low levels of food, mortality appears to be density independent. At all levels of food, cumulative mortality depends on numbers, but it is obscured at high levels of mortality because of the artificial constraint in days run in the model. At high food levels, mortality is less, as might be expected, but paradoxically, density dependence appears to be less at low food. This is because at low food levels mortality is already high at the lowest number of larvae, 1 m^{-3}. The general relationship is density dependent at all levels of food. If true, this would mean that the proportions of density dependent to density independent mortality would differ in each year class, and the hope that there was a constant ratio of one to the other has failed.

In Fig. 48, the 60 day restraint to the age of metamorphosis was extended to 100 days. Recruitment at metamorphosis is plotted on the initial numbers of larvae, 1 to 30 m^{-3} and at different levels of food organisms up to 40 000 m^{-3}. The linear relationship on the left of the figure expresses the maximal growth rate. At the present time the *initial* number of larvae on George's Bank is probably about 3 to 5 m^{-3} and the greatest number of food organisms is about 5000 to 10 000 m^{-3}. The number of larvae may have been greater in the unexploited stock. The sharp peak in recruitment at metamorphosis is unlikely to be observed at sea. The figure expresses an extension both in numbers of larvae m^{-3} and in numbers of food organisms. It is an extension well beyond the observed quantities of both. The very sharp form of the curve is perhaps absurd as the model is tested almost to destruction. The upshot is that the weaknesses are revealed.

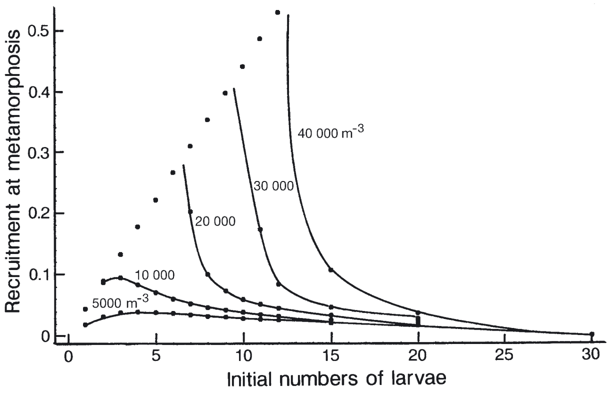


Fig. 48. Recruitment to metamorphosis as a function of initial numbers of larvae (1 to 30 m^{-3}) at different levels of food organisms up to 40000 m^{-3}. The time to metamorphosis was extended to 100 d. (After Cushing and Horwood 1994)

If larval production is not matched to that of the food, the growth rate is less, the maximum being reached less often, and the cumulative mortality to the age of metamorphosis declines more sharply with number of food organisms (because the mortality rate at age is fixed). The recruitment at metamorphosis will depend on numbers of food organisms less sharply. So the dependence of recruitment at metamorphosis on the initial numbers of larvae is of the same shape but the numbers of recruits are fewer. The same is true of the relationship of recruitment on numbers of larvae extended to high numbers of larvae and to high levels of food organisms. Similarly the degree of density dependence is lower. Thus the shift from match to mismatch leads to reduced recruitment and less density dependence; that is, within the limited structure of the model.

The model is too simple in 2 respects: mortality at age is constant and the numbers of food organisms are not reduced by the larvae. Evidence that food organisms are reduced by fish larvae has been presented above. This would have an effect analogous to the mismatch described above. But the nature of such a relationship has not yet been established for cod larvae and the *Calanus* cohorts. Differences in predation may take place, particularly as vulnerability shifts from one predator to the next, which is larger and less numerous. Here I assume that predators do not aggregate.

The real point about the model is that it illuminates the way in which the match/mismatch hypothesis can be tested, that is by estimating the growth and mortality of the food organisms. A study of predation would also be needed. This is no more than a study of how recruitment is generated.

Very recently, in a notable paper, Campana (1996) examined the growth rates of juvenile cod on George's Bank for the five year classes 1984 to 1988. Fifty larvae were sampled each year spread across each spawning period. The growth rate was measured by the width of the otolith radius at 90 days (about 30 mm in length, after the age at metamorphosis at 55 days). For the five year classes a positive relationship was established between growth at 90 days and year class strength ($r^2 = 0.80$). The differences in the width of the otolith radius were low (about 14%), but those in year class strength were high (by a factor of 4). This can only mean that recruitment depends on the growth attained in the face of mortality. The differences in year class strength are, of course, differences in mortality, and if modulated by growth, the relationship is a demonstration of the Ricker-Foerster thesis. It also implies that the predators do not aggregate on the patches of fish larvae. There is also the practical consequence that recruitment can be forecast to some degree at the age of 90 days (at least in cod).

Conclusion

There are 3 steps in the development of the simple view of recruitment. The first is the link between recruitment and climatic factors described in Chapter II. Such factors in the sea are few, wind stress, irradiance and heat input, all of which play parts in the production cycle in the sea wherever it occurs, spring or autumn outburst or point of upwelling. The second step in the development of the simple view of recruitment is the discovery that the magnitude of recruitment is probably determined between the late larval stages and the late metamorphs. This has not been revealed until recently because the late larval stages were not sampled very effectively. Perhaps the most important step is the demonstration by the masters of larval biology that fish larvae in the wild suffer from lack of food. This is linked directly to the production cycle by which food for the larval fish is generated.

The match/mismatch hypothesis does little more than express the dependence of fish larvae on their food. The model of match, in a primitive form, describes how recruitment might be generated as a function of food produced. This is no more than an indication of how a science of recruitment might develop. Lastly, the recent work of Campana demonstrates the Ricker-Foerster thesis that mortality is modulated by growth during late larval and post metamorphic life. If recruitment can really be forecast at an early age, then the science of recruitment has been profoundly simplified.

IV NATURE OF THE STOCK RECRUITMENT RELATIONSHIP

General Aspects

The Stock Recruitment Relationship displays the danger of recruitment overfishing. If the rate of exploitation is too high, recruitment is reduced and the fishery may be extinguished. In recent decades many stocks of herring, sardine and anchovy may have suffered recruitment overfishing. Four stocks of herring have recovered after catches had been banned, and in the last few years 2 cod stocks have failed.

The Stock Recruitment Relationship displays the density dependence of the recruitment processes by which the population stabilises itself. In recent years some of the density-dependent processes have been revealed but fuller studies are needed to elicit them fully. We also need to establish those processes by which recruitment is generated, which may or may not be linked to the density-dependent mechanisms.

The Stock Recruitment Relationship has not always carried conviction for 2 reasons: (1) the need for the curve to pass through the origin has sometimes been ignored; (2) the scatter of observations about a line parallel to the abscissa was often interpreted merely as lack of relationship and not worth consideration, whereas it is evidence of strong density dependence (Shepherd and Cushing 1980).

The present formulations demand that populations are in fact controlled by density-dependent processes. The necessity was stated by Haldane (1953) and by Moran (1962):

$$\text{Let } \delta N = B - D + I - E,$$

where N is the number in the population; B is the number of births yr^{-1}; D is the number of deaths yr^{-1}; I is the number of immigrants yr^{-1}; E is the number of emigrants yr^{-1}.

Then $\delta N/N = b - d + i - e$, in relative rates of change. If this were to approach zero in a number of generations, one (or all) of the functions cited above are functions of N and so a persistent population is controlled by density dependence. There are 2 basic processes: density-dependent mortality and density-independent survival, expressed as a straight line of Recruit per Stock, the slope at the origin of the Stock Recruitment Relationship. As density-dependent processes supervene, the curve departs from that at the origin. One of the simplest examples is shown in Fig. 49 where the number of eggs of pink and chum salmon at the end of spawning is plotted on the potential egg deposition (McNeil 1968); density-dependent processes occur presumably because more eggs are laid than can be supported by the oxygen in the redds.

Myers and Barrowman (1994) have used the hoard of Stock Recruitment Relationships (Myers et al. 1995) to show that Recruitment is indeed related to spawner abundance. With more than 200 stocks they have shown that the highest recruitment occurs when spawner abundance is high, that the lowest recruitment is found when the spawner abundance is low and that the mean recruitment is higher when spawner abundance is greater than the median. The methods used were non-parametric. In an optimistic world this substantial paper should establish that Stock Recruitment Relationships express real processes.

Four equations have been developed. Shepherd (1982) suggested that there was a general form,

$$R = a\,B\,f\,(B/K)$$

where $f\,(B/K)$ expresses the density-dependent processes.

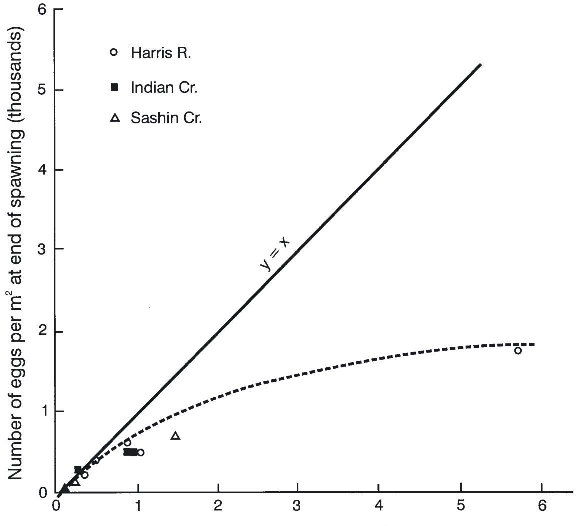


Fig. 49. Relationship between number of eggs of pink and chum salmon as a function of potential egg deposition, in 3 rivers in British Columbia. (After McNeil 1968)

Ricker (1958):	$R = a\,B \exp(-B/K)$
Beverton and Holt (1957):	$R = a\,B \big/ (1 + B/K)$
Cushing (1971):	$R = a\,B\,(B/K)^{-\beta}$
Shepherd (1982):	$R = a\,B \big/ [1 + (B/K)^{\beta}]$

where R is recruitment in numbers; a is the slope at the origin, the coefficient of density-independent survival (save in the Cushing equation); B is Spawning Stock Biomass in tonnes; K is the Threshold Biomass above which density-dependent processes predominate and at which recruitment is half that if only density-independent processes operated; β is the coefficient of density dependence.

Fig. 50 presents the 4 relationships with different values of β, in a plot of R/aK on B/K. The data would arrange themselves about any one of the curves chosen. Fig. 51g shows the Stock Recruitment Relationship for the stock of Iceland cod. The Shepherd curve passes through the origin and through the data parallel to the abscissa. Density-independent survival is expressed in the slope at the origin and just as in Fig. 49, density-dependent processes predominate when the curve departs from that slope with the observations arranged parallel to the abscissa.

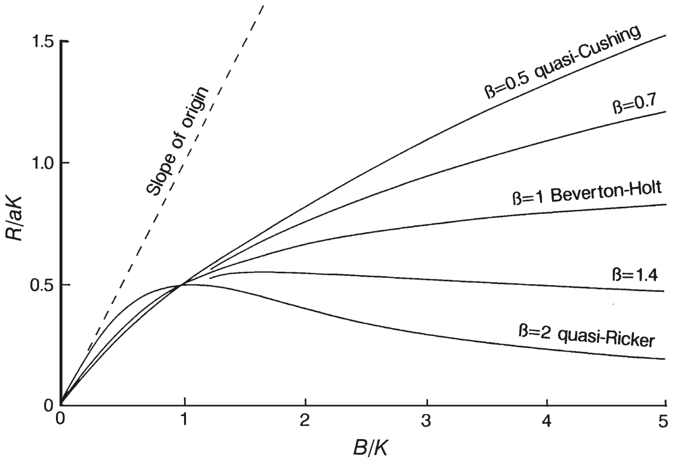


Fig. 50. Three Stock Recruitment Relationships with different values of β (= b), the coefficient of compensation expressed by the Shepherd curve. (After Shepherd 1982)

Stock Recruitment Relationships of the Nine Well-Known Stocks

The 9 well-known stocks are: Skeena sockeye salmon (Shephard and Withler 1958), Downs herring (Cushing 1992), North Sea herring (Anonymous 1993), North Sea sole (Anonymous 1993), North Sea plaice (Anonymous 1993), Pacific halibut (Myers et al. 1995), Iceland cod (Anonymous 1993), Arcto-Norwegian cod (Anonymous 1993) and Northern cod (Myers et al. 1995). All stocks were sampled for 3 decades or more. Data were fitted to Shepherd curves by ln Maximum likelihood; those of the North Sea herring were fitted by Solver in Microsoft Excel 4. Shepherd curves were used because they are more responsive to the data; the Beverton and Holt equation is constrained to an asymptote in recruitment and the Ricker curve yields a dome too readily.

Fig. 51a shows the Stock Recruitment Relationship (SRR) of Skeena sockeye salmon, with variance increasing to a middle stock; Fig. 51b shows the relationship of the Downs stock, a near linear one with variance increasing with stock; Fig. 51c shows that of the North Sea herring. Both Downs herring and North Sea herring suffered recruitment overfishing and the observations are well distributed about the slope at the origin. Fig. 51d shows the SRR for North Sea sole, with 3 very large year classes, much larger than the geometric mean. Two are associated with cold winters in the southern North Sea. Fig. 51e displays the SRR of North Sea plaice; it is unusual in that as stock increased in the 1970s and 1980s a possibly false dome was created. Fig. 51f illustrates the SRR of Pacific halibut, which is strange because recruitment declined in time and then subsequently increased. Fig. 51g displays the SRR of Iceland cod with a tendency for the most recent year classes at low stock to be a little lower. Fig. 51h shows the SRR of the Arcto-Norwegian cod, with a high variation in recruitment; from the time series of recruitment (Fig. 39) there may be some cyclical behaviour. Fig. 51i reveals the SRR for Northern cod, which is near linear, like that of the Downs herring; these are dangerous because as stock is reduced, so is recruitment.

The Stock Recruitment Relationships are well established and each differs from the others. Because the departure from the slope at the origin indicates density dependence, the differences between them represent different forms of density dependence. This is to be expected on general grounds. The 3 cod stocks evince completely different relationships, that of the Northern cod being near linear, that of the Iceland cod strongly density dependent with low variation, and that of the Arcto-Norwegian cod being very variable with

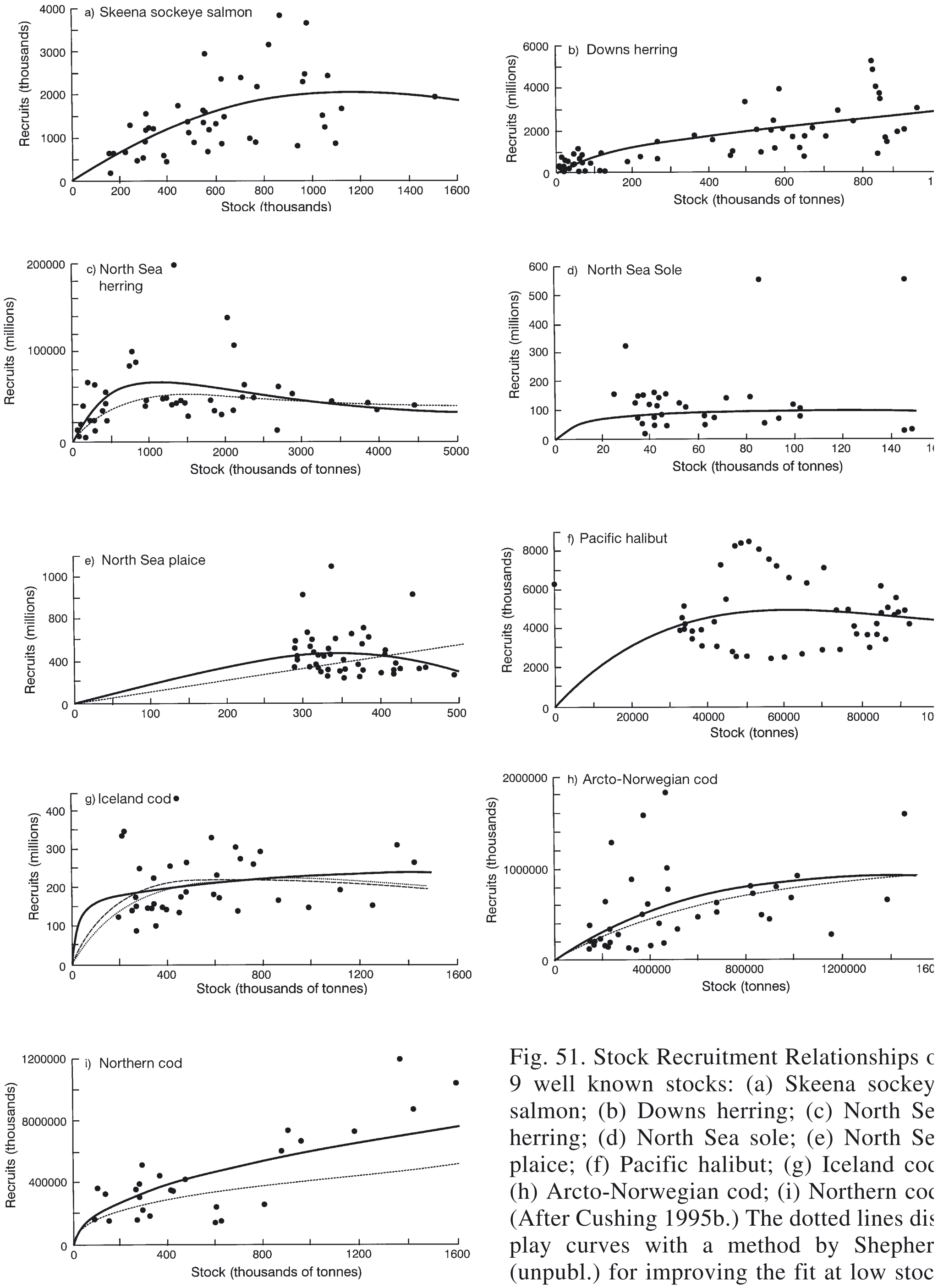


Fig. 51. Stock Recruitment Relationships c 9 well known stocks: (a) Skeena sockey salmon; (b) Downs herring; (c) North Se herring; (d) North Sea sole; (e) North Se plaice; (f) Pacific halibut; (g) Iceland coc (h) Arcto-Norwegian cod; (i) Northern coc (After Cushing 1995b.) The dotted lines dis play curves with a method by Shepher (unpubl.) for improving the fit at low stoc

perhaps some cyclical behaviour. Again the 3 flatfish stocks differ profoundly because each lives in quite a distinct environment.

Recruitment overfishing is the most dangerous condition which, strictly, can only be detected when the stock has recovered after a ban on catches. By this time the fishermen will have left the industry. One of the difficulties is that with a relationship like that of the Iceland cod (Fig. 51g) people will say that "a Stock Recruitment Relationship does not exist" because recruitment at low stock had not declined. Had it been observed, it would have been too late. The case of the Iceland cod is of some interest because the assessment biologists did detect a slight decline and acted to prevent recruitment overfishing, one of the few cases where this has happened.

Two Investigations

It is now well known that recruitment is lognormally distributed. This was shown by Hennemuth et al. (1980) and Garrod (1983), and by Myers et al. (1990) who observed more than a hundred stocks. The first of these investigations describes the consequences of a lognormal distribution of recruitment. Shepherd (in Shepherd and Cushing 1990) pointed out that in a lognormal distribution, the arithmetic mean was greater than the geometric mean by $\sigma^2/2$ and that as stock decreased, the excess in R/SSB increased. Fish stocks do not collapse when $F > M$ and they can remain stable even when $F \approx 5M$. Although weak regulation is all that is needed at high stock, very strong regulation is required at low stock. So, rare extreme year classes are to be expected at low stock and this has been observed (Fig. 51: Iceland cod, Arcto-Norwegian cod and North Sea herring, but not in the Downs herring or the Skeena sockeye salmon; flatfish stocks were not very heavily exploited).

A simulation model was constructed where R_o and P_o are the mean observations of recruitment and spawning stock biomass of the North Sea plaice. With Shepherd model parameters, $a = 2R_o/P_o$, $K = P_o$ and $\beta = 0.5$. The variance of recruitment was inversely proportional to biomass and the median recruitment was raised by $\sigma^2/2$. The result of a thousand year simulation is shown in Fig. 52; the Stock Recruitment Relationship is not unlike those in Fig. 51, and the larger year classes tend to appear at low stock.

A remarkable result was obtained when the simulation was run for a thousand years at high fishing mortality. The stock apparently goes extinct and then after some centuries it recovers with very strong year classes (like the

1904 recruitment of the Norwegian herring). This occurs by chance, but if climatic conditions were right on recovery, the stock would benefit very quickly.

The distributions of both predators and prey in the sea are patchy and lognormality is to be expected. As described in Chapter II, fish stocks respond to climatic changes. Indeed a stationary time series of recruitment must be uncommon. The lognormality of recruitment may allow the stock to exploit climatic change very quickly and effectively.

In the second investigation, Horwood (1995) made a considerable extension to the Cushing and Horwood (1994) model, described in Chapter III. The first step was to scale the model to the stock numbers of the George's Bank haddock, on which the model was based. Eggs from the Spawning Stock Biomass and prefeeding larvae died and numbers were divided by the depth of water on the Bank to yield numbers of larvae m^{-3}, the units used by Cushing and Horwood. Then 14 age groups of post-metamorphosis larvae, juveniles and adults were processed with the ordinary procedures of fisheries science.

The new models were run for 1500 years. In the following figures, results from the last hundred years are shown. Recalling Fig. 48, which describes the result of the Cushing and Horwood model, Fig. 53 shows the relationship of Recruitment and Spawning Stock Biomass at copepod densities of 10 and

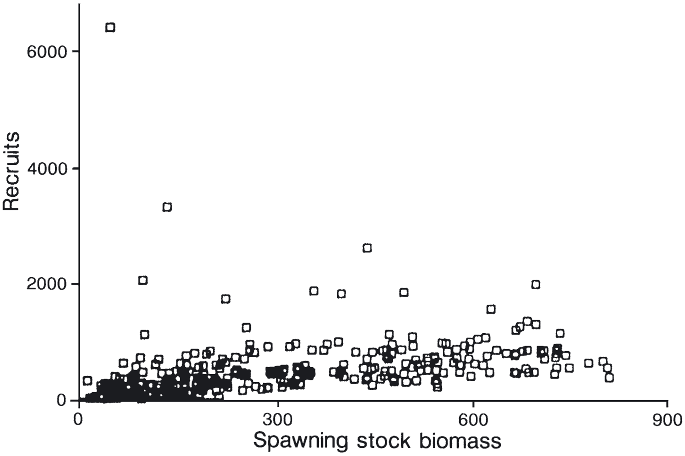


Fig. 52. The Stock Recruitment Relationship with lognormally distributed recruitment; the model was run for 1000 simulated years. Note the high recruitment at low stock. (After Shepherd and Cushing 1990)

$15 \times 10^3\ m^{-3}$ and the points represent the results of the new model. So the new and old models work on comparable scales.

Fig. 54 displays a series of relationships of Recruitment on Fishing mortality. At food densities of $>10\,000\ m^{-3}$, recruitment rises to a maximum at $F = 2.5$ (Fig. 54a). At higher levels of food, different patterns emerge; in Fig. 54b at $F = 1.25$, recruitment varies between high and low values and periods can be detected. At still higher food levels the high variation occurs at lower values of F and the periods tend to disappear. Fig. 54b illustrates stable equilibria up to $F = 1.1$; above that value the system becomes apparently chaotic and the variation is a representation of the bifurcations. It is characteristic of such systems that periodicities can occur.

Fig. 55 displays a time series of recruitment, stock and yield with randomly varying food levels. At 28 years, high recruitment occurred because in that year the food level was very high, but for the subsequent high year class (at year 37), the level of food was not high. Fig. 56 shows the Stock Recruitment Relationship derived from the model. It has the characters of those observed and particularly, it resembles that of Herrington (1948) for the George's Bank haddock.

It is still hard to distinguish the apparently chaotic dynamics from a complex of stochastic processes. But it is of some interest that the bifurcations can be found in a fairly simple model with different levels of food supply. Horwood pointed out that the model used resembled the "scramble" compe-

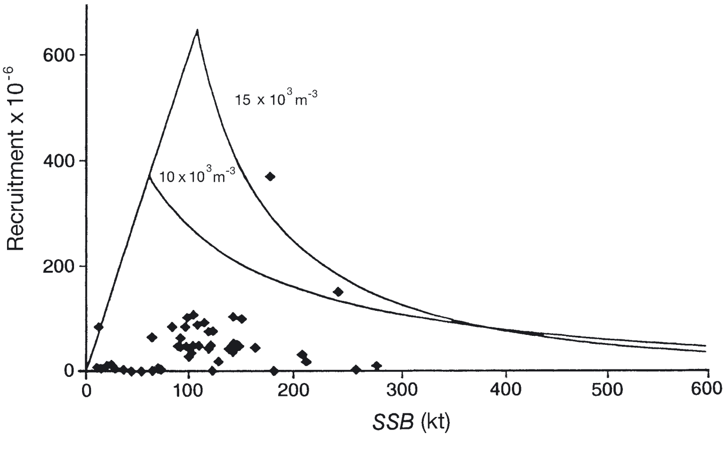


Fig. 53. Relationship between Recruitment and Spawning Stock Biomass of the George's Bank haddock, with food levels at 10 and $15 \times 10^3\ m^{-3}$. (After Horwood 1995)

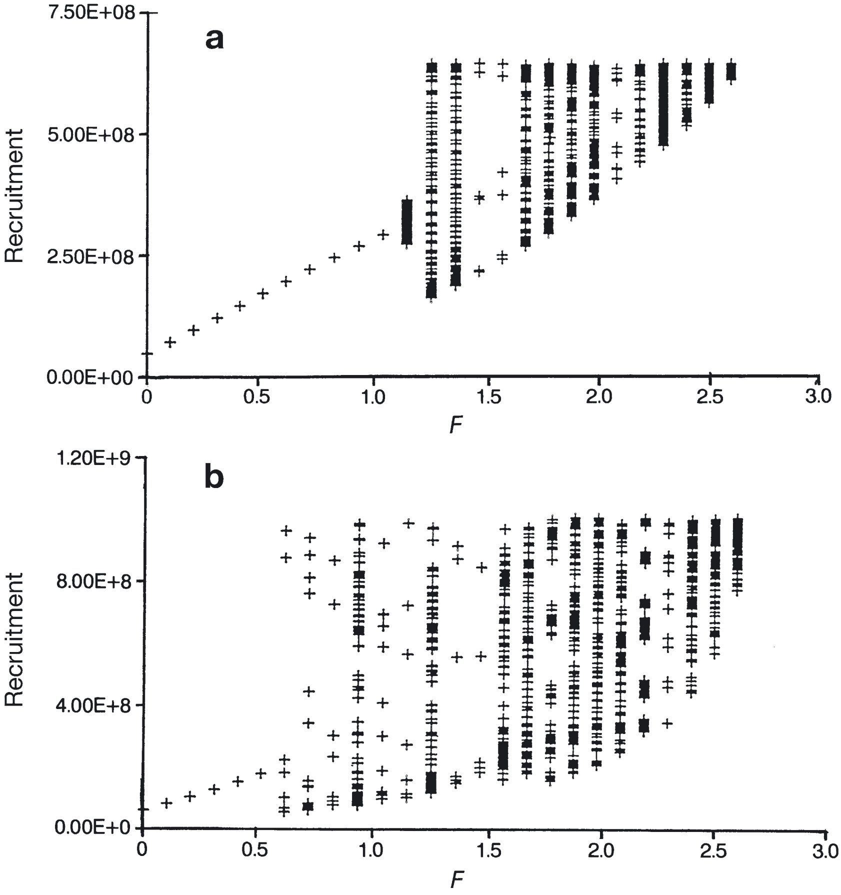


Fig. 54. Bifurcation diagrams at copepod densities of (a) 15 000 m^{-3} and (b) 20 000 m^{-3}, showing simulated recruitment as a function of fishing mortality. (After Horwood 1995)

tition of insects. With the right conditions biomass can build up and then both predator and prey may collapse.

Shepherd's approach examined the consequences of lognormal distributions of recruitment, characteristic of the sequences of mortality in a patchy environment. His simulation resembles the ordinary Stock Recruitment Relationship and makes the point that large year classes occur at low stock and indeed that such year classes can arise by chance and then can exploit climatic change. This approach does not demand that the generation of

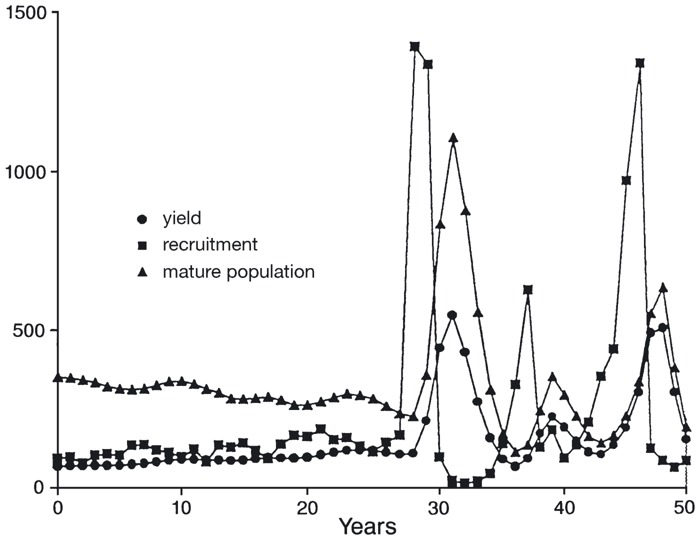


Fig. 55. Time series of recruitments with randomly varying levels of food. At 28 years high recruitment occurs because in that year the food quantity was very high. (Yield and mature population are in kilotonnes; recruitment is in numbers.) (After Horwood 1995)

recruitment is merely a random process but rather that the year classes are distributed lognormally quite independently of their origin.

Horwood's approach developed from the Cushing and Horwood (1994) model which linked differences in recruitment to levels of food for the larvae. The appearance of apparently chaotic behaviour is, of course, a sur-

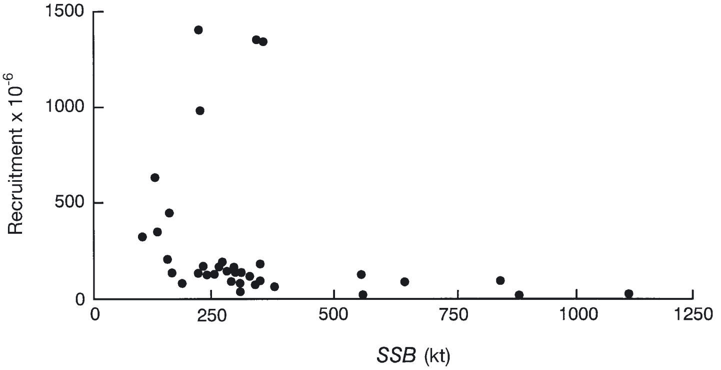


Fig. 56. Stock Recruitment Relationship derived from the Cushing and Horwood model. (After Horwood 1995)

prise, but the bifurcations occur at high food levels, perhaps higher than those usually observed at sea. The model operates within the bounds of existence of the George's Bank haddock and the variation in recruitment of that stock is high, up to 2 orders of magnitude. The conclusion from this study must be that a component of recruitment might appear to be chaotic when the production of larvae is well matched to that of their food.

Density-Dependent Processes

Ricker-Foerster thesis. The Ricker-Foerster thesis (Ricker and Foerster 1948) states that if fish larvae grow at less than the maximal rate, they suffer predatory mortality for longer. In the Cushing and Horwood (1994) model, as described in Chapter III, the constants are reasonable and model values lie within the range of the field observations. It describes the growth and death of haddock larvae on George's Bank with different levels of food. Predatory mortality diminished with age as the larvae grew, but the predator was an adventitious one which did not aggregate on its prey. With a growth rate less than the maximal the time to reach metamorphosis was extended and the cumulative mortality increased. Thus, part of this cumulative mortality was density dependent. Hence in the model the Ricker-Foerster thesis exists during the larval life of the George's Bank haddock. But there is no evidence from observations at sea, perhaps because the later larvae have not been very well sampled until quite recently, as noted in Chapter III.

There is one example of density-dependent mortality in fish larvae: Watanabe and Lo (1988) estimated the larval production of the Japanese saury *Coliolabis saira* in a very large area east of Japan for a period of 15 years. The observed lengths were converted to age from growth increments on the otoliths (Watanabe and Kuji 1991). The mortality rates were correlated with the initial larval production and so they were density dependent but the nature of the density dependence remains unknown.

There are 3 conclusions from the model study: (1) Recruitment at metamorphosis depends on the degree of match, that is, on the food available. (2) Up to one third of the cumulative mortality may be density dependent in the matched condition. In the mismatched state density dependence is less marked. Hence the degree of density dependence must differ in the model from year class to year class. (3) In the model, the slope at the origin is the maximal growth rate of the larvae, but in the true Stock Recruitment Relationship the slope at the origin represents density-independent survival.

Cannibalism. Cannibalism has always been a promising form of density dependence, but it has remained elusive. The first form of the Ricker equation expressed the density-dependent mortality as cannibalistic (Ricker 1954). It was later extended to a more general form of predation, based on aggregation (Ricker 1958). The Ricker equation readily displays a dome, particularly in the George's Bank haddock (Herrington 1948), Skeena sockeye salmon (Shephard and Withler 1958) and Arcto-Norwegian cod (Garrod and Jones 1974). The domed Stock Recruitment Relationship was attributed to cannibalism without evidence of gut contents. With more data and different fitting procedures the present Stock Recruitment Relationships (Fig. 51) of these 2 stocks cannot be described as domes. The presence of a domed Stock Recruitment Relationship is no longer putative evidence of cannibalism.

In an attempt to describe the dome, Harris (1975) distinguished stock-dependent from density-dependent mortality; the first is a function of the number of eggs, the second of numbers at any later age in the cohort. Harris proceeded to show the conditions under which a dome can be established, derived from the development of the Ricker equation by Beverton and Holt based on fish growth.

Cushing and Horwood (1977) put the problem in a form of the Beverton and Holt equation:

$$\mathrm{d}N/\mathrm{d}t = -(M_1 + M_2 N_0) N$$

where N is the number of larvae; M_1 is the instantaneous rate of density-independent mortality; M_2 is the instantaneous rate of density-dependent mortality; N_0 is the initial number (of eggs).

They showed that a dome could only be generated by a stock-dependent mortality, by cannibalism or by aggregating predators, but it was a light dome, hardly distinguishable from the asymptotic relationship of Beverton and Holt (1957). Cannibalism can potentially generate density dependence, where eggs or juveniles are eaten by fishes of the same stock of any age. As a regulatory mechanism, it is simple and plausible. But it is sometimes difficult to establish. For example, herring in the Southern Bight of the North Sea migrate away from their spawning grounds, leaving the eggs stuck on the gravel of the sea bed. In the same region, plaice spawn in spring and their eggs drift away to the northeast towards their nursery ground in the Wadden Sea. After spawning, the adult plaice migrate quickly by selective tidal transport on the western side of the North Sea. Thus the opportunity for cannibalism in these 2 cases at a very early age is limited. On the other hand, Cook and Armstrong (1986) have shown that the recruitment of North Sea haddock and whiting were reduced by large year classes 1 year older, so the cannibalism was measurable. However, the juvenile haddock and whiting are presumably eaten by other fish such as cod or saithe. According to Dwyer et al. (1987), Alaska pollock eat their juveniles in large numbers. The subtropical pelagic fishes in the eastern boundary currents feed on their larvae and juveniles as they live in the same drifting system and it has been suggested that the cannibal mortality is high (Smith et al. 1989). The question then is this: is the mortality generated by cannibalism a significant part of the total at whatever age it happens?

Following the very large study of gut contents in the North Sea in 1981, "the year of the stomach", multispecies virtual population analysis was developed in which predatory mortality was estimated (Pope 1991, Pope and Macer 1991). Nilssen et al. (1994) used gut contents of the Arcto-Norwegian cod to estimate the cannibal mortality of juveniles. They assumed that a fish of a given weight exerts a constant predatory mortality on each age group. Then the cannibal mortality, M_2 (per unit biomass, in million tonnes), is:

$$M_2 = \alpha_1 \exp\left[-0.5\left(\ln\left(\left(Wt_{\text{pred}}/Wt_{\text{prey}}\right)-\alpha_2\right)/\alpha_3\right)^2\right]$$

where Wt is weight and α_1, α_2 and α_3 are constants.

Fig. 57 shows the temporal changes in recruitment, M_2 and in M (= 0.2). There are 2 conclusions: (1) M_2 approximates very roughly the value of M =

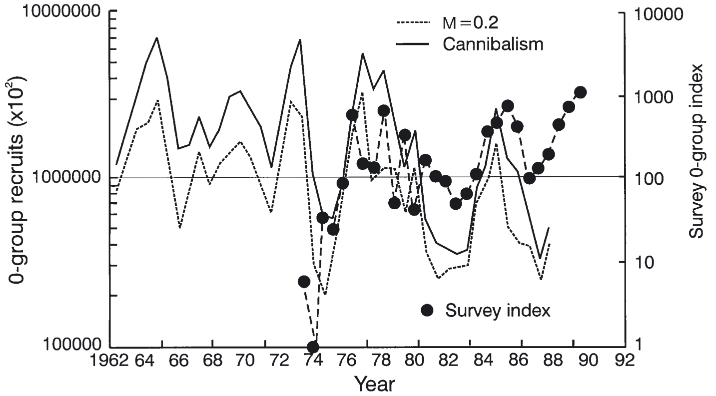


Fig. 57. Temporal changes in numbers of 0-group recruits with M = 0.2 and by cannibalism together with the survey index. (After Nilssen et al. 1994)

0.2; (2) the trend in recruitment is independent of M_2, which means that it is determined before the age of cannibalism on the juveniles. Nilssen et al. modelled the processes:

$$R = 3429\exp[0.772T-(5.408\exp-7)B]\mathrm{SSB}^{0.456}$$

where R is recruitment in numbers; T is temperature in °C; B is juvenile biomass in megatonnes; SSB is Spawning Stock Biomass in thousands of tonnes.

Fig. 58 illustrates the fit of this relationship to the data of the Arcto-Norwegian cod ($r^2 = 0.46$). It is a power law relationship and the line is drawn with a Lowess fit. There is no dome in this relationship but cannibalism is properly accounted for and indeed it plays a part in the regulatory mechanism. The numbers of recruits are reduced by cannibalism but the processes of recruitment are not modified. The earlier idea that a dome in the Stock Recruitment Relationship was caused by cannibalism is really a consequence of the nature of the Ricker curve.

Cannibalism has often been cited as a possible regulatory mechanism, but it has been demonstrated properly for the first time by Nilssen et al. The interesting question arises whether this is a sufficient mechanism or whether other mechanisms exist. It is already known that the mortality of the early juvenile Arcto Norwegian cod is density dependent (see below). Perhaps there are multiple systems of density dependence.

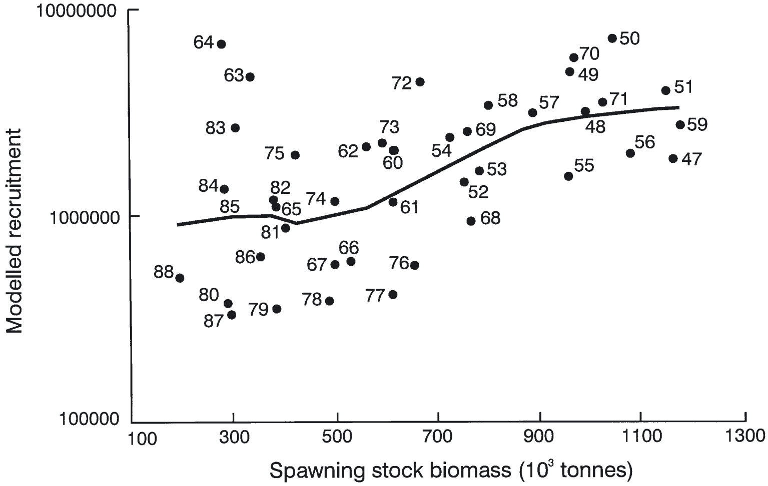


Fig. 58. Stock Recruitment Relationship of Arcto-Norwegian cod. Recruits as modelled 0-groups on a logarithmic scale and Spawning Stock Biomass (thousands of tonnes); the line is a Lowess fit. (After Nilssen et al. 1994)

Density-dependent mortality. The Ricker-Foerster thesis has been discussed. But growth and mortality need not be linked in this way. One example is the mortality of plaice larvae on settlement as they are eaten by shrimps at an age of about 100 to 120 days. Fig. 59 shows the density-dependent mortality at settlement (van der Veer 1986); it is a composite of observations over 3 years, 1980, 1981 and 1982. At the mean the density-dependent mortality is about twice the density-independent component. With enclosure experiments, van der Veer and Bergmann (1987) documented that shrimps were the responsible predators. The large 1963 year class of plaice might have owed its magnitude to the withdrawal of the shrimps to deeper water in the very cold winter. As the mortality must happen at the moment of settlement, it is not linked to growth at all (although the shrimps must select a size range).

Settlement from the volume of the sea to the surface of the seabed is a trap because the shrimps wait there for "manna from heaven". But it is not a necessary condition. Bjørke and Sundby (1987) displayed density-dependent mortality of early cod juveniles in the Barents Sea (at an age of 2 to 3 months, when they are still feeding on *Calanus* in the surface layers; Fig. 60). Density-dependent mortality at a middle range of stock is about the same as the density-independent mortality. The cause of this density-dependent mortality remains unknown. It is probably predatory but the predators have not been identified.

The mortality of flatfish on the nursery ground has been studied very fully, first by Zijlstra et al. (1982). For 7 years a grid of many stations was worked on the Balgzand in the Wadden Sea in northern Holland during spring, summer and autumn. 0-group plaice were grown by Fonds (1979) and were fed ad libitum at a range of temperatures. Fig. 61 shows the observed and simulated mean lengths of the 0-group plaice for the 7 years of

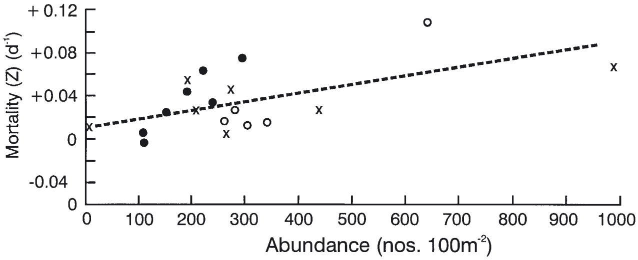


Fig. 59. Density-dependent mortality of 0-group plaice eaten by shrimps at settlement in the Wadden Sea from data in 1982, 1983 and 1984. (After van der Veer 1986)

observation between the beginning of June and the end of August, the main period of feeding. The little fish grow at their maximal rate, possibly at the least risk of predation.

The predatory mortality has been estimated by Beverton and Iles (1992a, b). They examined 3 flatfishes (plaice, dab, turbot) on the beaches for the first years of their lives. The little fish settle on the beaches over a period and remain there until they emigrate into somewhat deeper water in the winter, returning in the spring (sampling methods covered this small migration; Iles and Beverton 1991). Regressions were fitted to the data from the time of maximal recruitment to the beach in June to January of the following year. Beverton and Iles wrote:

$$\frac{1}{D}\cdot\frac{\mathrm{d}D}{\mathrm{d}t} = -(\mu_1 + \mu_2 \ln D)$$

where D is density; μ_1 is the instantaneous rate of density-independent mortality; μ_2 is the instantaneous rate of density-dependent mortality. Then,

$$D_t = \exp(\mu_1/\mu_2)\exp(\mu_2 t - 1)\,[D_0 - \exp(-\mu_2 t)]$$

where D_0 is the initial density and t is in days.

This expression is lightly curvilinear. Fig. 62 displays the dependence of mortality rate on ln Maximal density. The mortality rate due to predation is density dependent. Fig. 63 shows the decline of density-dependent mortality from the 10th of June, the average date of maximal recruitment to the beaches and the end of the second year of life. The decline in density-dependent mortality as cumulative mortality is estimated from Fig. 62 but is corrected for gear efficiency and the light curvilinearity of the model. Iles and Beverton's estimates were:

Period	Daily mortality, μ_2 (d^{-1})	Cumulative mortality, $\mu_2 t$
10th June to 10th July	0.015	0.450
10th July to 1st Jan	0.0044	0.761
1st Oct to 1st Oct (0-group to 1-group	0.0010	0.365

where t is time in days. In the first period, the estimate is valid for the smaller fish (<35 mm in length), but in the third period the upper confidence limit is less than 1 in some arrangements of the data; in one case (ICES continental) the upper confidence limit is less than 1). In the second period the simple regression in Fig. 62 yields $M = 0.572$ and the higher value in the

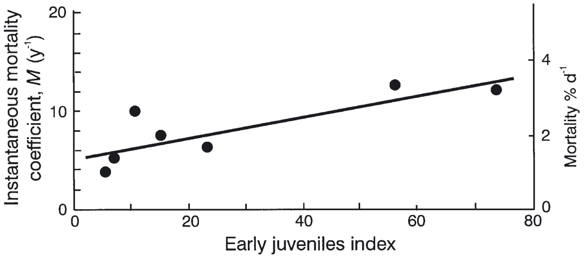


Fig. 60. Cod. Density-dependent mortality of early pelagic juveniles (2 to 3 months old) in the Barents Sea. (After Sundby et al. 1994)

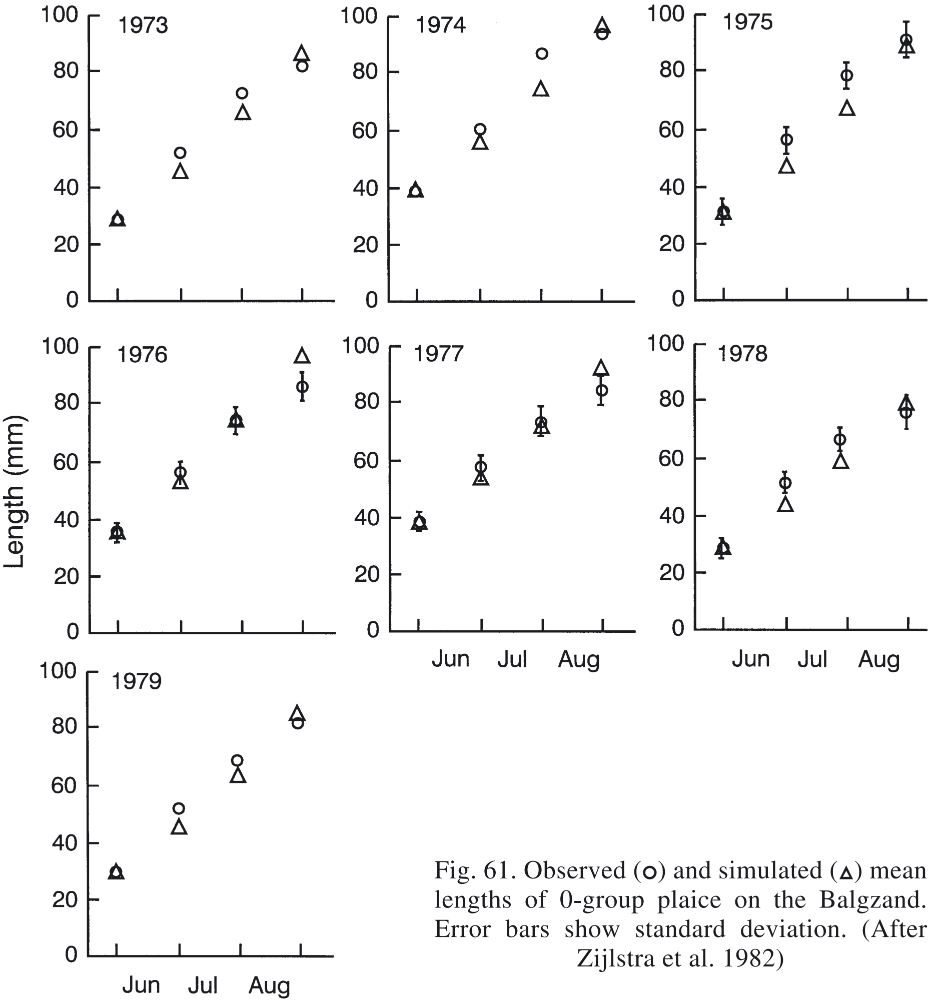


Fig. 61. Observed (o) and simulated (Δ) mean lengths of 0-group plaice on the Balgzand. Error bars show standard deviation. (After Zijlstra et al. 1982)

table derives from the use of the model. A reasonable conclusion would be that the density-dependent mortality of North Sea plaice lies between 0.6 and 1.6, as cumulative mortalities.

Myers and Cadigan (1993) extended this work to 17 populations of demersal fishes examined by survey on both sides of the North Atlantic. They wrote $\ln N_t = \lambda \ln N_0 - m$, where N_0 is the number on the first survey and N_t that on a later one, λ is the coefficient of density-dependent mortality and m is the density-independent mortality; the density-dependent mortality was expressed as $(1 - \lambda) \ln N_0$. Because surveys were used in this study a full analysis was given of the potential sources of error. In cod the density-dependent mortality amounted to 0.5 and similar figures were derived for plaice, sole and whiting. Myers and Cadigan (1993), with the same material, showed that the variability of recruitment owed little to density-independent mortality during the juvenile stages after metamorphosis. The same conclusion emerges from the study of Beverton and Iles.

Thus density-dependent mortality, as a function of predation, is firmly established. Of course it would be desirable to identify the predators, partly to balance the books but also to expose the cannibals. The question arises if this density dependence is sufficient. Reddingius (1971) noted that although density dependence was needed to avoid extinction, only a low value was necessary, but that is not the only purpose of survival (however, see the discussion above which points out that only light regulation is needed at high stock but at low stock, severe regulation occurs, with $F \gg M$). Myers and Cadigan (1993) believe that the observed density-dependent mortality is perhaps sufficient, that the generation of recruitment occurs during the larval stage and that the 2 processes are separate.

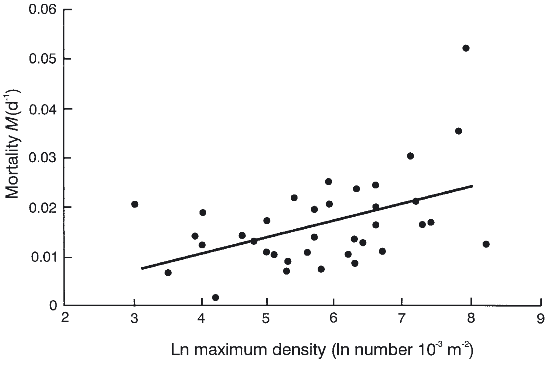


Fig. 62. Dependence of mortality rate on ln Maximal initial density (corrected for gear efficiency and curvilinearity from the model used). (After Beverton and Iles 1992a)

Another way of approaching the problem is to make use of the Stock Recruitment Relationship of the 9 well-known stocks used in this and earlier chapters. Fig. 64 shows the mortality rates as ln (Recruitment/Stock) as a function of stock in eggs [I assumed that except for salmon and halibut, eggs weighed 1 mg wet weight; the sizes of the sockeye eggs were taken from Foerster (1968) and those of the Pacific halibut from Scnitt and Skud (1975)]. Any fitted line of $1/x$ on x yields a biased result, but here the Shepherd curve is used as fitted by maximum likelihood by Myers et al. (1995) (with one exception as noted earlier in this chapter) so the bias is removed. Units of Stock, P, were converted to numbers of eggs: for example, P might be expressed in thousands of tonnes in the Iceland cod or $P \times 10^{-12}$ in eggs (1 tonne = 1×10^9 mg wet weight).

$$\ln(R/P) = -\ln(a) + \ln\left[1 + (P/K)^b\right]$$

where $\ln(R/P)$ is the total mortality from egg to recruit, $-\ln(a)$ is density-independent mortality and $\ln[1 + (P/K)^b]$ is the density-dependent mortality. More fully, $\ln(R/P) = M = -\ln(a) + b\ln(P) - b\ln(K)$. At low numbers of eggs, M tends towards $-\ln(a)$, but at high stock, $P \gg K$ and the slope of the line is b (I am very grateful to Dr J. W. Horwood, who has steered my progress through this problem). Each small figure shows an increase in mortality with stock. Estimates of density-dependent mortality are derived from the difference between the mortality on the fitted line at low stock and that

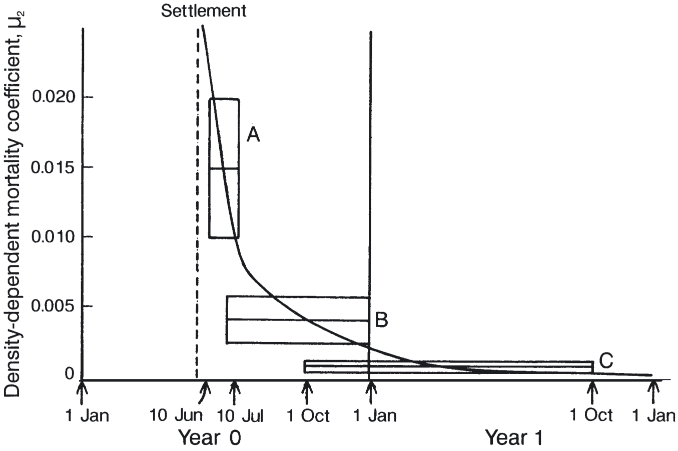


Fig. 63. Plaice. Decline of density-dependent mortality of 0-group individuals on beaches from 10th June to the following January. (After Beverton and Iles 1992b)

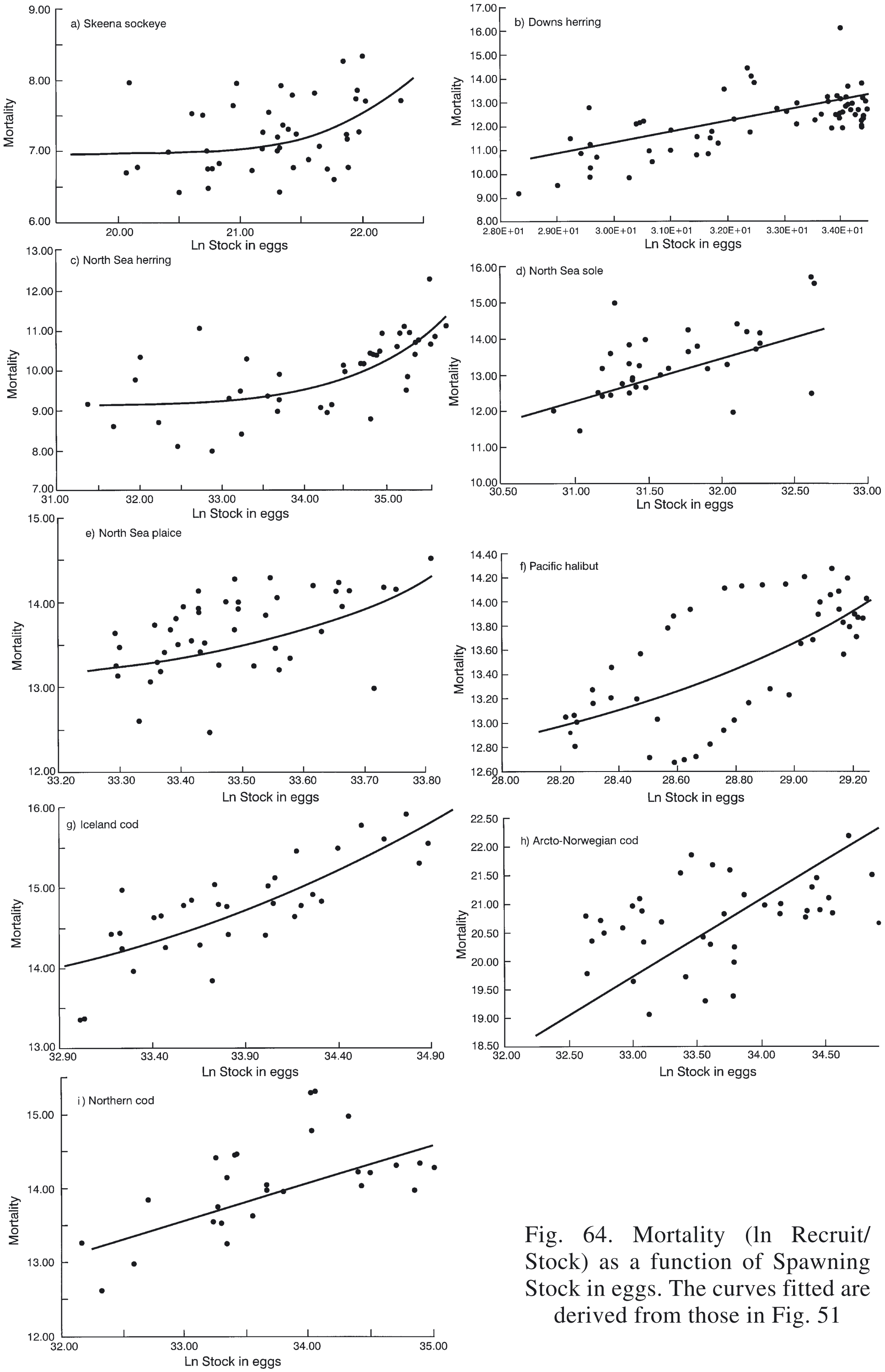


Fig. 64. Mortality (ln Recruit/Stock) as a function of Spawning Stock in eggs. The curves fitted are derived from those in Fig. 51

at high stock within the range of the data. Total mortality was estimated at a mean stock level. The results are summarized in Table 6.

It might have been possible to calculate the density-independent mortality directly from the Stock Recruitment Relationship, but as is very well known such an estimate is not supported by good observations. Where recruitment overfishing has occurred, the data at low stock are often of poor quality.

The proportion of density-dependent mortality is greater in those stocks that have suffered recruitment overfishing than in those that have not. So it is likely that the degree of density dependence displayed in Table 6 is minimal. This method of estimation includes all forms of density dependence and there may be more than one in any particular stock.

Cod suffered the greatest mortality, herring and salmon the least. Mortality of flatfishes was intermediate. The order—cod, flatfish and herring (or salmon)—is one of fecundity, the cod being most fecund and the herring least. This conclusion is the same as that in Cushing (1971) where a coefficient of density dependence was related inversely to the cube root of the fecundity or perhaps the distance apart of the larvae in the sea. At that time I concluded that this was evidence of density dependence in the larval stages.

It is a truism that the magnitude of recruitment is the result of mortality from eggs (or larvae) to recruitment. Then the remarkable point is the low

Table 6. Density-dependent mortality and total mortality of the 9 well-known fish stocks (within the range of exploitation)

Stock	Density-dependent mortality	Total mortality	Proportion of density dependence
Skeena sockeye	–1.00	–7.20	13.8%
Downs herring[a]	–2.70	–12.30	22.0%
North Sea herring[a]	–2.60	–11.00	23.6%
North Sea plaice	–0.80	–13.50	5.9%
North Sea sole	–2.10	–13.00	16.2%
Pacific halibut	–1.85	–13.50	25.0%
Arcto-Norwegian cod	–2.70	–20.50	13.2%
Northern cod	–1.30	–14.00	9.3%
Iceland cod	–2.00	–15.00	20.6%

[a] The estimates for the 2 herring stocks are larger because they both suffered from recruitment overfishing

variability of recruitment in the face of the enormous loss, a factor of 3 up to 2 orders of magnitude, as compared with a loss from stock to recruitment of 5 orders or more. This suggests that the processes are continuously modified. I do not believe that a succession of predatory fields would do this alone because it demands a rather rigidly organized ecosystem with a second predator succeeding the first at exactly the right time. If the larvae grew from one field to the next then a more sloppy ecosystem would suffice. If that is the case then the growth of the larvae plays an essential part, as shown by Campana (1996).

If this argument stands, then there are 2 forms of mortality: larval mortality modified by growth, and mortality of 0-groups, which in the case of the plaice, at least, is purely predatory. However, as will be discussed below, the growth of immature fishes in the open sea, is often density dependent, in which case the Ricker-Foerster process may continue.

In Chapter III, 2 examples were given of the loss of larvae from George's Bank and from the Labrador Current. The proportion was relatively high and by its nature must vary from year to year. From the studies of Beverton and Iles (1992b) and of Myers and Cadigan (1993) the mortality of juvenile fishes was predatory and mostly density dependent. In the model of Cushing and Horwood (1994) a fair proportion of imaginary larval mortality was density dependent but the larvae were not lost in the open ocean.

The physical oceanographers can now describe the larval drift properly, as for example that of the Northern cod from their spawning grounds on the shelf in the Labrador Current to their nurseries on the Grand Bank (de Young and Rose 1993). The losses can be estimated and in the future such estimates may be derived by particle tracking. Then estimates of true mortality should emerge. A very interesting problem arises as to what are the proportions of density-dependent and density-independent parts of this true mortality. It is likely that egg mortality is density independent unless the predators aggregate on them as "spawny haddocks" do on patches of herring eggs on the gravelly sea bed. Physical processes, of course, shape the biological ones (particularly in turbulence), but they find their expression in growth and mortality.

Density-dependent growth. Density-dependent growth in adults might lead to density-dependent fecundity. Then it is assumed that food is not abundant. In heavily exploited populations, like those of fishes, if the exploited stock is one tenth of the unexploited, there may be 10 times as much food per fish as in unexploited ones. Because fish in temperate seas can often be aged quite readily, the growth of fishes has been studied exhaustively for many decades. Yet density-dependent growth in adults has been hard to establish. If fish stocks are exploited heavily, as are most of them, more food should be available and so density-dependent growth amongst adults is necessarily hard to establish. Beverton and Holt (1957) compared W_∞ (weight at infinite age from the von Bertalanffy equation), based on samples of 10.7 to 13.7 years of age in 1945 and 1946 (3177 g), with the years before the Second World War (2177 g). This is one of the very few contrasts between an exploited and an unexploited stock. If stocks were exploited less heavily, as must eventually happen, it might become possible to establish density-dependent growth amongst the adults.

If the growth of adults were density dependent we should expect fecundity to be density dependent and so there would be control on the numbers of eggs produced. Horwood et al. (1986) examined the fecundity of plaice since the 1950s and found no density dependence; indeed, there had been an increment of fecundity during a period when the stock had increased, so the stock had not risen enough to bring in density-dependent growth and hence density-dependent fecundity.

Daan et al. (1994) summarized material from the North Sea on 8 species, mostly immature individuals, but data on 4 adult stocks were included. Fourteen out of 21 stocks displayed evidence of density-dependent growth. With one exception (the observation of Beverton and Holt), the adult series included immature fishes. The samples in which no density-dependent growth was shown included plaice and soles; we already know that the growth of plaice on the beaches was not density dependent. For the rest, cod, haddock, whiting, saithe, Norway pout and herring, the growth of immatures was density dependent. They were all individuals that did not grow up on the flats of the European coast. But some, such as cod and herring, led part of their immature lives not very far from the beaches. Daan et al. pointed out that the indication of density-dependent growth should be accompanied by a measure of food availability. If food were short for some environmental reason, density-dependent growth might appear to be present for reasons not linked to the abundance of the stock.

If immature fish grow quickly because their numbers have been reduced for one reason or another, they may mature earlier in their lives. Jørgensen (1990) showed that the median age of maturation of the Arcto-Norwegian cod declined from about $9\frac{1}{2}$ years in the 1950s to about $7\frac{1}{2}$ in the 1970s. The adult stock was reduced during the period by about a factor of 5. These changes were not related to density-dependent growth amongst the adults, but the immature fish were well exploited during this time. Indeed, it is likely that as the immature stock was exploited more heavily, so the young fish matured earlier in their lives because more food became available to them.

Not so long ago the Stock Recruitment Relationship was merely considered as a scatter diagram and little else. Shepherd and Cushing (1980) noted that the standard picture, like that of the Iceland cod (Fig. 51g) with the observations arranged parallel to the abscissa, displayed evidence of strong density dependence. In the decade or so since then, we have started to examine and even estimate the degree of density dependence. The Ricker-Foerster thesis is very well known and in the model of the growth and mortality of the George's Bank haddock, it was shown in an imaginary world that the density-dependent mortality amounted to about one third of the total (Cushing and Horwood 1994). Cannibalism is a potentially attractive regulatory mechanism which on the face of it is rather difficult to establish; however, Nilssen et al. (1994), with the quantities eaten of the juvenile Arcto-Norwegian cod, established the proportion of cannibalistic mortality in the Stock Recruitment Relationship and in fact were able to do so year by year for about 2 decades.

Density-dependent mortality of juvenile flatfish on European beaches was estimated by Beverton and Iles (1992a, b). An interesting point was that predatory and density-dependent mortality predominated, the density-independent component being low. Myers and Cadigan (1993) estimated density-dependent mortality for juvenile demersal stocks in the North Sea. Further estimates were derived from the 9 well-known stocks cited above and were shown in Table 6. The important point about the latter analysis is that the degree of density dependence must differ from year class to year class, which means that it must change under different conditions of growth and mortality, as in the model of Cushing and Horwood (1994).

Density-dependent growth in the adults of heavily exploited stocks does not appear to exist. As a consequence, it is unlikely that fecundity is density dependent, although if exploitation were reduced density-dependent fecundity might supervene. The growth of immatures is often density dependent, possibly if they are not exploited heavily. If they are exploited heavily there is more food available and they can mature earlier in their lives. Change in the age of maturation is a potential regulatory mechanism. The 2 processes should be distinguished.

There are 3 (or possibly 4) forms of density dependence: extension of predatory mortality by less than maximal growth, cannibalism, density-dependent and predatory mortality, and if exploitation were reduced, density-dependent fecundity. It is of some interest that 4 mechanisms have been identified. The Arcto-Norwegian cod is a cannibal and juvenile demersal fish suffer predatory and density-dependent mortality; an unexploited stock might display density-dependent fecundity, and in an imaginary world the larvae of George's Bank haddock suffered a density-dependent mortality. The early juveniles of the Arcto-Norwegian cod suffer a density-dependent mortality in addition to a cannibalistic one. Is it possible that all 4 mechanisms exist in the same stock, in the same species?

Recruitment Overfishing

When stocks are heavily exploited, recruitment can become reduced, as described below for the Downs stock of herring and for the Northern cod. Since purse seiners came into general use in the open sea most of the herring stocks in the North Atlantic were probably reduced by recruitment overfishing and the same is true of many sardine stocks in the upwelling areas. Fig. 65 (Shepherd and Cushing 1990) shows how recruitment overfishing is

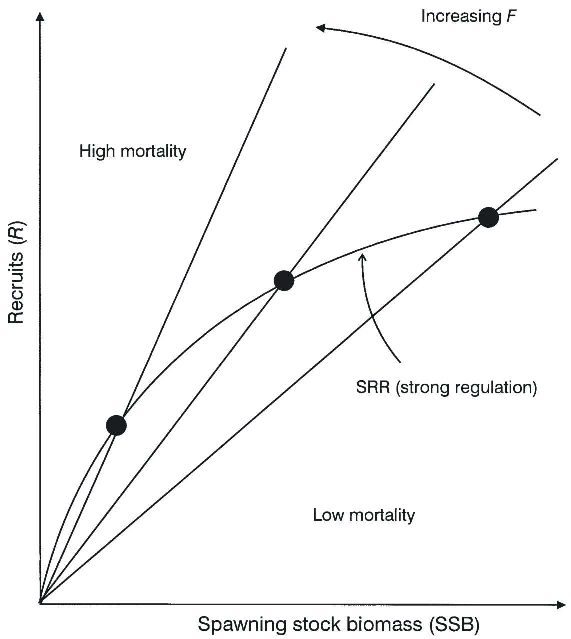


Fig. 65. Departure of the Stock Recruitment Relationship from the slope at the origin. *R*/SSB = 1/BPR, where BPR is Biomass per recruit, an index of survival. As *R*/SSB increases, survival decreases leading to collapse. (After Shepherd and Cushing 1990)

generated. The Stock Recruitment Relationship is shown as are the lines of Recruitment vs Spawning Stock Biomass, R/SSB (= 1/BPR, where BPR is biomass/recruit, an index of survival) which is sometimes called the replacement line. As fishing mortality, F, increases so does R/SSB, so survival declines, leading to collapse of the fishery. After the extinction of the fishery, the stock should recover after a time.

Obviously it would be desirable to prevent recruitment overfishing. A number of devices have been invented, the most prominent being F_{med}, the replacement line R/SSB on the Stock Recruitment Relationship at which half the observations lie above the line and half below. In Fig. 8 (p. 20) the argument is developed. The Stock Recruitment Relationship is that of the George's Bank haddock (Sissenwine and Marchessault 1985) and F_{med} is shown at $F = 0.5$. On the right of the figure is shown the yield per recruit curve and that of Spawning Stock Biomass per recruit (SSB/R), both as functions of fishing mortality. F_{med} is expressed in R/SSB which is inverted below to (SSB/R). The dotted line traces the link between F and R/SSB which shows that $F_{\text{med}} = 0.5$. If fishing is the only cause of reduced recruitment then this device should prevent recruitment overfishing. Serebryakov (1991) suggested a threshold at which the 90% recruit per stock line intersects the 90% level of recruitment. A number of other methods have been devised. However, if 3 poor year classes occur one after another (Fig. 7, p. 19) F_{med} is reduced a little, but recruitment overfishing supervenes quickly. This probably happened to the stock of the Peruvian anchoveta with the year classes 1971, 1972 and 1973. It is the environmental effects which make the whole system dangerous.

As shown in Chapter III, Fig. 39 (pp. 87–89) documents the variability of recruitment in 9 stocks for which there are relatively long time series. Two stocks, Downs herring and North Sea herring, which suffered recruitment overfishing are excluded from the search for sequences of poor year classes. The figures show the geometric means with 1 standard deviation. Sequences of poor year classes, of 1 standard deviation below the geometric mean, occur in the Arcto-Norwegian cod (5 year classes) and in the Pacific halibut (7 year classes). That in the stock of the Arcto-Norwegian cod is of some interest; the sequence of poor year classes (1976–80) was probably linked to the passage of the Great Salinity Anomaly of the Seventies, that mass of cool and freshish water that crossed the Atlantic from Iceland to the Grand Bank and thence to the Barents Sea (Dickson et al. 1988b, Cushing 1988c). But this stock suffered an earlier sequence of poor year classes (1965–67). There is one low sequence of 3 poor year classes in the

Skeena sockeye stock (1950–52). In the Northern cod there were 3 periods of 2 poor year classes each (1970–71, 1976–77, 1983–84). The general picture is of recruitment varying about a mean, but sequences of poor year classes do occur in 3 stocks out of the 7 examined. F_{med} does not prevent this effect; the poor year classes reduce F_{med} slightly, but recruitment overfishing happens quickly.

Two Examples of Recruitment Collapse

Collapse of the East Anglian herring fishery. During the 1930s and the immediate post-war years, a forecast of the age distribution of the Downs stock exploited by the East Anglian herring fishery was made each year (see Hodgson 1957 for a description). The herring recruited partly at 3 years of age and partly at 4; as the proportion was known, the age distribution of fours and older could be predicted with an estimate of total mortality. In 1950 and 1951, the forecast failed and in 1955 the recruitment of 3-year-old fish of the 1952 year class was reduced for the first time. Hodgson attributed the failure of the forecast to the new industrial fishery for pre-recruit herring in the eastern North Sea. Cushing and Burd (1957) showed that with an increase of *Calanus* in the North Sea, the herring had grown more quickly and so had matured earlier in their lives, at 3 years of age rather than partly at 3 and partly at 4.

The loss of recruitment to the Downs stock by the industrial fishery was estimated in 2 ways. First, the catches in the industrial fishery were estimated by age and year and converted to numbers. The ratio in stock of fours to threes was 1.8, so the apparent loss could be calculated, and in the crucial years 1948–51, the apparent loss to the Downs stock was greater than the industrial catch. Second, the percentage loss was modelled for different proportions of the Downs stock in the industrial fishery, and during the crucial years, 1949–50, the apparent loss was <5%. In 1955, when the industrial catch had reached 100 000 tonnes, the loss (with $M = 0.25$) might have been as high as 20% and if an unlikely half of the industrial catch had comprised Downs fish it would have been 34%. An international tagging experiment (Aasen et al. 1961) showed that the probable loss in 1957 was 16.5% and 18.5% in 1958. A loss big enough to account fully for the change in the pattern of recruitment would have been >60%. Hence the failure of the forecast in 1950–51 was probably due to an advance in maturation with increased weight at age from more food.

The collapse of the stock was probably due to increased fishing on the adult stock. Indeed, Tony Burd, my late colleague, made this point at a meeting with the industry in 1954. Cushing and Burd (1957) and Cushing and Bridger (1966) described methods to establish stock identity: mortality rates and recruitments were common to the fisheries in the Southern Bight and the eastern English Channel and, in contrast, there were distinct differences in mortality rates and recruitments between them and the Dogger fisheries further north. The stock in the Southern Bight is a unit and the estimates of mortality were right. But the Downs herring fed in the central and northern North Sea and the effort exerted there was assessed by relating catches per unit effort in the north to those in the south. During the 1950s an intense fishery flourished on the spawning grounds of the Downs stock, particularly between the Sandettié and Ruytingen Banks in the chops of the Channel. Pair trawlers and the large distant water trawlers worked the ground in November, December and January. From Dover the fishery looked like a naval battle. The large trawlers towed in lines 2 cables apart and there were usually between 100 and 150 of them. As result, the mortality rates of the older fish increased from about 0.30 before 1950 to more than 1.10 between 1951 and 1961.

Because I had seen the intense fishery at sea every year during the decade 1950–60, heard the radio communication, and had observed the extensive echo records in the 40 miles between the North Hinder Bank and the Sandettié Bank, I believed that the catches per unit effort of both trawlers and drifters in that area had become more efficient. An index of efficiency was developed from the ratio of catch per unit effort to stock in numbers (using the catch equation in numbers). This is a proper estimate of q, the catchability coefficient. The increase in efficiency was shown and the decline in recruitment was shown in efficient catches per unit of effort, which was confirmed in virtual populations (sensu Fry 1949).

We had to understand the decline in recruitment, which by the end of the 1950s was considerable, by a factor of 3 or 4. Larval surveys were started in 1956 in order to provide an independent estimate of stock. In Cushing and Bridger (1966), 3 Stock Recruitment Relationships were established in efficient catches per unit of effort, in virtual populations (sensu Fry 1949) and in numbers. The relationships were quite clear and accounted for the observed decline in recruitment. The results were presented to the International Council for the Exploration of the Sea in 1964 (Cushing and Bridger 1964). In 1966, there was a proposal to close the Southern Bight and eastern English Channel to herring fishing but it was rejected. Stock Recruitment Relationships were known, but at the time when the concept of yield per recruit was new, the idea of recruitment overfishing was still considered unlikely.

In 1987 I was asked, somewhat adversely, to put the record straight on the herring. I re-examined the material from 1923 to 1987. I found no relationship at all between recruitments to the Downs stock and those of the central and northern North Sea, which confirmed my earlier judgement on stock identity. I found an asymptotic dependence of catch per unit effort (of the drifters) on Spawning Stock Biomass, which supported my approach to the use of catches per unit effort. Further, I found a positive relationship of recruitment on ln *Para/Pseudocalanus* from the Continuous Plankton Recorder Network. The Stock Recruitment Relationship was confirmed, and it was a near linear one (Fig. 51b), as was shown earlier in Cushing (1968). As exploitation increases above a rather low level, recruitment must decline. The most interesting point was that this process was active in the years immediately before the second world war, leading to poor recruitment at age 3 in 1942, 1943 and 1944. This observation had led to the belief that a natural change had occurred during the Second World War but this was not so. Another interesting point is that the observations in the 1950s all lie below the line which may mean that the effect of the industrial fishery was to some degree underestimated, particularly as the stock became less abundant during the 1960s. Recovery did not take place until the fishery was banned between 1977 and 1982, perhaps because the industrial fishery was indeed having a disproportionate effect on recruitment to the Downs stock in the 1960s and 1970s.

When I recall the work and re-read the papers I am surprised by the complexity of events. In 1956 I was asked by the Permanent Secretary of the Ministry of Agriculture, Fisheries and Food how many ships I wanted and I said that all I needed was time. The solution emerged 7 years later and the last drifter sailed from Lowestoft in 1967.

The failure of the East Anglian fishery and its analogues in the Southern Bight of the North Sea was due to recruitment overfishing. It was the first time that such a condition had been recognized and described. Since that time many stocks have suffered from recruitment overfishing and a few have recovered, after catches were banned for a period.

Collapse of the Northern cod. The Northern cod has been exploited since the sixteenth century, originally by a transatlantic fishery from France, Spain, Portugal and Britain, yielding catches of about 200 000 tonnes yr^{-1} (Cushing 1988b). By the 1950s and 1960s the stock was exploited by the inshore gears (with traps, lines and gill nets), the Canadian offshore fleet and the foreign offshore fleet from European countries. During the 1960s total catches amounted to more than 500 000 tonnes (and 800 000 tonnes in 1968). In 1973 a quota system was introduced in ICNAF (International Commission on North West Atlantic Fisheries). In 1977 under the de facto Law of the Sea the foreign fleets left the Canadian 200 mile EEZ. A Canadian offshore fleet was created to take the place of the foreign fleets. By 1980–85 catches had reached 250 000 tonnes. However the catches of the inshore fishermen had declined to the detriment of the Newfoundlanders. This is often the first sign of overfishing.

In 1987 the Alverson Committee (Alverson 1988) was set up to enquire into the decline in inshore catches. They suggested that stock identity be examined, particularly the possibility of local stocks in the bays. Stock had increased since 1977, but perhaps its growth had been overestimated. Inshore weights at age had declined. Assessment techniques were standard, but fishing mortality was underestimated. Recruitment had declined since the 1960s (Fig. 51i). They recommended that fishing mortality be restrained to allow the stock to build up.

The managers were obviously concerned. The management objective was $F_{0.1}$ (an attempt to set an optimal economic yield being based on a marginal yield expressed as a tangent to the yield curve being one tenth of that at the origin). In 1988, the quota was 293 000 tonnes, up from 266 000 tonnes in 1987. In January 1989, the $F_{0.1}$ level was revised down to 125 000 tonnes because the Research Vessel survey in 1986 had yielded results which were “unrealistically high”. The quota was reduced to 235 000 tonnes. The Minister set up the Harris Committee and, in 1990, the quota was for $F = 0.32$ (i.e. half way between the observed value of $F = 0.44$ and the desired value of $F = 0.2$). By 1990, with $F = 0.32$, the quota was reduced to 132 000 tonnes. This account was taken from Lear and Parsons (1993).

The Harris Report (“Independent Review of the State of the Northern Cod stock”, 1990) wrote that the then rate of fishing mortality (0.45+) should be reduced to 0.20, which is the $F_{0.1}$ level. They recommended that the catches (and bycatches) of juvenile cod (2, 3, 4 and 5 year olds) should be eliminated. They also recommended that the Stock Recruitment Relationships be examined in detail. Further, they recommended that the relationships between cod, seals and capelin be investigated. A number of recommendations were made, including one that Canada should acquire management rights beyond the 200 mile limit (on the Nose and Tail of the Grand Bank). By far the most important conclusion was to establish the fishing mortality rate at 0.45. The management objective since 1977 was $F_{0.1}$, i.e $F = 0.18$, which had not been achieved.

All the cod stocks on the Grand Bank off Newfoundland have suffered substantial losses and in 1992 and 1993 a moratorium on catches was declared at the request of the industry (Martin 1994). There are a number of explanations; for example, a possible loss of recruitment was associated with cooler and fresher water from the north in the Labrador Current and an apparent movement of cod into deeper water (de Young and Rose 1993). Lear and Parsons (1993) established a potential link between recruitment and water temperatures.

Until 1987 the virtual population analysis for the Northern cod was "calibrated" by regressing standardized commercial catch per unit effort on exploitable biomass (from the virtual population analysis); with this method $F = 0.15$, close to the management objective. When calibrated with the catches per unit effort of the Research Vessel survey, $F = 0.45$ to 0.50 (Baird and Bishop 1986, 1987). In the autumn of 1987 the Alverson Report described the condition of the inshore fishery, the catches of which had been falling disproportionately. Amongst other conclusions, they said that fishing mortality had been underestimated.

Baird and Bishop (1989) made use of ADAPT, a calibration method which minimizes the differences between biomass and research vessel catch per unit effort in a cohort (Gavaris 1988). With ADAPT, they established that $F = 0.436$. Much more interesting, they found that a plot of ln Catches per unit of effort on exploitable biomass revealed that after 1977, q, the catchability coefficient, had increased sharply.

In 1990, the Harris Report on the state of the Northern cod was published (Harris Report 1990). They recommended a reduction in F to 0.20, an examination of the Stock Recruitment Relationship and the use of the Laurec-Shepherd method to "tune" or "calibrate" the virtual population analysis. Baird et al. (1991) using ADAPT reported that $F = 0.52$ and suggested a series of reducing TACs for the following 3 years. Baird et al. (1992) reported poor year classes and low catches in the north. They also reported a divergence between ADAPT ($F = 1.0$ in 1989 and 1990, 0.7 in 1991) and Laurec-Shepherd ($F = 1.2$, rising to 1.4). The Laurec Shepherd estimate corresponded to the results from the research vessel survey.

Hutchings and Myers (1994) reanalysed the state of affairs. First, Hutchings and Myers noted that the Stock Recruitment Relationship was a near linear one (Fig. 51i), which, like that of the Downs stock, means that as exploitation increases, recruitment declines. It also means that if the stock was overexploited, with a moratorium it should recover. This will provide the test of what has happened, because if the changes have been natural the stock need not recover.

Hutchings and Myers devised an index of sustainability:

$$1 = \sum l_x m_x \exp(-r_x)$$

where l_x is the survival from egg to the beginning of the breeding season at age x; m_x is the fecundity at age x; r_x is the natural rate of population increase at age x. If $r = 0$, the population neither increases nor decreases. They showed that the stock was sustainable if $M = 18\%$ and $F = 22\%$. Fig. 66a shows that the stock has rarely been sustained. Fig. 66b illustrates the numbers of harvestable cod from the harvest rate (catch/stock) and from the surveys. So the abundance was overestimated. Fig. 66c displays the changes in catchability during the period, which were considerable and account for the overestimate of abundance. In the analyses made, catch per unit of effort was assumed to be proportional to the abundance as estimated by the Research Vessel Surveys. But, as shown in the figure, $q = aN^{-b}$, where $b = 0.5$, as shown in the lower part of the figure (anticipated by Pope and Garrod 1975). Catch per unit effort does not depend directly on abundance; if $b = 1$, it is inversely proportional to abundance.

With the collapse of the Northern cod, a number of hypotheses were proposed. Lear and Parsons (1993) had suggested that an increase in natural mortality might be the result of cooler water temperatures but this was denied by Mertz and Myers (1995). de Young and Rose (1993) thought that the cooler water drove the spawners south and at the same time provided poor conditions for the larvae; they showed a positive relationship of recruitment on water temperature, so recruitment diminishes in the cooler water. Hutchings and Myers (1994) established a longer time series of water temperature in the cool intermediate layer. They showed that cold conditions had occurred in earlier years, that the mean number of cod per tow was not related to the long term temperature anomaly in 50 to 175 m and that recruitment (or residuals from the Stock Recruitment Relationship) was not related to temperature in the surface layers, 0 to 50 m. The deep distribution of cod did not change with time. Mass mortalities of cod occurred in 3 years of considerable catches and there was no evidence of higher mortality in the very cold years. The thesis of Sutcliffe et al. (1983) that recruitment was associated with high salinities from the north was re-investigated. According to Hutchings and Myers the relationship disappeared when salinity was related to the residuals from the Stock Recruitment Relationship. This remarkable study supported none of the potential natural changes and we conclude that the collapse was due to fishing.

The collapse of the stock since 1990 was attributed by Lear and Parsons (1993) "primarily to ecological factors" or to "large scale environmental perturbations". Presumably the reason for this view is that the estimate of fishing mortality with ADAPT was not as high as that with the Laurec-Shepherd method. However, Myers et al. (1995) have made use of long term tagging experiments on the Grand Bank and off Labrador (ICNAF areas 2J, 3K and 3L). Until 1987 the fishing mortality in 3K and 3L was about 0.6; in the period 1988–91, fishing mortality increased sharply to between 1.0 and 2.0 (there were no tagging experiments in area 2J in the period 1988–91). With this independent method, Myers et al. (1995) demonstrate that fishing mortality did in fact increase sharply. Very recently, Mertz and Myers (1995) have shown that there was no change in natural mortality.

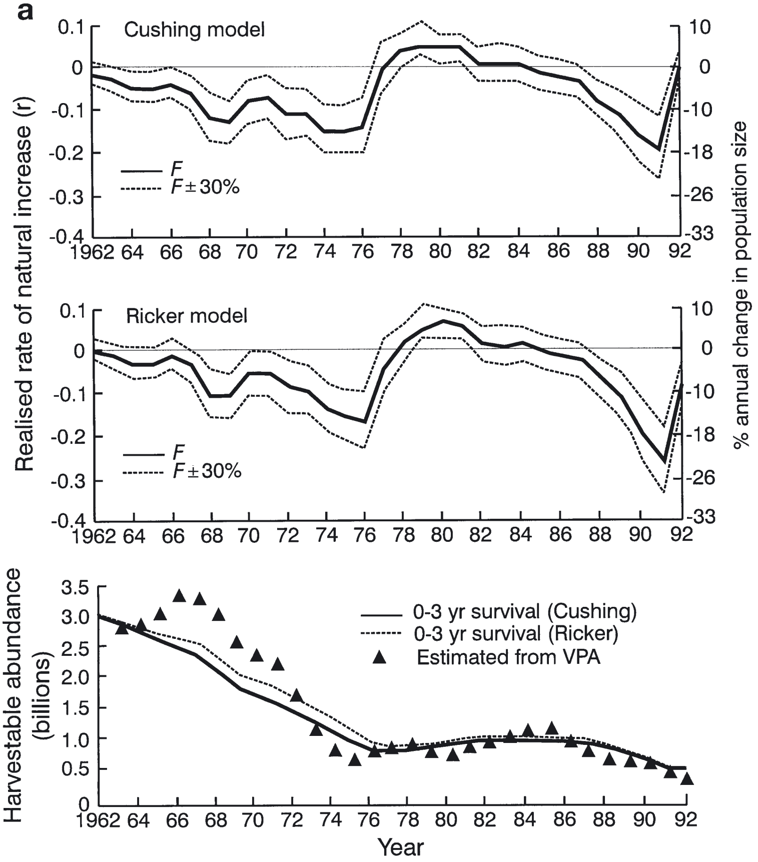
There were 3 sources of failure: (1) in the calibration of commercial catch per unit effort on exploitable biomass, q, the catchability coefficient was assumed constant whereas it has increased sharply from 1977 and indeed it must have increased again from 1988 to 1991 as stock diminished; (2) the second failure lay in the disregard of the Stock Recruitment Relationship from which Hutchings and Myers showed that $F = 0.20$ was the greatest that could be sustained; (3) ADAPT did not perform as well as Laurec-Shepherd: ADAPT must average observations in the cohort, whereas Laurec-Shepherd examines each age in the cohort separately.

The collapse of the Northern cod was a disaster for the Newfoundlanders. The real conclusion is that the near linear Stock Recruitment Relationship is the most dangerous of all. Virtual Population Analysis looks very simple, but tuning or calibration is not.

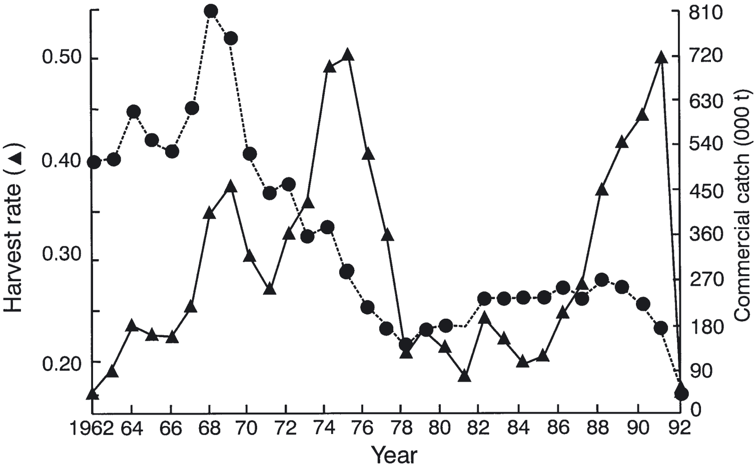
Comparison between the two stocks. The 2 stocks suffered collapse for rather similar reasons. First, environmental effects were cited in both cases. In the East Anglian fishery, the change in the age of maturation, with the increase of *Calanus* in the North Sea, had become confused with the possible effects of the industrial fishery for pre-recruits. A number of hypotheses were proposed for the decline of the Northern cod, all of which were feasible, and if the stock fails to recover, it will be investigated once again.

The second common feature of the 2 collapses was the complex nature of the problem. The fisheries on the Downs stock were very different, drifters off East Anglia, pair trawlers and bottom trawlers in the mouth of the Channel and industrial trawlers on the eastern nursery ground. The Northern cod has been exploited by inshore fishermen with gill nets, traps and lines, by

a


Cushing model
Ricker model
Realised rate of natural increase (r)
% annual change in population size
0.1
0
-0.1
-0.2
-0.3
-0.4
10
0
-10
-18
-26
-33
F
F ± 30%
1962 64 66 68 70 72 74 76 78 80 82 84 86 88 90 92
Harvestable abundance (billions)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
0-3 yr survival (Cushing)
0-3 yr survival (Ricker)
▲ Estimated from VPA
Year

b


Harvest rate (▲)
0.50
0.40
0.30
0.20
Commercial catch (000 t)
810
720
630
540
450
360
270
180
90
0
1962 64 66 68 70 72 74 76 78 80 82 84 86 88 90 92
Year

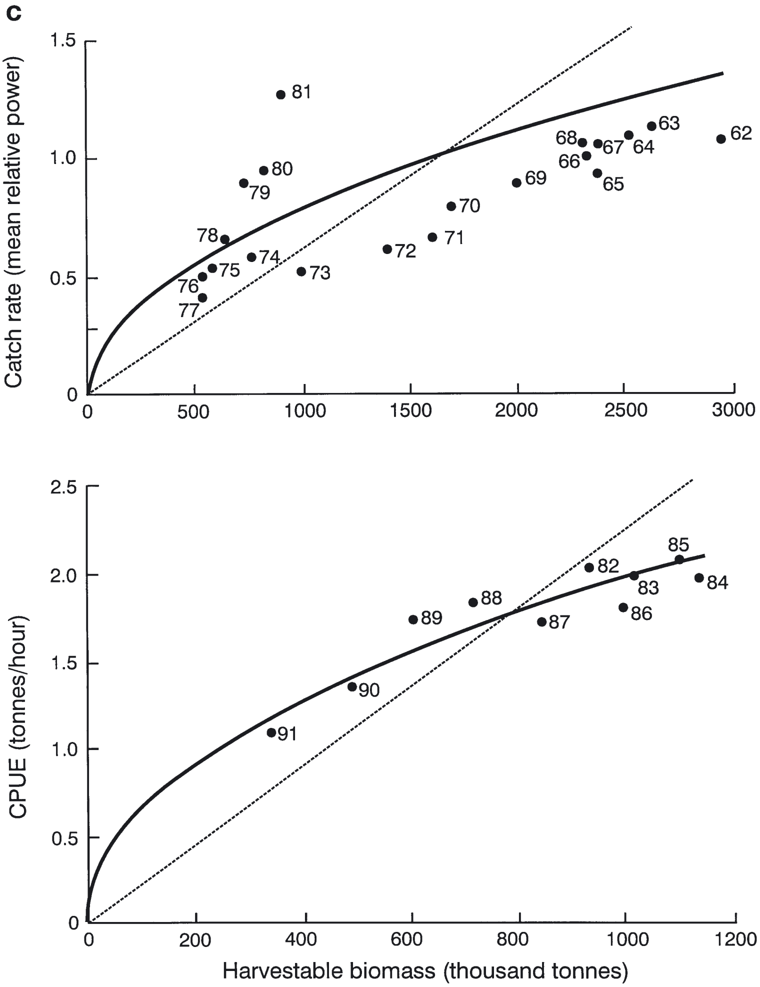


Fig. 66 (facing page and above). (a) Temporal variation in the natural rate of increase, *r*, of Northern cod using Cushing and Ricker Stock Recruitment Relationships. VPA: virtual population analysis. (b) Time series of harvest rate (commercial catch / harvestable biomass) and of commercial catches. (c) Catch rates as a function of harvestable biomass, 1962–81 (top) and 1982–92 (bottom). (After Hutchings and Myers 1994)

offshore fishermen with trawls and by foreign fishermen with large vessels and large trawls. Further, there were also questions of stock identity in both the Downs stock and in that of the Northern cod.

The use of catchability played a part in both stocks. I was much influenced by the contrast between the effectiveness of the drifter fleet off East

Anglia and that of the large distant water vessels working alongside the Sandettié Bank and estimated an increase in catchability. On the Grand Bank, research vessel surveys were carried out in detail on the assumption that an independent estimate of abundance was being made with the same vessels over a period of time. However the commercial fleet became more efficient after 1977. There is a more general issue here that fishermen may become more efficient all the time and that this problem has not been investigated.

When the Stock Recruitment Relationship is near linear, as in the Downs Stock and in the Northern cod, collapse really starts at a very early stage in the history of the exploitation. Then the decline in recruitment is steady if the rate of fishing mortality is too high to sustain the stock. This happened to both the Downs stock of herring and to the Northern cod.

Conclusion

The Stock Recruitment Relationship is the central problem of fisheries science today. For some decades, it was profoundly misunderstood because it was not realized that it usually expresses strong density dependence. Indeed, as shown above, it can now be used to estimate the degree of density dependence.

Common relationships are shown in Fig. 51 (p. 109). They are all different and most are reasonable representations. Two of them suffered recruitment overfishing and they evince the elusive slope at the origin. Many have considered the study of the Stock Recruitment Relationship a dead end, but it is now starting to yield information. Estimates of density-dependent mortality are displayed in Table 6 and when the physical losses of larvae are known it will be possible to estimate true density-independent survival.

Four forms of density dependence were identified. It is possible that all four coexist in the same population. Perhaps there are others which have not been identified. The proportions of the four must differ between stocks and might well change in time and certainly with degree of exploitation. Methods have been developed to estimate density dependence and presumably they will be applied to other stocks. In the end it might become possible to reconstitute the Stock Recruitment Relationship provided that we will learn more about density-dependent control and about the slope at the origin.

The dark side of the Stock Recruitment Relationship is recruitment overfishing. As stock is driven down towards the slope at the origin, recruitment declines, as do stock and fishery, and many fishermen leave the sea. Four stocks of herring recovered from recruitment overfishing, showing that it had taken place. It is likely that many more stocks suffered this fate, for which no account such as described here has been given. Recently, the Northern cod on the Grand Bank has collapsed and the North Sea cod is in danger of failure. Mechanisms have been devised to prevent recruitment overfishing assuming that it is due to fishing. But the 3 low year classes that destroyed the stock of the Peruvian anchoveta provides an example of the collapse through environmental factors when the pressure of fishing is high.

There is only one way out of this dilemma and that is to describe the generation of recruitment properly. I shall discuss this problem more fully in the next chapter. The point here is that recruitment overfishing is too large a problem to be ignored.

V THE SCIENCE OF RECRUITMENT

General Aspects

Fisheries science describes the exploitation of the stock; this may, however, include immature fishes. Originally, the recruits were those that joined the exploited stock. Today, the recruits are often defined as those that join the adult stock because of the great importance now of the dependence of Recruitment on Spawning Stock Biomass. In any case, the exploitation of the immatures may be undesirable in the long term because the Spawning Stock has so often been needlessly and dangerously reduced. In an ideal fishery, exploited moderately, the variance of quotas would be fairly low and the danger of recruitment overfishing would be remote. With heavy fishing, age distributions are dominated by the numbers of recruits and so the magnitude of the stocks, and hence quotas, are more variable than they need be. As described above, heavy fishing can lead to recruitment overfishing, which has occurred too frequently in recent decades. Under heavy exploitation, recruitment overfishing can follow the 3 very poor year classes which succeed one another and such dangerous conditions really do take place. Yet recruitment has not been investigated in any sustained way; of course, the immature fish are often sampled and such estimates provide inputs to the usual assessment procedure, merely a number, the origins of which remain unknown.

At its simplest, recruitment is the survival from the eggs that were laid. As noted in the last chapter, ln R/P is equally the simplest expression of mortality and such estimates vary from year class to year class. However, mortality declines as a function of age (see Fig. 33 on p. 79) because the larvae and juveniles grow through a succession of predatory fields and each predator in the sequence is larger and much less numerous than its predeceesor. Within each predatory field the little fish grow quickly or slowly and, if slowly, mortality is greater. Lastly there is continuous physical loss from the cohort, which can be high amongst the eggs and larvae, but which may persist to a slight degree even among the recruited adults. Such is the structure of recruitment processes and their study is quite distinct from the general biology of the early life history.

There are many, many studies on eggs, larvae and juveniles and much is known of their biology. However, the growth and the mortality of larvae and the juveniles have been studied only in a limited way, but never throughout the life histories of a number of cohorts. I have referred earlier to the work of Sette (1943) on the mackerel larvae off the Eastern Seaboard of the United States, of Harding et al. (1978) on plaice larvae in the Southern Bight of the North Sea. Further, I have already described the work of Beverton and Iles (1992 b) on the juvenile flatfish in European waters, and of Myers and Cadigan (1993) on the juvenile demersal fishes in the North Sea. Each work is a partial study of one stage in the life history. The whole sequence of events has to be studied from egg to recruit. I also referred earlier to a paper on this point, *Had I but world enough and time...* (Cushing 1987). *Time's winged chariot* has hurried near and the science of recruitment should be established (the italicized quotations are taken from Andrew Marvell's poem To His Coy Mistress).

The Troubled Fisheries

Most of the world's fish stocks are overexploited. Garcia and Newton (in press) have examined the state of the stocks in the oceans. They classified stocks as underexploited (U), moderately exploited (M, exploited at $<F_{\mathrm{msy}}$, where F_{msy} is the fishing mortality at maximal yield per recruit), heavily to fully exploited (F, exploited at F_{msy}) and overexploited (O, overexploited at $>F_{\mathrm{msy}}$). A stock should always be exploited at $<F_{\mathrm{msy}}$. Fig. 67a displays the proportions of stocks which are underexploited and overexploited in the statistical divisions of the Food and Agricultural Organization during the 1980s. Fig. 67b (from Garcia and Newton 1995) shows the biomasses of assessed stocks as function of fishing mortality, classified by the degree of exploitation (B_{msy}, biomass at maximal yield per recruit, corresponds to F_{msy}). Two thirds of stocks are heavily exploited or overexploited (as defined above) throughout the world ocean to the detriment of the fishermen.

Garcia and Newton developed a simple bioeconomic model of the world fisheries. Fig. 68 shows the dependence of revenue on a fleet capacity index (in millions of GRT, gross registered tonnes). By 1989 the maximum sustainable revenue is shown to be 43% less than the total costs throughout the world. This can only mean that most fisheries are subsidized and that fish prices are too low. The need for subsidies may be the consequence of heavy fishing which managers find difficult to curb.

Michael Graham (Graham 1943) wrote that "Fisheries which are unlimited become unprofitable" and Hardin (1968) commented on the Tragedy of the Commons, by which he meant that a common resource must lead by

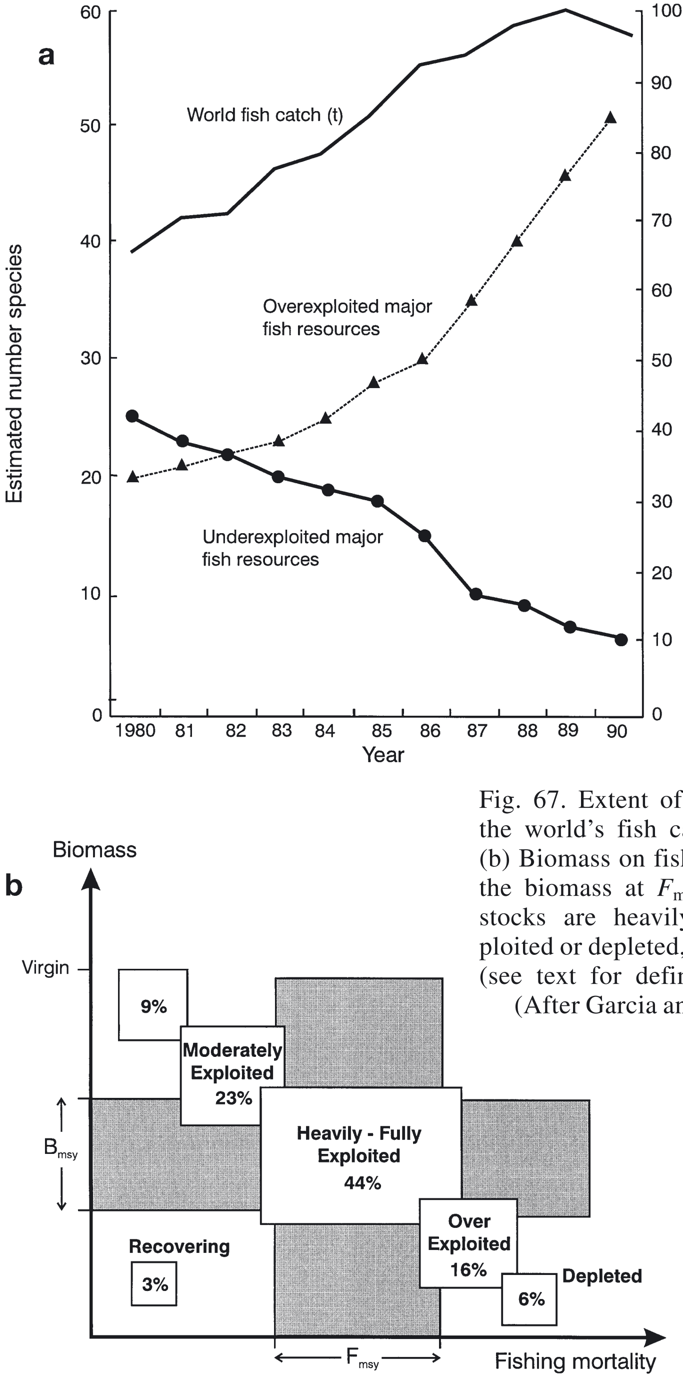


Fig. 67. Extent of overfishing. (a) Half the world's fish catch is overexploited. (b) Biomass on fishing mortality; B_{msy} is the biomass at F_{msy}. Two thirds of the stocks are heavily exploited, over-exploited or depleted, that is at F_{msy} or more (see text for definitions of the terms). (After Garcia and Newton in press)

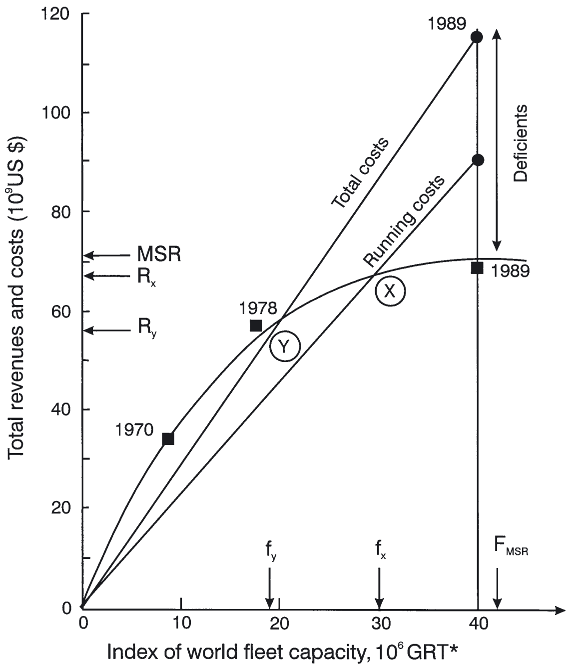


Fig. 68. Revenues and costs of world fish stocks as function of world fleet capacity (in gross registered tonnes, GRT). F_{msr} is the fishing mortality at maximum sustainable revenue. At X, revenue covers running cost, and at Y, total costs are covered by revenue. (After Garcia and Newton in press)

competition to overexploitation (see Chapter I). The de facto Law of the Sea agreed to in 1977 was supposed to overcome this problem because the stocks in the Exclusive Economic Zones would then be owned by each coastal state. The overexploitation displayed in Fig. 67 became serious during the 1980s after the de facto Law of the Sea was established. On a broad scale management has not been effective.

If most stocks in the world ocean are overexploited, the danger of recruitment overfishing must be high. The deep trouble is that it can only be identified properly by the recovery of stocks after a ban on catches. As noted above, 4 herring stocks did recover. Yet the Iceland spring spawners did not do so after a ban on catches, perhaps because the Great Salinity Anomaly of the Seventies passed over the spawning ground and the path of the larval drift. A number of sardine stocks may have suffered from recruitment overfishing. Indeed, Cushing (1971) produced some evidence that 4 pelagic stocks had collapsed for that reason, Japanese sardine, Hokkaido herring, Californian sardine and Atlanto-Scandian herring. I showed that Ricker's limiting exploitation rate might have been exceeded. The persistence of high effort during a time of falling stocks (and hence, probably recruitments) was demonstrated.

For a long time it was believed that the clupeid stocks were particularly vulnerable to recruitment overfishing because of their relatively low fecundity. Conversely, it was assumed that the highly fecund stocks, such as cod, would be secure from recruitment overfishing. Since 1988, the Northern cod has probably collapsed from recruitment overfishing, as described above, and now the North Sea cod may be in danger of such failure.

In the early 1960s the stocks of 5 gadoid species increased by a factor of 3 or more: cod, haddock, whiting, saithe and Norway pout (for a fuller account of the gadoid outburst consult Chapters II and III). Fig. 69 shows the catches of cod, haddock, saithe and whiting from 1903 to 1990. The result of the gadoid outburst is plain, as is the obvious benefit to the fishermen (Pope and Macer in press). Since the mid-1980s, cod recruitment has declined. This raises the possibility that the gadoid outburst is over and that the North Sea cod is in danger of recruitment overfishing.

Daan et al. (1994) created a data set of fishing mortality, Total Stock Biomass, Spawning Stock Biomass and Recruitment of the North Sea cod between 1910–14 and 1990–94. The data are displayed in 5 year blocks because the estimates of fishing mortality were derived from catches per unit effort which includes the annual variation in recruitment. Fig. 70 illustrates that the decline in Spawning Stock Biomass preceded that in recruitment.

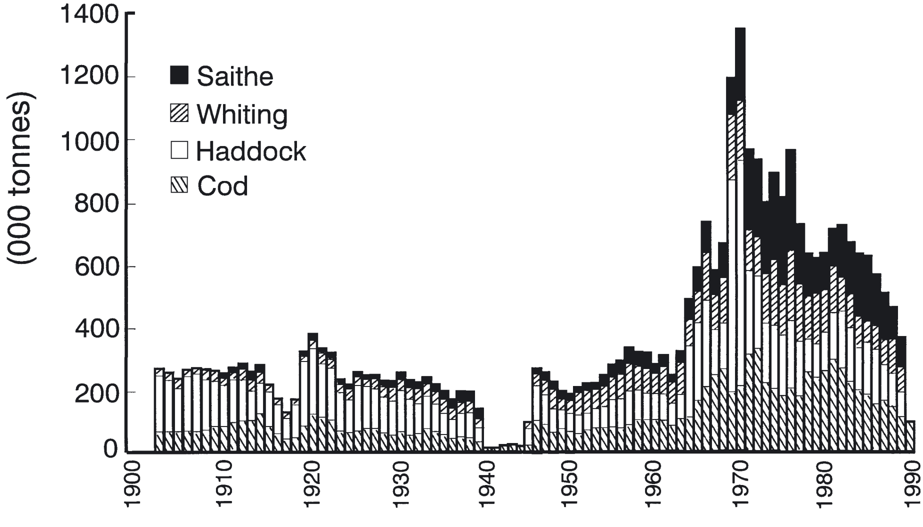


Fig. 69. Catches of 4 gadoid species in the North Sea from 1903 to 1990. (After Pope and Macer in press)

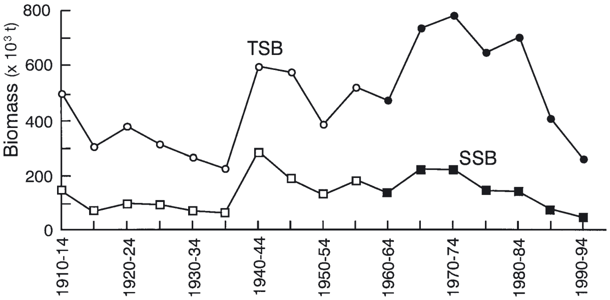


Fig. 70. North Sea cod. Trends in Total Stock Biomass (TSB) and in Spawning Stock Biomass (SSB) from 1910–14 to 1990–94. (Filled symbols show values based on virtual population analysis.) (After Daan et al. 1994)

This means that too many small cod were caught. So the stock was suffering first from growth overfishing which might then have led to recruitment overfishing. Indeed, the exploitation of immature stock might frequently be one of the prior conditions of recruitment overfishing.

Fig. 71 displays the Recruitments and Spawning Stock Biomasses of cod, haddock and whiting in the North Sea from 1921 to 1993 (Pope and Macer in press). The basic information for the years before virtual population analysis came into use was the estimates of fishing effort of Scottish trawlers from which measures of fishing mortality were derived; for the period of virtual population analysis (from 1962) the 2 estimates of fishing mortality corresponded quite well. John Pope tells me that the measures of whiting recruitment in 1944 and 1949 are probably biased upward.

Fig. 71a displays the results for the North Sea cod. Recruitment rose from 1964 onward and it remained high until 1987. Subsequently, the Spawning Stock Biomass fell sharply. The observations for North Sea haddock are shown in Fig. 71b; high recruitments occurred between 1962 and 1974, but not subsequently. Fig. 71c shows Recruitments and Spawning Stock Biomasses for North Sea whiting, the trend of which appears to have been independent of the trend in the gadoid outburst. However, Recruitment did increase in 1952 and it remained high until 1979. Thereafter it tended to decline.

The start of the gadoid outburst included the stocks of cod, haddock, whiting, saithe and Norway pout (stock estimates were taken from Andersen and Ursin 1977); all five were correlated with each other (Cushing 1982). It is now clear that this was not really true for the stock of whiting and that the correlation of the increase in stock of whiting in the early 1960s may have

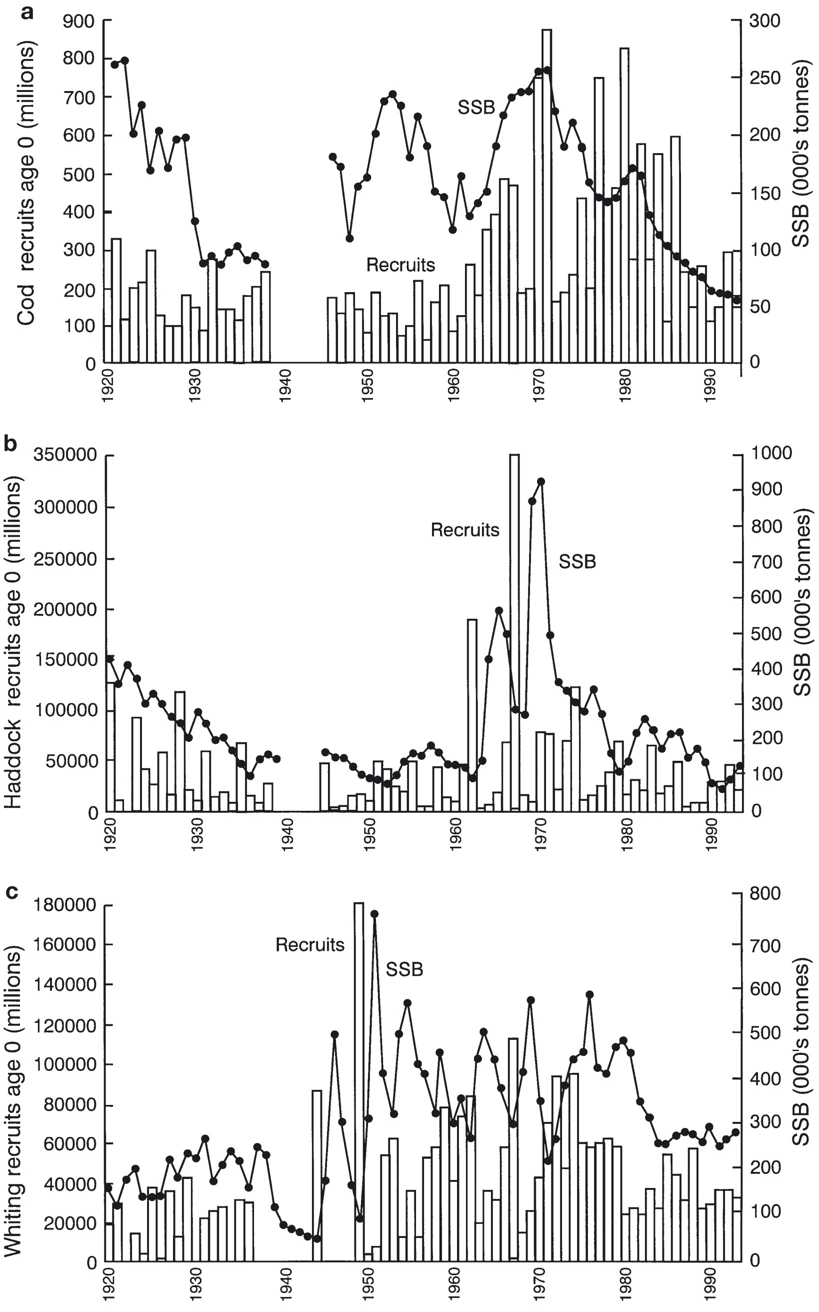


Fig. 71. Recruitments and Spawning Stock Biomass in the North Sea from 1920 to 1993 for (a) cod, (b) haddock and (c) whiting. (After Pope and Macer in press)

been spurious. Haddock recruitments had fallen after 1974; recruitments to the saithe stock have not declined. This leaves the cod stock, recruitment of which has fallen since 1986.

Was the decline in recruitment the result of the failing gadoid outburst or a direct effect of recruitment overfishing with no environmental concomitant? The end of the gadoid outburst may be a piecemeal affair or the decline in recruitment might be due to recruitment overfishing sensu strictu, particularly as $F > F_{\text{med}}$ for many years. But, of course, if the decline in recruitment was due to an unspecified natural cause such as the end of the gadoid outburst, recruitment overfishing would result. Both scenarios have the same result, recruitment overfishing. So far the only treatment for recruitment overfishing has been to ban catches until the stock recovers. Such a course in the mixed fishery in the North Sea would only be valid if all stocks suffered from recruitment overfishing, which is not true. Stocks of saithe, plaice, sole and whiting are probably not in the same danger. With luck the stock might recover, but it will require the most careful management.

From 1984 to 1988, the TACs agreed upon by the Council of Ministers (in the European Community, as the later European Union was then called) were greater than those proposed by the Advisory Committee on Fish Stock Management of ICES (ACFM) by nearly 15%. In 1990, ACFM abandoned the use of TACs for the North Sea cod and proposed that fishing effort be reduced in the North Sea to 70% of that in 1989. This advice was repeated each year to 1994 and the fishing mortality in 1993/4 remained high. Proposals for reducing effort by limiting the numbers of days at sea were not successful. However, fishing boats are being bought out by governments. In 1993, 135 boats left the UK industry and in 1994, 162 boats were to leave; similar reductions are under way in other countries bordering the North Sea. The scientific advice is being slowly carried out, but slowly.

As noted above many stocks have suffered recruitment overfishing. Of the 2 stocks described here, the Northern cod has almost certainly suffered recruitment overfishing and the North Sea cod may suffer it today. The only way in which such disasters, present and potential, can be prevented is to understand how recruitment is generated. Bradford (1992) has shown that the magnitude of recruitment is probably determined during the late larval stages. So the problem is to measure the growth and mortality in larval and juvenile life and to relate it to food available and to the predators.

Recruitment Science

The magnitude of recruitment is the result of physical loss and mortality from egg to recruit by the time the cohort joins the adult stock. Loss is the result of physical processes and mortality is caused by predation. The object of the study of the science of recruitment is to describe such processes in order to understand them.

In temperate and high latitudes fish spawn in the same place and at the same season each year, and the eggs and larvae are drifted in tide or current to their nursery ground which is also in the same place each year. The physical processes along the larval drift of 3 cod stocks were described in Chapter III. The Northern cod spawns on the shelf edge in the Labrador Current (Wroblewski et al. 1995) and the larvae are drifted to their nursery on the Grand Bank (Davidson and de Young 1994). On George's Bank, cod and haddock spawn on the northern part of the Bank, and the larval drift lies around the seaward edge of the Bank at a middle depth, proceeding towards the nursery ground on the southeast part of the Bank (Lough et al. 1994). The Arcto-Norwegian cod spawn in the Vestfjord in northern Norway and the eggs and larvae are carried north in the Atlantic Current, partly towards Spitsbergen and partly towards the North Cape and past it (Adlandsvik and Sundby 1994).

The larval drift from spawning ground to nursery ground is an ideal construct which can be displayed clearly in a diagram. For example, the larval drift of the plaice lies between the spawning ground in the centre of the Southern Bight of the North Sea and the nursery ground in the Wadden Sea, the flats in northern Holland. But the 0 group plaice are found all along the beaches in small numbers between the Wadden Sea and the estuary of the Scheldt, the next nursery ground to the south. So loss from the ideal larval drift is expected and from this arises the mixture between spawning groups.

In subtropical seas the major fisheries are found in upwelling areas. The pelagic fishes spawn at the points of upwelling where food will be available for their larvae as the upwelled water drifts away. Apart from the capes, where upwelling always occurs, the points of upwelling shift as the axis of wind direction changes from year to year. However, nurseries tend to be found inshore. It is a looser structure than that expected in temperate waters but the fishes appear to make use of the inshore jets and the major offshore drift to keep the stocks within the upwelling area.

In recent years, the physical oceanographers have demonstrated their ability to describe events in both coastal waters and in the ocean and more important where events take place in both. Bartsch and Knust (1994a) presented a 3-dimensional model which successfully described the drift of particles (or herring larvae) across the North Sea towards their nursery grounds in the east and these particles made diurnal vertical migrations, as the herring larvae do. Bartsch and Knust (1994b) described the larval drifts of sprats and sandeels in the German Bight of the North Sea. de Young and Davidson (1994) and Davidson and de Young (1994) displayed the drift of particles (or cod larvae) from the cod spawning grounds on the Labrador Shelf to the nursery ground on the Grand Bank. As described in Chapter III they were able to estimate the loss of eggs or larvae from this path of the larval drift. Davidson and de Young (1994) and Lough et al. (1994) were able to estimate the losses of larvae from the path of the larval drift, as did Adlandsvik and Sundby (1994) describing the passage of the larval drift of the Arcto-Norwegian cod.

Common to all these physical methods is the use of climatological information and the local wind stresses in each year of study. In other words the models are created and are run on computers. Although the development of such models costs some money it amounts to only a small fraction of the cost of running a research vessel at sea for many months. Such models are operated for quite long simulated periods. For example, that of Adlandsvik and Sundby is run for the simulated 2 or 3 months to take the eggs and larvae from the Vestfjord to the Tromsøflakket off the north coast of Norway. The particles in the sea reach their destination on the nursery ground or are lost. The real eggs and the real larvae are eaten and the survivors grow into little fish. If the net movement to the nursery ground can be described as remainder from the physical loss, there is no reason why the particles tracked should not be allowed to grow and die as they do in the Cushing and Horwood model. Then it might be possible to construct combined biological and physical models of the processes at sea.

The combined physical and biological model should describe the loss of fish eggs and larvae together with the growth and mortality of larvae and of juveniles. In the stocks alluded to above there are long time series of recruitment and perhaps of the numbers of prerecruits. Then it should be possible to make estimates of the order of magnitude of the parameters needed to reach the recruitment observed.

Work at sea is obviously needed, but research vessels are not always required. Fig. 34 (p. 80) shows the mortality of plaice eggs and larvae for 4 years of sampling (Harding et al. 1978). The research vessels surveyed the plaice spawning area and that of the larval drift towards the nursery ground on the flats of the Wadden Sea from December to April. The numbers of, for example, Stage 1 eggs, divided by the daily development rate at temperature, provided an estimate of production. Then curves of production in time for each stage were constructed. The ratio of production of Stage 11 eggs to that of Stage 1 provided an estimate of mortality. There are 2 points of interest: (1) The numbers of Stage 4 larvae in 1969 were 2 orders of magnitude larger than those of the other 3 cohorts. Yet (2) the 1969 year class was an average one, presumably because the excess numbers were eaten by shrimps on settlement in the Wadden Sea or on the beaches. I stopped the programme because I thought that the processes were so variable that it would take too long to arrive at sensible results. To produce the data shown in Fig. 34 cost 3.5 million pounds sterling in sea time alone at present-day prices, let alone the added costs. Of course, this helped to end the programme. Now I think that I was quite wrong to stop it because had it continued we would have learned whether the events of 1969 were abnormal or not. The heavy costs of sea time are the real reason why the science of recruitment has not developed.

The eggs of fishes (like cod or plaice) live mainly in the upper 20 to 30 m of the ocean, although those of herring and some other fishes lay their sticky eggs on the seabed. The development of the eggs depends on temperature, lasting 48 h in subtropical waters, 2 to 3 weeks in temperate waters, and perhaps 4 to 6 weeks in high latitudes. Very roughly there is 1 plaice egg m^{-3} in the Southern Bight of the North Sea in January to start with to be reduced by two thirds at hatching, and the numbers of Stage 4 larvae are reduced to between 0.0003 and 0.0734 m^{-3}; the whole development takes from about 110 to 130 days (from the meagre 4 samples available). The region is tidal with a maximal flow of about 5 knots. Perhaps a network of moorings could be placed across the area and along the path of the tidal drift.

Is it feasible to estimate numbers of eggs and larvae from an array of moorings for a period of months? Coombs (1980) showed that the Continuous plankton Recorder catches fish larvae from 2 to 55 mm in length. The problem then is to design a pump-driven development of the recorder which samples adequately up to the age of metamorphosis. The present recorder might sample plaice eggs properly for the 3 weeks before the larvae hatch. Two forms of progress are needed: to modify the machine so that it can sample metamorphosing larvae at densities of 0.001 to 0.05 m^{-3}; and to change the sampling bands after perhaps a week and store them for a period of months, after which they are recovered. Physical oceanographers use moorings all the time, some simple and some complex. If the array were arranged properly with respect to the larval drift, loss rates (as opposed to mortality rates) could be estimated directly.

Pannella (1971) discovered the daily rings on the otoliths and with proper practice they can be read well from larvae in many species. Hence, the larvae can be aged properly and growth and mortality can be expressed in daily rates. The distributions of numbers at age and of length at age are available at the time intervals produced by the sampling system. *The important point is that the sampling intervals will be quite short. As the larvae will be aged directly, growth rates and mortality rates will be estimated at these short time intervals.* Then the usual procedures of fisheries science can be applied directly to the samples of larval populations. Indeed, developments of virtual population analysis might be used to separate predatory mortality from physical loss or to separate the mortalities from different predators. Townsend and Graham (1981) constructed distributions of hatch dates of herring from larvae caught later. Such distributions would be of great value in establishing the optimal time of spawning for a successful year class, particularly when the rates of growth and mortality are established. Further, Townsend et al. (1995) has shown that the Sr/Ca ratio in the otolith provides a temperature history of the fish larvae when caught. Such methods will be of great value in establishing the proper rates of growth and mortality from the samples taken from the moorings.

The growth of fish larvae should also be examined experimentally. Larvae should be fed ad libitum on their usual food in order to establish maximal growth rates. The growth rates observed at sea can then be properly expressed as a proportion of the true maximum (in larger fish, a maximal growth rate is sometimes difficult to establish because the wild fish demand larger volumes than the tanks often used, but this problem should not arise with fish larvae).

As mentioned in Chapter III, Campana (1996) has described a link between growth rate and year class strength. The method of investigation is simple and estimates of growth can be made routinely. Hatch date, growth rate and temperature history (from the Sr/Ca ratio) provide a history of the biological processes, as sampled at sea. Further, in a particular year the tracked particles that grow and die in a model could be matched to the observed histories of growth at sea. Of course, Campana's method will be used directly to forecast recruitment as early as possible in the life history of the cohort. The real point, however, is to reconstruct the course of growth and mortality in the life of a cohort.

So far I have tried to show how the growth and mortality of fish larvae can be estimated relatively cheaply from moorings rather than with the use of expensive research vessels. Mortality may be estimated as well as possible, but it would be desirable to sample the predators and the predatory mortality. Harding et al. (1978) showed that whiting, haddock, dab, gurnard, herring, sprat and anchovies were potential predators of plaice larvae in the Southern Bight of the North Sea.

After a period of time the estimate of mortality will become reliable, based on rather short intervals of time. Presumably the predators will be sampled by midwater trawls and their abundance estimated as numbers $1000\,\mathrm{m}^{-3}$. Then from the stomach contents, the simple predatory mortality is (number of prey eaten)/(number of prey), both in units of $1000\,\mathrm{m}^{-3}$. Such a simple estimate is enough to assess the predatory mortality when the main estimate of mortality is to be made by other methods. Once the predators have been identified, there will be no need to sample them at the same rate as the larvae.

There are 3 components to the proposed science of recruitment: (1) Use of the physical model to describe the loss of larvae along the path of the larval drift and allow those particles to grow and die like fish larvae. (2) Estimation of growth and mortality at sea from moorings. (3) Estimation of predation at sea with research vessels.

Analogous procedures are needed to estimate growth and mortality of juveniles. Iles and Beverton (1991) and Beverton and Iles (1992a, b) have described the methods of estimating the mortality of juvenile flatfish. In the North Sea and neighbouring waters, numbers of juveniles are estimated routinely on international surveys. As pointed out above, Myers and Cadigan (1993) made use of these surveys to estimate the mortality of cod, whiting, haddock and plaice. Growth of juvenile flatfish is close to the maximal rate estimated from experimental work in tanks (Zijlstra et al. 1982). Whether this is so of juveniles in the open sea is not yet known.

In the North Sea, such surveys continue. Research vessel surveys on the Grand Bank are used each year for assessment purposes. Stomach surveys are likely to continue. It would take little modification to such surveys to make fuller analyses of the life of the juveniles including both their food and predators. It is possible that networks of moorings might be set up for other purposes and they could carry a little extra weight. Lastly, the computer programmes to describe the larval drift have been in principle written and could be adapted quite readily elsewhere.

The 3 components should be combined, based on the physico-biological model which would be run for as many years as estimates of recruitment are available. By this I mean that the long time series of recruitment estimates now available would be used in the models to estimate the upper and lower levels of growth rate, mortality rate and loss rate. The estimates at sea are needed to provide continuous information for use in the simulation models. The object of this procedure is merely to describe the formation of recruitment over a number of years.

Such a simulation model can be used to describe the generation of the recruitments as they occur. Much more interesting is the possibility of using the simulation model in a broader sense. Such a model would explain the nature of the rise of recruitment in the gadoid outburst and, much more important today, its decline. As noted above there is a question whether the decline in recruitment to the North Sea cod stock is due to the collapse of the gadoid outburst or to recruitment overfishing. Steele (1985) observed that the noise in the ocean is red, which means that long-term fluctuations are to be expected. Regime shifts occur such as sardine/anchovy in subtropical seas, herring/pilchard in the western English Channel, the appearance and disappearance of cod off West Greenland and events like the gadoid outburst in the North Sea. Jones and Henderson (1988) examined the possible switches between pelagic and demersal fish in the North Sea during the period of the gadoid outburst. They modelled such switches and found that the total energy flow remained the same; a similar point was made for the George's Bank ecosystem (Sissenwine et al. 1984). Obviously this is potentially a study in the generation of recruitment. This is an important part of the science of recruitment because we need to know when the shifts take place. It is possible that such shifts occur following recruitment overfishing as large gaps are blown in the ecosystem. Again, this can only take place if the science of recruitment is pursued properly.

In the North Sea, the distribution of primary production in time and space has been described as a function of wind stress and incident radiation (Elliott and Clarke 1991). The present distributions are arranged by month and area. There is no reason why they should not be estimated in the area of spawning and of the larval drift by the time intervals used to estimate the rates of growth and of mortality. The algorithms are relatively simple and could easily be incorporated in the physical models of particle trajectories in which they are allowed to grow and die just like fish larvae. It would be desirable to know the distribution of successful hatching dates and to compare the growth and mortality rates before and after the period of successful hatching. They may or may not be linked to the time of onset of primary production.

Such a development might be used to test the match/mismatch hypothesis. If the distribution of successful hatch dates occurred at the same time as that of primary production, growth rates would be greater and mortality rates less, as expected under the hypothesis. If the hypothesis is not true, such conditions would not be fulfilled. Much more important, such arrangements would allow us to understand how the magnitude of recruitment was generated.

The procedures outlined above were designed to promote the science of recruitment more cheaply than would have been possible 20 years ago. I have already referred to the international surveys in the North Sea which are used to provide indices of recruitment for the assessment procedures. Today such cooperation takes place in broad fields of fisheries science as a matter of routine. One could imagine that the procedures outlined above were shared amongst countries around the North Sea to their advantage.

The Tragedy of the Commons (Hardin 1968) drives the fishermen to compete and to bankrupt themselves. If enough fishermen are driven into bankruptcy then the cycle can start again, but with new fishermen. Since the 1950s the Tragedy of the Commons at sea has been mitigated but the ideal has not been approached. The 2 most troubled fisheries in the developed world are those for cod in the North Sea and on the Grand Bank. They are managed in the same way. Scientists provide a choice of options and the managers come from different countries. In both regions the scientific trouble was recruitment overfishing or its prospect and this is despite the devices invented to secure the stocks from such a fate. The real problem with recruitment overfishing is that when it is recognised it is often too late.

In a different world, management would be relatively simple. Fishing mortality would be much lower than it is today. Stocks would be exploited at the maximum economic yield. Catches per unit effort would be very much greater, even if total yield were only a little greater, and the fisherman would earn much larger profits. This has been known for the last half century and the question arises why management has failed.

It is true that if effort were cut back in the North Sea to 70% of the level in 1989, the prospect of recruitment overfishing of the cod stock should recede. This assumes that the problem was simply recruitment overfishing sensu strictu. The real trouble is that the scientists do not know how to handle this problem because it is only recognised when the fishermen have lost their means of living.

Many stocks appear to be well behaved for long periods and the scientists are lulled into a sense of false security. It is my belief that even if the North Sea cod is restored to security, a stock somewhere else will become vulnerable merely because history tells us that dramatic changes in the abundance of stocks are the rule and not the exception. Fishermen will then once more lose their livelihoods because the scientists cannot see what they are doing. There is only one way out of this appalling dilemma and that is to understand the nature of recruitment and how it is generated.

Present management is based on annual quotas and the management problem is how to divide them between countries (apart from the fortunate islands Iceland and New Zealand). If quotas bite, fishermen do not like them and catches may be misreported, making the jobs of scientist and manager hard. To avoid this a longer-term management is needed which does not look only 1 year ahead, but perhaps 5 years ahead. Fishing effort can be reduced gradually to a target some years ahead and this has started in the North Sea. Quotas will still be needed to divide the cake.

In the past the problem might have appeared daunting because so little was known of the physics and biology of the fishes in their early lives. Today, however, we can see how to solve the problems in a relatively straightforward manner. The managers should be delighted to spend the money on such work because this is the first step needed to move towards the ideal fishery.

Conclusion

The science of recruitment does not yet exist primarily because the work needed has so far been expensive. Two thirds of the stocks throughout the world ocean are heavily exploited or overexploited. This means that such stocks are vulnerable to recruitment overfishing.

Many are subsidized which is a poor substitute for management. Of course, if fishing effort were reduced enough the prospect of recruitment overfishing should recede. But fishermen resist the prospect of not going to sea and this is perhaps the main reason for the slow progress towards the ideal fishery where fishermen make regular profit from a high catch per unit effort and the need for regulation and inspection is low.

If fishing effort remains higher than that needed for the ideal fishery, recruitment overfishing can occur for 3 reasons: (1) the direct effect of heavy fishing, particularly if the catchability coefficient increases from year to year; (2) if 3 poor year classes follow each other; (3) if a regime shift occurs, which is more likely than the advocates of sustainability would have us believe.

If management were easy, the ideal fishery would pervade the world ocean. It is not, and because managers are often paymasters, they might admit their failure to manage and try to protect the fishermen by paying for research on recruitment. In the UK such payment would be very much less than the cost of enforcement. The result would be an understanding of how recruitment is generated. This would mitigate or even prevent the damage of recruitment overfishing. Then the managers could proceed peacefully towards an ideal fishery.

There are, of course, many other reasons for prosecuting the science of recruitment. One is the obsessive pursuit of knowledge that possesses the good scientist to the dismay of the paymaster. Another reason is to explore the ocean, the simplest and most important system in ecology, and to meet its political problems, primarily global warming. The third is the most important of all: to preserve the old contract with the fishermen who risk their lives at sea.

References

Aasen, O., K. P. Andersen, J. A. Gulland, K. Popp Madsenm, and D. Sahrhage. 1961. ICES Tagging experiment in 1957 and 1958. Rapp. P.-v. Réun. Cons. int. Explor. Mer 152: 1–50

Adlandsvik, B. and S. Sundby. 1994. Modelling the transport of cod larvae from the Lofoten area. ICES Mar. Sci. Symp. 198: 379–392

Alverson, D. L. (chair). 1988. A study of the trends of cod stocks off Newfoundland and factors influencing their abundance and availability to the inshore fishery. Dept. Fisheries and Oceans, Ottawa

Anderson, J. T. 1988. A review of size dependent survival during pre recruit stages of fishes in relation to recruitment. J. Northwest. Atl. Fish. Sci. 8: 55–66

Andersen, K. P. and E. Ursin. 1977. A multispecies extension of the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Danm. Fisk. og Havunders. 7: 319–435

Anonymous. 1993. Report on herring stocks south of 62° N. ICES CM 1993 / Assess. 6, Copenhagen

Anonymous. 1994a. Report of the Working Group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 1994 / Assess. 6

Anonymous. 1994b. Annual Report of the Sir Alister Hardy Foundation for Ocean Science for 1993, Plymouth

Astthorsson, O. A., I. Hallgrimsson, and G. S. Jonsson. 1983. Variations in zooplankton in Icelandic waters in spring during the years 1961–82. Rit Fiskideildar 7: 73–113

Bailey, K. M. 1981. Larval transport and recruitment in Pacific hake. Mar. Ecol. Prog. Ser. 6: 1–9

Bailey, K. M. and E. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. mar. Biol. 25: 1–83

Baird, J. W. and C. W. Bishop. 1986. Assessment of the cod stock in NAFO Divisions 2J3KL. NAFO SCR doc 86/47

Baird, J. W. and C. W. Bishop. 1987. Assessment of the cod stock in NAFO Divisions 2J3KL. CAFSAC Res. Doc. 87/42

Baird, J. W. and C. W. Bishop. 1989. Assessment of the cod stock in NAFO Divisions 2J and 3KL. CAFSAC Res. Doc. 89/6

Baird, J. W., C. A. Bishop, and E. F. Murphy. 1991. An assessmemt of the cod stock in NAFO Divisions 2J3KL. CAFSAC Res. Doc. 91/53

Baird, J. W., C. A. Bishop, W. B. Brodie, and E. F. Murphy. 1992. An assessment of the cod stock in NAFO Divisions 2J3KL. CAFSAC Res. Doc. 92/75

Bakun, A. and R. Mendelssohn. 1989. Along shore wind stress, 1953–1984; correction, reconciliation and update through 1986. pp. 77–81. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukuyama (eds.). The Peruvian Upwelling System: dynamics and interactions. International Center for Living Aquatic Resources Management, Manila

Bartsch, J. and R. Knust. 1994a. Simulating the dispersion of vertically migrating sprat larvae (*Sprattus sprattus* (L.)) in the German Bight with a circulation and transport model system. Fish. Oceanogr. 3: 92–105

Bartsch, J. and R. Knust. 1994. Predicting the dispersion of sprat larvae (*Sprattus sprattus* (L.)) in the German Bight. Fish. Oceanogr. 3: 292–296

Baumgartner, T. R., A. Soutar, and V. Ferreira Bartrina. 1992. Reconsruction of the history of Pacific sardine and Northern Anchovy Populations over the past two millennia from sediments in the Santa Barbara basin. Calif. coop. ocean. Fish. Invest. Rep. 33: 24–40

Beers, J. R. and G. L. Stewart. 1971. Microzooplankton of the plankton communities of the upper waters of the eastern tropical Pacific. Deep Sea Res. 18: 861–883

Berner, L. 1959. The food of the larvae of the northern anchovy *Engraulis mordax*. Bull. inter-Am. trop. Tuna Commn 4: 1–22

Beverton, R. J. H. and S. J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Fish. Invest. London 19: 1–532

Beverton, R. J. H. and T. C. Iles. 1992a. Mortality rates of 0 group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.), and turbot (*Scophthalmus maximus* L.) in European waters. II. Comparison of mortality rates and construction of life table for 0 group plaice. Neth. J. Sea Res. 29: 49–59

Beverton, R. J. H. and T. C. Iles. 1992b. Mortality rates of 0 group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters. III. Density dependence of mortality rates of 0 group plaice and some demographic implications. Neth. J. Sea Res. 29: 61–79

Bjørke, H. and S. Sundby. 1987. Distribution and abundance indices of larval and postlarval cod. pp. 127–144. *In*: H. Loeng (ed.). The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Institute of Marine Research, Bergen

Blacker, R. W. 1957. Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. Fish. Invest. London 20(10): 1–49

Blacker, R. W. 1965. Recent changes in the benthos of the West Spitsbergen fishing grounds. Int. Commn Northwest. Atl. Fish. Spec. Publ. 6: 791–794

Blaxter, J. H. S. 1988. Pattern and variety in development. pp. 1–58. *In*: W. S. Hoar and D. Randall (eds.). Fish Physiology X1 a. Academic Press, Chichester and New York

Boeck, A. 1871. On silden og silde fiskeriene, naunlig om der norske varsildfisket. Indberetning til den Konglige norske Regierung Department for der Infre am foretagst Praktisch-vidensk avelige Undersøgelser, Christiania

Bolster, G. C. and J. P. Bridger. 1957. Nature of the spawning area of herring. Nature 179: 638

Bradford, M. J. 1992. Precision of recruitment predictions from early life stages of marine fishes. Fish. Bull. U.S. 90: 437–457

Brander, K. M. 1992. A re-examination of the relationship between cod recruitment and *Calanus finmarchicus* in the North Sea. ICES Mar. Sci. Symp. 195: 393–401

Brander, K. M. and A. B. Thomson 1989. Diel differences in avoidance of three vertical profile sampling gears by herring larvae. J. Plankton Res. 11: 775–784

Brothers, E. S., C. P. Mathew, and R. Lasker. 1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. U.S. 74: 1–8

Brown Goode G., Collins, J. W., R. E. Earll, and A. H. Clark. 1884. A history of the mackerel fishery. Bull. Bur. Fish. for 1881. US Govt. Printing Ofiice, Washington, D.C.

Bückmann, A. 1942. Die Untersuchungen der biologischen Anstalt über die Ökologie der Heringsbrut in der südlichen Nordsee. Helgoländer wiss. Meeresunters. 3: 1–17

Burd, A. C. and W. G. Parnell. 1971. The relationship between larval abundance and year class strength. Rapp. P.-v. Réun. Cons. int. Explor. Mer 164: 30–36

Butler, J. L. 1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax*, larvae in the Californian Current. Can. J. Fish. Aquat. Sci. 48: 1713–1723

Campana, S. 1996. Year class strength and growth rate in young Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 135: 21–26

Carrasco, S. and O. Lozano. 1989. Seasonal and long term variation of zooplankton volumes in the Peruvian Sea, 1964–1987. pp. 82–85. *In*: D. Pauly, P. Muck, J. Mendo and I Tsukuyama (eds.). The Peruvian Upwelling System: dynamics and interactions. International Center for Living Aquatic Resources Management, Manila

Chambers, R. C. and W. C. Leggett. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can. J. Fish Aquat. Sci. 44: 1936–1947

Cohen, E., M. Grosslein, M. Sissenwine, F. Steimle and W. F. Wright. 1980. A comparison of energy flow on George's Bank and in the North Sea. Can. J. Fish. Aquat. Sci. 59: 95–107

Cook, R. M. and D. W. Armstrong. 1986. Stock related effects in the recruitment of North Sea haddock and whiting. J. Cons. int. Explor. Mer 42: 272–281

Coombs, S. H. 1980. Continuous Plankton Records; a plankton atlas of the North Atlantic and North Sea: Suppl. 5, Young fish, 1948–72. Bull. mar. Ecol. 8: 229–281

Costello, J. H., J. R. Strickler, C. Marrasé, G. Trager, R. Zeller, and H. J. Freise. 1990. Grazing in a turbulent environment: behavioral response of a calanoid copepod, *Centropages typicus*. Proc. natl Acad. Sci. USA 87: 1648–1652

Crecco, V. A. and T. F. Savoy. 1987. Effects of biotic and abiotic factors on growth and survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42: 1640–1648

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic recruitment fish success in upwelling areas. Can. J. Fish. Aquat. Sci. 46: 670–680

Cushing, D. H. 1961. On the failure of the Plymouth herring fishery J. mar. biol. Ass. U.K. NS 41: 799–816

Cushing, D. H. 1966. Biological and hydrographic changes in British seas during the last thirty years. Biol. Rev. 41: 221–258

Cushing, D. H. 1967. The grouping of herring populations. J. mar. biol. Ass. U.K. NS 47: 193–208

Cushing, D. H. 1968. The Downs stock of herring during the period 1955–1966. J. Cons. int. Explor. Mer 32: 260–269

Cushing, D. H. 1969. The regularity of the spawning season in some fishes. J. Cons. int. Explor. Mer 33: 81–92

Cushing, D. H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer 33: 340–362

Cushing, D. H. 1980. The decline in the herring stocks and the gadoid outburst. J. Cons. int. Explor. Mer 39: 70–81

Cushing, D. H. 1982. Climate and Fisheries. Academic Press, London and New York

Cushing, D. H. 1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 5: 847–854

Cushing, D. H. 1984. The gadoid outburst in the North Sea. J. Cons. int. Explor. Mer 41: 159–166

Cushing, D. H. 1985. Had I but world and time: the study of a single year class. ICES CM 1985/H 71. 6 pp.

Cushing, D. H. 1987. Had I but world enough and time.... ICES CM 1987, Copenhagen. 8 pp.

Cushing, D. H. 1988a. The Provident Sea. Cambridge University Press, Cambridge

Cushing, D. H. 1988b. The study of stock and recruitment. pp. 105–128. *In*: J. A. Gulland (ed.). Fish Population Dynamics. John Wiley, Chichester

Cushing, D. H. 1988c. The northerly wind. pp. 235–244. *In*: B. J. Rothschild (ed.). Toward a Theory on Biological-Physical interactions in the World Ocean. Kluwer, Dordrecht

Cushing, D. H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. Adv. mar. Biol. 250–293

Cushing, D. H. 1992. A short history of the Downs stock of herring. J. Cons. int. Explor. Mer 49: 437–443

Cushing, D. H. 1995a. The long term relationship between zooplankton and fish. ICES J. mar. Sci. 50: 611–626

Cushing, D. H. 1995b. Population Production and Regulation in the Sea. Cambridge University Press, Cambridge

Cushing, D. H. and J. P. Bridger. 1964. The stock of herring in the North Sea and changes due to fishing. ICES 1964 / H: 1–76 (mimeo)

Cushing, D. H. and J. P. Bridger. 1966. The stock of herring in the North Sea and changes due to fishing. Fish. Invest. London 25(1): 1–122

Cushing, D. H. and A. C. Burd. 1957. On the herring of the Southern North Sea. Fish. Invest. London Vol. 20, Part 11. 31 pp.

Cushing, D. H. and R. R. Dickson (1976) The biological response to climatic change. Adv. mar. Biol. 14: 1–122

Cushing, D. H. and J. W. Horwood. 1977. Development of a model of stock and recruitment. pp. 21–35. *In*: J. H. Steele (ed.). Fisheries mathematics. Academic Press, London and New York

Cushing, D. H. and J. W. Horwood. 1994. The growth and death of fish larvae. J. Plankton Res. 16: 291–300

Daan, N., H. J. C. Heessen and J. G. Pope. 1994. Changes in the North Sea cod stock during the twentieth century. ICES Mar. Sci. Symp. 198: 229–293

Dahl, K. 1907. The scales of herring as a means of determining age growth and migration. Rep. Norw. Fish. Mar. Invest. Vol. 2, Part 6. 1–36 pp.

d'Arcy Thompson. 1947. A glossary of Greek fishes. Oxford University Press, Oxford

Davidson, F. and B. de Young. 1994. Modelling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. 4: 33–51 de La Fontaine, Y. and W. C. Leggett. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Can. J. Fish. Aquat. Sci. 45: 1173–1190

Devold, F. 1963. The life history of the Atlanto-Scandian herring. Rapp. P.-v. Cons. int. Explor. Mer 154: 98–108

de Young, B. and F. Davidson. 1994. Modelling retention of cod eggs and larvae (*Gadus morhua* L.) on the Newfoundland shelf. ICES Mar. Sci. Symp. 198: 346–355

de Young, B. and G. A. Rose. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. 50: 2729–2741

Dickson, R. R. and K. M. Brander. 1993. Effects of a changing wind field on cod stocks in The North Atlantic. Fish. Oceanogr. 2: 124–153

Dickson, R. R., K. R. Briffa, and T. R. Osborn. 1994. Cod and climate: the spatial and temporal context. ICES Mar. Sci. Symp. 198: 280–286

Dickson, R. R., P. M. Kelly, J. M. Colebrook, W. S. Wooster, and D. H. Cushing. 1988a. North winds and production in the eastern North Atlantic. J. Plankton Res. 10: 151–169

Dickson, R. R., J. Meinke, S.-A. Malmberg, and A. J. Lee. 1988b. The Great Salinity Anomaly in the northern North Atlantic, 1968–1982. Progr. Oceanogr. 20: 103–151

Dickson, R. R. and J. R. Namias. 1976. North American influences on the circulation and climate of the North Atlantic sector. Monthly Weather Rev. 104: 1255–1265

Duhamel du Monceau. 1769. Traité Général des Pêches et Histoire des Poissons. Vols 1–3. Saillant et Nyon, Desaint, Paris

Dwyer, D. A., K. M. Bailey, and P. A. Livingston. 1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Barents Sea with special reference to cannibalism. Can. J. Fish. Aquat. Sci. 44: 1972–1984

Ellertsen, B., P. Fossum, P. Solemdal, and S. Sundby. 1989. Relations between temperature and survival of eggs and first feeding larvae of the Arcto-Norwegian cod (*Gadus morhua*). Rapp. P.-v. Cons. int. Explor. Mer 191: 209–219

Ellertsen, B, P. Fossum, S. Sundby, and S. Tilseth. 1987. The effect of biological and physical factors on the survival of Arcto-Norwegian cod and the influence on recruitment variability. pp. 101–126. *In*: H. Loeng (ed.). Proceedings of the Third Soviet-Norwegian Symposium. Institute of Marine Science, Bergen

Ellett, D. J. and J. H. A. Martin. 1973. The physical and chemical oceanography of the Rockall Channel. Deep Sea Res. 20: 585–625

Elliott, A. J. and T. Clarke. 1991. Seasonal stratification in the North West European Seas. Cont. Shelf Res. 11: 467–492

Erlandsson, S. 1936. Dendrochronological studies. Stockholms Hogskalas Geokronol Inst. 116 pp.

Foerster, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Bd Can. 162:1–422

Fonds, M. 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperature in a natural daylight cycle. pp. 151–156. *In*: E. Naylor and R. G. Hartnoll (ed.). Proc. 13th Eur. Mar. Biol. Symp. Pergamon, Oxford

Fortier, J., W. C. Leggett, and S. Gosselin. 1987. Pattern of larval emergence and their potential impact on stock differentiation in beach spawning capelin. Can. J. Fish. Aquat. Sci. 44: 1326–1330

Frank, K. T. and W. C. Leggett. 1981a. Wind regulation of emergence and early larval survival in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 38: 215–223

Frank, K. T. and W. C. Leggett. 1981b. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic and biological factors. Can. J. Fish. Aquat. Sci. 38: 1327–1338

Frank, K. T. and W. C. Leggett. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and predator prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991–1003

Frank, K. T. and W. C. Leggett. 1984. Selective exploitation of capelin (*Mallotus villosus*) eggs by winter flounder (*Pseudopleuronectes americanus*): capelin egg mortality rates and contribution to the annual growth of flounder. Can. J. Fish. Aquat. Sci. 41: 1294–1302

Fry, F. E. J. 1949. Statistics of a lake trout fishery. Biometrics 5: 27–67

Fuiman, L. A. and A. E. Magurran. 1994. Development of predator defences in fishes. Rev. Fish Biol. Fisheries 4: 145–183

Garcia, S. M. and G. Newton (in press) Current situation, trends and prospects in World capture fisheries. *In*: Conference on Fisheries Management, Global Trends

Garrod, D. J. 1983. On variability of year class strength. J. Cons. int. Explor. Mer 41: 63–66

Garrod, D. J. and B. W. Jones. 1974. Stock and recruitment relationship in the Northeast Arctic cod stock and the implications for the management of the stock. J. Cons. int. Explor. Mer 36: 35–41

Garstang, W. 1900. The impoverishment of the sea. J. mar. biol. Ass. U.K. N.S. 6: 1–69

Gavaris, S. 1988. An adaptive framework for the estimation of population size. CAFSAC 88/29 12pp

Gerritsen, J. and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Bd Can. 34: 73–82

Gislason, A., O. S. Astthorsson, and H. Gudmundsson. 1994. Zooplankton, *Calanus finmarchicus* and fish eggs south west of Iceland, 1990–1993. ICES Mar. Sci. Symp. 198: 423–429

Glover, R. S. 1979. Natural fluctuations of populations. Ecotoxicol. environ. Saf. 3: 190–203

Graham, M. 1935. Modern theory of exploiting a fishery and application to North Sea trawling. J. Cons. int. Explor. Mer 10: 264–74

Graham, M. 1943. The Fish Gate. Faber, London

Gray, J. A. B. and E. J. Denton. 1991. Fast pressure pulses and communication between fish. J. Mar. Biol. Ass. U.K. NS 71: 83–106

Gulland, J. A. 1965a. Recent changes in the North Sea plaice fishery. J. Cons. int. Explor. Mer 31: 305–322

Gulland, J. A. 1965b. Estimation of mortality rates. Annex to the Arctic Fisheries Working Group. ICES CM 1965 Gadoid Fish Committee 3. 9 pp.

Haldane, J. B. S. 1953. Animal populations and their regulation. New Biol. 15: 9–24

Hansen, P. M. 1954. The stock of cod in Greenland waters during the years 1924–52. Rapp. P.-v. Cons. int. Explor. Mer 136: 65–71

Hansen, P. M. 1968. Report on cod eggs and larvae. Int. Commn Northwest. Atl. Fish. Spec. Publ. 7: 127–138

Hardin, G. 1968. The Tragedy of the Commons. Science 162: 1243–1248

Harding, D., J. H. Nichols, and D. S. Tungate. 1978. The spawning of plaice (*Pleuronectes platessa* L.) in The Southern North Sea and English Channel. Rapp. P.-v. Cons. int. Explor. Mer 172: 102–113

Harding, D. and J. W. Talbot. 1973. Recent studies on the eggs and larvae of the plaice (*Pleuronectes platessa* L.) in the Southern Bight. Rapp. P.-v. Cons. int. Explor. Mer 164: 261–269

Hardy, A. C. 1924. The herring in relation to its animate environment. Part 1. The food and feeding habits of the herring with special reference to the East coast of England. Fish. Invest. London 7 (3): 1–53

Harris, J. G. K. 1975. The effect of density dependent mortality on the shape of the Stock Recruitment curve. J. Cons. int. Explor. Mer 36: 144–149

Harris Report. 1990. Independent Review of the State of the Northern Cod stock. Dept. Fisheries and Oceans, Ottawa

Hennemuth, R. C., J. E. Palmer, and B. E. Brown. 1980. A statistical description of eighteen selected fish stocks. J. North Atl. Fish. Org. 1: 101–111

Herrington, W. 1948. Limiting factors for fish populations. Some theories and an example. Bull. Bingham. Oceanogr. Coll. 11: 229–278

Hickling, C. F. 1927. The natural history of the hake. Fish. Invest. London Vol. 10, Part 2. 100 pp.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapp. P.-v. Cons. int. Explor. Mer 20: 1–20

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. J. Cons. int. Explor. Mer 1: 1–54

Hjort, J., Jahn, G. and P. Ottestad. 1933. The optimum catch. Hvalr. Skr. 7: 92–127

Hodgson, W. C. (1957) The Herring and its Fishery. Routledge and Kegan Paul, Aylesbury and London

Höglund, H. 1972. On the Bohuslán herring during the Great Herring fishery period in the eighteenth century. Rep. Inst. Mar. Res. 20: 1–86

Hollowed, A. B., K. M. Bailey, and W. S. Wooster. 1987. Patterns of recruitment in marine fishes in the Northeast Pacific Ocean. Biol. Oceanogr. 5: 99–131

Hollowed, A. B. and W. S. Wooster. 1992. Variability of winter ocean conditions and strong year classes of North east Pacific groundfish. pp. 433–444. *In*: R. R. Dickson, P. Malkki, G. Radach, R. Saetre and M. P. Sissenwine (eds.). Hydrobiological Variability in the ICES area, 1980–1989. Rapp. P.-v. Cons. int. Explor. Mer 19

Horwood, J. W. 1995. Plankton-generated chaos in the modelled dynamics of haddock. Phil. Trans. R. Soc. Lond. B. 350: 109–118

Horwood, J. W., R. C. A. Bannister, and G. J. Howlett. 1986. Comparative fecundity of North Sea plaice (*Pleuronectes platessa* L.). Proc. R. Soc. B. 228: 401–431

Hovgard, H. and E. Buch. 1990. Fluctuations in the cod biomass in the West Greenland sea ecosystem in relation to climate. pp. 36–43. *In*: K. Sherman, L. M. Alexander and B. D. Gold (eds.). Large Marine Ecosystems: Patterns, Processes and Yields. Am. Ass. Advmt Sci, Washington, D.C.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. mar. Res. 7: 459–82

Hunter, J. R. 1972. Swimming and feeding behavior of larval anchovy, Fish. Bull. U.S. 70: 821–838

Hunter, J. R. and G. L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy, *Engraulis mordax*. pp. 559–574 *In*: J. H. S. Blaxter (ed.). The Early Life History of Fish. Springer, Berlin

Hutchings, J. A. and R. A. Myers. 1994. Timing of cod reproduction: interannaual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21–31

Hutchings, J. A. and R. A. Myers. 1994. What can be learned from he collapse of a renewable resource? Can. J. Fish. Aquat. Sci. 51: 2126–2146

Iles, T. C. and R. J. H. Beverton. 1991. Mortality rates of 0 group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters. 1. Statistical analysis and estimation of parameters. Neth. J. Sea Res. 27: 217–235

Johnstone, R. and P. G. W. Jones. 1965. Inorganic nutrients in the North Sea. Folio 11, Serial Atlas of the Environment. American Geographical Society, Washington, D.C., 3 pp.

Jones, R. 1961. The assessment of the long term effects of changes in gear selectivity and fishing effort. Mar. Res. Scot. 2:1–19

Jones, R. 1964. Estimating population size from commercial statistics when fishing mortality varies with age. Rapp. P.-v. Cons. int. Explor. Mer 155: 210–214

Jones, R. 1973. Density dependent regulation of the numbers of cod and haddock. Rapp. P.-v. Cons. int. Explor. Mer 164: 166–173

Jones, R. and E. W. Henderson. 1988a. The dynamics of energy transfer in marine food chains. pp. 447–465. *In*: A. L. Payne, J. A. Gulland and K. H. Brink (eds.). The Benguela and comparable frontal systems 5. S. Afr. J. Mar. Sci. 12

Jones, R. and E. W. Henderson. 1988b. Simulation studies of fish larval survival. pp. 343–372. *In*: B. J. Rothschild (ed.). Toward a Theory on Biological-Physical Interactions in the World Ocean. Kluwer, Dordrecht

Jones, R. and J. R. G. Hislop. 1978. Changes in North Sea haddock and whiting. Rapp. P.-v. Cons. int. Explor. Mer 172: 58–71

Jørgensen, T. 1990. Long term changes in age at sexual maturity of North east Arctic cod. J. Cons. int. Explor. Mer 46: 235–248

Kawasaki, T. 1983. Why to some pelagic fishes have wide fluctuations in numbers. F.A.O. Fish. Rep. 291(3): 1065–1080

Kondo, K. 1988. General trends of neritic-pelagic fish populations—a study of the relationships between long-term fluctuations of the Japanese sardine and oceanographic conditions. pp. 178–184. *In*: Proceedings of the 25th Anniversary Symposium Fisheries and Fisheries Oceanography in the coming century held in Tokyo November 10–13 1986. Jap. Soc. Oceanogr.

Kushnir, Y. 1994. Interdecadal variation in North Atlantic sea-surface temperature and associated climate conditions. J. Climate 7: 141–157

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. 73: 453–462

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. Rapp. P.-v. Cons. int. Explor. Mer 178: 375–388

Lasker, R., Feder, H. M., G. H. Theilacker and R. C. May. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5: 345–353

Laurec, A. and J. G. Shepherd. 1983. On the analysis of catch and effort data. ICES CM 1982/G8: 1–8

Laurence, G. C. 1982. Nutrition and trophodynamics of larval fish, review, concepts, strategy, recommendations and options. pp. 1–22. *In*: Fish Ecology, Vol. III. Coop. Inst. Mar. Atmos. Sci., University of Miami

Lea, E. 1927. Investigations in Norwegian herrings. Appx. B. Rapp. P.-v. Cons. int. Explor. Mer 41:105–136

Lear, W. H. and L. S. Parsons. 1993. History and management of the fishery for the Northern cod in NAFO Divisions 2J, 3K and 3L. pp. 55–90. *In*: Perspectives on Canadian Marine Fisheries management. Dept Fisheries and Oceans, Ottawa

Leggett, W. C. 1986. The dependence of fish larval survival on food and predator densities. pp. 117–118. *In:* S. Skreslet (ed.) The Role of Freshwater Outflow in Coastal and Marine Ecosystems

Leggett, W. C., K. T. Frank, and J. T. Carscadden. 1984. Meteorological and hydrographic regulation of year class strength in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 41: 1193–1201

Litvak, M. K. and W. C. Leggett. 1992. Age and size selective predation on larval fishes: the bigger the better hypothesis revisited. Mar. Ecol. Prog. Ser. 81: 13–24

Ljungman, A. 1882. Contribution towards solving the question of the secular periodicity of the great Herring fisheries. U.S. Commn. Fish. Fisheries 7(7): 497–503

Lohmann, H. 1908. Untersuchungen zur Feststellung des völlstandligen Gehaltes des Meeres an Plankton. Wiss. Meeresunters Kiel 9: 1–122

Longhurst, A. R. 1967. The pelagic phase of *Pleuroncodes planipes* Stimpson (Crustacea, Galatheidae) in the California Current. Calif. coop. ocean. Fish. Invest. Rep. 11: 142–154

Lough, R. G., W. G. Smith, Werner, F. E., J. W. Loder, J. H. Page, C. G. Hannah, C. E. Nairn, and R. I. Perry. 1994. Influence of wind driven advection on interannual variability in cod egg and larval distributions on George's Bank, 1982 and 1985. ICES Mar. Sci. Symp. 198: 356–378

MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. coop. ocean. Fish. Invest. Rep. 20: 72–82

MacKendrick, A. C. 1926. Applications of mathematics to medical problems. Proc. Edin. Math. Soc. 40: 98–130

MacKenzie, B. R. and W. C. Leggett. 1991. Quantifying the contribution of small scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar. Ecol. Prog. Ser. 73: 149–160

Mackenzie, B. R., W. C. Leggett, and R. H. Peters. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? Mar. Ecol. Prog. Ser. 67: 209–225

Mackenzie, B. R. and W. C. Leggett. 1991. Wind based models foe estimating the dissipation rates of turbulent energy in aquatic environments. Mar. Ecol. Prog. Ser. 96: 209–215

Mackenzie, B. R., T. J. Miller, S. Cyr, and W. C. Leggett. 1994. Evidence for a dome shaped relationship between turbulence and larval fish ingestion rates. Limnol. Oceanogr. 39: 1790–1799

Marak, R. R. 1974. Food habits of larval cod, haddock and coalfish in the Gulf of Maine and George's Bank Area. J. Cons. int. Explor. Mer 25: 147–157

Martin, C. 1994. The collapse of the Northern cod stock. Fisheries 20 (5): 6–8

May, R. C. 1974. Larval mortality in marine fishes. pp. 3–19. *In*: J. H. S. Blaxter (ed.). The Early Life History of Fish. Springer-Verlag, Berlin

McNeil, W. J. 1968. Survival of pink and chum salmon eggs and alevins. pp. 101–120. *In*: T. G. Northcote (ed.). Symposium on Salmon and Trout. Institute of Fisheries, University of British Columbia, Vancouver

Mertz, G. and R. A. Myers. 1994. Match/mismatch prediction of spawning duration versus recruitment variability. Fish. Oceanogr. 3: 236–245

Mertz, G. and R. A. Myers. 1995. Estimating the predictability of recruitment. Fish. Bull. U.S. 93: 657–667

Miller, T., L. B. Crowder, and F. P. Binkowski. 1990. Effects of changes in the zooplankton assemblages on growth of bloater and implications for recruitment success. Trans. Am. Fish. Soc. 19: 483–491

Mitchell, J. M. 1864. The herring, its natural history and national importance. Edmonston and Douglas, Edinburgh

Moran, P. A. P. 1962. The statistical processes of evolutionary theory. Oxford University Press, Oxford

Morse, W. 1989. Catchability, growth and mortality of fish larvae. Fish. Bull. U.S. 87: 417–446

Murphy, G. I. 1965. A solution of the catch equation. J. Fish. Res. Bd. Can. 22: 191–202

Myers, R. A. and N. J. Barrowman. 1994. Is fish recruitment related to spawner abundance? ICES CM/G: 37 10 pp.

Myers, R. A., N. J. Barrowman and J. M. Hoenig. 1995. Estimates of cod mortality in the Newfoundland region from tagging data. DFO Atl. Fish. Res. Doc. 95/93: 1–29

Myers, R. A., W. Blanchard, and K. R. Thompson. 1990. Summary of North Atlantic fish recruitment, 1942–1987. Can. Tech. Rep. Fish. Aquat. Sci. 1743

Myers, R. A., J. Bridson and N. J. Barrowman. 1995. Summary of worldwide spawner and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. 2024

Myers, R. A. and N. G. Cadigan. 1993. Density dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50: 1576–1590

Mysak, L., W. W. Hsieh, and T. R. Parsons. 1982. On the relationship between interannual baroclinic waves and fish populations in the North East Pacific. Biol. Oceanogr. 2: 63–101

Nesis, K. N. 1960. Variations in the bottom fauna of the Barents Sea under the influence of fluctuations in the hydrological regime. pp. 129–138. *In*: Soviet Fishing Investigations in North European Seas. Nauka, Moscow

Nilssen, E. M., T. Pedersen, C. C. E. Hopkins, K. Thybolt, and J. G. Pope. 1994. Recruitment variability and growth of North East Arctic cod: influence of physical environment, demography and predator-prey energetics. ICES Mar. Sci. Symp. 198: 449–470

Nival, P., F. Carlotti, and A. Sciandra. 1988. Modelling the recruitment of marine species. pp. 321–342. *In*: B. J. Rothschild (ed.). Toward a Theory on Biological-Physical Interactions in the World Ocean. Kluwer, Dordrecht

Ording, A. (1940/41) Arringanalyser på gran of furu. Medd. fra. det. Norske Skogversoksvesen 7: 105–354

Ottestad, P. 1969. Forecasting the annual yield in sea fisheries. Nature 185: 183

Ottestad, P. 1986. Time series described by trigonometric functions and the possibility of acquiring reliable forecasts for climatic and other biospheric variables. J. Interdiscipl. Cycle Res. 17: 29–49

Owen, R. W., N. C. H. Lo, G. H. Theilacker, A. Alvarino, J. R. Hunter, and Y. Watanabe. 1989. Spawning and survival patterns of larval northern anchovy *Engraulis mordax* in contrasting years: a site intensive study. Fish. Bull. U.S. 87: 673–688

Page, F. H. and K. T. Frank. 1989. Spawning time and egg stage duration in North West Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on George's Bank and Brown's Bank. Can. J. Fish. Aquat. Sci. 46 (suppl. 1): 68–81

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science 173: 1124–27

Parmanne, R. and V. Sjøblom. 1984. The abundance of spring spawning herring larvae around Finland in 1982 and 1983 and the correlation between zooplankton abundance and year class strength. ICES CM/1984 J:18 (mimeo)

Parmanne, R. and V. Sjøblom. 1987. Possibility of using larval and zooplankton data in assessing herring year class strength off the coast of Finland in 1974–1986. ICES CM/1987 J:19 (mimeo)

Parrish, R. H. and A. D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Fish. Bull. Calif. Fish. Game 167: 1–110

Pedersen, T. 1984. Variation of peak spawning of Arcto-Norwegian cod (*Gadus morhua*) during the time period 1929–82 based on indices estimated from fishery statistics. pp. 72–81. *In*: E. Dahl, D. S. Danielsson, E. Moksness and P. Solemdal (eds.). The Propagation of Cod, *Gadus morhua* L. Flødevigen Biological Station, Arendal

Pepin, P. and R. A. Myers. 1991. Significance of egg and larval size to recruitment variability of temperate marine fish. Can. J. Fish. Aquat. Sci. 48: 1810–1828

Peterman, R. and M. J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy, *Engraulis mordax*. Science 235: 354–356

Peterman, R., M. J. Bradford, N. H. C. Lo, and R. Methot. 1988. Contribution of early life stages to interannual recruitment of northern anchovy (*Engraulis ringens*). Can. J. Fish. Aquat. Sci. 45: 8–17

Petersen, C. G. J. 1894. On the biology of our flatfishes and on the decrease of our flatfish fisheries. Rep. Dan. Biol. Sta. 1V. 1893 1–146

Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Res. Bull. int. Commn NW Atlantic Fish. 1: 163–169

Pope, J. G. 1991. The ICES Multispecies Working Group: evolution, insights and future problems. ICES Mar. Sci. Symp. 193: 22–33

Pope, J. G. and D. J. Garrod. 1975. Source of error in catch and effort quota regulations with particular reference to variations in the catchability coefficient. Res. Bull. I.C.N.A.F. 11: 17–30

Pope, J. G. and C. T. Macer. 1991. Virtual population analysis of North Sea predators for the years 1963–1987. ICES Mar. Sci. Symp. 193: 46–49

Pope, J. G. and C. T. Macer (in press) An evaluation of the stock structure of North Sea cod, haddock and whiting since 1920 together with a consideration of the impacts of fisheries, and predation effects on their biomass and recruitment. ICES J. Mar. Sci.

Pope, J. G. and J. G. Shepherd. 1985. A comparison of the performance of various methods for tuning VPAs using fishing effort. J. Cons. int. Explor. Mer 42: 129–151

Radcliffe, W. 1921. Fishing from the earliest times. John Murray, London

Rau, C. 1884. Prehistoric fishing in Europe and North America. Smithsonian Institute, Washington, D.C.

Reddingius, J. 1971. Gambling for existence. Acta Biotheor. 20 (Suppl. 1): 1–208

Ricker, W. E. 1944. Further notes on fishing mortality and effort. Copeia 1944 1: 23–44

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd Can. 11: 559–623

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd Can. 119: 1–300

Ricker, W. E. and R. E. Foerster. 1948. Computation of fish production. Bull. Bingham oceanogr. Coll. 11: 173–211

Rogers, J. C. 1984. The association between the North Atlantic sea surface temperature and the Southern Oscillation in the Southern hemisphere. Monthly Weather Review 112: 1999–2015

Rollefsen, G. 1934. The cod otolith as a guide to race, sexual maturity and mortality. Rapp. P.-v. Cons. int. Explor Mer 88: 11

Rothschild, B. J. and T. R. Osborn. 1988. Small scale turbulence and plankton contact rates. J. Plankton Res. 10: 465–474

Runnstrøm, S. 1941. Racial analysis of herring in Norwegian waters. Fisk. Dir. Skr. (Ser. Havunders) 6 (7): 1–98

Russell, E. S. 1931. Some theoretical considerations of the overfishing problem. J. Cons. int. Explor. Mer 6: 3–20

Russell, F. S., A. J. Southward, G. T. Boalch, and E. I. Butler. 1971. Changes in biological conditions in the English Channel off Plymouth during last half century. Nature 234: 468–70

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial fish populations. Fish. Bull. U.S. 52: 191–203

Schlesinger, M. E. and N. Ramankutty. 1994. An oscillation in the global climate system of period 65–70 years. Nature 367: 723–726

Schmidt, J. 1909. The distribution of the pelagic fry and the spawning regions of the gadoids in the North Atlantic from Iceland to Spain. Rapp. P.-v. Cons. int. Explor. Mer 10(4) 11pp

Schopka, S. A. 1991. The Greenland cod at Iceland, 1941–1990 and its impact on assessment. NAFO Scr. Doc. 91/102, Halifax, NS. 7 pp. (mimeo)

Scmitt, C. C. and B. E. Skud. 1975. Relation of fecundity to long term changes in growth, abundance and recruitment. Int. Pac. Halibut Commn. Sci. Rep. 66: 1–31

Scura, E. D. and C. W. Jerde. 1977. Various species of phytoplankton as food for larval northern anchovy, *Engraulis mordax*, and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra.* Fish. Bull. U.S. 75: 577–583

Serebryakov, V. 1991. Predicting year class strength under uncertainties related to survival in the early life history of some North Atlantic commercial species. NAFO Sci. Council Studies 16: 49–55

Sette, O. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I. Early life history, including growth, drift and mortality of the egg and larval populations. Fish. Bull. U.S. 38: 149–237

Shephard, M. P. and K. C. Withler. 1958. Spawning stock size and resultant production for Skeena sockeye. J. Fish. Res. Bd Can. 15: 1007–1025

Shepherd, J. G. 1982. A versatile new stock recruitment relationship for fisheries and the construction of sustainable yield curves. J. Cons. int. Explor. Mer 40: 67–75

Shepherd, J. G. and D. H. Cushing. 1980. A mechanism for density dependent survival of larval fish as the basis of stock-recruitment relationship. J. Cons. int. Explor. Mer 39: 160–167

Shepherd, J. G. and D. H. Cushing. 1990. Regulation in fish populations: myth or mirage? Proc. R. Soc. B. 330: 151–164

Shepherd, J. G. and J. G. Pope. 1993. Alternative methods for the estimation of immigration to the Icelandic cod stock. Fish. Oceanogr. 2: 254–259

Shepherd, J. G., J. G. Pope, and R. G. Cousens. 1984. Variation in fish stocks and hypotheses concerning their links with climate. Can. J. Fish. Aquat. Sci. 42: 602–608

Sinclair, M., M. J. Tremblay, and P. Bernal. 1989. El Niño events and variability in Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608

Sissenwine, M. P., E. B. Cohen and M. D. Grosslein. 1984. Structure of the George's Bank ecosystem. Rapp. P.-v. Cons. int. Explor. Mer 183: 243–254

Sissenwine, M. P. and J. G. Shepherd. 1989. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci. 44: 913–918

Sissenwine, M. P. and G. D. Marchessault. 1985. New England groundfish management : a scientific perspective on theory and reality. pp. 255–278. *In*: T. Frady (ed.). Fisheries Management Issues and Options. Univ. Alaska Sea Grant Program, Juneau

Smith, P. E. 1985. Year class strength and survival of 0 group clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 69–82

Smith, P. E. and H. G. Moser. 1988. Calcofi time series: an overview of fishes. Calif. coop. ocean. Fish. Invest. Rep. 29: 66–77

Smith, P. E., H. Santander and J. Alheit. 1989. Comparison of the mortality rates of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, eggs off Peru. Fish. Bull. U.S. 87: 497–508

Somerton, D. A. and D. R. Kobayashi. 1989. A method for correcting catches of fish larvae for the size selection of plankton nets. Fish. Bull. U.S. 87: 447–455

Soutar, A. and J. D. Isaacs. 1974. Abundance of pelagic fish during the nineteenth and twentieth centuries as recorded in anaerobic sediments off California. Fish. Bull. U.S. 72: 257–75

Southward, A. J. 1962. The distribution of some plankton animals in the English Channel and Western Approaches. II. Surveys with the Gulf III high speed sampler, 1958–60. J. mar. biol. Ass. U.K. 42–375

Southward, A. J. 1963. The distribution of some plankton animals in the English Channel and approaches. III. Theories about long term biological changes including fish. J. mar. biol. Ass. U.K. NS 43: 1–29

Southward, A. J. 1967. Recent changes in abundance of intertidal barnacles in south west England: a possible effect of climatic deterioration. J. mar. biol. Ass. U.K. NS 47: 81–95

Southward, A. J. and G. T. Boalch. 1994. The effect of changing climate: past events and future predictions. Exeter Maritime Ser. 9: 101–143

Southward, A. J., E. I. Butler, and L. Pennycuick. 1975. Recent cyclic changes in climate and in abundance of marine life. Nature 253: 714–717

Steele, J. H. 1985. A comparison of marine and terrestrial ecosystems. Nature 313: 355–358

Steele, J. H. (in press) Ocean Science and Policy issues. Fish. Res.

Steele, J. H. and E. W. Henderson. 1981. A simple Plankton Model. Am. Nat. 117: 676–691

Sundby, S., B. Ellertsen, and P. Fossum. 1994. Encounter rates between first feeding cod larvae and their prey during moderate to strong turbulent mixing. ICES Mar. Sci. Symp. 198: 393–405

Sundby, S. and P. Fossum. 1990. Feeding conditions of North east Arctic cod larvae compared with the Rothschild Osborn theory on small scale turbulence and plankton contact rates. J. Plankton Res. 12: 1153–1162

Sutcliffe, W. H., Loucks, R. H., K. F. Drinkwater, and A. R. Coote. 1983. Nutrient flux on to the Labrador Shelf from Hudson Strait amd its biological consequences. Can. J. Fish. Aquat. Sci. 40: 1692–1701

Taggart, C. T. and K. T. Frank. 1990. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. pp. 151–164. *In*: K. Sherman, L. M. Alexander and B. D. Gold (eds.). Large Marine Ecosystems: Patterns Processes and Yields. Am. Assn. Advmt Sci

Taggart, C. T. and W. C. Leggett. 1987a. Wind forced hydrodynamics and their interaction with larval fish and plankton abundance: a time series analysis of physical-biological data. Mar. Ecol. Prog. Ser. 44: 438–451

Taggart, C. T. and W. C. Leggett. 1987b. Short term mortality in post emergent capelin *Mallotus villosus*. I. Analysis of multiple in situ estimates. Mar. Ecol. Prog. Ser. 41: 205–217

Tåning, A. V. 1937. Some features of the migration of cod. J. Cons. int. Explor. Mer 12: 1–35

Templeman, W. 1948. The life history of the capelin (*Mallotus villosus* O. F. Muller) Newfoundland waters. Bull. Newf. Govt. Lab. 17: 1–151

Thompson, W. F. 1937. Theory of the effect of fishing on the stocks of halibut. Rep. Inst. Fish. Commn. 12:1–22

Thoradottir, T. 1977. Primary production in north Icelandic waters in relation to recent climatic changes. *In*: M. J. Dunbar (ed.). Polar Oceans. Arctic Institute of North America, Québec

Townsend, D. W. and J. J. Graham. 1981. Growth and structure of larval Atlantic herring, *Clupea harengus harengus*, in the Sheepscot River Estuary, Maine, as determined by daily growth increments in otoliths. Fish. Bull. U.S. 79: 123–130

Townsend, D. W., Radtke, R. L., D. F. Malone, and J. P. Wallinga. 1995. Use of strontium:calcium ratios for hindcasting larval cod (*Gadus morhua*) distributions relative to water masses on George's Bank. Mar. Ecol. Prog. Ser. 119: 37–44

van der Veer, H. 1986. Immigration, settlement and density dependent mortality of a larval and post larval 0 group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29: 223–236

van der Veer, H. W. and M. J. N. Bergmann. 1987. Predation by crustaceans on a newly settled 0 group plaice population (*Pleuronectes platessa* L.) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 35: 203–215

Walford, L. A. 1931. Northward occurrence of southern fish off San Pedro in 1931. Calif. Fish. Game 17: 401–405

Watanabe, Y., and Y. Kuji. 1991. Verification of daily growth increments in saury otoliths by rearing larvae from hatching. Jap. J. Ichthyol. 36: 1–10

Watanabe, Y. and N. C. H. Lo. 1988. Larval production and mortality of Pacific saury, *Coliolabis saira*, in the north west Pacific Ocean. Fish. Bull. U.S. 87: 601–613

Wooster, W. S. and K. M. Bailey. 1989. Recruitment of marine fishes revisited. Can. Spec. Publ. 108: 153–159

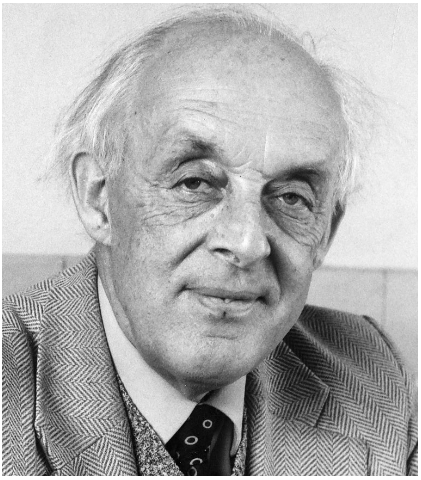
Wroblewski, J. W., D. W. Kilka, S. Narayanan, S. Collins, and B. D. McGrath. 1995. Winter distribution and movements of northern Atlantic cod (*Gadus morhua*) along the Newfoundland-Labrador continental shelf edge from observations on commercial trawlers. Fish. Oceanogr. 4: 128–146

Yamazaki, H. and T. J. Osborn. 1988. Review of oceanic turbulence: implications for biodynamics. pp. 215–234. *In*: B. J. Rothschild (ed.). Toward a Theory on Biological-Physical Interactions in the World Ocean. Kluwer, Dordrecht

Xie, L. and W. W. Hsieh. 1991. Upwelling winds along the west coast of North America, 1899–1988. Oceanography, University of British Columbia, MS Rep. 58: 1–40

Zijlstra, J. J., R. Dapper, and J. Ij. Witte. 1982. Settlement, growth and mortality of post larval plaice (*Pleuronectes platessa* L.) in the western Wadden Sea. Neth. J. Sea. Res. 15: 260–272

About the Author and the Book



David H. Cushing

Dr. David H. Cushing received the ECOLOGY INSTITUTE PRIZE 1992 in marine ecology. He was born in Alnwick, Northumberland, England, and completed his studies at Balliol College, Oxford. Thereafter he joined the scientific staff of the Fisheries Laboratory, Lowestoft, Suffolk, where he became head of the Biology Section in 1965 and Deputy Director in 1974. He and his research group have shaped essentials of today's knowledge on fisheries and plankton ecology.

Chaired by Professor John D. Costlow (formerly director of Duke University Marine Laboratory, Beaufort, NC, USA), the ECI Jury selected David Cushing for his outstanding contributions to various fields of marine ecology. His pioneering studies on the dynamics of plankton patches, the feeding of copepods, the 'match-mismatch' theory of fish-stock-recruitment and the impact of climate on plankton and fisheries remain cornerstones of our efforts to investigate and harvest the seas.

About the Ecology Institute (ECI)*

The international ECI is a not-for-profit organization of research ecologists. Director and scientific staff — 54 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: (1) educational travel, e.g. visits to renowned research institutions, participation in important scientific meetings; (2) research projects; (3) purchase of scientific equipment and publications. 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 more than ever before on definitive ecological knowledge for planning our present and future.

---

* Nordbünte 23, D-21385 Oldendorf/Luhe, Germany
Tel: (+49) (0) 4132 7127; Fax: (+49) (0) 4132 8883; E-mail: ir@int-res.com;
Internet: http://www.int-res.com