EXCELLENCE IN ECOLOGY

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O. Kinne, Editor

Robert T. Paine

Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective

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MARINE ROCKY SHORES AND COMMUNITY ECOLOGY: AN EXPERIMENTALIST'S PERSPECTIVE

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Robert T. Paine

Department of Zoology NJ-15
University of Washington
Seattle, Washington 98195,
USA

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Introduction

Otto Kinne

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

The book series "Excellence in Ecology" (EE) is published by the International Ecology Institute (ECI) and made available at cost price.* EE books may also be donated to scientific libraries in Third-World countries.

EE books are authored by recipients of the Ecology Institute Prize, which honors the sustained high performance of outstanding research ecologists. Prizes are awarded annually, in a rotating pattern, for the fields of marine, terrestrial and limnetic ecology. Prize winners are selected by a jury of seven ECI members appointed by the director. EE books offer the laureates the chance to publish their personal views on the state of the art of their fields of expertise and to bring to the attention of a world-wide audience their insights into the knowledge, problems and realities that form the biological basis for human existence.

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

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

The ECI Prize carries a stipend of US $5000. In addition to this prize, the ECI awards an annual IRPE Prize (International Recognition of Professional Excellence) which carries a stipend of US $750 and which honors a young (not more than 40 years of age) research ecologist who has published uniquely independent and/or challenging papers representing an important scientific breakthrough and/or who must work under particularly

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difficult conditions. The ECI also supports, via the Otto Kinne Foundation (OKF), promising postgraduates in environmental sciences in East European countries — especially in the fields of ecology, diseases of organisms, and climate research. The OKF aids postgraduates — without distinction of race, religion, nationality or sex — by providing financial assistance for professional travel and/or scientific equipment. For details write to the ECI.

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

Nominations for OKF Fellows, addressed to the ECI and accompanied by a letter of support as well as a documentation of the nominees' performance, are invited from ECI members and members of the Editorial Staffs of the three international Inter-Research journals.

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: <u>Ecology – Potentials and Limitations.</u> (Published 1987; price DM 67 plus postage and handling)

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

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

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

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

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

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

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

Quotation of the Jury (Chairman: Tom Fenchel, Helsingør, Denmark)
Robert T. Paine has made substantial and original contributions to marine biology and to ecology in general. In particular the Jury mentions the discovery of the role of patch formation and properties of food web structure

in shaping communities of sedentary organisms. These studies (of which several have become classics of marine ecology) have fundamentally changed the way in which we view marine benthic communities. This work has also served as an inspiration for innovation in the mathematical description of community processes and has had a lasting impact on our understanding of "landscape dynamics", of equal importance to the development of the science of ecology and to conservation ecology.

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

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

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

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

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

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

Book 6: <u>Science and Limnology.</u> (In press.) 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: <u>Recruitment in Marine Fish Populations.</u> (To be published 1995/96)

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

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

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

IRPE Prize Winners and Their Major Scientific Achievements

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

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

nevertheless proved to be correct. The Jury acknowledge Dr. Cavanaugh's brilliant and independent research in understanding chemosynthetic energetic pathways.

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

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

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

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

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

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

Ecology Institute Jury 1989 for the Field of Marine Ecology

Recruited from the Institute's scientific staff, jury members are appointed by the ECI's Director. They elect among themselves the chairperson.

PROFESSOR T. FENCHEL (Chairman), Marine Biological Laboratory, University of Copenhagen, DK-3000 Helsingør, Denmark

PROFESSOR F. AZAM, Marine Biology Research Division, 0202, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093-0202, USA

PROFESSOR J. GRAY, Institutt for Marinbiologi og Limnologi, Universitetet i Oslo, Postboks 1064, Blindern, N-0316 Oslo 3, Norway

PROFESSOR B.-O. JANSSON, Askö Laboratory, University of Stockholm, S-10691 Stockholm, Sweden

DOCTOR G. I. MÜLLER, Scientific Secretary, The Romanian Marine Research Institute, 300 Bvd. Lenin, Constanta, Romania

DOCTOR S. W. NIXON, The University of Rhode Island, Graduate School of Oceanography, Narragansett Bay Campus, Narragansett, RI 02882-1197, USA

PROFESSOR G. G. POLIKARPOV, Institute of Biology of South Seas, Academy of Sciences, 2, Nahimov St., Sevastopol, Ukraine

I am grateful to the jury and its chairman, Professor T. Fenchel, for their critical work. Several other outstanding ecologists nominated for the prize were also considered highly eligible, and the final decision was difficult to make.

Ecology Institute Staff 1994 (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)

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Prof. T. Fenchel, Helsingør, Denmark (1985)

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Prof. J. Gray, Oslo, Norway (1984)

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Prof. B. L. Wu, Qingdao, China (1993)

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Prof. M. Gadgil, Bangalore, India (1985)

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. 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. S. Ulfstrand, Uppsala, Sweden (1986)

Prof. E. O. Wilson, Cambridge, MA, USA (1988)

Limnetic Ecology

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)

Prof. J. G. Tundisi, São Paulo, Brazil (1990)

Dr. D. Uhlmann, Dresden, Germany (1989)

Prof. R. G. Wetzel, Tuscaloosa, AL, USA (1993)

Prof. W. Wieser, Innsbruck, Austria (1987)

Prof. W. D. Williams, Adelaide, Australia (1986)

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R. Friedrich	J. Kunert	

## Book 4: Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective

Excellence in Ecology Book 4 was written by the recipient of the Ecology Institute Prize in marine ecology 1989, Robert T. Paine of the University of Washington, USA. Chaired by Tom Fenchel, Helsingør, Denmark, the ECI jury 1989 (see above) has summarised the outstanding scientific performance of Robert T. Paine in a statement which is part of the Prize document, reprinted on p. XVI.

Robert T. Paine's book focuses on "the heartland of ecology" (p. XXI). His central topics are population biology and community ecology, as viewed from the perspective of a naturalist – in the fullest sense of this word. As he sees it, the historical roots of modern community ecology can be traced to a population biology inspired by thinking in terms of dynamics.

Based on these convictions, Bob Paine examines multi-species interactions on rocky shores and paints fascinating pictures of the origins of community ecology, competitive interrelations among coexisting forms of life, and the patterns of constructing communities from populations.

Stating, and rightly so, that ecology is ultimately founded on observations in the field, Paine concludes that the historically grown concepts of ecology are of interest not only "as a humbling experience" (p. 8), but that they are also a stimulating, generative force for new ideas. The roots of much of today's ecology are old and they originate in applied issues. Consequently, the book pays much attention to documenting how it all began and developed. For a long time ecologists remained reluctant to delve into experimentation and to apply ecological theory and mathematically based modeling.

Experimental simplification and verification of multi-species assemblages constitute important tools in the hands of research ecologists. They have yielded a rich harvest, especially in investigating details of competitive interactions, both among individuals and among species. Competition is a major motor of evolution and of structuring organismic coexistence.
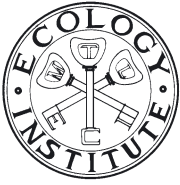
ECOLOGY INSTITUTE PRIZE 1989

In Marine Ecology

Professor Robert T. Paine

(Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195, USA)

has been elected by the Marine Ecology Jury of the Ecology Institute (ECI) as the winner of the 1989

ECOLOGY INSTITUTE PRIZE

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.

ECI Marine Ecology Jury 1989:

Professor T. Fenchel, Helsingør, Denmark
(Chairman)
Dr. F. Azam, La Jolla, USA
Professor J. Gray, Oslo, Norway

Professor B.-O. Jansson, Stockholm, Sweden
Dr. G. I. Müller, Constanta, Romania
Dr. S. W. Nixon, Kingston, USA
Professor G. G. Polikarpov, Sevastopol, USSR

ECOLOGY INSTITUTE

The Director

Kinne

Professor Dr. Otto Kinne

Oldendorf/Luhe, Federal Republic of Germany, November 9, 1989

Hierarchical, unbuffered competition should reduce the capacity for coexistence, while loops or intransitivities, and variable interaction rates and linkage patterns should work to enhance coexistence. Most studies based solely on observation have described species coexistence, but manipulative studies have attempted to delve into and understand the forces that organize coexistence and build communities. Experimentation has provided powerful analytical tools for the modern ecologist.

Communities are structured, to a considerable extent, by trophic interactions and by the quality of the habitat (site). The author especially considers the roles of predation and disturbance in generating a richer pattern of coexistence. He distinguishes three interrelated views: metapopulation models, source-sink dynamics and supply-side relations. Bob Paine concludes that writing this EE book consolidated his "personal viewpoint that community ecology is deceptively demanding" (p. 123).

Increasingly detailed description of nature has not really enhanced our understanding of nature, i.e. has failed to reveal how organismic assemblages work, what significant processes are involved, or how natural assemblages might be conserved. Nevertheless, descriptive compilations of species lists have caused increasing concern about progressive losses in biodiversity (see also EE Book 2: "Success and Dominance in Ecosystems: The Case of the Social Insects" by Edward O. Wilson), awakened awareness of detrimental human impacts, and stimulated theoreticians to search for forces that affect and determine organization.

Experiments that involve addition or elimination of selected species in a defined area reveal major influences on assemblage patterns. The magnitude of changes caused in this way provides important clues for the recognition and interpretation of assemblage structure.

The key to understanding community ecology lies in intuition and in studying nature as it evolved free of human deformation. In the future, ecologists should, more so than in the past, attempt to disentangle the multiplicity of factors and the complexity of nature by experimentation in the field.

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Ecology Institute Prize 1989 in the field of limnetic ecology. Reproduction of the prize awarding document

Robert T. Paine:
Recipient of the Ecology Institute Prize 1989 in Marine Ecology. A Laudatio

Tom Fenchel

Marine Biological Laboratory (University of Copenhagen), DK-3000 Helsingør, Denmark

Thirty or forty years ago, biotic communities were largely viewed as static entities; attempts to understand them were mostly based on equilibrium considerations and community ecology was still mainly a descriptive science. Papers on marine invertebrate communities, in particular, usually consisted of lists of species and of their abundance combined with (mostly unsuccessful) attempts to provide criteria for the delimitation of spatially discrete and defined communities. Theories or ideas on causation which sometimes accompanied these exercises often echoed a debate from the beginning of the century on whether communities "exist" (viz. as a kind of "super-organism") or, alternatively, whether they are assemblages of largely non-interacting species populations. Since then, our approach to and understanding of biotic communities have radically changed. This change in our way of looking at nature is, to a large extent, a result of Robert T. Paine's work.

Robert T. Paine was born in Cambridge, Massachusetts (USA), in 1933 and studied at Harvard and at the University at Michigan, which awarded him a Ph.D. in 1961. Since then, he has been Professor of Zoology at the University of Washington and has thus remained close to his favourite laboratory: the magnificent intertidal flora and fauna of the Pacific coast of North America. Robert T. Paine's starting point was (and is) natural history and, in this way, he has continued the tradition of many great evolutionary biologists and ecologists from Darwin onward. The early love of Robert T. Paine seems to have been birds; and, throughout his career, he has published papers on snowy owls, wrens and peregrine falcons. But, primarily, his early work was concerned with different aspects of the biology of marine benthic invertebrates, and this resulted in many important discoveries. Several of Robert Paine's earlier studies on ecological diversification of sympatric prosobranch congeners point toward his later fundamental

interest in food webs and the structure and species richness of marine benthic communities.

Undoubtedly, the most influential single paper by Robert T. Paine (and indeed a highly influential paper on marine ecology in general) is *Food Web Complexity and Species Diversity*, published in *The American Naturalist* in 1966 (several of Robert Paine's later papers have been reprinted in different "benchmark paper collections", but the 1966 paper has been reprinted in four such books!). Like most other innovative and important papers, this one was not produced in a vacuum: it was clearly inspired by ideas and problems presented by the Hutchinson school of ecology, and it was probably also inspired, in part, by J. H. Connell's (1961) experimental study of barnacle zonation. But the paper presented truly original approaches and ideas: it demonstrated the value of experimental work in community ecology, the role of food web topology and interaction strength between species populationsand, especially, the fundamental role of spatial and temporal patchiness and successional patterns for the maintenance of species diversity. The significance of the paper for marine community ecology was soon widely recognised, and it has since served as an inspiration for countless ecological studies. The basic themes of the paper, food web topology and experimental manipulation, remain central to community ecology today.

These concepts have also been central to Robert T. Paine's more recent research. His work is of wide and general significance for ecology, but it is still primarily inspired by the intertidal faunas of rocky shores; and, it is always based on profound knowledge of the natural history of the individual species. Through collaboration with Simon A. Levin, his ideas have been cast in a mathematical mold, and this has provided a valuable extension and generalisation of the concepts of disturbances and patch dynamics in maintaining the diversity of landscapes and of species in nature.

J. B. S. Haldane has been quoted as saying that "a scientist has really made it if his ideas and results have become so generally accepted and applied that it has been forgotten who originally generated them". It is generally acknowledged that Robert T. Paine has made fundamental contributions to marine ecology, and he has deservedly received much recognition (such as membership in the National Academy of Science, as President of the Ecological Society of America in 1979–80 and as the recipient of the Ecology Institute Prize in 1989). However, he has also been successful in Haldane's sense since the approaches and ideas he initially developed for understanding intertidal animal communities have proven so general that they have become widely accepted and integral parts of contemporary ecology.

Preface

I knew writing a book, even one intentionally short and probably especially a first, would be hard work. Because of this perspective, I had never seriously contemplated the task until accepting the honor and challenge of the international Ecology Institute Prize. Whether the award is richly deserved recognition of half a lifetime of "barnacle bites", a novel form of book advance, or a thinly veiled bribe is immaterial. It worked for me as it has for my illustrious predecessors, almost certainly because it provides an unfettered opportunity to explore some favorite ecologic subject. I acknowledge with gratitude Professor Otto Kinne.

Ecology is awash in both texts and more specialized books as even casual perusal in a good academic bookstore proves. Inspection of the titles suggests that most topics on organisms and even some others can be called "ecology". My own effort falls solidly in the heartland of ecology, somewhere along the boundary between population biology and community ecology. My subject lies on the more traditional side because of my lifelong interests in natural history. That reflects the attitudes of permissive, long-suffering and forgiving parents who let me roam what then seemed to be uninhabited wilderness 30 miles west of Cambridge, Massachusetts (USA), and now is suburbia. I was forgiven for having pockets stuffed with earthworms and salamanders, taken on mushroom hunts, encountered beer and flying squirrels as part of a moth attractant recipe, and was encouraged to become a boy bird-watcher. I dedicate this book to my parents Robert Treat and Barbara Birkhoff Paine.

Becoming a naturalist almost has to be an individualistic enterprise. Practicing it professionally requires support and some measure of understanding. Support has come primarily from the National Science Foundation. A John Simon Guggenheim Memorial Foundation fellowship permitted a personal examination of foreign shores. The Makah Indian Nation has allowed access to its land or islands where my students and I have worked for over three decades; for this I remain deeply grateful. Certain individuals stand out: my mentors F. E. Smith and N. G. Hairston, Sr.; past and current students P. K. Dayton, B. A. Menge, J. T. Wootton, C. A. Pfister and J. Ruesink; and especially my friends Simon Levin and Peter Kareiva, who have made their

credo, "Better ecology through mathematics," believable and in the process enhanced my naturalist's perspective. In vastly different ways, all are responsible. I alone remain culpable.

Seattle, Washington, USA, November 1993   Robert T. Paine

I GENERAL CONSIDERATIONS

Numerous species often share limited areas or volumes of habitat: 70 species found in association with an articulated coralline alga (Dommasnes 1969), over 300 coexisting in just a few square meters of mussel bed (Suchanek 1979), and in excess of 2000 shallow water fishes at the northern end of the Australian barrier reef complex (Sale 1976). Such numbers almost certainly would be the rule, not the exception, if microorganisms were routinely included in quantitative surveys. The residents also interact within the shared environment, killing, eating, excluding, facilitating and breeding. These and other relationships in which the presence and even importance of more than two species is acknowledged is the domain of community ecology. As I define it, community ecology acquires its intellectual traditions from population biology with an interest in dynamics, and an acknowledged significance for density, population responses, growth, and the consequences of both intra- and inter-specific interactions. One style, and the one espoused here, also shares with population biology an increasing reliance on experimental manipulation as the surest means of both testing and rejecting hypotheses and generating novel insights. It differs from population biology primarily in its interest in elucidating the consequence of interactions embedded in a species-rich matrix, thus enhancing recognition and discussion of such potential phenomena as indirect effects, diffuse competition and trophic cascades. The intellectual price of such focus is a reduction in extensively quantified information on single species, an approach characterizing most traditional studies of commercially significant natural resources in which, unfortunately, non-focal species tend to be ignored. Thus precision in community studies tends to be sacrificed for reality. The degree to which these more encompassing studies approach generality, in Levins' (1966) sense, remains to be determined. However, even when attention is expanded from one or a few species to perhaps 10 to 20, this still can be viewed as a mockery of the natural world. Community ecology therefore attempts to confront a multiplicity of factors and the natural complexity of ecological assemblages.

Perhaps the most famous metaphor identifying this complexity is the concluding paragraph of *The Origin of Species* (Darwin 1859) where nature is described as a "tangled bank". Other landmark publications in which numer-

ous species play roles but where the character of the entire ensemble is the dominant theme would be Forbes' (1877) essay on the "Lake as a Microcosm" and Cowles' (1899) convincing reconstruction of successional patterns along the shores of Lake Michigan. Elton's (1927) grand little book caught the essence of community interactions, describing trophic levels, niches, food cycles (= food chains and webs) and numerical pyramids for the first time. It was A. S. Watt (1947), however, as far as I can tell, who introduced the phrase "pattern and process" to describe the coupling between descriptively obvious features of natural assemblages and dynamics at the level of both landscapes and interspecific interaction. Watt clearly believed that within limits process generated pattern, and such a bias is the dominant theme of my endeavor. Description, of course, plays a central role in presenting facts and stimulating the identification of patterns. It may well be an essential first step. However, I place little faith in inferences drawn about underlying processes culled from such observations: nature is too subtle, too many equally appropriate, alternative hypotheses can be proffered to explain the observed pattern. Rather, I believe that ecologists must continue the task of disentangling Darwin's bank by experimentally exploring and expanding upon mechanistically understood interactions.

Patterns come in many forms but the universal denominator to all is that the facts are garnered by observation or sampling — of behavior, abundance, distribution or habitat features. Structure is a closely allied term especially when observable properties of mixed species populations, or characteristics of the landscape (or seascape), are being described. Table 1 provides general definitions of these and other terms that form the basic vocabulary of community ecology.

There is not, and perhaps shouldn't be, any complete acceptance of these definitions. For instance, Allee et al. (1949) defined a community as that collection of species which, if given radiant energy, would be self-sustaining. Not only does this restrict community limits to the photic zone, unless one incorporates vast and unworkable volumes of space as would be necessary to accomodate deep-sea assemblages, but it also implies a balanced, equilibrial nature. At the other extreme, application of a generally useful collective term to a taxonomically limited subset, e.g. a plant, bird or fish "community", seems equally inappropriate. For these latter, the term assemblage is both more accurate biologically and less imbued with implied constraints or characteristics. Are ecological terms then useless? Of course not, because there remains an appropriate vagueness and imprecision which is probably required when considering mixed populations of organisms, which vary con-

Table 1. Definition of ecological terms. (Adapted from Menge 1982)

Term	Definition
Community	A collective term for organisms at a site. Should include all species and trophic levels.
Assemblage	A subset of a community chosen for study. The term implies taxonomic incompleteness.
Guild	A group of species within a community of comparable trophic status or which utilize similar foods or spatial resources in comparable ways (Root 1967).
Community structure	Collective expression referring to the "appearance" of a community; determined by quantifying distribution, abundance, body size, trophic relationships and species diversity.
Community organization	Collective expression referring to the mechanistic dynamics which can produce community structure; determined by evaluating the role of competition, predation, other biotic interactions, disturbance, colonization and spatial and temporal heterogeneity.
Interspecific competition	Mutual striving by two (or more) species for a resource or resources in short supply.
Predation	Consumption of one species by another. It may be complete, resulting in victim mortality, or partial, in which the victim survives.
Biotic disturbance	Disruption of habitat or organisms caused by the nontrophic activities of organisms. Usually leads directly or indirectly to mortality of the affected organisms.
Physical disturbance	Disruption of habitat or organisms caused by the physical environment. Leads directly or indirectly to mortality, or temporary impairment, of the affected organisms.
Experiment	Deliberate, controlled alteration or perturbation of a biotic or physical characteristic with subsequent monitoring of the response of the relevant populations. Controls include both unmanipulated populations and experiments testing for effects of any artificial devices used in the experiment other than the intended effect.
Species diversity (= richness)	Number of species in a community, assemblage or guild.

siderably in space and time, and which rarely if ever share common boundaries. Two observations support my belief that obsession with semantic exactness or becoming overly prescriptive about the meaning of jargon is a waste of time. First, ecologists rarely turn to the available dictionaries of ecological terms, unless it is to identify the meaning of ancient jargon. And second, ecology did not benefit during the era of over-definition, and thus, for example, ready interpretation of the results of many early studies by Clements and his followers is essentially impossible.

How, then, does one justify identifying one style of ecological endeavor as "community ecology" if there remains no agreement on whether or how a community might be identified, the extent to which it may or may not be organized, whether consistent emergent properties exist, or whether its boundaries in space (and time) can be specified? The weakest answer, but perhaps the best or least misleading, is that the term implies only that more than two or three species will be seriously considered. This is the essence of Underwood's (1986) evaluation: the examination of communities as units of study will be less rewarding than specific studies on when, where and how often species interact, the intensity and consequences of their interactions, the relative permanence of interdependencies, and how the interpretation changes when different habitats are examined or spatial and temporal scales are employed. Perhaps this view is more accurately termed an expanded population biology. However, by broadening the perspective to more than just a few species, and addressing questions on complex, multi-trophic-level interactions, the relationships within an assemblage are being considered. Calling such study "community ecology" seems appropriate.

The terms pattern and structure need not imply anything about underlying causal mechanisms. The latter are processes, for instance competition, predation, disturbance, or parasitism. It is often suggested that they "organize" the assemblage, and that local variations in their intensity and outcomes generate the observable patterns mentioned above. The term mechanisms is essentially synonymous with process in implying some specific interaction with a characteristic dynamic. One of the themes developed in this book is that natural assemblages are so malleable in structure, so reactive to the specifics of particular interspecific relationships that what is observed is almost an illusion containing little reliable information about underlying causes. Changing the processes by altering the biological composition often yields a massive secondary response. In some sense, one should believe one's eyes, but infer no underlying mechanism. To gain deeper understanding one must intrude experimentally.

Because experimentation has played an important role in the development of community ecology concepts, and because of its lengthy tradition in ecology generally (explored in Chapter II), I discuss now various styles of ecological endeavor and what I mean by an experiment.

Ecological facts are gathered and hypotheses derived from some combination of observation, contemplation and, when appropriate, enumeration. Behavior is observed and classified, abundances quantified, distributions described and so forth. These are or can provide quantitative descriptors of the real world. I call these *observations* and prefer to distinguish them from *measurements* which involve assessing in some secondary fashion physical attributes (e.g. temperature, salinity, current velocity, nutrient concentration) or biological ones (gonadal volume, individual mass, respiratory rate). The information acquired in these ways rarely focuses on interspecific interactions in their natural setting but rather produces estimates of presence, abundance, position and performance, all characteristic of, and central to, ecological description. *Field experiments*, on the other hand, involve a planned alteration of some natural situation, and in the sense employed here can be identified by the presence of at least two treatments, one of which is a "control".

The word "experiment" is loosely applied in western science, probably in part because it suggests that impressive or important research is being accomplished and also because that word provides a vowel essential for sexy acronyms. Hurlbert (1984) almost apologetically acknowledges the semantic jungle of distinguishing straightforward measurement from what he reluctantly calls a "mensurative experiment". I have decided not to accept conventional or current usage and dignify even technically demanding comparative sampling or observational routines by calling them experiments. They remain measurements because, as identified by Hurlbert, all the sampling units are treated equivalently and no between-unit manipulation is imposed despite the fact that striking differences may occur naturally. On the other hand, the purposeful alteration of one or more factors, properly controlled, produces what Hurlbert terms a "manipulative experiment". These are the real thing. Their application, limitations and abuse in ecology have been discussed by Hurlbert (1984), Underwood (1990, 1991) and many others. Hairston's (1989) critical yet constructive discussion remains the best source from which to glean a feeling for both the challenge and resolving power of manipulative field experiments.

There are at least two intrinsically different kinds of experiments. The first is really an exploration, almost a fact-finding mission, guided by inves-

tigator intuition. These are often minimally designed or replicated, in part for economic reasons: no one wants to commit major effort or funds to an enterprise in which any result is highly uncertain. Today's funding climate renders such gambles generally unprofitable. I prefer to call such efforts controlled manipulations. In contrast, when one has a fair grasp of the fundamental biology, the setting, the necessary duration or spatial scale, and the consequences, one can do an experiment in the sense of Underwood (1991). This should be hypothesis testing at its best, but it requires prior information and its accompanying biases. To design well an experiment of this sort and its control(s), one must have substantial knowledge about the situation. Biases certainly lurk everywhere and I know of no way to avoid them. For instance, randomization of treatments effectively counters bias associated with placement, but the choice of species to be, or not to be, studied remains entirely subjective as does the spatial extent of the experiment and even its duration. To determine these haphazardly would be tantamount to denying the value of prior data, experience and intuition.

There are certainly other kinds of experiments. Medawar's (1969) delightful essay on the structure of scientific thought identifies four, two of which have been considered above. What I have termed an "exploration" is called a "Baconian" experiment, described as an attempt to answer the question, "I wonder what would happen if..." (his p. 35). Medawar suggests, and I agree, that most original research, especially in unfamiliar circumstances or on poorly understood phenomena, starts with this kind of manipulation. It should generate the foundation for "Critical or Galilean" experiments which permit hypotheses to be discriminated amongst, rejected, modified, or extended. Medawar's remaining categories seem less like science. "Demonstrative or Aristotelian" experiments involve the assembly of facts or observations to support some belief or conjecture. There is a strong element of self-serving and self-perpetuating bias here. On the other hand, it is commonplace to believe that an observation "fits" one or another scheme. The notion of generalization is built on such actions and it seems inappropriate and economically foolhardy (and probably impossible in a funding sense) that every new situation, fact or factoid be rigorously scrutinized. Last are the "Deductive or Kantian" experiments. Although these could be called thought experiments, they also encourage the generation of a different perspective on whatever the common observation might be. The recent rediscovery of and interest in "supply side ecology", or whether and the extent to which larval stages determine the population characteristics of the reproductive stock (Young 1990, Grosberg and Levitan 1992), seems to provide an

ideal example. There need be no proof that the alternative view is important or capable of modifying previously drawn conclusions. However, to the extent that thought experiments reflect biologically plausible forces, they provide both a cautionary note and an appropriate stimulation to new and different research.

Is the controlled manipulation of variables the most effective form of hypothesis testing in community ecology? I believe the answer to be yes despite the widely understood limitations. For instance, it is clearly unacceptable to disturb or alter the density of certain species because of legal constraints generated by their rarity, roles as national emblems, or great public esteem. For numerous conditions, the technology necessary for cost-effective study has yet to be invented or employed. And certain species seem to be essentially intractable. For all these circumstances, other approaches are necessary. Diamond (1986) has discussed these, even generating a comparative scorecard of relative effectiveness. Although Diamond's category of "natural experiments" would be called observations here, the major points are these. Manipulations and regional comparison both have their limitations, and should be natural allies. The longest continuously maintained experiment known to me was initiated in 1843: this time span is trivial at the scales basic to interpreting the rates of faunal build-ups. Experiments have obvious spatial restrictions as well, showing an inverse relationship between replication and spatial extent (Kareiva and Anderson 1988); no such boundaries need plague comparative ecology. Studies employing the latter technique can consider hundreds of species simultaneously; experimental community ecology is currently limited to less than, and usually much less than, a score. Although the comparative method may receive the highest grades for "realism", there is often little assurance that the cause of the observed differences has been correctly identified. Hairston (1989) comments on the pitfalls of such weak inference applied to ecologically complex situations characterized by patterns for which alternative explanations are readily proposed.

Experimentation has no single hallmark, and whether some comparative studies qualify as an experiment, or are simply sophisticated measurements, is often context-dependent. For example, measuring (sampling) simultaneously the temperature of ten different tidepools is not an experiment. This is measurement: no factor is systematically manipulated and no *a priori* control is identifiable. Suppose an oceanographer samples a volume of water simultaneously with nets of three different mesh sizes. Is this a field experiment? I would claim "no" despite the presence of three identifiable treat-

ments because it is the equipment, not the organic world, that is being varied. I would place in the same non-experimental category larval settlement plates established at different times or places (these are thermometer equivalents) or surfaces manufactured from three different materials (net equivalents). In both cases the object being manipulated is extrinsic to the real world. On the other hand, identical settlement blocks paired with and without grazers, or paired plankton exclusion trials employing either no or different grades of mesh, would qualify as an experiment despite potential uncertainty as to designation of a control. The critical difference between these latter studies and those described immediately before is this: the latter explore consequences of variation enforced on the natural world; the former examine how different equipment samples a variable natural world.

There is a time-honored tradition in experimental field ecology to designate natural sites adjacent to the experimental treatment(s) as the "control". That is, following Connell's (1974) identification of the tactical difference between laboratory and field experimentation, to hold one (or a few variables) constant in the field, and to evaluate effects against a variable background represented by an unmanipulated control. I will expand on an idea later that this traditional approach maximizes the difficulty (and expense) of detecting all but the most blatant signals, suggesting that community ecology will be effectively served by using an experimentally simplified state, or possibly even a theoretically determined "null" condition, as the basis for comparison rather than a potentially variable portion of the real world. I have used the term "reference state" when discussing such treatments (Paine 1984, 1992).

This book examines the study of multispecies interactions on rocky marine shores, an environment rich in both pattern and species, and asks the question, "Can underlying process be inferred from pattern?" Three biases permeate my answers. First, patterns are the product of processes and therefore interactions between populations promote and even enhance complexity. Second, experimental manipulations performed in rational and morally acceptable ways must be done to understand the perceived complexity. And last, because ecology is fundamentally based on observation, many of the major and even subtler relationships have been recognized for decades. Therefore, the conceptual history of ecology is interesting, not only as a humbling experience, but also as a source of ideas.

Chapter II contains my attempts to create or invent a convenient historical context in which the ideas central to this book developed. I do this in part because there is an intrinsic merit to the process and in part because I have

no interest in rediscovering the wheel. The roots of much of today's ecology are ancient, and there is more than an element of truth to the statement that "Darwin thought of it first."

Chapter III provides evidence supporting my basic claim that multi-species assemblages, especially those characterizing essentially planar surfaces, can be experimentally simplified. The resultant monocultures are formed competitively with a local dominant usurping the limiting resource at a rate commensurate with life history features. Such monocultures, even though unnatural in the sense that they may rarely exist in nature, or if they do, do so under restricted circumstances, provide a common baseline or reference state against which to calibrate the ecological importance of individual species. The presence (generally) of a two-dimensional resource (space), ease of observation, and direct accessibility of these surfaces to experimental investigation have yielded a rich harvest of data and ideas on such competitively based concepts as priority effects (in invasion) and whether nature is essentially hierarchical or transitive in organization.

Chapter IV develops specifically the roles played by predation and disturbance in distorting potential monocultures and thus generating a landscape richer in pattern and coexisting species. Communities are assembled from populations whose local abundance may be influenced by trophic interactions, whose actual presence could be determined by intrinsic site quality and in which the dispersal ability of the component species differs vastly. Consideration of communities in this way leads naturally to three inter-related views of assemblage spatial structure: metapopulation models, source-sink dynamics and supply-side ecology. Trophic relations are another source of local variation, and I compare the potential contributions to understanding assemblage structure of static and dynamic approaches.

The final chapter is a personal perspective, not a summary. I have little doubt that humanity is devastating all natural assemblages, especially terrestrial ones. As species are lost and interactions distorted or otherwise modified, the ecologists' capacity to understand the processes causal to the observed patterns becomes increasingly difficult, and diminished in parallel with that is the ability to manage and restore. If a glimmer of optimism exists, it is represented by the results of J. C. Castilla's "human exclusion" work in coastal Chile. At the best, this suggests that some degradation is reversible; at the most disheartening, it provides a vision of what has been or is being lost. I conclude that experimental ecology has a major role to play in understanding the massive complexity of nature, especially when collaborative efforts with theoreticians blossom.

II HISTORICAL ORIGINS OF COMMUNITY ECOLOGY

The sources of ideas or concepts are important, not only because the historical development and perspective hint at why some approaches flourished, being compatible with the technology and prevalent social attitudes, but also why others floundered. This chapter collects the threads leading to my version of marine community ecology into an interrelated and loosely interdependent fabric. Because I am hardly a historian by intention, and this book is not meant to be a history, I make no apologies for lack of completeness or for omissions. However I have attempted to track the themes I believe to dominate the development of community ecology to their origins and to provide references to these if they seemed self-evident or hopelessly obscure. My motivation is straightforward. Community ecology as practiced today is certainly pluralistic, maybe even increasingly so. One extreme viewpoint, "macroecology" (Brown and Maurer 1989), attempts to infer underlying relationships from comparative surveys of large areas with the analysis usually restricted to a single, higher taxon (e.g. birds, mammals). Another extreme might be called "hard-core experimentation", in which the focus is on some specific interaction. A third would be mathematical or theoretical ecology which in its purest form may bear slight semblance to reality. All attempt to make sense of and even integrate the interplay between process and pattern. They also share common origins.

Here I examine and develop some of the evidence for four primary roots: observation which underlies all natural history and related qualitative endeavors; sampling which developed into quantitative methodologies; and hypothesis testing, which eventually led to manipulative experiments under field conditions. A fourth attribute of current community studies — theory based in mathematical models — while nourished and even stimulated by the above roots, appears to have progressed initially independently. It will be treated as a separate enterprise.

Although in the sections which follow I discuss these roots as though they were distinctive and readily separable, such is not the case, and one may not be a root at all but rather simply a requirement. That is, natural history or knowledge based on it suffuses ecology to such an extent that Elton (1927), clearly one of the discipline's founders, could define ecology as "scientific

natural history". The remaining roots — the development of quantitative techniques, experimentation, and the application of mathematical models — all could be classified as technical roots. Each involves the discovery that employing or even developing a technique — quadrat sampling, controlled manipulation, differential equations — would enhance understanding of nature. I have purposely omitted genetics, because its tie to community ecology historically seems remote, and statistical inference, because it was developed initially outside the domain of ecology.

Other classifications exist. For instance, there are conceptual roots involving major ideas such as natural selection, equilibrium/disequilibrium or "niche". But the past of most of these is murky and involves value judgments I am unwilling to make about appropriate antecedents. There is also merit to considering the role that focused "schools" of thought played, for instance the development of ideas on succession by the American ecologist Clements and his mentor, C. E. Bessey (Tobey 1981), or the development of quantitative plankton research under the direction of the German biologist V. Hensen (Mills 1989). I have chosen a technical root classification both because it appears more general and because it seems directly germane to my perception of the ontogeny of community ecology.

(1) Natural History/Observational Ecology

All four dominant community ecology roots had their origins at least partially in applied issues. It seems certain that precise knowledge of the whereabouts and habits of potential prey organisms conferred immediate benefit to aboriginal hunters. That is, knowing where and how the next meal might be acquired was an intimately applied issue. To the extent that success depended on understanding much of what is now called natural history, our remote ancestors must have been at least adequate practitioners. It can be argued that the rapid Pleistocene extinction of many North American mammals attests to human hunting efficiency. Codifying the knowledge came much later, beginning seriously with the Greeks about 500 BC and continuing to the present (Allee et al. 1949, McIntosh 1985). Bates' (1950, p. 7) definition of natural history as "...the study of life at the level of the individual — of what plants and animals do, how they react to each other and their

environment, how they are organized into larger groupings like populations and communities" catches the essence of the term. It is not mindless observation (though it can be); it does provide essential facts and the fodder basic to more synthetic approaches. Much of ecology may in fact be "scientific natural history", and as Hairston (1989) insists, any field study benefits from, and perhaps requires, presenting the natural setting in sufficient detail so that the reader can readily visualize the observational/experimental conditions. Any number of examples of this ecological style could be identified that catch its flavor, excitement and the implicit observational skills. For example, there is no dearth of information or stimulation in such "pure" natural history expositions as Beebe (1944), Crompton's (1950) descriptions of spider behavior, Forbush's tomes (1925) on New England birds, or Yonge's (1949) details of the British seashore. Population and community ecology clearly require an adequate basis in observational ecology. Natural history would survive without quantitative development.

Natural history in a modern sense was developed on numerous fronts. One unambiguous source can be attributed to individuals Worster (1977) calls the "arcadians", represented by Gilbert White, Linnaeus, Thoreau and even Darwin. White (1720–1793), a parson by vocation, became famous for his book, *The Natural History of Selborne*, which laid the foundation for essays on natural history and "was also one point of origin, representative if not seminal, for the modern study of ecology" (Worster 1977, p. 5). White clearly enjoyed both observing and thinking about nature: his counts of bird numbers have been used in discussions of long-term population trends. To support his views of the economy of nature, White even described a food web of sorts. Similar attributes characterized his contemporary, Linnaeus (1707–1778). At the age of eight, Linnaeus had developed a passion for flowers, by 28 had published the first edition of *Systema Naturae* and by 30, a flora of Lapland. A 1749 essay on "The economy of nature" was praised by its contemporaneous translator as providing "a more comprehensive and distinct view, as it were in a map, of the several parts of nature, their connections and dependencies, than is anywhere else to be found" (Worster 1977, p. 34). Furthermore, amateur biologists actively supported these endeavors. Such individuals tended to dominate entomology and ornithology, despite lack of any formal training, and they constituted an important resource to contemporary professionals. Darwin's voluminous correspondence provides a wealth of examples. Wallace, on his trip to South America in 1849, sent back, as promised, lengthy letters to the Mechanics Institute at Neath, one of his sponsors (Wallace 1905, in MacKenzie 1990). It seems certain that in the

17th and especially the 18th and 19th centuries, serious and accurate attention began to be paid to ecological details, to ways of organizing this detail, and to the development of schemes to relate taxonomically the flood of new species to those previously described.

Other suggestions that natural history was actively practiced prior to 1800 can be found in the origins of what is now called environmentalism and conservation biology. Grove (1990) has described the interaction between profit motives underlying British colonialism and the stark fate of island biotas. Mauritius was stripped of its ebony forests before 1670; the dodo went extinct during that decade. Such events spurred the birth of a remarkably modern environmentalism: a 1769 Mauritean ordinance required landholdings to maintain some proportion (25 %) of native forest, and forbade cutting on steep mountain slopes to minimize soil erosion. Reforestation, restrictions on clear cutting and even a forest service, established in 1777, were in place. As Grove (1992, p. 44) has written:

> The early laws were not confined to forests. Pollution of water by effluent from indigo factories and sugar mills engendered more laws in 1791. In 1798 regulations were introduced to control vital but diminishing fish stocks.

Destruction of habitat brought extinction of native species; forest clear-cutting appeared to reduce rainfall and thus diminish the quality of life for European residents. The plant physiologist Stephen Hales (1677–1761) identified transpiration as a process connecting plant physiology with the atmosphere. As a direct consequence, forest reserves were established in 1764 on the West Indian island of Tobago. Their initial purpose was to maintain urban rainfall and a high-quality life; they remain the oldest forest preserves in the world.

In fact, landscape alteration and its consequences must have been particularly apparent on islands. Moutia and Mamet (1946) describe a purposeful and apparently successful importation of mynah birds from India to Mauritius (in 1762!) to control locusts, an economically important pest. Although few details of this initial introduction for biocontrol exist, it cannot have been easy; it speaks well for the depth of biological knowledge essential to the undertaking.

Natural history and observation played major roles in these and related events. The British East India Company employed by 1838 some 800 "surgeons" in India alone. These individuals often served as town doctor, curator of a local botanical garden, game warden and even engineer in charge of

developing transportation systems. Most were highly educated; many were concerned about the destruction they were witnessing and even overseeing. Some were dedicated to the concept of containment and regulation of the activities underlying environmental change. They were not trained biologists in any sense; many were natural historians and regularly reported observations and transmitted specimens to established academies and museums. However, they drew the tie between human-induced change (mining and natural resource exploitation including over-fishing and clear-cutting) and environmental effects. An 1858 paper by J. S. Wilson (Grove 1992) even discusses changes in the global atmosphere driven by human alteration of the plant community. Biodiversity was not yet an issue although the conspicuous extinction of the Polish auroch in 1627 and the dodo in the 1670's had broached the subject. To the extent that biodiversity concerns reflect an interest in the consequences of interactions between large numbers of species, rather than being a fundamental rationale for habitat preservation, they point naturally towards community ecology. If these early conjectures were primarily focused on global events associated with deforestation, they presage an ecosystem perspective. In either case, their source can be traced to pre-1800 concerns about the economic consequences of human-induced changes.

Although such interests were focused on organism welfare, and linked to global effects through the medium of physiology (an ecosystem perspective only maturing in the 1960's), there is little evidence for attention to specific distributions, and even less to abundance unless a species was pushed to or beyond the brink of extinction. The major exception would be Humboldt's initiation of studies in quantitative plant geography, and its immediate stimulation to mapping the large-scale spatial distribution of land plants.

I believe marine shorelines have always provided a stimulus for biological research. Accessibility, great diversity at both phyletic and specific levels, the conspicuousness of biological interaction (e.g. Wertheim 1984) have all contributed to interest in this environment. Of the roots of marine community ecology, the one I have called "natural history/observational ecology" seems least influenced by economic concerns or demands. Curiosity generated by intertidal patterns led first to their description, initially in 1812 (Gilsén 1930), and eventually to experiments designed to explore the patterns' causes. These threads are united at the end of this chapter.

(2) Quantitative Methodologies

One means of distinguishing natural history from population biology or community ecology might be found in the level of quantitation. Recording a phenomenon or verbal description does not necessarily entail measurement or quantitation; measuring a rate or estimation of density does. Alexander von Humboldt is credited with founding plant biogeography with the publication (1807) of *Essai sur la géographie des plants* (Tobey 1981). His techniques of regionally censusing the number of plant species and relating this to the average annual temperature provided a means for comparing floras, and relating distributional patterns to climate. An early application involved a study in the Rhine Valley (Hoffmann 1879, in Tobey 1981): distributional patterns and frequency of occurrence were evaluated in 21.4 km^2 quadrats. Methodologies practiced at these large spatial scales led to Oscar Drude's studies of the plant geography of Germany. They described pattern and were amenable to generalized survey techniques but bore little relation to the ecologically critical issues of abundance or spacing, and could provide no information on density measured as numbers per unit area. I believe it reasonable to conclude that these generalized and simple plant mapping techniques encouraged the similar British surveys ("botanical cartography") organized by Tansley (1904b). These exercises also provided a geographic context in which measurements of plant structure and function could be placed. A whole generation of German physiologists worked to relate performance to habitat features through the medium of physiologically oriented studies. Their accomplishment was:

> ...to broaden the scope of botanical science by redirecting the focus to the plant in its natural surroundings. Their botanical training had a strong physiological orientation and, equally important, they were among the first generation of German botanists to come of age, so to speak, within a Darwinian universe; they attended universities in the late 1870's and early 1880's, when Darwinism was enjoying its greatest popularity in Germany. With their backgrounds in plant anatomy and physiology, they saw in the concept of natural selection the key to explaining the manifold complex adaptations of plants to biotic and abiotic factors....   (Cittadino 1990, p. 4)

Although their efforts were essentially autecological, their eventual impact on the development of experimental field ecology is readily traced from them to Drude to Pound and Clements (Tobey 1981). Drude's descriptions of plant assemblages and their coherence had inspired Pound and

Clements to describe the prairies of Nebraska, as reflected in Pound's (1896) endorsement of Drude. Drude's techniques failed, however, to provide an adequate description of the Nebraska prairie because they were qualitative and because of the subtlety of prairie grass distribution. The solution was a 1 m^2 quadrat in which individual plants were counted and their numerical (rather than relative) abundance could be given. Although others (Greig-Smith 1954, Oosting 1956) credit Raunkier (1908, in Raunkier 1934) with originating quantitative estimates of abundance, I believe Clements (and Pound) have priority. For example, Pound and Clements (1898) describe 5 m^2 square plots in which all individuals were counted, work in which "...deficiences resulting from the small size of the plots are corrected by taking a large number of plots at each station and averaging the results" (p. 20). In any case, one quantitative root of empirical ecology traces directly to the stimulus and shortcomings of phytogeography as practiced in Germany in the second half of the 19th century.

However, a second equally plausible origin of the root exists. The German government, after the Franco-Prussian War of 1870–1871, was increasingly involved in economic enterprises. Colonialism provided both the incentive and opportunity for extensive study of plant geography and economic development (Cittadino 1990). At home, North Sea fisheries commanded similar attention under the direction of Karl Möbius and Victor Hensen. I have been unable to find either hints or evidence that the plant physiologists and their marine compatriots interacted or stimulated one another, suggesting an independent origin of their quantitative approach to nature. The place was the Port of Kiel. There, Mobius studied benthic ecology in the Gulf of Kiel and the Helgoland oyster bank, coining the term "biocenoses" in perhaps the first community ecology study (Möbius 1873, translated 1883). He and Hensen were initial members of the German marine commission, with Hensen having been diverted from physiological research by a desire to improve and manage the North Sea for fishing. It was known at the time that the eggs of cod floated freely, an observation Hensen extended to plaice and flounder.

> Hensen was interested in these observations because they suggested the possibility of estimating the size of parental fish population on the basis of an egg sample. Later in this period [1871–1885], Hensen became increasingly interested in the small organisms the fish feed upon. He introduced the term "plankton" for these organisms, and concentrated on sampling their number because he felt that the productivity of fisheries would depend on the size of the plankton population.
>
> (Lussenhop 1974, p. 324)

Hensen's procedures involved reinventing (actually discovering independently) the plankton net, calibrating the volume of water swept per unit time hauled, counting the eggs in subsamples, and concern for the errors involved in his procedures. He appears to have been beaten by the latter problem, eventually solved by R. A. Fisher, and thus assumed for convenience as much as anything else that fish eggs were uniformly distributed in the ocean's waters. The resultant controversy, with E. Haeckel who believed plankton to be patchily distributed, provides the first, and one of the prime, examples of ecological debate centered on technique (Egerton 1983).

One of Hensen's associates was F. Dahl. Although his background was in entomology, he participated in some of the plankton collecting expeditions, and in 1889 began studying the invertebrate assemblage of the Elbe estuary (Damkaer and Mrozek-Dahl 1980). The animals were dug from areas ranging from 0.24 to 4.0 m^2, sieved, identified and counted (Dahl 1893). This work appears to be the first quantitative sampling of the marine benthos (incidentally, I cannot find reference to the experimental blocks alluded to by Hedgpeth 1957; Dahl's 1893 work appears to have involved sampling only). Dahl's studies led directly to the much more extensive research of the Dane C. G. J. Petersen who became the first Director of the Dansk Biologisk Station in 1889. In the next three decades, a quantitative bottom sampler — the Petersen grab — was invented, and animal assemblages in Danish coastal waters extensively investigated. The initial publication of this effort (Petersen and Jensen 1911) established the utility of the technique for quantitative marine ecology. Petersen was, essentially, a fisheries biologist interested in charting the quantitative distribution of benthic invertebrates and in measuring both the sources of energy and rates of production, the latter as an estimate of annual production of fish food. He showed little interest in defining these animal-dominated benthic assemblages as communities (Thorson 1946) and as Hedgpeth (1957, p. 7) writes, "Petersen himself considered his method an extension of Hensen's investigations."

It may be unsurprising that this root developed as recently as it did, or that its genesis can be traced to at least two, apparently independent, schools of thought. That these were sympatric and simultaneous is a troubling problem. There is no doubt, though, that marine biologists, motivated by economic considerations, participated actively and successfully.

(3) Experimental Manipulation

Natural history has been rendered more scientific by the quantitation of real world phenomena and especially the development of hypotheses capable of being examined experimentally. I have considered the former first because of the central role it has played in the conceptual development of marine community ecology and now turn to the latter, which also has a long history of development.

I like to think of experimental ecology beginning not with Darwin in 1859 but on a pleasant English day in 1843 when the Rothamsted experiments were initiated by J. B. Lawes (Tansley 1904a). Lawes had inherited the Rothamsted property in 1834. By 1842, convinced that turnip production was enhanced by the addition of fertilizers, he had patented the manufacture of "superphosphates". Lawes

> ...seems to have been partially spurred [to begin the systematic experiments in 1843] by the lectures of Liebig delivered at the Royal Institution. Liebig taught that plants derived not only their carbon but also their nitrogen from the atmosphere, and on this he founded his doctrine of *mineral manuring*.... Lawes found that this theory did not square with his practical experience, and selecting certain fields from his estate, and devoting a barn to the purposes of an agricultural laboratory, began the great series of experiments which have been carried on continuously from 1843 till the present day.   (Tansley 1904a, p. 171)

Lawes' idea was to examine the effects of barnyard manure and chemical fertilizers, especially nitrogen and phosphate, on the production of wheat. It is especially satisfying that Lawes was interested essentially in testing Liebig's law of the minimum. Liebig favored nitrogen as the limiting nutrient and, ironically, was eventually proven correct. The manipulation continues to the present and has yielded insights about slow, long-time base change in community composition (Silverton 1980). Perhaps the most important derived consequence was the development by R. A. Fisher of techniques for analysis of variance and randomized factorial design. Taylor's (1989) essay on long-term ecological research, for which the "Broadbalk" experiment at Rothamsted provides the prototype, sets these impressive results into a historical context. It seems certain that field experimental manipulation entered ecology under the appropriate banner of hypothesis testing.

The concept of experimental examination of ecological ideas was clearly well established before the mid 1800's. Darwin, sometimes called the first ecologist (Harper 1967), often calibrated the generality of his observations

with manipulations. Chapter 3 of the *Origin* (1859) includes tests of how grazing (or mowing) influences grass species richness, and how herbivores affect weed germling survival. His worm (vegetable mould) book (1881) provides a quantitative exploration of worm behavior. Darwin had observed that *Lumbricus terrestris* tended to haul leaves into their burrows by their apices. He then explored this behavior by offering the worms, in replicated trials, triangles of different apical angles cut from moderately stiff writing paper. His plant breeding book (Darwin 1876) serves as a remarkable example of his willingness to explore unknown phenomena, in this case the adaptations of land plants to cross and self fertilization. Darwin's studies, carried out on numerous species with some of the experimental crosses maintained for ten generations, revealed almost uniformly that progeny from cross fertilizations were superior in height or fertility to those from self-fertilizations. Fisher (1960, p. 27) chose this work as an example "...to illustrate the principles on which biological experiments may be made conclusive."

Manipulative exploration of field biological phenomena seems to have characterized at least some of the *terrestrial* ecological work of the period. There certainly was no opposition or hostility towards field manipulation; many of the practitioners struggled with the recognized problems of data analysis but proceeded anyway. For instance, in the first paper in the first journal devoted to ecology (*Journal of Ecology*), Oliver (1913) mentions but provides no details of the dramatic changes in plant community composition introduced by excluding rabbits by fencing. He was referring to the ongoing work of Farrow (1916, 1917a) in which a fence was built in 1903 and later supplemented with rabbit-proof cages. Farrow's results have a remarkably modern tone: browsing by rabbits influences the competitive ability of heathland plants differently, with grazing favoring grasses over dicotyledons; the intensity of grazing (examined by cages in high and low rabbit density areas) directly determines the plant species richness (basically an early version of the intermediate disturbance hypothesis); these grazers impact tree growth and hence succession. Farrow (1917b) also tested an alternative hypothesis that water limited plant growth. The methodology, adding water and simultaneously excluding rabbits, led to the conclusion that water supply determined the specific rate of plant growth while rabbit activity controlled the vegetation's luxuriance. This paper is unique in other ways as well: it introduces a simple differential equation showing how the balance between the rate of plant growth and rate of rabbit consumption will underlie the dynamics of "luxuriance". In the same year, Jeffreys (1917) experimentally examined the influence on plant growth of diminished water

supply and Tansley (1917) described experiments, initiated in 1911, on competition between two species of *Galium*. Although inconclusive in some ways, this latter study illustrated a deep appreciation of how such work should be conducted: replication, variation in soil type, and inter- and intra-specific effects are all considered.

I provide the above detail to suggest that experimentation as a way of conducting field ecological studies was alive and well in Britain at that time. One gets the feeling that people talked to one another and read the appropriate papers, that the role of terrestrial vertebrate grazers was appreciated, and that there was no applied/basic ecology dichotomy. I will suggest shortly that none of these attitudes penetrated to the other side of the English Channel. But first, what was happening concurrently in North America?

The intellectual counterpart to Tansley in Britain was F. E. Clements, best known now for his development, sometimes excessive, of ideas of plant community structure and its identity as a superorganism, the central role of change or succession, and an almost pathological interest in coining novel terminology. It may have been the latter as much as the former which led to his fall from grace. It certainly renders many of his papers essentially uninterpretable, and has probably contributed to the reappearance of many Clementsian concepts in new guises (McIntosh 1985). For instance, I have haphazardly sampled 6 pages of the glossary in Clements' 1905 classic on *Research Methods in Ecology*. This section is a mother-lode of abandoned and useless terminology. I estimate that less than 15 % of the scores of terms either invented or applied by Clements to plant ecological phenomena have been retained. The book, however, contains much more than the title suggests: personal opinion and philosophy, social commentary on other kinds of botany, the role of humans and "natural experiments", pictures of geotomes (they are not shovels), and even a taxonomy of quadrats. It was an important and acknowledged source at the time, and yet it deals with experimental methodology in a rather indirect, naive fashion. Furthermore, Clements seemed to have been unaware of Rothamsted despite Tansley's (1904a) advertisement of the activities there. Clements wrote (1905, p. 4), "...the experimental study of ecology dates from Bonnier (1890, 1895), although it is well understood that experimental adjustments of plants to certain physical factors had been the subject of investigation before this time." Apparently disregarding the accomplishments of applied ecology was as commonplace then as it is now. In addition, Clements' (1935) paper on "Experimental ecology in the public service" really does not identify experimental programs unambiguously focused on process. Rather, much of it

deals with the devastation to the American landscape by overgrazing, the interplay between periodic drought and soil erosion, and even fire. Exploratory manipulations are described, but Clements writes pessimistically about "control experiments" performed out-of-doors. The major problems identified were the length of time necessary to the investigation, cost, a large enough space to contain a representative assemblage and, of course, the absence of control in a laboratory sense, a list familiar to all current practitioners. Clements' authoritative 1905 book was similarly vague about field manipulation and I can find almost no mention of experiments in Adams (1913), perhaps the first book devoted to animal ecology.

Were field experiments performed in North America during the interval 1890–1940? The answer seems to be "few", and none were developed with the focus of Farrow, the explicit attention to design of Tansley, or the plant-herbivore interest of Summerhayes (1941). And this was despite the presence of numerous biologically or ecologically oriented journals embracing a variety of environments. *The American Naturalist* first appeared in 1867; in the interval prior to 1925 the dominant theme was the nature of inheritance and sources of genetic variation. There appears to have been little interest in what today would pass for population or community ecology. The *Biological Bulletin* began publishing in 1900 a strange mixture of ant work and laboratory studies on the early development of marine organisms. All experiments were lab experiments, and little interest in applying this information to field populations is evident. The *American Midland Naturalist* began in 1909, and was "devoted to natural history, primarily that of the prairie states." The early issues are essentially descriptive (e.g. bird migration dates and lists, species habits, regional floras); later ones acquire a paleontological emphasis. There is no experimental ecology of any flavor. And, finally *Ecology* appeared in 1920: the dominating preoccupation was with the role physical factors played.

Few North American efforts appeared to match the developing sophistication of the British effort during this interval. One possible reason is the slow, inefficient communication of the time. On the other hand, both Cowles and Clements (and their wives) participated in the "International Phytogeographical Excursion", 1911, basically a tour of Britain personally guided by Tansley (Sheail 1987). The hospitality was reciprocated, and in 1913 Tansley visited the United States under the auspices of another phyto-geographical excursion (Dachnowski 1914). In addition, the quantitative methodologies invented in Germany and Denmark were rapidly adopted, so time-lags in communication appear to have posed few problems. Three

other factors seem equally plausible candidates. First, Clements championed successional change leading to a climax community as the unifying theme in ecology. Although this was the first such ecological paradigm, it was burdened with a wealth of terminology. The specialized vocabulary alone could have inhibited or destroyed interest in complex natural assemblages and the experiments necessary to identify significant processes.

Second, I have already commented on the communication that appears to have characterized British ecology. Many of their studies appear almost linear, in the sense that one discovery led to a new generation of experiments. I could develop no sense of unification in the early American ecological literature and, in fact, perhaps the contrary state existed. Clements' botanical interests were nurtured in Nebraska with an approach originally inspired by the German plant geographer Oscar Drude (Tobey 1981). An alternative interpretation for vegetational change coexisted with Clements' views. It was championed by H. C. Cowles at Chicago, and was based on the ideas of a Dane, Eugene Warming. Although the passage of time and rampant misinterpretation (or advocacy) have blurred the distinction between these two approaches to succession and the nature of the plant community, the philosophical differences remain important. Clements believed that climatic forces outweighed biological processes, and therefore that the climatic climax was a potentially inevitable terminal state to succession, whether or not it was actually achieved. Cowles believed that these same biological processes, because they operated with intensity at local spatial scales, would prevent the attainment of a regional equilibrium. Therefore a plant community, integrated in a Clementsian sense and ideally suited to the regional climate, was an illusion. The conceptual distinctions were apparent enough so that Cowles (1898, p. 372) could write:

> It may be too early yet to predict whether the direction to future work in plant geography will be given by Warming or by Drude; and so whether we shall speak of ecology or phytogeography, or life forms or vegetational forms, or plant societies or formations, is yet to be decided.

It is tempting to detect in this passage a persistent dichotomy between styles of ecology, recognizable today as population ecology on one hand and ecosystem studies on the other.

As a second example of reduced communication or ecological deafness, Gleason (1926) repeatedly challenged Clements' ideas (McIntosh 1985 and many others): Gleason seems to have had little influence until after World

War II (Hagen 1992). Physical forces and their ecological impact dominated most early American ecological thinking. Combined with an intense interest in assemblage disruption and distribution, it could well have reduced interest in process.

Finally, the simple immensity of the landscape, and seascape, could have played a role. Ecologists were rare, natural history had fallen on hard times, little was known about the habits and often identity of the local organisms. Description, just a simple inventory of what was present, may well have been the top priority of the day. The early American ecologists lacked the cohesiveness which characterized British ecology. There was no national "Vegetation Committee" (formed by Tansley in 1904) and no ordinance survey maps which encouraged vegetational mapping at scales varying from six inches to one inch per mile. Under these circumstances, process-oriented experimental work could well have been unlikely.

There was a burgeoning interest in the environment as an economic resource in the 19th century. As the European invasion of North America expanded westward, vast territories came under agrarian influence. In the United States, enhanced agricultural productivity appears to have attained the status of a national goal and with it came "government". The federal role was supportive and minimally paternalistic and helped agriculture make a significant and essential contribution to the nation's economic growth. In 1866 an experimental farm was formed at the University of Wisconsin. It languished. However, in 1875 the State of Connecticut established an agricultural station and other states followed this example of public support for research into means of enhancing farmer productivity. In 1887 the Hatch Experiment Station Act was passed by Congress. Each state with a preexisting agricultural "experimental" station was provided with $15 000 per year, a princely sum in those days (True 1937, Rosenberg 1971). The Department of Agriculture's Office of Experimental Stations played an especially important role by supporting the notion that professional scientists were the appropriate individuals to conduct the expected research. The Hatch Act contained provisions designed to discourage exploitation and reassignment of agricultural station personnel to teaching duties, and attempted to restrict other diversion of funds (Rosenberg 1971). In 1906 the federal monies were increased to $30 000 per year, with the stipulation that the funds were to be used for "original" scientific research.

There is little doubt about the effect of federal involvement. Scientists supported in these applied ventures discovered vitamin A and hybrid corn. Departments of plant pathology, microbiology and bacteriology were often

generated as the result of attacks on strictly applied problems. By 1901 it was possible to proclaim that the development of a test for the butterfat content of milk "had been worth more to the State of Wisconsin than the cost of running the entire university throughout its history" (Rosenberg 1971, p. 208).

These and other success stories must have been visible to the biologists in the basic science departments. I can only guess at why receptivity was so low. The scientists at the agricultural stations, often trained in Germany and usually chemists, were required to teach courses ranging from German to biochemistry, despite stipulations about their primary responsibilities. The university administrations often found it expedient to divert the Hatch (and Adams) Act funds towards what is now known as overhead. And intellectual snobbery, especially rampant in leading American universities, reinforced the attitude that agricultural station scientists were second rate and primarily concerned with improving fertilizers or advising farmers on how to manage their lands for profit. Although the traditional lack of understanding and communication between biologists in basic science departments and those at agricultural stations seems finally to be breaking down (as of 1993), the lengthy gap in communication has served neither group well. I believe it contributed substantially to the slow acceptance by biologists in basic science departments of field manipulative techniques.

Experimental field research did exist in the United States, but such efforts were buried deeply in what must have passed for the "gray" literature of the day. A fine and very early example is the study of the cause and transmission of "Texas Fever", a disease of cattle carried by ticks (Smith and Kilborne 1893). The field studies were repeated in time (1889–1892), were often replicated within and between seasons, and were controlled. They were also definitive, and any reader of their report should be convinced of the robustness of their conclusion that, essentially, the old ranchers were correct: there was a causal link between ticks and cattle disease. In another study Hildebrand (1920) investigated the capacity of mosquito fish (*Gambusia affinis*) to control mosquito larvae and thus the practical value of this fish in anti-malarial work. Although few numbers are given, and one can only guess at how many ponds were examined or manipulated, the paper generates an impression of both scientific care and robustness. Spatial variation was addressed by observation and experiment. Highly acidic ponds provided suitable habitat for abundant mosquito larvae whereas fish transplants to these sites failed (often in a few minutes). On the other hand, *G. affinis* effectively eliminated mosquito larvae when introduced elsewhere, a result

shown to be dependent on the presence and quantity of rooted or floating aquatic vegetation. Hildebrand had an accurate feeling for the role that refuges or safe sites might play in moderating prey-predator interactions, and even attempted to estimate a per capita consumption rate. My point in mentioning both the *G. affinis* and cattle fever research is that examples of experimental attacks on applied field problems were visible before 1920. However, their success in clarifying difficult issues seems to have had little influence on how North American ecology was performed. Experimental manipulation of natural populations remained unappreciated and was rarely practiced by university-based ecologists until approximately 1960.

If one looks beyond ecology to other biological disciplines, one finds a rich, varied and substantially earlier development of experimentation, especially in what would now be called applied areas. Many of the studies are true experimentation in that focus on an *a priori* question, adequate controls and straightforward manipulation are easily recognized. They stand in stark contradiction to the current self-proclaimed "experimental biology" dominated by biochemists and molecular biologists, much of whose research involves highly inventive measurement and related description.

Lenhoff and Lenhoff (1986) date the birth of "experimental biology" as 1744 with the publication of Abraham Trembley's (1710–1784) observations and research on *Hydra*. Trembley's work was acclaimed and internationally recognized within his lifetime; such 19th century luminaries as Cuvier and Von Baer readily acknowledged its seminal role. It seems immaterial whether Trembley's research was truly experimental. Despite the difficulty of recognizing a control treatment, the hallmarks of insightful and critical observation, planned manipulation, an eagerness for duplication of the results and even hypothesis testing of a sort are all apparent. Trembley clearly intervened in the biology of *Hydra*, and his observations on movement, regeneration, feeding and even individual and population growth appear to provide an appropriately primordial start.

The Italian priest and biologist Lazzaro Spallanzani (1729–1799) may well have performed the first real experiments replete with controls in his efforts to test the hypothesis of spontaneous generation of life. Broth when sterilized and effectively closed to invasion remained unspoiled. Comparable material when exposed to air rapidly became contaminated. Edward Jenner's (1749–1823) proof of the effectiveness of vaccination against smallpox bears the readily recognized hallmarks of appropriate field experimentation. Folk wisdom held that there was a natural antagonism between cowpox and smallpox. Jenner's early research suggested two forms of cowpox, only one

of which could protect against smallpox. In 1796 he innoculated an 8 year old boy with material collected from cowpox lesions on the hands of a milk-maid; two months later the boy was innoculated with smallpox virus but the disease did not appear. Publication of the results (1798), controversy, and recognition followed. Given the disfigurement and occasional mortality associated with smallpox and Jenner's successful development of a means of protection, most biological scientists must have been aware of the resolving power of experimental intervention in natural phenomena. Louis Pasteur's (1822–1895) investigations into the causes of fermentation and the proce-dures for the preparation of artificial vaccines provides examples of widely acclaimed, experimental research. Perhaps, however, his most audacious work involved isolation of the bacterial cause of anthrax, developing a heat-weakened innoculum, and then inviting an international group to examine an experimental test in May 1881. The control animals, twenty-four sheep, one goat and six cows, were inoculated with the attenuated and weakened anthrax strain. Twenty-six days later these and twenty-nine unvaccinated animals were injected with a fully virulent strain. Although the controls remained healthy, within three days all the unvaccinated sheep were dead and the cows terminally ill (Harré 1983). Finally, the 1892 work of Dmitri Iwanovsky on what eventually was recognized as tobacco mosaic virus sup-ports the view that well-designed experimentation was an acceptable, inter-nationally recognized and appreciated way to explore and understand applied problems. Iwanovsky investigated a wilting disease of tobacco by extracting juices from infected plants and placing these fluids in contact with healthy plants. The infection was transmitted despite state-of-the-art filtra-tion through porcelain filters. It is immaterial that viruses remained uniso-lated until 1935: Iwanovsky's research identified an unknown, and at the time invisible, agent. Subsequent work, by testing alternative hypotheses, further characterized the agent.

   These examples imply that the experimental investigation of biological hypotheses probably began in the 18th century and was internationally rec-ognized and broadly employed in the 19th century. The Rothamsted station was inaugurated in 1843, also with an applied mission. Why was it, then, both in other English-speaking nations and continental Europe that the approach wasn't immediately emulated by students of the natural world when the message of new insights and powerful, convincing discovery was clear? This root is increasingly characteristic of current efforts to understand the complexities of natural, multi-species assemblages. Why experiments were rarely performed before 1900 and infrequently before 1960, especially

in North America and continental Europe, remains unfathomable to me. The answer must lie beyond the cataclysm of the second world war: ecologists were beginning to do revealing experiments under laboratory conditions (e.g. Gause 1934) well before that event. It cannot be for lack of convincing examples from a variety of fields of biology: many prominent ones were widely acknowledged. There appears to have been no sustained fear of numbers, and the statistical problems which had vexed pre-1900 ecologists (Tobey 1981) were well on the way to being solved. For whatever reasons, what has seemed so obvious and relevant since Connell's (1961a, b) experimental investigations of species interactions cannot have been so compelling prior to that date.

(4) Mathematical Ecology

> More generally, even a potentially erroneous theory is an enormous advance over having no theory at all, for the incorrectness of the theory, when tested, is in a sense a measure of how far wrong are the postulates on which the theory is based. Once this has been determined, we can start modifying the theory; if we had no theory, there would be nothing to modify and we should get nowhere.

So wrote Hutchinson (1978, p. 40) in concluding a chapter richly imbued with history on the entry of mathematics into population biology. Scientific demography is portrayed as beginning in 1662, and led rapidly to the concepts of doubling time and geometric increase in human populations, with the consequences of the latter being recognized. Malthus's 1798 essay on population was doubly significant: it provided a convincing perspective on the dynamics and checks to population increase, and it made an important contribution to how both Darwin and Wallace thought about the selective nature of mortality. It remained, however, for Verhulst in 1838 to identify a sigmoidal growth curve or "logistic", and to imbue it with an upper boundary to population size. Details of the rediscovery of Verhulst by Raymond Pearl in 1931, himself developing techniques for projecting the consequences of continued human growth, and mathematical generalization by A. J. Lotka and Vito Volterra can be found in Kingsland (1985).

Applied biology contributed significantly to the later stages of this root. Kingsland (1985) suggests that Lotka was always searching for biological

examples appropriate to his nascent theme of systems ecology. He found them in data on malaria epidemiology. Volterra, on the other hand, already a famous and established mathematician, was essentially coaxed into applying mathematics to biology by his son-in-law, Umberto D'Ancona, who had identified population recoveries in certain Adriatic Sea fishes during the First World War, and sought a mathematical explanation. In this sense, then, early support for the appropriateness of mathematical approaches to ecology came from cyclical predator-prey interactions. It was these that stimulated Volterra; equally, in the first truly experimental application of the Lotka-Volterra equations (Gause 1934), cycles were sought in protozoan systems.

Mathematics, stimulated by a desire to understand and even predict the consequences of human demographic trends, entered ecology early in the 19th century. The root is a robust one, at times confusingly so; it is probably also critically important for the future development of community ecology, especially when experimentalists communicate with theoreticians. Demographic prediction is an art form and effectively applied as matrix manipulation to size- and age-structured populations (Caswell 1989). Dispersal and population spread into homogeneous and heterogeneous environments can be routinely analyzed by diffusion-reaction models (Levin 1974, Okubo 1980). Mathematical studies of possible chaotic behavior are proliferating everywhere. Yet these and a host of similar examples involve single- or two-species interactions, and most have been initially investigated with the time-worn and overly simplistic but still useful Lotka-Volterra equations. Mathematics is necessary to unite spatial variation and multispecies relations including trophic interactions — all central to the domain of community ecology — into a conceptually rich framework capable of prediction. I do not believe this surge of mathematization can or should be avoided. Without it, community ecology will be awash in facts, even those based solidly in natural history and supported by convincing statistical analyses. Thus further analytical development will be required to even begin to unravel Darwin's tangled bank.

If such optimism is justified, it should be tempered with a dose of reality. I commented earlier on the seeming reluctance of ecologists to embrace experimentation, and time may likewise pass before all ecologists are acquainted and comfortable with ecological theory. Banse (1992) has discussed an equivalent scientific "sociological puzzle," the slow and still only partial integration of marine phytoplankton performance and zooplankton activity despite almost 60 years and perhaps a century of recognition of their coupled dynamics in which mathematically-based modeling plays a central

role. There is an intellectual inertia in ecology and all sciences to incorporating new approaches, and as Banse suggests, the delays may have well-disguised causes.

(5) A Marine, Benthic Perspective on "Roots"

As an amateur digging into the dusty past of ecology, I attempted to be sensitive to my "first impressions" and surprises. Three predominated. First, much of the older and largely forgotten or ignored literature is rich in current ideas if not detail; Baker (1910) and Fischer-Piette (1935) come especially to mind. Second, applied biology has made special and continuing contributions to attitudes and approaches. It too is a wasteland of neglect and what is now termed gray literature has a lengthy tradition. There could be immensely revealing records buried unpublished in theses or the records of marine laboratories, just as I know exist in hidden reports to government agencies. I was struck by the substantial contribution to ecological understanding generated by the economics of exploitation. Ecology was internationalized early in its development by recognition of the consequences of overpopulation and other human excesses. And finally, I remain puzzled why certain attitudes or approaches failed to spread rapidly, why these invisible barriers even existed.

The study of ecological interactions on rocky shores contains elements of all of these. Most people live close to shorelines (Steele 1991) and historically, because almost all international trade was conducted port to port, maritime cities became capitals and seats of higher learning. Shorelines were readily accessible, observable and showed conspicuous changes in assemblage composition along an environmental gradient. Furthermore, extensive travel was not a pre-requisite: the pattern of change was visible at a site. There were at least two immediately derived consequences.

First, it was obvious that many marine species constituted a highly valuable resource yet one which could be overexploited. Economic concerns, abetted by industrial cities linked by rail to the coast, identified the significance of marine fisheries, both invertebrate and vertebrate. In Britain, a Royal Commission to Investigate Fisheries Problems was formed in 1863. Both the United States Fish Commission and the German Kommission zur

wissenschaftlichen Untersuchung der deutschen Meere were founded in 1871. This was also the period for the organization of major marine research stations. The first, established by the French at Concarneau in 1859, was rapidly followed by others: the Zoological Station at Naples, Italy, in 1872, the Marine Biological Laboratory at Plymouth, England, in 1884 and the Woods Hole Marine Biological laboratory in Massachusetts, USA, in 1886 (Yonge 1956). There must have been numerous more modest efforts as well. For instance, the University of Minnesota established a field station at Port Renfrew on the outer coast of Vancouver Island in 1901. Oberlin College (a small private school in Ohio) sent an excursion to Tatoosh Island on the outer coast of Washington State in June 1912. These latter two sites are not easily accessible even now. The heroics involved in transportation and other logistics in these earlier times must have been awesome. In addition, organism-centered debate appears to have been commonplace in scientific circles, e.g. the origin of coral reefs, the nature of life in the deep sea, the relationship between ontogeny and phylogeny and so forth. Such essentially marine issues commanded attention in both the scientific community and government circles, and public funding of marine stations and biologically centered expeditions followed. The German and British governments were especially involved (usually motivated by some economic incentive), and even R. F. Scott's ill-fated and badly planned attempt to reach the South Pole (1911–1914) resulted in a wealth of scientific data (e.g. Cherry-Garrard 1930). Hedgpeth (1957) describes classes in marine biology for "ladies and gentlemen" conducted in 1890. All the above imply that there was a lively awareness of and interest in the biology of marine organisms by at least 1850, and that it was expressed in governmental, scientific and lay circles. The marine natural history root aided by economic considerations gives every appearance of having been vigorous.

The second consequence of early familiarity with the coast — description of intertidal zonation patterns — was strictly academic in origin, motivated by individual curiosity, and is the oldest scientific marine interest barring systematics. Gilsén (1930) reviewed zonation as an important precursor to his subtidal research on the "epibiosis" of the Gullmar Fiord (Sweden). He began his history of marine "sociology", meaning the characteristics of a mixed species assemblage, with the contribution in 1812 of a countryman, Wallenberg. That work, credited with being the first on zonation, concentrated on algal patterns along the west coast of Norway, but remained hidden from general view until rediscovery in 1917. The period 1812 to 1925 produced numerous studies dominated by Scandinavian and French biologists,

most of which are descriptive with an emphasis on pattern. Few hints on the possible processes underlying pattern exist; there is a detectable influence of jargon in terms of association and collective properties. On the other hand, if one believes that comprehensive reviews catch the state of a subject, much changed within a decade. Fischer-Piette[1] (1940) in presenting his views on intertidal zonation analyzed sampling techniques, the role of interannual variation, and the consequences of interaction, and made a very clear statement (p. 401) that both physical and biological factors needed to be considered. A brief section even highlights the capability of field experiments to explore the causes of zonation. Thus zonation patterns attracted an attention which continues to the present. For instance, Stephenson and Stephenson (1972) devoted many years to descriptive studies seeking "universal" patterns of zonation. Lewis (1964) added detail and sought causes for the pattern. His emphasis on physical factors as the major consideration clearly reflected contemporary attitudes. Both books contain convincing summaries and photographs showing that the phenomenon is easily recognized at many places along the shores of all continents, although perhaps especially at mid and higher latitudes. Conspicuous boundaries offer a challenge for dynamical explanations, and the temptation has stimulated both "modern" experimental studies (Connell 1961a, b; Paine 1966, 1971a) and constructive discourses on experimental protocol (Underwood 1991).

Although marine studies contributed extensively to the development of quantitative methodologies, especially through the work of Hensen and Petersen, very little of this expertise was extended to rocky shorelines. Thus there were few if any extensively quantified rocky shore studies attempted from 1900–1950; few even exist today and most that do tend to be restricted to a limited set of species. Perhaps the best early example is Hewatt's (1935) 110×1 yard (ca. 100×0.9 m) transect across the intertidal zone at what is

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[1] Because Edouard Fischer-Piette (1899–1988) remains a little-appreciated persona, but interesting and important in any history of marine ecology, and because of (my) confusion or uncertainty concerning his name, I am appending this note. Supporting bibliographic materials published anonymously can be found in *J. Conch.* (1968; 107: 93) and *Bull. Soc. Zool. Fr.* (1990; 115: 5–7). He was born E. Fischer and published under that name until he decided in 1929 to honor his mother's family's distinguished record in paleontology and hyphenate her patronym to his name. His importance resides in his contributions to both malacology and ecology and, probably especially, his interaction with Harry Hatton, the author of, perhaps, the seminal field experimental study (Hatton 1938).

now the Hopkins Marine Station, Monterey, California. Others would be Shelford and Towler's (1925) description of rocky shore assemblages in Puget Sound, Washington State, and Oliver's (1923) in New Zealand. In contrast there were large numbers of soft sediment studies, in which assemblage characteristics such as species composition, size structure, biomass, and even spatial pattern were quantified (Thorson 1957). At least three reasons underlie the differences. One can sample unconsolidated sediments with coring devices and grabs with relative ease and such habitats provide a comforting illusion of relative homogeneity. Neither sampling ease nor apparent spatial homogeneity characterizes rocky shores. Second, marine soft sediments are relatively commonplace in comparison to rock-dominated habitats, which introduces an element of availability. And last, the sparse paleontological record of many rocky shore invertebrates, and the petroleum industry's interest in the sedimentary sources of oil, have favored sampling studies in marine muds and sands.

Although hard rock studies did not add much to the sampling root of ecology, they have been integral to the development of experimentation, largely because the obvious zonation patterns stimulated interest in their causes. All the early (pre-1940) marine experimental studies dealt with zonation and all such studies known to me were attempted on rocky shores. The earliest example I can find in which questions on ecological processes were posed and explored is the work of Sarah M. Baker (1909, 1910) who explicitly investigated "the causes of zonation". She worked at the Isle of Wight, and although her research was not a legitimate field experiment, neither was it a laboratory one. She deserves mention because of the nature of her approach, and her intent to explain on the basis of desiccation tolerance the orderly zonation of six species of brown algae on a gently sloping limestone shore. Her measurements suggested that tolerance characterized the higher species but not those growing lower down. An accompanying set of measures examined how desiccation influenced gamete maturation, release and attachment for four species — a truly pioneering attempt to relate the interplay between reproductive output and post-establishment performance. Interestingly, she also articulates a concept of trade-offs: species capable of rapid growth seemed more susceptible to the stresses of desiccation. Thus her focus was on understanding pattern and the physical correlates associated with it. She replicated her measures, employed three treatments per species in the 1909 study, and interpreted her results in the context of the natural distribution pattern. On the other hand, the work was comparative and without obvious controls, and involved no field manipulation.

All the subsequent and relatively infrequent studies prior to 1932 fall into two broad categories: (1) benthic algal growth as it related to zonation patterns, and (2) rocky surfaces, either of novel materials or denuded by scraping, as a means of examining succession. The following examples are provided not so much to illustrate early experiments (some are uncontrolled) but to suggest a gradually developing trajectory for rocky shore ecology.

Scraping natural rock surfaces is an easy and obvious way to investigate an assemblage. Although Dahl (1893) is reported to have done this (Hedgpeth 1957) I cannot identify this activity in the cited paper. However, Hariot (1909) denuded intertidal rocks in Brittany. That effort, done in parallel with observational studies on *Fucus* spp., suggested a rapid recovery towards *Fucus* domination initiated with a mat of ulvoids. By the 1920's, the sweeping influence of Clements' ideas on succession were directing the nature of marine ecology. Wilson (1925), employing both denuded natural and novel surfaces, investigated the "early phases of the successional development of the algal associations" near La Jolla, California. Pierron and Huang (1926) placed barren rocks at three intertidal sites in protected waters of Washington State, and observed their repopulation by animals. There is little of elegance in either of these studies, but they suggest an increasing willingness to investigate the causes of pattern in nature, and to quantify the results.

During this same interval there are examples of algal physiology being investigated in the field by controlled manipulation. Fallis (1915) appears to be the first. Her intent was to understand factors influencing the growth rate of a giant kelp, *Nereocystis luetkeana*. Her approach involved creative devices, numerous treatments, quantitation of results and even frond hole punching to measure growth. Another study (Klugh and Martin 1927) tested ideas on algal zonation by transplanting to different depths pieces of wood on which the algae were naturally growing. The focus was on growth rate evaluated as frond elongation, with the ecological consequences inferred. In North America, studies such as these never developed any intellectual momentum and no or little experimental research was done on recruitment issues, factors determining zonation or the consequences of interaction until well after the Second World War.

That was not true in Western Europe. Beginning in the 1920's, Fischer-Piette and the "preparateur" of the Saint-Servan Laboratory, H. Hatton, began a series of studies which are entirely "modern" in their intent and approach. The Hatton and Fischer-Piette (1932) study addressed two issues: factors influencing recruitment of the barnacles *Balanus balanoides* and *Chthamalus stellatus*, and factors setting upper and lower limits to their dis-

tribution. A companion piece (Hatton 1932) examined the recruitment of *Fucus vesiculosus* onto 25 cm^2 denuded surfaces. The culmination of this work (Hatton 1938) reported detailed observations and experiments on 2 barnacles, a limpet, 3 brown algae and concludes with a discussion of pairwise interactions between the majority of the species. If one were challenged to select a single study to mark the birth of marine field experimental ecology it would be this one. Although Hatton apparently never published again, his research was a prominent and acknowledged precursor to Connell's (1961a, b) incisive studies, and remains a tour de force in its own right.

If the Hatton-Connell line indicates the genesis of experimental studies on recruitment rates generally, and barnacles as especially suitable subjects for experimental study, another thread began to appear in Ireland. Renouf and Rees, working at Loch Ine, published (1932) an intriguing advertisement for research either in progress or planned. Their approach was highly experimental, centered around understanding distributional patterns, and motivated by a belief that "biotic factors play an important, and perhaps decisive part." As far as I can tell, none of this was ever published; J. A. Kitching, in numerous papers and reviews (1987), rarely alludes to it. However, it is unlikely that the research attitudes and beliefs were developed independently and in isolation. Renouf and Rees identify both growth rate and substratum angle as a determinant of competitively based outcomes, state their interest in recruitment phenomena, and specify spore buoyancy as a factor in algal colonization and distribution.

It had been recognized for some time in English-speaking nations that the large limpet *Patella vulgata* cleared paths through green algae (Orton 1914). When Eslick (1940) in a taxonomic work removed all limpets from 5 m^2 of surface at the Isle of Man, he observed changes (unpublished but later communicated to D. A. Jones) in the algal assemblage. Six years later Jones (1946) reported the consequences of another limpet removal at the Isle of Man, but this time with the specific intent of quantifying the algal response. Major changes occurred, as essentially all subsequent marine grazer removals have demonstrated. Jones' report triggered an outburst of related notes and papers: Conway (1946), Jones (1948), Lodge (1948) and Burrows and Lodge (1950). That these studies initiated a growth industry of sorts in marine plant-herbivore interactions is reflected in numerous reviews (Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Underwood 1991). It is these earlier studies, I believe, which ushered in the current era of marine community ecology. Just as Hatton (1938) combined measures of recruitment with novel, single-species adult manipulations (denuding rocks,

experimental increases of moisture, transplantation) to which Connell (1961a, b) added cages (and their controls) and a focus on predators, the plant-herbivore studies conclusively indicated the interactive linkage between trophic levels on rocky shores. In many senses these few studies form the foundation from which experimental ecology, and not just its marine morph, has expanded.

The mathematical root of ecology has a well-understood progression from Malthus and his precursors to Verhulst and eventually to Lotka and Volterra. The almost overwhelming detail and creativity of *Elements of Physical Biology* (Lotka 1925) shows little indication of having been influenced by marine experience except in the discussion of food chains. That could not be said for Volterra, and I have provided only minimal detail on how the apparently cyclical responses of marine fisheries stimulated his interest in biological phenomena.

There is a side-shoot (derivative) of this mathematization of ecological processes that almost certainly deserves much closer scrutiny. A Russian, trained as a geochemist, moved to Paris in the late 1920's, made contact with Volterra (Scudo and Ziegler 1976, Kingsland 1985) and developed an interest in biology. Vladimir Kostitzin subsequently published Lotka-Volterra models of atmospheric CO_2 concentration as mediated by plant and animal components, a model of symbiotic interactions, and eventually a book, *Mathematical Biology* (1939). The latter, if nothing more, is a testament to the power of marine systems to inspire and challenge. Kostitzin employs the anecdotal suggestion of cyclical relationships between starfish and mussels (Fauvel 1901), and the unquantified, completely descriptive studies of Fischer-Piette (1935) to bolster his mathematics. There is no suggestion that the interacting populations must cycle. However, the appearance that natural populations do fluctuate due to predator-prey interactions provided sufficient justification for the mathematical generalization. In addition, his book addresses such marine biological phenomena as hermit crab behavior and crab molting. Two of Kostitzin's interests, symbiotic or mutualistic effects, and organic inputs into global carbon cycles, remain current and important today.

III COMPETITIVE INTERACTIONS ON HARD SURFACES

Competition is the simultaneous use by two or more individuals or species of some resource in short supply. In a practical or analytical sense there should also be some consequence of the presumed interaction measurable at the individual or population level. That is, supposition or interpretation derived from observation might provide acceptable argument for some form of competition, but one which should also be supported by independent lines of evidence. Connell's (1980) "ghost of competition past" identifies the cautionary note: simply because two species differ does not necessarily imply that competitive processes led to the observed variations. In this chapter I examine the outcome of competition for a planar, two-dimensional resource, space, and develop further the view that whenever such a homogeneous resource is simultaneously occupied by two or more species, the causes of coexistence must be sought in factors extrinsic to the situation. Although it may seem unproductive to examine the simplest of ecological resources, the rich harvest of ideas and insights generated by experimenting with it should dispel that notion. Thus patterns of utilization and sharing of more complex resources — e.g. food, which is discontinuously distributed in space and will vary enormously from item to item in quality and availability — are highly unlikely to be simpler, though they may well be different.

The conceptual development of competition can be traced to antiquity. Qualitative notions of resource shortages and a struggle for existence predate Darwin who stated the consequences clearly, and experimental field studies had been completed early in this century (e.g. Tansley 1917). Placing the outcome of resource competition into an evolutionary perspective followed, eventually leading to Hardin's (1960) "competitive exclusion principle" and numerous views on niche diversification and evolved means of coexistence. Although now called Gause's hypothesis, the proposed inability of similar species to persist in stable coexistence appears to have been first clearly articulated in 1932 by the Argentine mammologist Angel Cabrera who wrote (as given by his rediscoverer Hedgpeth):

> In the same locality and same geological period, directly related animal forms always occupy different habitats or ecological stations. This leads the author to formulate the following law: related animal forms are ecologically incompatible, and their incompatibility is the more profound, the more directly related they are.   (1978, p. 54)

Quantitative ways of examining single or mixed populations had their genesis in human demographic studies. Hutchinson (1978) and especially Cole's (1957) lively historical sketch provide some details: for instance, human population censuses made in Biblical times, life insurance annuities sold in ancient Rome, and a 13th century report on how the Chinese registered vital statistics and tracked population trends all suggest a continued interest in population numbers (probably primarily for tax revenue generation). In 1588 an Italian, Giovanni Botero, two centuries before Malthus, enunciated the principles of a human capacity for geometric growth and a finite environmental carrying capacity. Malthus (1798) catalyzed a growing interest and concern for human population numbers, and mathematical elaboration followed (Verhulst 1838, Pearl and Reed 1920). The notion of a "competition coefficient", which describes the per capita influence of one species on the growth rate of another, was inspired by Volterra's work (Hutchinson 1978) and placed into an experimental context by Gause (1934, 1935). Gause's research may well have been, and might well still provide, the best example of ecological experimentation motivated by theory. Gause chose a vehicle appropriately matched to many of the mathematical assumptions (e.g. individual equality, minimal time lags, numerous generations within the experimental time frame), controlled for potential changes in the bacterial food resource, independently evaluated both intra- and interspecific effects on the rate of growth (r) and carrying capacity (K), and replicated, though without statistical evaluation, these experiments. He clearly understood the interplay between theory and experimentation, and his research underlay much of the subsequent development of such ideas as niche diversification, width, or breadth, resource allocation and coexistence, and when numerous species were involved, limiting similarity. Equally, much of his work concentrated on two fundamental aspects of competition: demonstrating that the resource was in short supply, i.e. was potentially limiting; and providing a protocol which allowed the density-dependent effects of intraspecific competition to be isolated from and evaluated in the context of multi-species interactions.

Gause's demonstration that competition in test tubes between yeasts or between protozoans could be quantified established the reality of competition as a natural force. The compartmentalization into the experimentally difficult components of intra- and interspecific influences was soon forgotten and ecologists began to develop strictly inferential approaches to evaluating competitive interactions. One ultimate consequence has been an ecological war (Simberloff 1982, 1983, Roughgarden 1983) which arose from

both philosophical and tactical differences. The battle was essentially over the reliability of inferences drawn from sometimes quantified observations: did these portray or even suggest the outcomes of competitive interactions? I believe it instructive that roughly half of Simberloff's examples of experimental study of competition in nature are drawn from marine environments. Rock surfaces provide ideal though perhaps not typical situations in which to identify how process produces pattern.

(1) Kinds of Competition

Competition can obviously be con- or hetero-specific, and the process has not escaped compilation and analysis by reviewers (e.g. Miller 1967, Colwell and Fuentes 1975, Connell 1983, Schoener 1983, Branch 1984, Underwood 1990). Although Schoener (1983) discusses six basic kinds of heterospecific competition, these seem reducible to two traditional and fundamentally different categories. *Exploitation competition* occurs when the probability of encounter with the limiting resource is reduced by the presence of one or more other species. Hallmarks are that the resources are undefendable and both the competitors and resources tend to be mobile. *Interference competition* involves mechanisms by which access is denied through direct contact or spatially restricted influence. All examples which follow, as might be anticipated from studies on essentially planar surfaces, are of the latter type. My intent is to develop a line of argument about one context within which competition can be studied. That is, organisms obviously compete for resources. That presented no difficulties to Malthus at the intraspecific level, nor for Darwin and the others inspired by that observation. The early experimental study by Tansley and Adamson (1925) on plant competition retains its luster especially when the problems of design and execution are forgiven. Most studies of competition, either observational or experimental, have treated the external environment and its potential physical and biological influences as a given. The question seems to have been, "What can be learned about competitive processes in the real world?" For instance, Connell's (1983) review expressly excludes "exclosure" experiments in which predation as a factor might be considered. Buss (1986) takes much the same tack, following Miller (1967), and argues that the outcome of interspecific competitive conflicts are best studied and understood in the

context of a real world situation. I believe that these views, in a way which seems so defendable on the basis of being natural, deny often acknowledged influences of predators, parasites, disease and disturbance. The natural world is filled with uncertainty. A clearer vision of an unfettered competitive outcome is gained when such external factors are reduced in influence. One example, among many, is Park's (1948) demonstration that the competitive abilities of *Tribolium confusum* are influenced by the presence of a sporozoan. *T. confusum* defeats its congener *T. castaneum* in the presence of the parasite under specified environmental conditions yet loses in its absence. Park was correct in eliminating the parasite and its confounding influence and thereby reducing his study to an examination of the intrinsic abilities of two similar species.

It is unlikely that such detail (or precision) will ever be available for manipulative studies conducted under natural conditions. However, the almost universal tendency, involving numerous authors, disparate places and various phyla for "total exclusions", whatever the treatments might be, to approach single species domination of the resource in question suggests that spatially homogeneous resources are unlikely to be shared and that some single species will eventually prevail in the contest. A corollary of this viewpoint is that inferences made about innate competitive ability, when the study has been conducted without attention to or attempts to control the numerous extraneous influences, will generate erroneous conclusions. It is like betting on the outcome of a race between a lame, elderly horse and a potentially superior thoroughbred, yet one burdened with an invisible handicap reducing the assurance of victory to some greatly lower probability. Depending on the severity of the handicap, the older horse might predictably win. Thus the clearest view of intrinsic competitive abilities should come when neither of the contestants is burdened with conditions reducing its abilities to acquire resources at the expense of other species.

(2) General Statement of the Problem

Most rocky shores, beginning especially at mid-shore levels and extending lower, teem with life. The organisms may be sessile or mobile, clonal or unitary, prey or predator, or range in mass over many orders of magnitude. Perhaps the most impressive attribute is that most of the space is occupied by something living; their polyphyletic nature and spatial continuity essentially

guarantees that the process of interspecific competition is unabated. Examination of overgrowth patterns at interspecific boundaries, changes in species abundance patterns through time, and little available free space (e.g. 5%, Dayton 1971) or estimates of >100% cover in point sampling (e.g. Russ 1980) suggest that the spatial resource is typically in short supply. What was naively called primary or free space (Paine 1966, Dayton 1971) was a misleading convenience implying that space potentially invadable by barnacles or mussels existed. The term ignored the fact that such space could be dominated by a veneer of crustose coralline or other low profile algae, or even if appearing superficially barren, was almost certainly occupied by a species-rich assemblage of bacteria, diatoms and even cyanobacteria, as convincingly illustrated in the scanning electron micrographs collated by Sieburth (1975). One must assume that most rock (and organic) surfaces contain living material and that these resident, microscopic species are not benefited from being overgrown under most circumstances (but see Sebens 1986a). Competition should be characteristic and continuous; the descriptive problem is how to evaluate it.

Buss (1980, 1986) suggests that body size of clonal organisms, measured as thallus or colony thickness, is a useful measure. I agree, and would extend the reasoning to unitary species as well. Small barnacles, e.g. *Chthamalus* spp., have a body dimension measured as a diameter of 2 to 4 mm. I believe it legitimate to discuss their competition for space with some sponges, crustose algae, and other organisms with bodies more or less equivalent in size (say varying by a range of 4× or less in critical dimension). Describing as competition the contests between these same barnacles and the holdfasts of large benthic algae or 10 cm adult mussels encroaching from the side is much less meaningful because of the inequitable nature of the contest. It was the lack of satisfactory description of the natural assemblages and their complexity as much as anything else which led to the view that, if a predator restricted the density and distribution of a competitively superior prey, resources would be made available and more species could thus coexist in an atmosphere of reduced competition. More species will coexist on the primary surface (Paine 1966, 1974) but is competition reduced? Almost certainly not, given saturation of the space by a variety of different taxa. The necessity for a distinction seems especially clear when dealing with benthic algae (and I am ignoring microalgae). One can roughly classify them as "canopy" and "understory" (e.g. Dayton 1973, 1975). They certainly compete for space (and light and nutrients) but the differences in eventual size and especially growth rate make the comparisons uninformative: larger

species, once established, generally will win. The examples of interspecific competition described below are either between species more or less equivalent in major body dimension or, when substantially dissimilar, for which the author considered the consequences of size inequality. The species need not be closely related since interphyletic and even interkingdom competition is commonplace on marine hard surfaces (Woodin and Jackson 1979). Furthermore, the fact that one species may come to dominate at the expense of others need not imply that interspecific competition has been eliminated at the site. It may still occur vigorously at different temporal, spatial and body size scales. Whether these invisible or unconsidered events influence or even can alter the outcome of the primary one remains an important unresolved issue.

(3) Competition for Space in the Presence of Consumers

When resources are fully or nearly saturated, one can assume inter- (and intra-) specific competition to exist. Resident species, probably in proportion to their relative abundances, suggest the existence of successful but necessary compromises driven by evolutionary trade-offs. Local survival will require some ability to fend off consumers which, in turn, could reduce innate competitive abilities. Thus, where individuals grow into contact, one can usually draw inferences about the possible outcome: an individual or colony may conspicuously overgrow another or the common boundary may appear static. Scoring these patterns and calling species "winners" or "losers", or stating that a "standoff" exists, has produced an extensive literature. The strengths of this approach, despite its purely observational basis, are the possibility of large sample sizes, the ability to include numbers of similar species in the analysis and the blatant nature of most interference competition. Fig. 1 suggests the ease of direct observation and the security of inferences relating competitive directionality and presumed outcome. Lang's (1973) field study on corals and the assumed direction and outcome of their interspecific interactions was one of the first. Others (Stebbing 1973; Osman 1977, Buss and Jackson 1979, Quinn 1982, Russ 1982, Sebens 1986a, b, Chornesky 1989, and many more) indicate the taxonomic and regional breadth of such endeavors. One question is common to all these
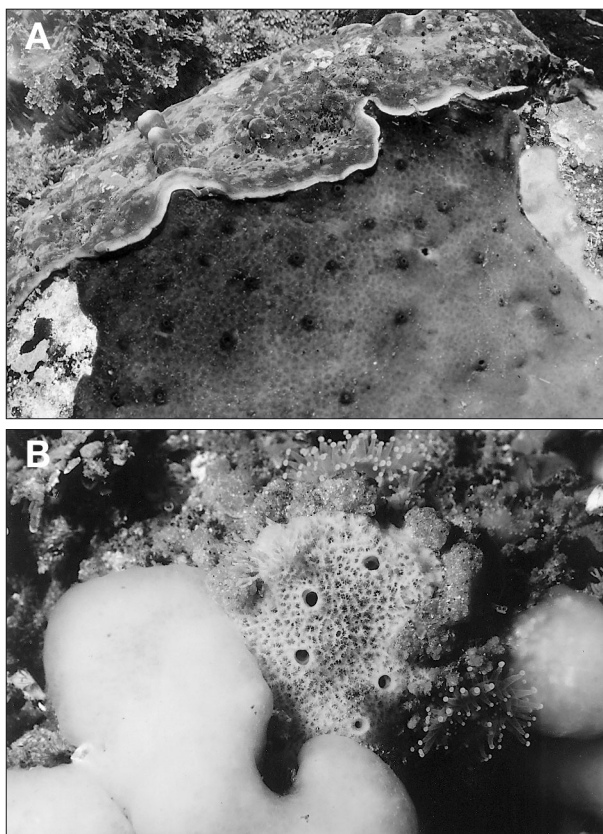
Fig. 1. (A) The encrusting coralline alga *Lithothamnion* sp. overgrowing an encrusting sponge. Port Elizabeth, South Africa. (B) A compound ascidian (*Cystodytes lobatus*) overgrowing an unidentified sponge which in turn is overgrowing other sessile benthos. Monterey Bay, California, USA; courtesy of D. R. Brumbaugh

studies: what insights can such observations provide into the processes underlying multispecies coexistence under natural conditions?

Quantitative assessment is aided by the intuitively attractive interpretation of ratios of wins:losses. High ratios suggest a potential for competitive dominance of the subordinate species. Numerous ways to expand such indices exist, and some ingenious ones have been developed by Sebens (1986b). Thus, in addition to discovering who wins or loses, it is useful to know how common the interaction is, whether potential interactors ever meet, seasonal variation in the results, and especially biologically significant quirks. Excessive losses in pair-wise comparisons indicate that the species is at risk. Species can then be linked together and evaluated as to whether the complex is generally transitive (A > B > C; A > C) or intransitive (A > B > C > A). The former condition implies potential single-species monopolization of the resource; the latter suggests high levels of uncer-

tainty, that in general all species could be maintained in the system, and therefore the persistence of continued coexistence and diversity. Intransitivity especially has caught the attention of theoreticians (Gilpen 1975) because of its capacity to promote coexistence and the promise of complex dynamics (e.g. limit cycle behavior).

The six examples chosen for scrutiny exemplify the great variation characteristic of observational studies. They present "nature" as it is, often as a snapshot in time, and usually draw inferences about the underlying mechanisms and their consequences. My intent is not to criticize the results, since data should be accepted as given and I usually have no familiarity with either the species or the research system. Rather, I present these now to provide a foil for the next section which asks, what happens in these or comparable competition systems if one intervenes by removing presumed consumers? The sample size in the next section, eleven papers, is purposefully larger because I believe the results for space-limited assemblages to be essentially uniform and generalizable, and to present an unanswerable challenge to a style of ecology based on observation alone. My intent is to suggest that even detailed observations on competitive relationships in the absence of experimentation fail to reveal the innate capacities of the species in question.

Example 1. Lang (1973) examined how coral species legislate space on tropical reefs. The competition is essentially three-dimensional because light for the corals' algal symbionts, nutrients from the water column, and space are all significant factors. However, 2-D photographs remain the method of choice for identifying and quantifying events before and after physical contact between two or more species. Thus I call this interaction competition for "space" while recognizing the inherent inaccuracies.

Lang discovered that competition was essentially hierarchical although with quirks. Successful competitors tended to dominate all lesser species. The mechanism — extracoelomic digestion by extruded filaments — was observable. Laboratory observations tended to confirm what was seen in the field: winners tended to constitute winners, and winners could digest at least two losing species simultaneously. Further, she identified a paradox which remains unresolved: competitively superior species constitute relatively minor components of the reef complex, although by employing aggression, they effectively limit overgrowth by more rapidly growing subordinate species. The robustness of her conclusions has withstood the tests of time. The pattern even seems general, for Connell (1976) has observed hierarchical competitive relations in unmanipulated Indo-Pacific reefs. However, it is not known how adding other and usually unrelated taxa, many of which

compete aggressively with corals for space, might influence these relationships. For instance, Sebens (1976) convincingly demonstrated with field experiments that an anemone was able to destroy or overgrow corals, Suchanek et al. (1983) showed that sponges can overgrow other scleractinians, and Sebens and Miles (1988) have added octocorals to the network.

Lang's seminal study remains convincing and also characteristic of work of this genre: the biological detail, often offered casually, suggests that the author really understands the basic structure of the system; there is almost no quantitation but a pattern is identified and discussed; the phenomenology is supported by appropriate photographs. Her student Chornesky (1989) has added detail but not necessarily clarification to the interaction within a complex assemblage.

Chornesky reports on a 20-month, primarily photographic study of a subset of the Caribbean species examined by Lang. Twenty-four pairwise interactions were followed: in 23 of these, no consistent patterns of overgrowth success against a contiguous competitor were identified. Rather the common boundaries oscillated in time. There were no apparent effects of season or other environmental factors. Instead, successful attacks by one species resulting in local death of a portion of the second would be eventually countered by responses of the second species employing other attack mechanisms. Chornesky reports cycles of alternating reciprocal injury with neither species gaining over substantial intervals (although 20 months is still but an instant in the potential lifetime of corals or, indeed, any clonal species). Her conclusions are reasonable: the arms race is neither to the swift nor vicious, but rather results in a standoff of sorts. The status quo amongst the set of species examined should persist until a novel procedure evolves, assuring competitive dominance at least in the short run. The message is that snapshot views may not (though they can) reveal the ultimate winner and that reversals should be anticipated. Thus the spatial and temporal scales of observation make an essential contribution to interpretation.

Example 2. Stebbing (1973) chose a system remarkably different in its traits: short-lived epibionts on the fronds of *Fucus serratus*, a brown alga. The epibionts are a polyphyletic assemblage of bryozoans, worms and a hydroid. The resource is again space, but a surface which is both temporary in persistence and growing. Seven species of epiphytes were studied; no manipulations were employed. The basic observation was "on what appeared to be occurring". Species could be touching, fusing, overgrowing, retreating or degenerating. Because growth in Bryozoa can be directional, an unprotected flank which is relatively easily overgrown is often exposed.

A case can be made for a weakly hierarchical arrangement of overgrowth abilities (3 species of essentially competitively equivalent bryozoan can overgrow a fourth bryozoan species, and all can overgrow *Spirorbis spirorbis*, a worm). Such an interpretation disguises three much more interesting findings. First, three bryozoans seem more or less equal competitively. When heterospecifics meet, Stebbing found little evidence for overgrowth. Rather in 100%, 90% and 95% of the pairwise interactions, growth stops or is simply redirected to where it is unimpeded. Second, intraspecific competition is also minimal in all 4 bryozoans. Again, growth simply stops or is redirected after initial contact with a conspecific. It is not known how the energy which could have gone to lateral growth is used — perhaps in reproduction. Last, the stoloniferous hydroid *Dynamena pumila* is also a member of the assemblage. Stolons creeping over the *Fucus serratus* surface are readily overgrown by Bryozoa. However, emergent erect portions bearing the feeding and reproductive hydroid polyps are little affected, and Stebbing concluded that the hydroid's substantially different morphology permitted it to avoid most direct competition and therefore coexist.

As in the Lang/Chornesky studies, the most typical competitive outcome is a stalemate with no single species capable of exercising superior ability. There are even legitimate doubts about whether such a species might exist within the assemblages as described because few predators were observed and other disturbances, however defined, seemed minimal. Rather, local abundance appears related to the intensity of larval recruitment, species-specific behavior or growth patterns.

Example 3. In a series of influential papers (Jackson and Buss 1975, Buss and Jackson 1979, Jackson 1979) the details of competitive encounters between invertebrates inhabiting the undersides of Caribbean corals were examined. Free space was found to be a rare commodity (1 to 5% maximum) and spatial competition intense. Coral colonies were collected and the direction of overgrowths in the cryptic assemblage tabulated. Few examples were discovered where growth had ceased along the margin of interspecific contact, and these data were ignored. Twenty species, primarily bryozoa and sponges, were evaluated. The intent was to identify and describe qualitatively the existence of competitive loops or intransitivities, and to discuss the implications of these for such phenomena as the probability of single-species resource monopolization and the development of coevolved relationships.

Although the interactions were recognized as a "snapshot" view, catching the relationship instantaneously, they were presented without the accompa-

nying numbers as results. The contact matrix is thus qualitative and not susceptible to statistical interpretation. (This may be a common pattern. Observation is both easy and easily biased by observer conviction or convenience. Sampling all such competitive events in an unbiased fashion and with sufficient frequency to include most relationships has proven to be a daunting, and unmet, challenge to biologists.)

Most of the pair-wise interactions were observed: for 20 species 190 interactions are possible and of these, 152 are represented. Fig. 2, taken from Buss and Jackson (1979), shows lots of competitive uncertainty. A tunicate wins most encounters followed by a coralline alga. Losers tend to be bryozoans. Although I find it unlikely on biological and especially morphological grounds that a coralline alga could dominate either sponges or ascidians, I accept their description. If that occurs, then loops appear in the contact matrix. Quinn (1982, p. 133) has noted that "their analysis can be arranged into an order such that in only 10 of 152 interactions do lower ranking species consistently overgrow higher ranking species." Further, if one subsamples their matrix drawing species at random, most of the resulting arrays are ordered hierarchically. Such a process might well be analogous to the haphazard recruitment thought to characterize smaller habitat areas.
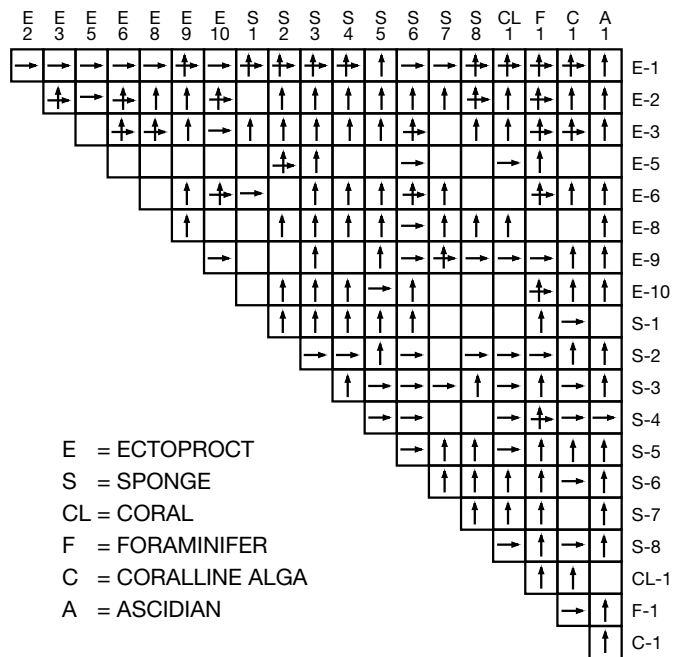
Fig. 2. The contact matrix of pair-wise competitive interactions between cryptic coral reef species. Arrows point in the direction of the presumed dominant in each species pair. (From Buss and Jackson 1979)

E = ECTOPROCT
S = SPONGE
CL = CORAL
F = FORAMINIFER
C = CORALLINE ALGA
A = ASCIDIAN

Buss and Jackson's studies highlighted both the uncertainty in the outcome of many pair-wise competitive encounters and the possible role that transitive relationships might play in how communities are structured. In particular "position effects", that is, species placement with respect to local topographic relief, and size differences between the competitors were emphasized. While such factors are certain to be important in all assemblages, they may attain special significance when Bryozoa comprise a substantial fraction of the community. As Jackson (1979), Quinn (1982) and others have noted, Bryozoa tend to grow directionally (rather than radially), in the process leaving a flank of older and often senescing zooids to be fouled or overgrown. Under such conditions age or angle of attack could well contribute to the observed competitive indeterminancy.

Example 4. Osman (1977) studied an epifaunal assemblage encrusting rock and other surfaces near Woods Hole, MA, USA, which was not taxonomically dissimilar to that examined by Stebbing (1973). Predators were assumed to play a minor role in the dynamics, allowing Osman to focus on a complex interplay between recruitment, competitive abilities, and the role of disturbance. Only one manipulative experiment was performed, although settling plates were used to measure the intensity, substrate size selectivity and patterns of larval recruitment. That manipulation, a temporally confounded exclusion (via cages) of possible benthic predators, suggested that consumers were unimportant as factors influencing distribution and abundance.

What was significant then? Space in these glacial outwash boulder fields is both limiting and discrete. Once an individual attaches and survives, success is determined by its ability to defend itself from lateral encroachment, grow, expand its domain and eventually reproduce. Although such a scenario may seem particularly characteristic of epibenthic clonal organisms, it describes well the challenges facing barnacles, mussels and other unitary species. One of Osman's conclusions, based on observation of both the settling plates and rock surfaces, was that "intraspecific competition has been greatly reduced in the epifaunal community being studied" (p. 44). It was also possible "to rank many of the species in a linear sequence of dominance based on their ability to overgrow or outcompete one another" (p. 45). Thus the compound ascidian *Botryllus schlosseri* never on average lost a competitive encounter with eight other species, and absolutely (100% of encounters) dominated four of them. *Spirorbis pagenstecheri* and a barnacle uniformly lost all observed encounters. Uncertainty of outcome, where it existed, characterized the higher ranked species, and was usually polarized

in the sense that in the determination of the top six competitors, ratios of wins to losses greater than 6:4 characterized two-thirds of the participants. There were no persistent reversals and hence no intransitivities apparent in this system. Solitary (unitary) species, in accord with Jackson's prediction (1979), were the losers in competition for space with clonal species.

Why then no spatial dominance? The answers are found in Osman's documentation of two presumably independent processes, disturbance and predation, both of which generate uncertainty. The boulder field, much like others (Sousa 1979a), is formed from rocks of variable size. Smaller rocks, albeit of similar attractiveness to settling larvae, are disrupted much more frequently than more massive ones. This size- or mass-dependent disruption produces opportunity. Superimposed on these spatially uncertain events are those generated by a complex of factors influencing the eventual concentration of potential larval recruits at a space in time. This is also highly variable; the combination yields a diverse mixture despite a convincingly linear competitive hierarchy, for winners do not necessarily find the spatial resource first, and may not persist long enough for competitive overgrowth and elimination to occur simultaneously at all sites and times.

Example 5. Kay and Keough (1981) examined the invasion and subsequent acquisition of space in artificially cleared patches on subtidal pilings. The work, in South Australia (35° S), envisions the assemblage as a mosaic of space-requiring species. Patches varying from 1 cm^2 to 1 m^2 form naturally and then are invaded by recruits from the plankton or encroached by lateral growth of the surrounding biota. Competition for space is intense and polyphyletic.

Kay and Keough made their own replicate patches, which were varied to purposefully include 4 seasons of formation, 3 sizes (100, 625, and 2500 cm^2), and a predetermined composition of the surrounding assemblage. Subsequent events were recorded by non-destructive photography, and standard techniques were employed to evaluate the competitive process. Particular attention was paid to establishing a sufficiently large sample of pair-wise interactions so that the contact matrix could be evaluated statistically both for wins and losses, but also for situations in which neither species wins and therefore the contestants are competitively equal. As they note, without such data it is difficult to distinguish transitive hierarchies from intransitive networks.

Most of their patches were reinvaded from the edges. Such a process is vegetative and need not involve larval recruitment: more than 75 % of the space was recovered in this fashion. And of course that process tends to pit

an established, adult organism against a recent settler bound to be physically smaller. Size differences strongly bias the eventual outcome. An effort was made to record all the potential 324 pair-wise interactions between the resident species. However, only 98 were observed and of these, only 40 occurred frequently enough to be analyzed statistically. Their results are thus restricted to a severely but understandably limited subset of the total.

Many of the species were essentially equivalent competitively. That and the holes (non-observations) in the contact matrix make conclusions based on the entire ensemble tentative. However, they found a taxonomic pattern which basically scales with major body dimension: tunicates overgrow sponges (five overgrowths, two ties) which overgrow bryozoans (eight overgrowths, three ties), and all overgrow worms. Thus there should be a general tendency towards patch domination by tunicates. That this does not occur is attributable to disturbance frequency relative to the organism's life span, and the low densities of tunicate larval recruitment. Local history at the physical scale of cm^2 plays a major role in the coexistence of this species-rich piling assemblage. Coupled with recruitment uncertainty, and variable and probably size-dependent competitive outcomes, these factors in combination produce high local diversity. Predation, though not examined, did not seem to be influential.

Example 6. Sebens (1986a, b) studied the patterns of space utilization, competitive processes and their outcomes, and resultant shifts in species' abundances on subtidal rock walls at Nahant (42° N), MA, USA. The assemblage is dominated by potentially long-lived clonal organisms and rock surfaces are inhabited by a rich mixture of plant and animal species. Most space was occupied with interspecific competition being apparent and often vigorous. Perhaps the best way to describe the assemblage, as Sebens does, is as a mosaic. Even at these small spatial scales (<1 m^2) "history" is important because one of the potentially dominant species both recruits poorly and is slow growing. Some species are locally ravaged by consumers, others grow, senesce, and then slough off. Sebens monitored the assemblage for about 3.5 years. Specific sites were photographed, the boundaries traced onto a map, the species identified and their areas digitized. Comparison of pairs of photographs, usually at a monthly interval, permitted gains and losses of area, and changes in the perimeter space common to competitors, to be analyzed.

Sebens recorded 2254 interactions. Of these 41% (934) were "standoffs" in the short term, with neither gains nor losses occurring in the 30 days between censuses, while the remaining 1320 interactions tended to be hierarchical. The best competitor was a colonial ascidian, *Aplidium pallidum*,

which had good overgrowth capabilities, resisted being overgrown, and lived for several years. Poorly ranked species in the hierarchy were those of low profile. They persist in the assemblage by two distinct mechanisms. Some can survive long periods under some superior competitor after having been overgrown. Others are typical ruderal or invasive species characterized by rapid recruitment and subsequent growth.

Sebens' studies are informative about the nature of competition for space for various reasons. First, despite the small spatial dimensions of the photographs (18×25 cm), each picture contained hundreds of discrete and identifiable individuals or colonies. When the abundance shifts are portrayed for 3.5 years, perhaps the most surprising aspect is that they are as invariant as they are. One possible dominant, *Alcyonium siderium*, remains essentially unchanged; another, *Aplidium pallidum*, seems to increase or decrease on a two-year cycle, a time frame appropriate to its natural dynamics. Increasing the spatial scale or number of replicate photographs would surely dampen the local fluctuations and increase the assemblage's stability, as measured by persistence and constancy in percent cover. Second, the photographs permitted indices relating immediately to a species' competitive ability to be calculated. Thus, in addition to the observed pattern of edge overlap (the traditional win:loss ratio; Jackson 1979), Sebens calculated how rapidly one species might be overgrown as a function of encounter rate, the competitive importance of a species in the assemblage (what portion of all area acquired could be accounted for by the activities of that single species), and even the ability to resist being overgrown.

Sebens (1986a) portrayed this assemblage as a mosaic of four alternative, locally stable states (sensu Sutherland 1974): large bodied *Metridium senile* or *Alcyonium siderium*, capable of protecting their juveniles from predation; *Aplidium pallidum* which can acquire space rapidly when sea urchin densities are low or reduced; and an urchin-dominated condition characterized by a pavement of coralline algae. What would transpire ecologically with the reduction of the host of consumers associated with these rock walls? Sebens alludes to both exclusion and addition experiments, especially of sea urchins, and concludes that they "...had little effect on those assemblages" (1986a, p. 365). However, he goes on to temper that opinion based on the results of parallel manipulations on horizontal surfaces usually dominated by erect fleshy algae. If these are shaded, and urchins are excluded by standard caging techniques, an invertebrate assemblage comparable to that on vertical walls develops. "These experiments provide evidence that at least some of the observed states of the community can, in fact, be interconverted

by manipulating only two factors, light and urchin density" (Sebens 1986a, p. 365).

However, some of the ordering of taxa by competitive ability may be an artifact of precisely which organisms were chosen for comparison. Because Sebens' papers include such extensive detail reanalysis is possible using different taxonomic choices. Table 2 is my interpretation of his Table 5, exposed sites only, in Sebens (1986b). There is little question that when all 11 taxa are compared, a competitive hierarchy exists. I have disaggregated this table, in the process omitting a sponge thought to be an epibiont (*Leucosolenia cancellata*) and an enigmatic, multispecific aggregation termed "complex". The large anemone *Metridium senile*, one of the potential alternative states identified in Sebens (1986a), is absent because, though locally present in low yet consistent abundance, it was not represented in the photographs used to quantify competitive outcomes. My subdivision is based on body size: larger, essentially three-dimensional species have been separated from the more nearly planar and smaller algae, bryozoans and worms.

Table 2 suggests that the apparent hierarchy in competitive abilities may simply be due to the competitive advantage generated by large body size or increased dimensionality. *Aplidium pallidum* overgrows the other 3 members of the larger species set, but these latter are characterized by standoffs amongst themselves. The smaller, more truly planar taxa provide minimal evidence for a hierarchy: the top two taxa (Bryozoa and *Spirorbis* spp.) are equivalent competitively, *Spirorbis* spp. were not observed to compete with two "lesser" ranked algae, and within the three animal taxa, two of the possible three interactions were judged to be standoffs. I believe Sebens' hierarchy to be the result of pooling species of substantially different body sizes since opponents of a given morphology seem generally fairly well matched.

Sebens' fine study highlights two problems of continuing importance. First, there is the arbitrary choice of what species to include. In this case the common denominator for all sizes was that they co-occur and share the need for a spatial resource. Second is the role of size itself. Large species generally must pass through a life history stage during which they will be equivalent in body dimension to those species destined to remain small. What happens during the period of equivalence? The answer is "lots", as clearly acknowledged by Sebens, with effects including preemptive exclusion, overgrowth and possibly even facilitation.

Table 2. The percent of non-standoff interactions won at exposed sites in Sebens (1986b). N signifies that no contacts occurred; S indicates that all contacts were judged to be standoffs

A. Larger taxa

		LOSER			
		Aplidium	*Alcyonium*	*Mogula*	*Dendrodoa*
WINNER	*Aplidium pallidum*	–	94	100	65
	Alcyonium siderium		–	S	S
	Mogula spp.			–	S
	Dendrodoa carnea				–

B. Smaller taxa

		LOSER				
		Bryozoa	*Spirorbis*	*Litho.*	Red crusts	*Phymat.*
WINNER	Bryozoa	–	50	N	100	100
	Spirorbis spp.		–	N	100	N
	Lithothamnion glaciale			–	S	100
	Red crusts				–	S
	Phymatolithon laevigatum					–

Summary. If these six examples can be taken as representative of their genre, few convincing patterns emerge. All share a common interest in whether naturally occurring interspecific competitions for space can be ordered as a hierarchy of winners and losers, or whether sufficient reversals (or loops or intransitivities) occur to prevent possible domination by a single species. This focus may well have been the product of intense interest in the 1950s and 60s in patterns of species diversity (Hutchinson 1959, Pianka 1966, MacArthur 1972). If nature is essentially hierarchical, unimpeded competition should reduce the capacity for species to coexist. Intransitivities, in proportion to their frequency, interaction rates and exact linkage patterns, should either slow or eliminate competitive exclusion, and thus work to enhance the prospects for coexistence.

The two most informative patterns which emerge are the high proportion of apparent short- or long-term standoffs and that intraspecific competition appears to have been minimized. The latter is intriguing since classical competition theory would predict the opposite in these species-rich assemblages. In most cases, the authors identified size as a significant factor influencing

and possibly even determining the eventual outcome. Early life history, e.g. immediately post-recruitment interactions, was also deemed important though basically unknown. Many of the multispecies interactions were roughly hierarchical although the high proportion of standoffs and reversals renders such decisions tentative. When assemblages are subdivided by taxon (Buss and Jackson 1979, by Quinn 1982) or by relative size (Sebens 1986b, in this chapter) the inferred pattern is altered. And, finally, most of the authors suggested that events extrinsic to the system, especially predation, disturbance, and the vagaries of larval recruitment, could play significant roles.

As articulated by Quinn (1982) the significance of departures from a strictly hierarchical organization is unclear. If a competitive dominant exists, that is a species capable of invading, resisting invasion and acquiring space at the expense of all others, some forces external to the system must constrain it. These are most likely disturbance or predation, otherwise competitive monopolization will occur independent of the number of reversals or intransitivities. Another way of phrasing this is that, to retard inexorable monopolization, a loop must involve the top local competitor. On the other hand, intransitivities can alter the dynamics and species abundance patterns. If size, age or position-dependent reversals involving the dominant occur occasionally, they will increase the persistence of transitional species and hence local diversity. Such speculations remain untested.

(4) Competition for Space when Predation has been Substantially Reduced

Numerous possibilities exist for enhancing the capacity of two or more species to coexist: the activities of other species and resource heterogeneity including refugia seem to be the most significant. Here I encapsulate the results of 11 experimental studies in which consumers were removed or had their numbers consistently reduced. Although I have made no effort to audit all such studies, neither do I believe there is any systematic bias, either historical or regional. The competition is for space: on artificial surfaces there is often little structural heterogeneity so its influence on potential coexistence is moot. Where the surfaces are natural, and hence variable, I simply

report the results since without exception no quantitative measures of structural or habitat heterogeneity are provided. I have made no attempt to balance the sample size of such studies with that of the previous section. It is vastly easier to make observations than to combine those with experimental manipulation. Hence most "competition" studies have been performed in the real world, in the presence of extrinsic agents like disturbance or predators and with little knowledge of whether the species under investigation have saturated their resources or not. In contrast, the authors discussed below have manipulated their study systems in various ways. No total predator removal is possible because means of excluding the "mesograzers" (Brawley and Fei 1987) and maybe especially micrograzers remain unknown, and therefore their influence has not been quantified. Despite this limitation, the consumer removal treatments uniformly differ dramatically from the controls, where the latter are unmanipulated portions of the natural world. I believe this tendency to be robust for space-limited studies and therefore the message to be important.

Example 1. Connell's (1961a, b) studies initiate this section because they provide a defendable starting point for the rebirth of experimental marine ecology, and it is experimental manipulation which has provided fundamental insights on how communities are organized. Connell's work in Scotland was planned as an examination of the population ecology of two barnacle species which compete for space. It was never intended to be a community study and therefore we are told little about the associated organisms, with the exception of the carnivorous snail *Thais lapillus*. For instance, starfish were common at his lowest level, disrupted at least one experimental treatment and, though effective barnacle predators, were not considered further. Because the results are couched in terms of barnacle density, percent survival, or numbers consumed, it is almost impossible to generate a feeling for the degree to which space, as the commodity being competed for, was available. However, the results are robust and generalizable to other, if not most other, rocky shores. Limpets do bulldoze barnacle cyprids and very recent metamorphs, in the process clearing space. When *Patella vulgata* (two per cage) were enclosed with recently settled barnacles, the barnacle mortality was 3.7% per day. In the limpet-less controls it was 1.6% per day (Connell 1961a). Limpet activity makes space available, even if only briefly. When *Chthamalus stellatus* is present, this smaller, flatter species is less susceptible to either bulldozing or predation (see also Dayton 1971, Paine 1981) for reasons which remain unknown, and therefore a species mix at small spatial scales is favored.

Connell (1961b) performed a two-factor experiment in which both predation and the intensity of interspecific competition were manipulated (his Table 7, showing as percent mortality of *Chthamalus stellatus* the consequences of excluding *Thais lapillus* and eliminating *Balanus balanoides*). No statistical analysis was given, but the results seem reasonable. Under all conditions crowding by *B. balanoides* accounts for about 50% of *C. stellatus* mortality. *Chthamalus* had slight influence on *B. balanoides* and also showed little evidence for consequential intraspecific competition (6 of 167 deaths, or 3.6%). The role of *T. lapillus* is argued to be "to lessen the interspecific competition" and therefore to enhance the possibility of coexistence. One message, though inferential, is very clear: the persistence of *C. stellatus* in the zone of overlap is abetted by two important factors extrinsic to the process of interspecific competition, because the competitive superiority of *B. balanoides* is diminished by size-selective predation and limpet bulldozing.

Example 2. I (Paine 1966, 1974) manually removed, beginning in 1963, the seastar *Pisaster ochraceus* from a 13.8 m^2 portion of a mid-intertidal rocky surface at Mukkaw Bay, Washington State, USA. An adjacent and contiguous 20.3 m^2 area served as the control: although the manipulation was unreplicated, its outcome has been repeated at another exposed site 10 km distant (Paine 1984). The original intent, motivated by a curiosity about how high species richness might be maintained on these shores, was to explore the role played by a conspicuous and abundant (1 to 5 m^{-2}) consumer. The initial exclusion lasted 5 years (the other has continued from 1970 to the present). At the termination of the 1963 removal, judged to have reduced *P. ochraceus* density by about 84% during winter but only 50% during a six-month "summer" interval when they were actively moving and feeding, the percent cover of *Mytilus californianus* had increased from 1% to 95% on the removal and remained essentially unchanged at between 2% and 5% on the control. There were concomitant shifts in species richness patterns when the more conspicuous and identifiable plant and animal species were compared. No other species were manipulated, and despite normal variation in the texture or rugosity of such natural substrata, mussels predominated.

Although the jargon term "keystone species" did not appear until Paine (1969a), it was the sweeping compositional change mentioned above which catalyzed its introduction. Since then I have preferred the term "critical species" to identify single species whose presence and activities are major determinants of community structure and organization.

The influence of *Pisaster ochraceus* is due to its preferential consumption of mussels, and the capacity for mussels, when unimpeded by predation or disturbance, to outcompete all other local species for the spatial resource. Mussels are thus a competitive dominant, though this ecological potential often is unrealized. That they provide a habitat for a rich array of other species (Suchanek 1979) is a different issue. Left undisturbed for a sufficient interval (which may be measured in years), mussels and mussels alone remain attached to the rock substratum. Perhaps the most significant aspect of this manipulation, putting the diversity issue aside, is that a single species exclusion produced a "monoculture" composed of the competitive dominant while the natural control retained its characteristic richness in pattern and species diversity. Wootton (1993, 1994 and as Example 11 below) has experimentally explored the direct and indirect roles of other species in influencing this particular outcome.

Example 3. If Connell (1961a) signals the rebirth of experimental marine ecology, Dayton's (1971) opus is the benchmark publication identifying the application of experimental manipulation to multispecies interactions. His study system was the assemblage characteristic of the marine shores of Washington State. Although the cast of characters is necessarily limited to but a small fraction of the species pool, his focus was free or available space and the factors making it available for occupancy. It is thus a description of multispecies interactions examined by experimental manipulation.

Dayton's study sites encompassed a broad range of wave exposures and were, without exception, higher on the shore than that described in Paine (1966, 1974). The most conspicuous space occupiers at these levels are barnacles; the major consumers are gastropods, as in Connell's studies. Limpets also can play a major role. I have chosen two sets of experiments among many to illustrate a general outcome. The data show that "free space" is usually limiting on exposed shores, varying from 7 to roughly 27%, but that it also is influenced by tidal height of the sampling and overall benignness of the site. More space exists in calm areas and higher on the shore suggesting the need for caution in interregional comparisons.

Dayton described as controls those sites with "access to all biological disturbers" and expressly contrasted them to events under total exclusion devices. In manipulations designed to identify the role of limpets, at three exposed sites and three tidal levels, barnacles dominated the total exclusions in contrast to the controls in which barnacles were minimally represented. The amount of space eventually occupied by barnacles is related to tidal height and relative exposure (his Figs. 7 to 9): in all cases there are signifi-

cant differences in percent cover between the real world and total exclusion treatments, and for the latter, there are always tendencies towards monospecific domination of the space. When this is not conspicuous, the data often (7 out of 9 times) indicate that the larger and more rapidly growing barnacle species would have excluded its competitors if the manipulation had been maintained for more than 8 months. In longer-term experiments (his Figs. 14 to 16) spatial dominants developed from initially low percent covers: at total exclusion sites mussels initially represented by 0% cover developed to between 30 and 100% representation. Although mussels were occupying secondary space, i.e. were growing over and attached to barnacles, they would have eventually killed the barnacles and established themselves on the primary surface. Similar manipulations at a protected site gave equivalent results, in that the large barnacle *Balanus* (now *Semibalanus*) *cariosus* rapidly attained dominance at all four tidal levels despite being essentially absent in the presence of its consumers.

Dayton's study, by focusing on the spatial resource and its occupancy under varying regimes of predation, demonstrated how space could serve as a common denominator to multispecies marine studies. Although the focus was not novel, being an expanded version of Hatton (1938) and Connell (1961a, b), the multispecies attitudes, emphasis on space as the ultimate limiting resource, and some of the manipulative procedures were. The study showed that predator removal alone could radically alter the biological assemblage inhabiting a rock surface, again indicating that extrinsic forces play important roles in organizing assemblages on space-limited surfaces. One byproduct of the manipulations was an unambiguous signal that competitive interactions between four common species were fundamentally hierarchical, with the largest individuals, mussels, being dominant, and the smallest, most slowly growing barnacle a consistent loser.

Example 4. A time-honored tradition continues to exist in marine ecology of either preparing natural surfaces or setting out artificial ones, and then simply waiting to see what happens next. The life history of fouling organisms, their natural reliance on exotic substrata patchily distributed in space and time, and their relatively brief life spans all predispose them for this style of work. Sutherland's (1974) paper embodied a critically important addition: he performed experimental manipulations in an effort to understand factors influencing the assemblages' eventual species composition.

The paper showed that interaction-dependent "multiple stable points" or alternative community states existed. Whether they were "stable", capable of self-maintenance, or were even truly alternative depends on one's choice of

definitions. What his study illustrated was that the fouling assemblage at Beaufort, NC, USA, could be manipulated into forming statistically distinct assemblages. The basic procedure involved suspending 232 cm^2 unglazed ceramic tiles 0.3 m below the water's surface. In one of a series of experiments, and the one germane here, four replicate tiles were surrounded by nylon fish net of ca. 6 mm mesh; controls (four) lacked the mesh but were otherwise identical. The manipulation lasted from April through December 1972.

Because those enclosed tiles were themselves designated as controls for other manipulations (dominant species removals inside the netting), the comparison is between "controls" inside and outside the netting. Sutherland was impressed by the "dramatic contrast". Inside, the tunicate *Styela plicata* occupied more than 75 % of the space from July to October, and usually more than 95 % of it. On the outside controls, *S. plicata* never occupied more than 5 % of the surface. Fig. 3 (overleaf) illustrates the resultant and divergent patterns of assemblage development. Sutherland's interpretation, with which I concur, is that given protection from some enemy, presumably grazing fish, small tunicates would survive to a size at which they were no longer attractive prey. A canopy of mixed hydroids and arborescent Bryozoa could also suffice for protection, as did the fish netting. I draw a further conclusion: tunicates, especially *S. plicata*, are the legitimate competitive dominants in this system. However, they need protection to demonstrate their superiority. Without it, competition for space still exists and other species come to dominate because, in the natural world, *S. plicata* is severely handicapped, an outcome most convincingly shown under conditions of reduced or eliminated fish predation.

Figs. 4 and 5 show better than words can describe the differences Sutherland observed. *Styela plicata* in the absence of its consumers invades surfaces characterized by a veneer of barnacles and the bryozoan *Schizoporella unicornis*. The reverse is not true, and therefore interspecific competitive interactions are strongly asymmetric. Another viewpoint is that observations and measurements on even artificially homogeneous surfaces are incapable, in the absence of manipulation, of revealing the true nature of *S. plicata*. Sutherland's experiments provided both that insight and a convincing argument for the importance of pre-emptive competition (fresh plates were submerged to measure recruitment during the above experimental interval). In particular, this work developed a plausible link to the mathematical ideas of alternative community states (Lewontin 1969).

Example 5. Menge (1976) explored several aspects of community organization along the shores of Maine and Massachusetts, USA, from 1972 to
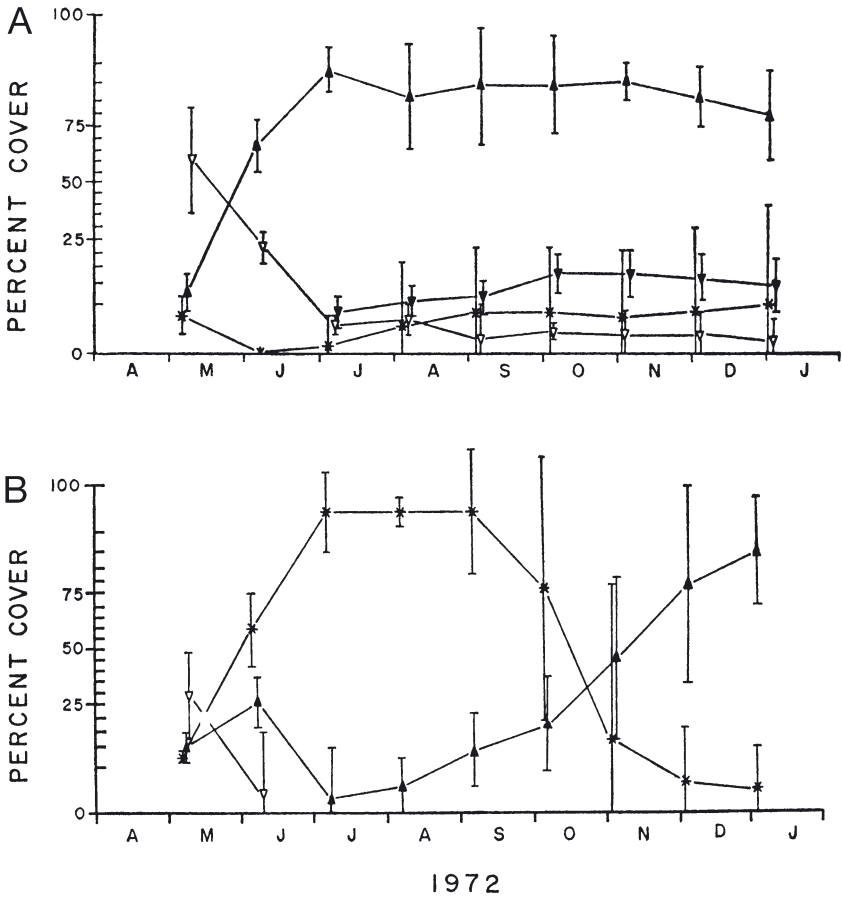
Fig. 3. Percent cover estimated photographically on replicate ceramic tiles suspended 0.3 m below water under docks at Beaufort, NC, USA. Error bars are 95% confidence intervals. (▲) *Schizoporella unicornis*; (▽) *Balanus* spp.; (∗) *Styela plicata*; (▼) *Hydroides dianthus*. Refer to Sutherland (1974) for additional detail. (A) Control series outside fish-exclosure net. (B) Control series inside net. (From Sutherland 1974)

Fig. 4. From the experiments reported in Sutherland (1974): development of the epifaunal assemblage outside the fish-exclusion net. The settling plates were unglazed ceramic tiles with a surface area of 232 cm^2 (6 inches on a side), suspended horizontally 0.3 m below low water. (A) Barnacles (*Balanus* spp.) dominate the surface on June 1, 1972. (B) Several weeks later (July 28) the surface is dominated by the bryozoan *Schizoporella unicornis*, a condition persisting through December. Courtesy of J. P. Sutherland

A
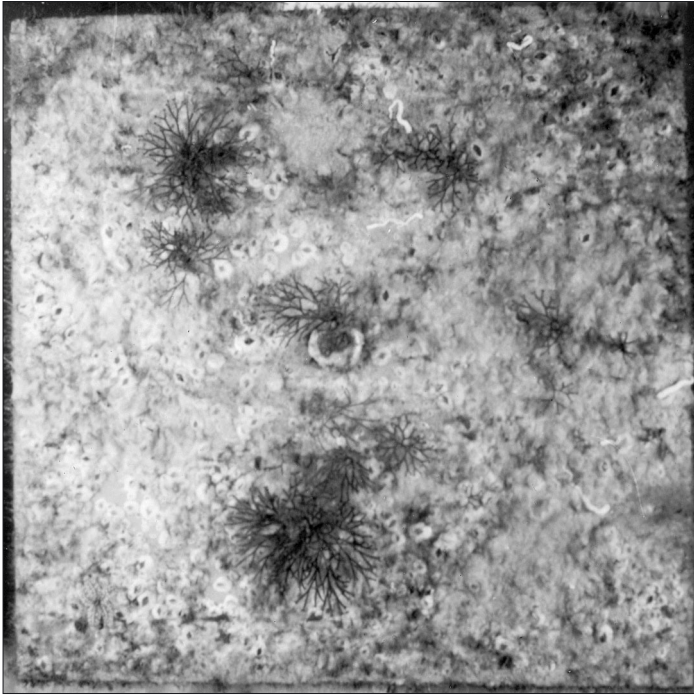
B

A
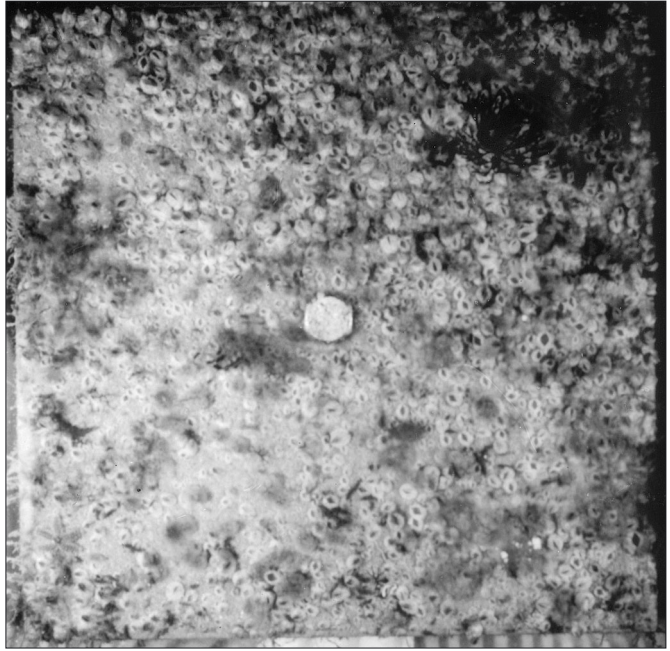
B
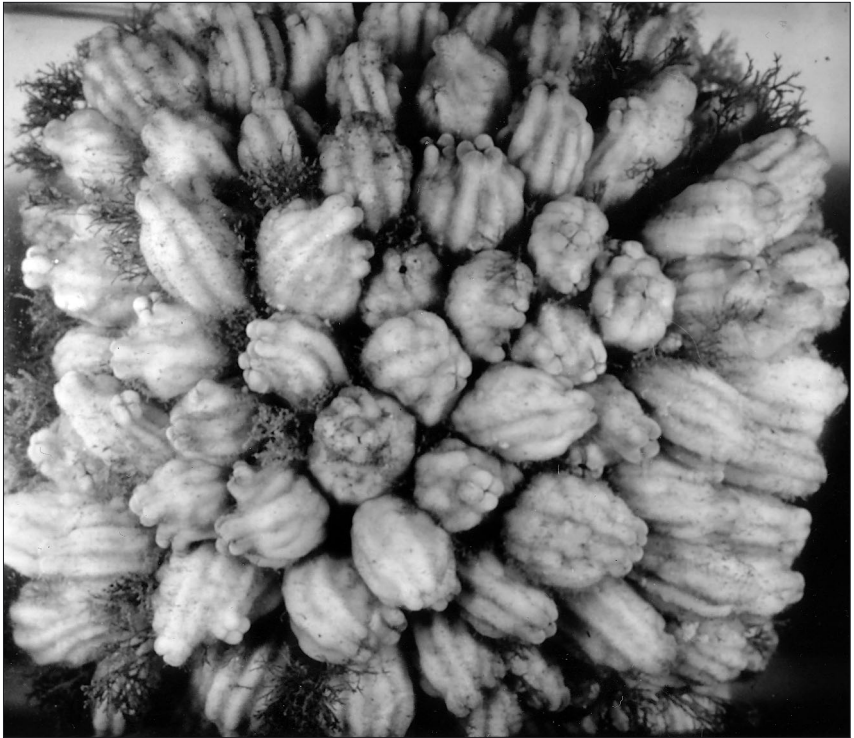
1975. His study sites were chosen to represent gradients in environmental rigor from exposed to protected. The high and mid-intertidal surfaces were inhabited by a species-poor assemblage characterized by one barnacle, a mussel and fucoid algae. The high zone at all sites tended to be inhabited by *Balanus balanoides*. At mid-intertidal levels, exposed sites were covered by mussels whereas protected ones had ample "free primary space", a lush algal canopy, relatively dense populations of invertebrate consumers, and few mussels.

Menge's observations and experiments suggest that ecological events in the barnacle zone, anywhere along the exposure gradient, are most easily interpreted as consequences of barnacle population dynamics, including regional variations in larval recruitment. An exception probably occurs near their lower limit where competition with mussels becomes important. The same generality does not characterize the mid-intertidal because *Mytilus edulis* covers about 80% of the primary space on exposed shores and is barely represented at Canoe Beach Cove, the most protected site. However, under predator (i.e. *Thais lapillus*) exclusion cages at all protected sites mussels increased to the detriment of barnacles, suggesting both that interspecific competition was involved and that all mid-intertidal sites regardless of exposure could be dominated by mussels. The level of dominance attained by mussels approximates that at exposed mid-intertidal shores at which predation is naturally reduced: 84% on vertical walls, and between about 70 and 95% on horizontal surfaces. I am tempted to argue that this comparability in fundamental patterns of space utilization which appears only after manipulation is convincing evidence that these New England shores, despite their apparent observationally based differences, represent two phases of the same basic assemblage rather than different communities associated with exposed and sheltered shorelines.

Example 6. Peterson (1979) examined the organization of an assemblage characteristic of wave-exposed jetties and more protected pilings in coastal New Jersey, USA. The major macroscopic species were sampled quantitatively along the exposure gradient, and free space was identified; experi-

Fig. 5. From the experiments reported in Sutherland (1974). (A) Development of the epifaunal assemblage inside the fish-exclosure net. The surface is dominated by barnacles, and the composition is statistically indistinguishable from that in Fig. 4A; May 17, 1972. (B) The *Styela plicata* "monoculture"; August 2, 1972. Courtesy of J. P. Sutherland

mental manipulation included both consumer inclusion and exclusion. As seems typical in almost all marine intertidal environments (e.g. Stephenson and Stephenson 1972), a band of barnacles (here *Balanus balanoides*) dominated the high intertidal zone. The mid and low zones, treated collectively, were more variable. At exposed sites, free space was scarce (<10%) and the blue mussel *Mytilus edulis* predominated in the natural absence of consumers. At the protected end of the inlet, on pilings, free space was plentiful during the summer (>40%), species richness was relatively high, mussels were uncommon and known mussel predators plentiful.

Peterson's manipulations were of three sorts: he excluded all larger mobile predators (2 crab species and a carnivorous gastropod) from access to the piling surface by encasing the latter in cylindrical cages composed of 6 mm mesh; cage controls included the mesh but were open at the bottom, permitting consumer access; and some pilings were encased completely with the usual complement of consumers except the blue crab *Callinectes sapidus*. Some of the results for the combined mid and low zones are shown in Table 3. The unmanipulated ocean and cage control bay pilings — representative of their portion of the real world — were conspicuously different in dominance patterns, resource availability and species richness and composition. The differences tended to disappear when predators were excluded from the protected site. In other words, the manipulation transformed the protected site to a condition reminiscent of the exposed one. And finally, the predator inclusions produced little difference between them and the total exclusion treatment, suggesting that the two included consumers were relatively unimportant, and conversely, that the highly significant assemblages differences were attributable to the effectiveness of blue crab as consumers

Table 3. Natural assemblage differences in the mid-low intertidal zone along an exposure gradient (ocean versus bay), and after a predator exclusion experiment at the latter. Values are percent coverage. (Modified from Peterson 1979)

Resource category	Ocean piling site	Bay piling site	
		Cage controls	Predator exclusion
Mytilus edulis	98.0	8.0	67.0
Balanus balanoides	0.5	6.0	15.0
Benthic algae	0	Not given	Not given
Free primary space	1.5	47.0	6.0

of mussels in calmer waters. Such patterns, familiar to European ecologists (Kitching et al. 1959, Seed 1969), have been minimally investigated on this side of the Atlantic.

Peterson's study, like many in this section, shows how one assemblage can be translated into another, quite different one through the simple expedient of single predator manipulations. That inference is derived from the differences in community composition between the cage controls and an inclusion treatment of two weakly interacting species. Comparison of the inclusion treatment to an unmanipulated (uncaged) control is less revealing because the roles of the weak interactors are masked by *Callinectes sapidus*. The most useful standard against which to judge species roles is the total exclusion treatment whenever, as here, a competitive dominant is revealed. Not only are strengths and consequences of interactions suggested but sites characterized by significantly different species compositions can be demonstrated to be but phases or alternative states of a common condition.

Example 7. Russ (1982) evaluated overgrowth patterns between 52 species on 30×20 cm sand-blasted bakelite panels suspended under a dock at Victoria, Australia. Immersion times ranged from 2 to 42 months, data were reported for the 15 most abundant encrusting species (but excluding an unknown number of consistent losers), and criteria were established for wins, losses and standoffs, called a "delay/tie". As seems typical in such studies, there is much uncertainty in the outcome of any particular pair-wise interaction despite the overall hierarchical nature of the rankings. For instance, when the colonial ascidean *Botrylloides nigrum* and the bryozoan *Celleporaria fusca* interact, the former wins 65/67ths of the time, indicating the presence of an occasional reversal, and 53 interactions were judged as delay/ties. Taking the relative sizes of the interacting species into account helps explain some of the pattern: regardless of identity, the larger individual always wins. In general, however, there remains a lot of uncertainty when the whole assemblage is examined. In an assemblage of 15 species there are 105 possible interactions: Russ observed 101 of these. Delay/ties occurred in 72 interactions and reversals in 34.

Russ found that relative size and growth rate generally determined the identity of a winner in an essentially hierarchical arrangement. The pattern would have been yet more convincing if born losers — barnacles, polychaetes, tubiculous amphipods and hydroids — had been included. There was no single competitive dominant although the ascidian *Distaplia virides* is a potential candidate: it invariably won competitive encounters when it was the larger of the pair although it lost to 5 other species when it was

smaller. In a fouling assemblage such as this one, winning seems to be strongly biased by priority, which in turn will be a function of propagule availability and at what season the panels are set into the environment.

The above is what one might expect to see in an epifaunal assemblage living on a surface exposed to whatever exigencies nature might provide. Russ (1980), however, also manipulated the assemblage in an effort to understand how the interplay between fish grazing and character of the substratum influences the epifauna. Bakelite panels were again used, only in this study panels were individually caged with galvanized mesh wire. Cage control panels had half the roof and one side removed, permitting easy access by fishes or other mobile grazers. Although two further treatments involving artificial arborescent Bryozoa were employed, I report here only events on the flat surface treatments. Percentage cover on the panels was estimated by a point sampling technique. Because when an encrusting species existed beneath a canopy species at a given point both were counted, estimates of >100 % were the rule. After 7 months immersion, the assemblages in the open and closed treatments were strikingly different: for colonial ascidians, coverages were 1 % (open) and 73 % (closed); for arborescent Bryozoa, 91 % and 37 %; for encrusting Bryozoa, 27 % and 6 %. Russ attributed a reduction in bryozoan cover, relative to panels immersed for only 4 months, to a developing competitive domination of the space by colonial ascidians due to their larger size and rapid growth. He made no attempt to distinguish the relative abilities of the two top competitors (the ascidians *Distaplia viridis* and *Botrylloides nigrum*) because interactions at their common boundaries always ended in standoffs.

Russ' work highlights the challenge of interpreting spatial competition. Both with and without the consumers, unquestionably fishes in this case, space is a limiting resource and competition for it is occurring. In the presence of fishes, diversity is high, and within taxa of comparable body dimension, much uncertainty in the outcome of competition exists. When fish are excluded, the competitive milieu changes, and previously handicapped dominants emerge and reduce diversity by excluding via overgrowth and subsequent smothering species of lesser stature.

Example 8. Keough (1984b) describes patterns of spatial occupation on the shells of a large bivalve, *Pinna bicolor*, living in the subtidal (ca. 7 m depth) of southern Australia. The bivalves, which protrude from the sand, represent a biologically active resource of moderate density (about 0.5 *P. bicolor* m^{-2}) patchily distributed in space. Because they are relatively long-lived (average age ca. 13 years), *P. bicolor* tend to be potentially predictable

in time. Keough's study, which lasted for 22 months, involved scoring the possible outcomes of competitive encounters between colonial tunicates (didemnids), sponges, Bryozoa and spirorbid worms.

One measure of the relative competitive ability of the epifauna was judged by evaluating changes in boundaries: if one species had covered 25 % of the surface of another, the former was judged the winner; if there had been little change in the previous 4 months, it was scored as a tie or standoff. Results suggest that most *Pinna bicolor* shells were characterized by Bryozoa occupying 23 to 37 % of the surface, with unused shell surface varying from 40 to 66 %. Clearly, on *P. bicolor*, space is not in short supply. However, the epifauna compete when they meet at a common boundary, and Keough provides a contact matrix showing the outcome of competitive interactions.

In addition, $60 \times 60 \times 30$ cm high mesh cages were placed over individual *Pinna bicolor* to exclude all predators, primarily gastropods, seastars and fishes, and the change in abundance recorded photographically as before. Table 4 suggests the direction of change: sponges were statistically equal in abundance at all times, under all treatments; bryozoa were heterogeneous in time, but tended to decrease in % cover during the terminal 7 months of predator exclusion; tunicates both recruited to *P. bicolor* and grew.

Keough's observations at competitive borders suggest tunicates to be superior to other epifauna on these bivalve shells. One interpretation is that, in a predator- or disturbance-free world, such as approximated by the cages, tunicates would dominate the space. In fact, in Keough and Butler (1983) further detail on this same assemblage suggests that if didemnid tunicates

Table 4. A reconstruction of Keough's (1984b) results. Controls which were uncaged are compared with complete predator exclusions. Data, by taxon, are given as % cover at the beginning and end of the manipulation

Category	August 1978	June 1980
Uncaged sponges	7	4
Caged sponges	1	1
Uncaged Bryozoa	24	37
Caged Bryozoa	13	17
Uncaged tunicates	3	0
Caged tunicates	7	15

recruit to *Pinna bicolor* valves, the number of associated resident species declines precipitously. If a didemnid dies, which many do seasonally, species richness increases. Juvenile fish are the only predators of "obvious importance"; their effect is "...to remove colonial tunicates and prevent these species from monopolizing *Pinna* shells" (p. 237).

Keough (1984b) favors an alternative view that variations in recruitment ability and intensity, rather than post-recruitment competition or predation, determine the species composition of spatially isolated, acceptable habitat. Such an evaluation discounts his own experimental results. Whatever the ultimate mechanism, it seems that low recruitment rates of tunicates and sponges to spatially fragmented and relatively small sites play an important role. Equally, once established, tunicates have the capacity to exclude other species or inhibit their settlement, and thus potentially could dominate the resource through superior competitive ability in the absence of their consumers.

Example 9. Perhaps all communities are complex but some are surely more complex than others as measured by the apparent richness of identifiable taxa. Menge et al. (1986) purposely chose to examine the diverse assemblage of consumers and their sessile prey in the Gulf of Panama. In almost every sense it was a heroic effort and remains unique to my knowledge as a preliminary attempt to disentangle the complex interactions on a tropical rocky intertidal shore, let alone anyplace else. Much of the study lasted for about three years. Four consumer groups were identified: slow-moving invertebrate predators, primarily gastropods; slow-moving invertebrate grazers, primarily limpets; small, fast-moving consumers, a heterogeneous group composed of small fishes and trophically-mixed crabs; and large-bodied, fast-moving fishes. Decisions about group assignment were based on how the species in question foraged [called "functional groups" to distinguish them from Root's (1967) concept of a guild in which resource commonality is emphasized]. Although the treatment extremes (all consumer groups present, all absent) were achieved, the design was not orthogonal because the influence of small fishes and crabs could not be experimentally isolated. For instance, it is possible to exclude all consumers and large consumers, but not small consumers while simultaneously permitting access to the resources by large consumers. As Menge et al. state, such problems have generally been ignored in experimental investigations of community organization.

In one sense, no novel generalities were discovered, and the skeptic could note that ecologists have long suspected complex dynamics to be character-

istic of complex systems. Thus it comes as no surprise that indirect effects are commonplace, that non-additivity is the rule (that is, there is little compensation for the role of removed consumer groups by those remaining), or that diffuse competition (MacArthur 1972) might exist. What is significant is that none of these details could have been guessed by observation alone. Lubchenco et al. (1984) had shown that space utilization patterns in unmanipulated plots changed little through time. Rock surfaces in the low zone tend to be dominated by brown, blue-green and red algal crusts. Usually more than 90% of the space was covered, and the patterns of species occupancy seemed both constant in time and characteristic of the region. Community structure, in contrast, changed dramatically in the experimental absence of consumers. Different treatments tended to have different effects, with the greatest effects attributable to situations in which slow-moving herbivores (a complex of 13 species) or large fishes (a 15 species complex) or both were excluded. In general, the greater the number of groups excluded, the greater the departure from the unmanipulated natural condition. In such circumstances, maximum differences should have been found in the total deletions, and they were. The bivalve *Chama echinata*, covering less than 2% on unmanipulated surfaces, accounted for approximately 50% of the primary space in the total exclusions. The tendency was convincing enough for Menge et al. to suggest that a bivalve dominated shore (including a mussel and oyster in addition to *C. echinata*) was "...likely to eventually replace the crustose algal monopoly..." (p. 254). Later, they identify *C. echinata* as the dominant competitor and imply that it is, somehow, controlled collectively by the consumer groups.

The messages I derive from the tropical research of Menge, Lubchenco and co-workers is that meeting successfully the intrinsic challenge of understanding even a modest fraction of how truly complex, species rich assemblages are organized will depend on the development of cleaner, more specific experimental procedures. However, and yet again, manipulation produced highly significant differences between treatments, with the real world state being barely recognizable in the species abundance patterns of the total exclusions. Solitary, not colonial or clonal species, tended to dominate, and within them a candidate for competitive dominant was identified. Perhaps most importantly, the authors suggest that the striking differences in composition between temperate and tropical rocky shore assemblages is due to differences in the rates and kinds of interactions, rather than the presence of novel relationships in the tropics, thus furthering the possibility of interregional generalizations.

Example 10. Robles (1987) has investigated how predation on mixed species of mussels influences the biological character of the upper levels of a sheltered shore in southern California. The natural assemblage appears as a coralline algal turf intermixed with a fucoid alga, *Pelvetia fastigiata*. Two barnacle species are conspicuously present, bare rock accounts for 18% or less of the space coverage (except at the highest tidal levels), and mussels are insignificant (0.3% cover). A minimum list of consumers includes whelks and shore crabs restricted to the intertidal, and highly mobile crabs, fishes, octopuses and spiny lobsters which advance and retreat with the tides. Robles' focus was on resolution of a biological paradox: measured high rates of mussel recruitment to the high algal turfs, no conspicuous mussel bed, and substantial transient populations of mobile consumers on the site at high water.

The experimental approach was standard though hardly easy. Large predators were excluded by the placement of 20 cm high by 35 cm long dome shaped cages covered with mesh. Other treatments included cage controls (open-ended arches) and open plots. Possible physical effects introduced by the cage treatments were monitored by examining the diversity and condition of benthic algae. Although baseline data were accumulated from 1981 to 1984, the primary experiment ran for only a year, beginning in November 1981, and was terminated because storm-generated swells damaged one of the replicates.

The cage mesh (2.5 cm square) permitted ready access to the experimental plots by small bodied consumers. Robles' observations on predators suggested that only spiny lobsters specialized on mussels; the remaining potential consumers tended to eat other kinds of prey. The experimental conditions generated striking changes in the mussel populations which can be attributed to effective restriction of lobster foraging. After the year during which the experiment remained balanced with all (3) replicates intact, *Mytilus* spp. coverage in the open and arch (cage control) plots remained at 0%. In the cages it had risen to 22%. Furthermore, the density of *M. edulis* had increased from 51 to 182 per 230 cm^2 census plot in comparisons of open and cage treatments, and mussels longer than 1 cm had increased from 4 individuals to 77. A single exclosure plot "followed an additional 6 mo developed nearly 100% primary cover of *Mytilus* spp." The principal lesson of this study is that even in mixed assemblages, with little available "free" resource and in which competition can be presumed to be intense, no dominant is recognizable until predators are excluded. Manipulation again reveals the existence of competitively dominant

monopolizers and a single consumer species capable of holding them in check.

Example 11. I terminate this collection of experimental papers with two by Wootton (1993, 1994), in part because they extend the theme of massive differences between experimental and control sites, in part because they reiterate the dominance of *Mytilus californianus* on western American exposed rocky shores, but primarily because they address how ecologists might analyze multispecies interactions. The latter problem is hardly new, having been wrestled with initially by Gause (1934), Vandermeer (1969), and Wilbur (1972), and more recently by Wilbur and Fauth (1990), amongst many. At the heart of the issue lie the problems of interaction additivity (can combined pair-wise studies account for the outcome of multispecies interactions?) and the prediction of the role indirect effects play in community dynamics and organization.

The 1993 paper first posed a traditional question: How would this portion of the rocky shore differ if the component species were hierarchically vs. intransitively arranged in competitive hierarchies? Wootton then proceeded to add two new elements to this problem: the role of competitor body size and sufficient time for successional changes to occur under the stated experimental conditions. The study lasted for nearly five years, and was conducted on the outer coast of Washington State, on essentially the same shores explored by Paine (1966, 1974) and Dayton (1971). There are two major competitive protagonists, the mussel *Mytilus californianus* and goose barnacle *Pollicipes polymerus*, and two consumers, gulls and carnivorous gastropods. Treatments included controls (the real world), cages (29×34 cm vinyl covered wire letter baskets), gastropod removals, and both a mussel deletion and a large mussel addition. The presence or absence of gastropods exercised little or no influence on the rate of mussel domination. However, gull predation essentially accelerated the process by differentially removing *P. polymerus* (as illustrated in Fig. 6, overleaf), as did the addition of large mussels. Thus initial body size asymmetries and predation change the dynamics, successional pattern, and rates of disturbance to mussel beds, but not the ultimate, inexorable mussel domination.

This study provided some of the data for a more ambitious attempt to link the effects of various chains of interactions between mussels, barnacles, dog whelks (*Nucella* spp. here; formerly *Thais*, and birds, the last actually a three-species conglomeration. of which gulls are the most significant. A small starfish (*Leptasterias hexactis*) attaining abundances of 100's m^{-2} in the mussel bed was included. Wootton (1994) applied the statistical tech-

nique of path analysis for assessing the known or suspected interspecific relationships. Because the procedure requires *a priori* hypotheses, it can be used to predict the consequences of chains of interactions, and to suggest which among several alternatives is most likely correct. As such, as noted by Wootton, it depends on accurate knowledge of or superior investigator intuition about the relative importance of species. Omitting a major player or a strong interactor could lead to spurious conclusions. However, even a 10-
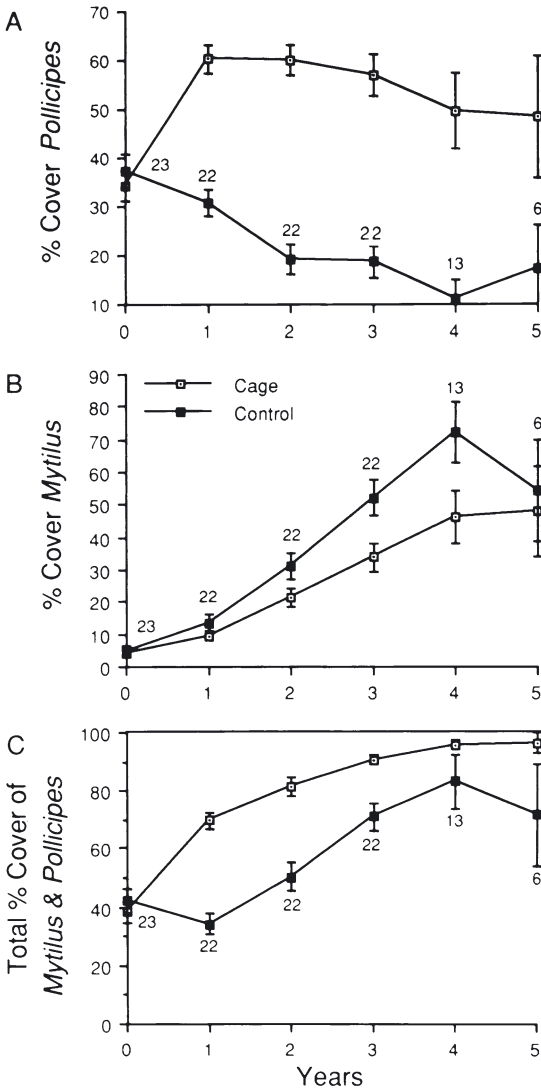

Fig. 6. Changes in percent cover over time of (A) the goose barnacle *Pollicipes polymerus*, (B) the mussel *Mytilus californianus*, and (C) their combined space utilization. Error bars represent 1 SE; sample sizes are indicated above or below the error bars. (From Wootton 1993)

species assemblage will have 45 possible pair-wise interactions; examining these experimentally with adequate replication is not only logistically difficult, but also has proven inconclusive as a means of determining the relative importance and even presence of indirect effects (e.g. Vandermeer 1969, when only four species were present). Wootton's suggested alternative to earlier brute force, multi-species examinations is path analysis. He showed experimentally that the presence of birds altered the abundances of mussels and goose barnacles, which in turn interact with an acorn barnacle. These are also eaten by two invertebrate predators. All are consumed by birds. A rich mix of known direct and inferred indirect effects are possible. Path analysis was used to generate three hypotheses about how the assemblage was organized. One was indicated as most likely to be correct. Eleven falsifiable predictions about possible directions of abundance change under various experimental treatments were then made. All were supported. New procedures must be found to evaluate how species interact in multispecies, multitrophic-level situations. Wootton's arguments favoring path analysis, at least for the time-being until something better is invented, are persuasive.

Summary. I cannot guess why the mania for experimental manipulation re-entered marine benthic ecology shortly after World War II, but it did with the limpet-bashing work of Jones (1948) and Burrows and Lodge (1950) (see p. 35 for an account of experiments prior to that date). These and Connell's 1961 papers were attempts to explain observable patterns by understanding the immediately underlying processes. Unlike observation-based studies, the majority of which attempted to explore how species coexisted (and hence had their inception in diversity issues), the manipulative studies rapidly evolved their own focus: community organization. Connell's work emphasized that properly controlled and replicated experiments could be done, and the subsequent ten studies reported here illustrate the often spectacular changes in assemblage structure attributable to consumer exclusion. The latter are summarized in Table 5 (overleaf). In every case, a species normally considered to be rare or uncommon attains or approaches domination of the primary space resource. In these studies little attention has been paid to the role of intraspecific competition, probably because the emphasis has been shifted from competition to predation. However, the near saturation of the spatial resource under all conditions, both in the initial, real-world or natural setting and after manipulation, attests to the ever-present possibility of competition. Competitive interactions are thus not diminished in the presence of consumers. Rather, their intensity or rate must change, and it seems likely

Table 5. Abundance of potential competitive dominants measured as percent cover of primary space, before and after caging out or manual removal of consumers from solid surfaces

Situation	Eventual dominant	% Cover Before	% Cover After	Duration of experiment	Source
Exposed rocky intertidal shore	Mussel	1	95	5 yr	Paine (1966)
Semi-protected rocky intertidal shore	Mussel	17	30–100	17 mo	Dayton (1971)
Fouling community	Tunicate	5	>75	9 mo	Sutherland (1974)
Protected rocky intertidal shore	Mussel	<1	70–95	19 mo	Menge (1976)
Fouling community	Mussel	7	67	13 mo	Peterson (1979)
Fouling community	Tunicates (2 spp.)	1	73	7 mo	Russ (1980)
Fouling community	Tunicates	7	15	22 mo	Keough (1984b)
Protected rocky intertidal shore	Clam	2	50	3 yr	Menge et al. (1986)
Protected rocky intertidal shore	Mussel	0 0	22 100	1 yr 1.5 yr	Robles (1987)
Exposed rocky intertidal shore	Mussel	1	46	5 yr	Wootton (1993)

that interspecific relationships attain greater importance in the presence of consumers, assumed to limit competitive dominants, than in their absence. This is because of an increased variety of contacts. As in the non-experimental studies, changes in the distribution of body sizes both within and between taxa are of major significance. Larger species tend to be able to overgrow ones of lesser stature in a "might is right" world (Paine 1977). Conversely, the former seem more susceptible to the destructive influences

of size-selective predation and/or disturbance. The tradeoff between stature and competitive vigor, as mediated by extrinsic forces, appears as the principal determinant of the structure of marine hard-surface assemblages.

In some sense the ecological significance of extrinsic factors was deduced by J. B. S. Haldane (1949, in Haldane 1985) who argued for the general importance of infectious disease as a necessary component of population control. He reasoned that predators, generally larger and with lower intrinsic rates of increase than their prey, could never limit prey growth. Other factors operating in a density-dependent manner were required. Disease and lack of food or space were his choices, and it is probably not coincidental that he wrote (p. 184), "Lack of space is certainly effective on dominant species such as forest trees or animals like *Mytilus*."

What else of conceptual substance did these manipulations produce? Certainly the notion of critical or keystone species (Paine 1969a) and verification that history- or interaction-dependent alternative states represented possible developments within a set of interacting species (Sutherland 1974) were two immediate outcomes. I am tempted to suggest that, because experimental procedures must be maintained for some time for trends to be expressed, longer-term studies began to replace "snapshot" overviews. Although long-term observations have merit in their own right, the manipulative studies testing hypotheses and focused on mechanism clarified a position that duration (or temporal scale) was an important consideration, as identified in the "press" experiments of Bender et al. (1984). Finally, the experiments have led progressively towards the development of increasingly powerful analytical methodologies. For example, the diagrams of Paine (1980), Dethier and Duggins (1984), and Dungan (1986) with their implied interactions are being superceded by techniques based on dynamics and especially sensitive to indirect effects (e.g. Wootton 1994). The latter is but an example of a necessary step, acknowledging that these assemblages are internally interactive, and characterized by complex multilevel relationships which themselves are subject to and generate change.

IV CONSTRUCTING COMMUNITIES FROM POPULATIONS

I begin this chapter by discussing how monocultures — unispecific occupation of a resource that arises in the absence of external disturbance — relate to models or other devices intended to stimulate hypothesis formation and testing, and by this route, facilitate a mechanistic interpretation of nature. Based on this relationship I nurture the view that an idealized, even unnatural, state can play a critical role in developing understanding of how the processes of disturbance and predation contribute to ecological patterns. These major subjects reduce in part to a set of components common to them all. Disturbance may disrupt assemblages sufficiently to both alter patch quality and introduce spatial pattern into otherwise monotonous environments. Predation by herbivores and carnivores generates an equivalent influence. Thus I consider ways of evaluating intrinsic patch quality and its consequences for reproductively competent, generally sessile inhabitants. In a patterned environment the patches are interconnected by dispersing propagules, usually larval stages. It is this collage of interactions, patch quality, individual performance and dispersal, all of which are minimally understood, which generates the next set of challenges to marine community ecologists. My intent is to forecast a future direction, one that might nurture and in turn be nourished by mathematical theory that copes satisfactorily with natural complexity, including especially spatial pattern and trophic dynamics, and thus might contribute meaningfully to that mechanistic understanding essential for preservation of our global biotic resources.

(1) Models and Monocultures

Models can be thought of as a scientific shorthand for ready communication of ideas and relationships. They vary greatly in their fundamental character, ranging from the analytical to the entirely descriptive; both kinds are capable of prediction. All must be incomplete if for no better reason than human understanding remains incomplete. As such they represent a simplification of the study system, guided by an intent to catch the essence of the situation.

Some may be simplified on purpose and therefore rendered even less "natural", for example the "neutral" models explored by Caswell (1976), as a means of evaluating whether the component(s) simplified (by assigning randomly chosen values) were important or not. Model utility is tied closely to a capacity to generate testable predictions, not to any innate naturalness, and can provide a baseline against which to evaluate departures. I give examples of both physical and biological models below, in part because I wish to avoid the accusation of "physics envy", but equally because I think ecology has much to gain from the power of a comparative approach in which one state may be partially imaginary yet relatively well understood.

The prime example of a physical model is Newton's (1642–1727) law of universal gravitation, postulating attraction between any two masses. Newton had taken the astronomer Kepler's laws, which essentially were phenomenologically based descriptions of planetary orbits, and added a mechanistic basis to their paths around the sun. Kepler in turn had relied on the meticulous observations and measurements of the Danish astronomer Tycho Brahe. Uranus, the seventh planet and minimally visible to the unaided eye, was discovered and named in 1781. However, the eighth planet Neptune is invisible and was discovered on the basis of unexplained wobbles in the orbit of Uranus. Newtonian mechanics predicted not only Neptune's distance, but also its celestial position and mass. As is often suggested, empiricists do the labor and theoreticians garner the glory. Gause (1934) employed the above chronicle in an expanded way:

> For the development of a theory it is particularly advantageous if experimental methods and observations do not at once furnish data possessing a great degree of accuracy and in this way enable us to ignore a number of secondary accompanying phenomena which make difficult the establishment of simple quantitative laws.
>
> (p. 42, quoting his countryman P. P. Lasaroff)

In other words, excessive detail can obscure dynamically based pattern. Later, in developing a tighter analogy to physical laws, Gause (p. 35) suggests that the now notorious logistic equation was a starting point only, "for the rational construction of a theory of the struggle for existence." Perhaps. My point is that it is the departure from expectations or model predictions which should guide further work. The history of observationally based community ecology is replete with failed and even misleading laws or quantitative models. If we are to derive lessons from the physicists' book, it is that cooperative interactions between experimentalists, theoreticians and those given to observation can stimulate understanding, and that data challenging

the prediction of some pet theory, or departures from some special state, are not to be viewed with fear and loathing but as an incentive to further research.

Another and conceptually different example of the value of prediction would be Mendeléyev's law or the periodic table. This mid 19th century model was entirely phenomenological, but based on the fact that elements display a periodic recurrence of properties, increasing approximately with atomic weight and number. The "law" predicted successfully the presence of the elements gallium and germanium, and challenged chemists to reexamine, and correct, the atomic weights of others. Mendeléyev himself believed that verifiable prediction was the hallmark of scientifically reliable natural laws.

It would be naive in the extreme to believe that ecologists could ever achieve the accuracy of the above dynamical or phenomenological predictions. That is not the point. Both the above models provided a basis for identifying a departure from the expected (Neptune) or holes in the logical structure of nature (periodic table). Thus they served as effective reference points. Competitively formed monocultures, in space limited systems, have the potential to fill much the same role. When they fail to exist, one should always ask what complex of events might prevent their formation. If they do exist, or can be developed through appropriate procedures, they provide a baseline against which departures might be measured, individual species influences calibrated, and so forth. The fact that they may not exist naturally should not detract from their utility. Frictionless planes do not exist; the Hardy-Weinberg equilibrium is a starting place for evaluating departures from the expected in population genetics.

Prediction in ecology

Can ecological models predict — defined as providing a verifiable prophesy of some unknown value or consequence? Most can't, don't and perhaps never will, and in this sense I agree with Peters (1991). However, it is important here to distinguish between quantitative models, whose outputs are a precise number or an arrangement of organisms at a particular time, and qualitative models that are more concerned with trends and directions of change. Thus quantitative forecasts embodying the detail required to resolve the controversy of whether niches are filled or not (e.g. Lawton 1982) or to state the exact identity and sequence of events following a successful ecological invasion seem unlikely at present. However, as Lehman (1986) dis-

cusses, prediction comes in a variety of flavors. That espoused by Peters (1986, 1991) is basically satisfied by regression equations giving mean values and their error terms. It acknowledges and even anticipates improved predictions as a consequence of a magnified data set and comfortably permits statements about values to be expected when the dependent variable's value is identified. Another kind of prediction exists, one characteristic of ecology's many qualitative models, and one to which Peters and others object. That is, if one state is known, it is often possible to forecast the direction of change following a perturbation (e.g. addition of a predator, extinction of some resident), and possibly even the magnitude of the change. Such predictions, clearly lacking the illusory rigor of the first style, are often rooted in understanding of some underlying process or mechanism. However, they accept as reality a dynamic and constantly changing natural world. As Lehman (1986, p. 1165) observes, "Static descriptions don't lend themselves to predictions about perturbations, or to the understanding they provide." The example of qualitative ecology which Peters (1991, p. 19) presents as a "simple theory to predict the density of racoons and other mammals" has broad confidence intervals spanning 2 to 3 orders of magnitude and would constitute what most ecologists still call a "ball park" or "order of magnitude" guesstimate.

Most of the approaches to coping with natural complexity discussed later are shamelessly qualitative. They purport to reflect some of the variation characteristic of nature, and by identifying processes possibly causal to this variation, to suggest why changes occur, or even whether they will. They lend themselves to the exploratory power of mathematical modeling. Although many are in their infancy, some have provided a basis for examining local shifts in biological pattern, thereby permitting novel insights into how pattern is driven by process.

Reference states and ecological experiments

For most ecologists, the "reference" state in their analyses is a control against which the results of a manipulation can be compared. The use of such controls is undeniably essential to statistical analysis but it does not represent a conceptually insightful baseline state, and is moreover often logically impaired. In particular, because the standard control is usually identified as unmanipulated nature, it has no *a priori* theoretical meaning that lends itself to comparison between systems and no hypothesized mecha-

nisms that produce it. In addition, such controls themselves are often extraordinarily variable because at the least they are intended to provide an unbiased representation of the natural variation characteristic of the study site and system. This time-honored procedure makes recognition of an experimentally caused effect just that much more difficult. By contrast, I am suggesting that use of reference states that arise from a coherent theoretical view, or are generated in the field by an experimental protocol, will enhance both comparison and understanding.

Chapter III discussed examples showing that a variety of assemblages inhabiting rocky shores, or at least solid, planar surfaces, could be simplified. In many cases, especially when the manipulation was carried out for a sufficient time interval and the investigator adequately tended the treatments, single species initiated and sometimes completed the process of usurping all the space. These monopolies or monocultures are formed by competitively superior species, and can serve as reference states (Paine 1984). Their ubiquity and some qualifications on application of this approach are discussed next.

Competitively formed monocultures

The dominance of hard surfaces by single species under marine conditions is common and plays a historically important role in marine biology because it provided the basis for the classification of shorelines into "universal" zonation patterns (Stephenson and Stephenson 1972). Monocultures can clearly be developed with experimental manipulations; Figs. 7 and 8 (overleaf) illustrate their polyphyletic nature under normal conditions. One consequence of competitive dominance is an enhanced susceptibility to disturbance. Gaps or patches are apparent in the otherwise continuous distribution of the tunicate *Pyura praeputialis* (Fig. 7A) and an annelid worm *Galeolaria caespitosa* (Fig. 8B). Such spatial variation in an otherwise monotonous landscape has numerous and important ecological implications. The domination can often be extensive and persistent, as is the case for *Mytilus californianus* (Fig. 7B). Indeed, the competitive mechanisms involved in both acquiring space and defending it from encroachment may be as varied as the species involved. I have suggested (Paine and Suchanek 1983) that spatial domination by both these *Mytilus* and *Pyura* species is in some measure a product of their assemblage of associated species through the actions of a complex and minimally understood multispecies facilitation. Fig. 8A illustrates both a
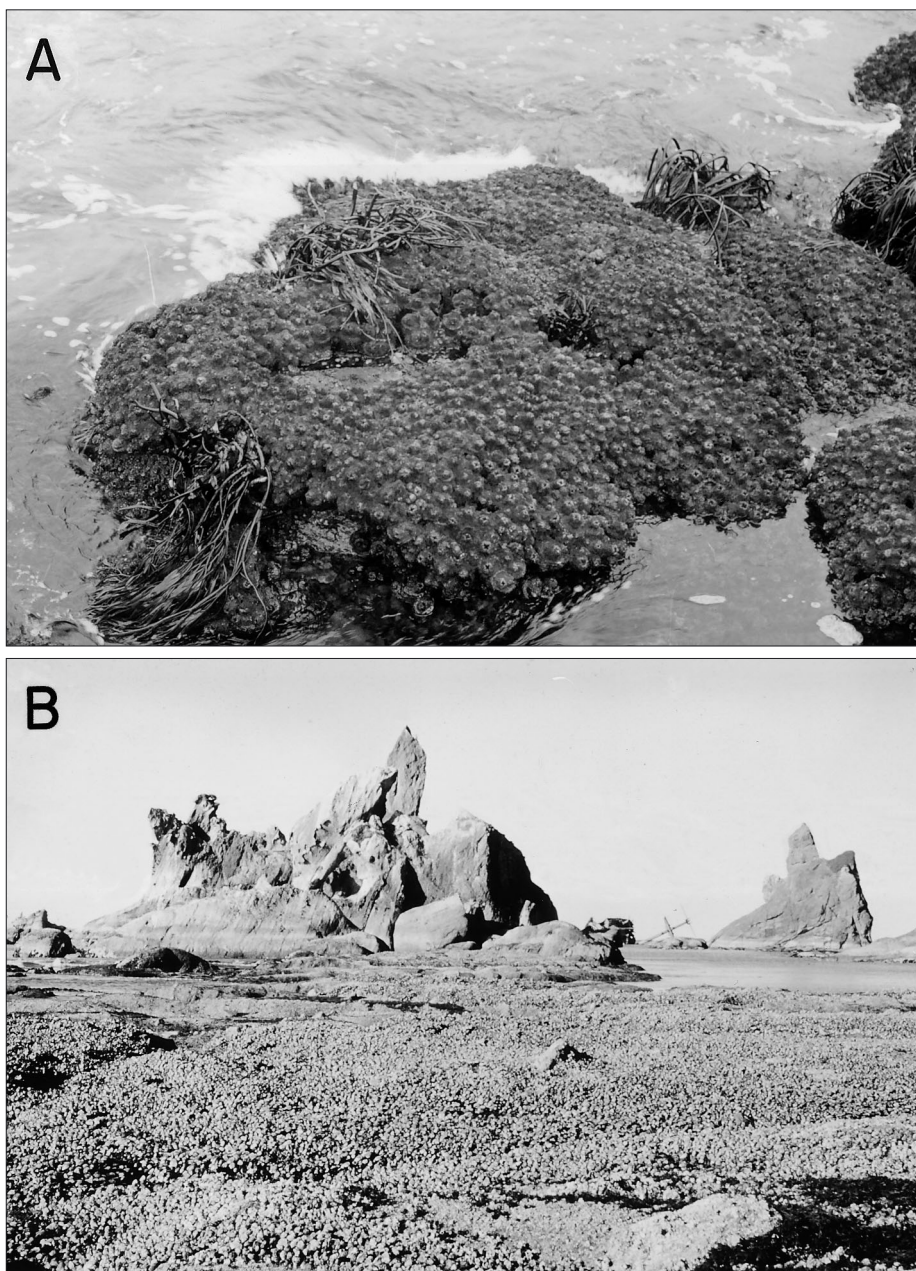
Fig. 7. (A) Nearly complete spatial monopolization by the tunicate *Pyura praeputialis* at the north side of the Bay of Antofagasta, Chile. A few gaps are visible. The alga is *Lessonia nigrescens*. (B) Extensive development of the mussel *Mytilus californianus* near Portage Head, Cape Flattery region, Washington, USA
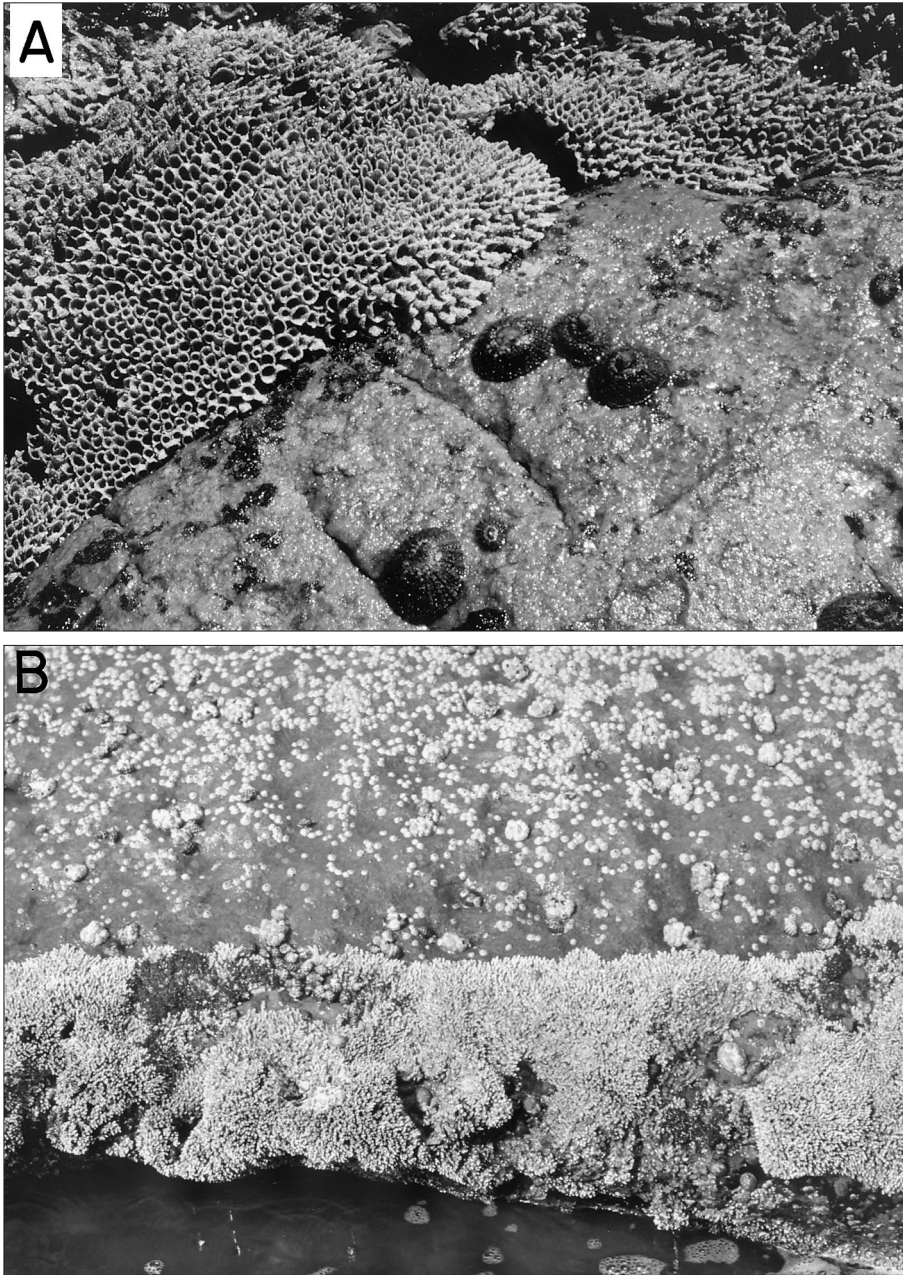
Fig. 8. (A) Tubes of the polychaete worm *Gunnarea capensis* growing onto rock surfaces required by patellid limpets. Cape Town, South Africa. (B) A band of another polychaete worm, *Galeolaria caespitosa*, on a vertical surface north of Sydney, Australia. Gaps in the distribution are obvious

more conventional competitive process and its polyphyletic nature, as the tubeworm *Gunnarea capensis* extends onto rock surfaces necessary for limpets, *Patella* sp., and in the process renders the habitat unsuitable.

A key question is what processes lead to spatial monopolies or monoculture formation. An answer relies on the efficacy of pre-emptive competition. If the space is small enough and the time interval short, a normally transitional species might be able to usurp the resource completely albeit briefly. Such ecologically interesting situations are too capricious to be of general utility as experimental reference states. Of greater significance, two states of the original intermediate disturbance hypothesis could be characterized as monocultures, as suggested by Paine and Vadas (1969) and Connell (1978) and as demonstrated by Lubchenco (1978). For a more complete discussion of the history of this idea, see Fox (1979). The extreme states should be composed of the competitive dominant in the absence of consumers and the most resistant species in their presence. Both would constitute "monocultures", but since the processes responsible for their formation are fundamentally different, I believe it essential that they be distinguished, if for no better reason than to expose the all-too-frequent mistake of equating abundance with competitive ability (see Dayton 1971 for discussion). The experiments summarized in Table 5, and many others, indicate why this decoupling is so necessary. I use the term monoculture in reference to resource domination by a single species characterized by superior interspecific competitive abilities. When interference competition is the prevalent mode, the resource is usually primary space.

Such monocultures exist as single-species stands only in the sense that the dominant has usurped the great majority of the primary spatial resource, and in the process, denied other species direct access. The dominant, by being larger-bodied, enhances the site's dimensionality and thus is often associated with a species-rich community. Surveys (e.g. Suchanek 1979) reflect and confirm this. When the intent is to understand ecological processes, the resource focus seems most appropriate; if the interest is in faunistics or diversity patterns, the entire assemblage should comprise the sample unit. Because what constitutes, or does not constitute, a monoculture is arbitrary, the resource being dominated should be identified as clearly as possible, as should the level of domination (e.g. is the most abundant species the dominant, or should dominance be defined by the amount of resource controlled by a single species?). The temporal scale is equally important since it is likely that early successional stages may be momentarily abundant, only to be eventually replaced by competitively superior ones. Such

detail is significant and no set criteria exist (Sutherland 1974, Connell and Sousa 1983, Paine et al. 1985). It is also reasonable to ask why monocultures seem characteristic of intertidal hard surfaces and especially those on exposed shores. At least three possibilities exist: harsh local physical conditions may limit occupancy to a few tolerant species (Connell 1975); violent wave action may constrain the activities of predators (Menge 1978); intense predation may generate an assemblage characterized by a predator-resistant life-form (Lubchenco 1978, Paine 1984).

I tend to use the terms spatial monopoly and monoculture interchangeably, although both have other possible interpretations. A monopoly could be absolute, with no other species admitted. Monoculture conjures up the image of cultivated single-species stands. Both terms suggest a community state essentially frozen in time until some uncontrollable and usually catastrophic event alters the condition, or until the dynamics of the situation are purposefully changed. Because the nature of the local assemblage is being manipulated and altered, even directed, it is important to distinguish between the above terms and Clements' (1905, 1916) concept of monoclimax and the related concept of succession. The resemblances are superficial: one involves sequences of species replacements or "natural" change in the presence of a rich complex of associated species; the other, my usage, depends on experimental alteration of crucially important interactions.

Because succession is a temporal trajectory in which variable processes (Connell and Slatyer 1977) generate pattern, it is impossible to side-step the influences of "Clementsian" thinking. One vastly oversimplified interpretation would be that pioneer species gradually are replaced by superior competitors, a process eventuating in a local climax in which further change was impossible. Climatic change could alter the outcome just as localized catastrophes could postpone or deflect the inevitable. Nonetheless, a monoclimax — a stable, self-replacing and seemingly permanent assemblage — in which successive competitively induced replacements power the process bears only superficial resemblances to what I term a competitively formed spatial monopoly, especially if one focuses on the dominant plant or sessile invertebrate species. First, there is little similarity, and certainly none if one considers the role that experimental manipulation plays, in the means used to identify why, how and under what circumstances one species replaces another. Even at its simplest, Clements' monoclimax was a complex and stable mixture of species, the culmination of a lengthy development. Second, spatial scale provides another difference. Most ecological experiments are done in limited dimensions — cm^2 or m^2 (Kareiva and Anderson 1988), not

at the landscape level envisioned by Clements. Third, Clements' 1916 magnum opus on *Plant Succession* ignores the roles of grazers: although their influence in terrestrial assemblages continues to be debated, there is little doubt about their role in structuring marine benthic systems. Finally, although these differences are sufficient to distinguish a monopoly from a monoclimax, others, probably due to Clements' sweeping vision about the nature of climax vegetation, exist. There is nothing "superorganismic" about a spatial monopoly, and as Chapter III shows, such a monopoly usually remains unexpressed in the absence of experimental intervention. Equally, a monopoly is hardly a whole, integrated stable flora (or fauna). It need not be formed by a linear process, and recent syntheses (Drury and Nisbet 1973, Horn 1975, Connell and Slatyer 1977), drawing on a wealth of objection developed during Clements' lifetime, identify numerous often antagonistic mechanisms. Finally, Clements remained an ardent believer in the inheritance of acquired morphological characteristics (Hagen 1992). That seems especially unlikely when species broadcast their gametes freely and settlement is to a spatially variable postlarval environment. Single species, at local spatial scales, can monopolize a spatial resource under specific conditions. They bear at best a superficial resemblance to the Clementsian monoclimax.

(2) Unifying Dynamics in Intertidal Communities

One perspective is that the holy grail of community ecology is the integration of the interaction of habitat structure and trophic dynamics as identified by Root (1973) and Kareiva (1987, 1990) with patch dynamic models such as those of Levin and Paine (1974) and Paine and Levin (1981). An alternative possibility is that the petty details of local patch dynamics might be irrelevant at sufficiently extensive spatial and temporal scales. A macroscopic approach is often justifiable and may well be unavoidable. It also tends to hide how individuals (or populations) contribute to natural variation, and it is the latter which has proven attractive to biologists like myself. Therefore, I have retained a focus on ecological studies involving small spatial scale though not necessarily brief duration.

Fig. 9 presents a static and planar version of this ultimate goal. The bounded areas could be patches, gaps, islands, even populations. The lines

connecting them represent exchange of individuals, which could be uni-
directional (as in source/sink relationships) or reciprocal if the interactions
were ecologically panmictic. I have attempted to superimpose on each patch
an indication of trophic structure with larger patches tending to support both
more numerous and more complex interactions. Such a diagram contains no
dynamics but they exist by implication. Exchange or dispersal is best identi-
fied as a rate (Okubo 1980), as would be the changes in patch (Paine and
Levin 1981) or population structure, as identified in metapopulation dynam-
ics (Harrison et al. 1988). If the bounded areas of Fig. 9 were islands, local
rates of invasion and extinction would be implied. As species enter, interact,
flourish or go extinct, the trophic structure will surely change, and with it the
relative abundances of the resident species (Hairston et al. 1960, Menge and
Sutherland 1976, 1987, Fretwell 1987, Abrams 1993). If artistically easy,
one could expand the horizontal scale to include the spatial limits of practi-
cal study. Perhaps only a single patch can be examined, a procedure blinding
the observer to a bigger universe. Conversely, more synthetic overviews
could lose track of significant local or small-scale events. A synthesis may
remain unlikely, even impossible, but the following sections attempt to iden-
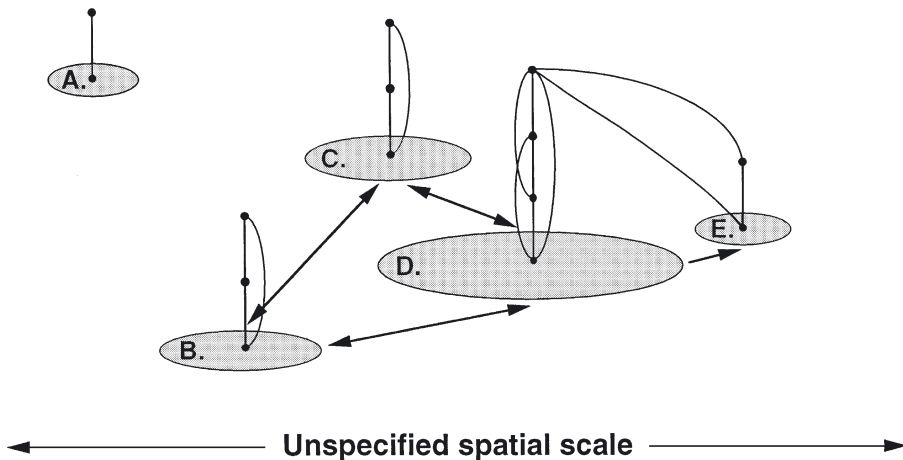

Unspecified spatial scale

Fig. 9. A patterned environment with trophic structure. Patches B, C and D exchange
individuals through dispersal (arrows): they form the core of a metapopulation. The
resident trophic structure (indicated wth points joined by lines or curves) is assumed
to vary with patch size. Patch E is a satellite of this core group, and is a sink as
suggested by the one-headed arrow. Patch A is too distant from the source group
(B, C, D), implying the restrictions that spatially limited dispersal imposes on meta-
populations or gap dynamic models. Graphics by A. Sun

tify the basic importance, reality and interdependence of: (1) habitat patterning, as generated by disturbance; (2) life history events focused on within-patch dynamics, as well as dispersal which counters local extinction, drives much of the successional interactions and generally is scale-dependent; and (3) predation, a process whose influence will vary with local density and the general composition of the assemblage of both prey species and consumers.

Disturbance

All assemblages are subject to alteration of the standing stock number or mass, and although conventions have evolved over the years, I continue to prefer and use here a distinction employed by Dayton (1971) and endorsed by Sousa (1985). Biological disturbance is attributable to the actions of other organisms: predation is probably the most usual but bulldozing, exfoliation following senescence, and whip-lashing all produce spatially localized injury or mortality. Physical disturbance is generated by such inorganic environmental factors as log-bashing, wave action, sand scour or climatic events exceeding the morphological or physiological tolerance limits of the organisms in question. It may be estimated as diminished productivity (Grime 1977). Some authors have combined the two (Grime 1977, Dethier 1984), since both physical and biological processes can cause mortality, alter distribution, and influence productivity as, for instance, when extreme temperatures or partial predation reduces individual growth and subsequent reproductive output. Disturbance manifested as a reduction in efficiency remains particularly difficult to identify. Both sorts of disturbance are also capable of leaving long-lasting or transitory imprints on the assemblage, especially as they influence spatial pattern. Perhaps the strongest argument for retaining the distinction is how natural selection might be expected to act. Physical disturbance is certain to be more general and less targeted, suggesting that selective but specific responses to different stresses are unlikely. When biological forces are involved, leading to reactions like induced defenses (Gilbert 1966, Harvell 1984), the resultant pattern will be individualistic and increased spatially or temporally localized variation should be apparent.
    Fig. 10 illustrates the type of pattern under discussion here. In general the patches are larger than a single barnacle, mussel or benthic alga; although pattern surely is present and identifiable at these reduced spatial scales, I know of no attempts to quantify it, and benthic ecologists tend to treat it as predation rather than disturbance. These patches (Fig. 10) all have recogniz-

B.

C.

A.

D.

G.

**Competitively
formed monoculture**

**Single resistant
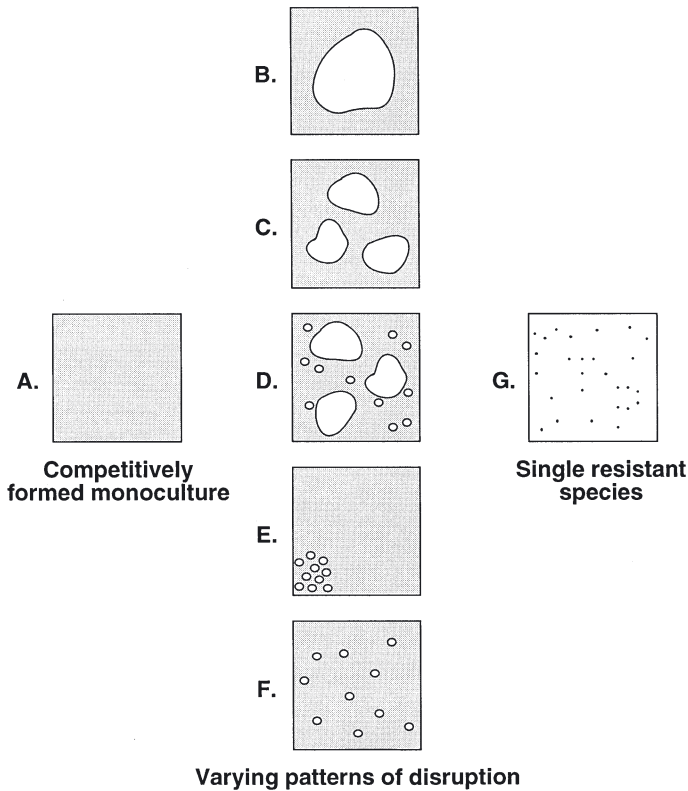species**

E.

F.

Varying patterns of disruption

Fig. 10. Pattern in imaginary planar landscapes subjected to varying intensities and size distributions of localized disturbance. (A) With no disturbance a monoculture composed of the competitively dominant life form develops. (B to F) Pattern generated under varying disturbance regimes. All have different biological connotations (see text). (G) At high disturbance frequency, only a single resistant species exists.
Graphics by A. Sun

able and sharp boundaries, are apparent because they are contrasted against a background reference state formed by a monoculture, and qualitatively appear to provide an important source of enrichment for both pattern and species.[1] It is not my intent to argue for the relevance of patches to intertidal ecology. Rather the following paragraphs present the case that such pattern

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[1] The term "gap" is often employed by terrestrial ecologists to describe discontinuities in a forest's canopy: I consider it and "patch" to be synonymous and will use the terms interchangeably.

is dynamic at workable spatial and temporal scales, is characterized by parameters which are both realistic and can be estimated in the field, and therefore that their study can provide useful insights into the consequences of pattern generation at landscape scales by human agencies. Two inter-related attributes are considered below.

Disturbance dynamics. Gaps or patches form naturally or can be produced experimentally, and can be followed until recovery, however defined, has been achieved (see Sousa 1984b, 1985 for reviews). For mussel beds on the coast of Washington State, a minimal interval will be 6 to 7 years (Paine and Levin 1981), and for nearby stands of a dominant benthic alga, *Hedophyllum sessile*, the interval ranges from 17 to 39 months (Paine 1977, 1984). Recovery in these examples is defined by the patch essentially disappearing into or becoming indistinguishable from the background assemblage. The significance of understanding the ecological factors associated with these presumed background or reference states has been explored by Paine (1984). Mussels are a legitimate, competitively formed state. *H. sessile*, on the other hand, is replaced by *Alaria* spp. in the absence of certain grazers. Although *H. sessile* monopolizes the canopy cover, its ability to do so is grazer-dependent: low *H. sessile* cover is found at high chiton or sea urchin densities (Duggins and Detheir 1985, Paine 1992); nearly complete domination occurs at intermediate grazer concentrations; and low cover reappears in the absence of grazers as a high percentage of *Alaria* spp. characterizes the canopy. Such biologically induced variation greatly reduces the value of *H. sessile* as a reference state, both locally and more generally.

The boulders studied by Sousa (1979a, b) provide a further example of how a mechanistic appreciation of process, leading to reference state formation, might increase our understanding. At his site, the competitively dominant alga is *Ulva* sp., and other algae and even barnacles are enhanced when it is removed experimentally or by grazers. Focus on *Ulva* sp. rather than the late successional red alga *Gigartina canaliculata* provides a means for identifying the impact of specific grazers and calibrating the degree and rate of approach to the background species composition which is dependent on both grazers and boulder size.

It seems ironic that the intimately coupled processes of patch or gap "birth" and "death" are usually considered under different headings: formation as disturbance, and recovery as succession. Formation will have at the least a magnitude and a frequency associated with it. Harper (1977) has argued that infrequent major events, catastrophes, may be less important than more regularly occurring events, disturbances, because the former

evoke no adaptive responses from the impacted populations. However, unknown or unrecorded catastrophes could well leave a historical signature if they produced local extinctions or introduced pattern into a "slow" system. As in all ecology, scale is significant: the landscape or seascape features will often appear to be in a dynamic steady state with formation and disappearance rates in balance if a sufficiently large region is considered (Paine and Levin 1981, Pickett and White 1985). It remains an important desideratum to discover whether the variation characteristic of comparable sites studied concurrently might be reflected at a single site sampled on a long-term basis. That is, can time be substituted for space?

Patch or gap traits. Disturbance on a scale that generates recognizable and readily quantifiable pattern is most easily considered if the successional clock is reset at zero. This, of course, doesn't always happen: it is unlikely to happen in terrestrial communities because of seed banks, low profile shrubs protected by benign boundary-layer conditions (in the case of hurricanes) or fire-resistant species (where burning is the mortality source). The importance of the residual, surviving species composition to the subsequent process of recovery has been recognized since at least Clements (1916). Pickett and White (1985) provide numerous examples.

For marine solid surfaces the assumption of relatively complete macrofaunal destruction seems more reasonable. The holdfasts of large algae overgrow and kill benthic invertebrates (e.g. Dayton 1973). When storms dislodge an entire plant, relatively clean space is revealed. Similar conditions occur when long-persistent stands of mussels, oysters, worms and tunicates are removed: by and large the surface, though biologically conditioned by the prior inhabitants, is relatively free of macro-fauna or flora. What may persist falls into three categories. Some species may have been overgrown and have tolerated that condition in the short term. For example, mussels readily overgrow barnacles. Under old stands of multilayered mussels which have accumulated a dense layer of shell and organic debris, few if any barnacles survive. If the barnacles have been recently overgrown, many, though showing signs of shell abrasion, will still be alive. In this circumstance, disturbance enhances barnacle survivorship. Some species can tolerate overgrowth and almost seem to require it. The enigmatic fleshy crust "*Waernia*" (Sebens 1985a) is probably such a species. Overgrowth is thus a condition for local survival, and may well be positively correlated with fitness. Last, the dominant life form often provides a secondary habitat for scores or even hundreds of associated species. Mussels (*Mytilus californianus*) harbor at least 300 species (Suchanek 1979, Paine and Suchanek 1983). Giant tuni-

cates (*Pyura stolinifera*) in South Africa are associated with a minimum of 70 residents (Van Driel 1979) and benthic algae in Tasmania with hundreds (Edgar 1983). When their habitat is destroyed, these dependent species can no longer persist on the exact same site. Dayton (1975) classified the associated assemblage into three types. That being considered, the dependent or obligate species are those requiring a measure of protection afforded by the dominant. In the absence of such protection they disappear locally. Dayton tested this idea by surveying the flora at his study sites and then removing the canopy species. Although I do not agree with some of the species assignments, the number of sites manipulated (6), their distribution across a broad range of wave exposures, and the uniformity of response is convincing. The obligate understory constituted 10 to 52% of the algal species. It would be fascinating to know how general this result is and how the numbers would change if the abundant local invertebrate grazers had been removed.

Although within a study system patches or gaps may form at a known frequency and provide an estimate of a rate of disturbance, the subsequent influence of this disturbance is very much dependent on a suite of patch traits. On a local scale, the most important trait is area. Fig. 10 illustrates how a fixed magnitude of disturbance might be achieved by either a calamitous event generating a single huge gap or less severe events generating numerous smaller gaps. The rates might be comparable when disturbance is calculated as spatial resource made available per unit time. The biological consequences of these two patterns (see below) would be dramatically different, especially as they influenced the rate of recovery (succession) and the identity of the early invaders. In Paine and Levin (1981), the size-frequency distribution of patches in a mussel bed approximated a log-normal distribution with gaps ranging from less than 100 cm^2 to over 35 m^2 during the observational interval on the most exposed shoreline. Both the rate of disturbance and mean patch size decreased in more benign, less wave-swept environments, and there are no compelling reasons to suppose that other patterns might not exist. In Sousa's (1979a) study boulders were overturned with a frequency dependent on their mass relative to wave energy. Presumably large boulders were immune or at best rarely overturned. As such they constitute an important habitat resource for long-lived species and might be generally inappropriate for opportunists.

Patch shape is also important and in marine benthic environments remains generally uninvestigated. Two patches of similar area or volume can have very different shapes. Shape is significant for two reasons. First, depending on the primary biological mechanisms of patch closure, patches

identical in area can disappear at very different rates if, for instance, closure depends on invasion by planktonic propagules versus vegetative growth from the surrounding biota. Levin and I (Paine and Levin 1981) calculated an eccentricity function for rectangular patches. Assuming inward migration or vegetative growth from all boundaries, square patches always persist longer than rectangular ones, and the greater the eccentricity, the more rapid the recovery. A long narrow disruption is thus likely to be of less ecological significance than a square patch of identical area. Second, although the patch itself may be biologically barren or initially hostile terrain, the surrounding assemblage has proven to be a rich source of mobile invaders. An extensive literature, often accompanied by photographs of "browse lines" in patches, exists on localized grazer or carnivore effects (e.g. Dayton 1973, Suchanek 1978, Paine and Levin 1981, Sousa 1984a for grazers, Menge 1978 for carnivores). A browse line becomes visible at the external margins of patches, when mobile consumers residing in the mussel bed are able to venture into patches and produce a 10 to 15 cm band relatively free of colonizing, fleshy macroalgae. Depending on the dimension or radius of influence, grazer presence suggests that small patches or exceptionally eccentric ones may be entirely incorporated into a browse zone whereas larger ones will not be. The phenomenon generates systematic edge effects with consequences for the patch inhabitants: in large, low-eccentricity patches, grazers or carnivores may be uncommon away from the edge, thus permitting more susceptible species to invade and survive. Conversely, grazer-resistant but weakly competitive species such as coralline algae may flourish in the browse zone. One expression of this interaction between process and habitat shape is that of a dart board pattern or concentric rings of species (Fig. 11, overleaf). In all events, patch shape, in conjunction with size, makes an important contribution to the influence of disturbance on community composition.

Fig. 10 alludes to a final key attribute of patches: their distribution in space. Most patches are invaded from the plankton. If the propagule has some capacity to persist while water-borne, the normal vagaries of current will provide potential access to suitable habitat even kilometers apart. However, for those plants and animals tending to lack dispersal stages in which the larval interval is suppressed or even omitted, interpatch distance becomes a significant aspect. That such species tend to be found at higher latitudes, in more seasonal environments or colder waters (Thorson 1950) conveys clear implications for latitudinal effects on marine patch dynamics. Thus, at higher latitudes interpatch distance assumes an increasing significance. Under all circumstances, the spatial distribution of patches (or
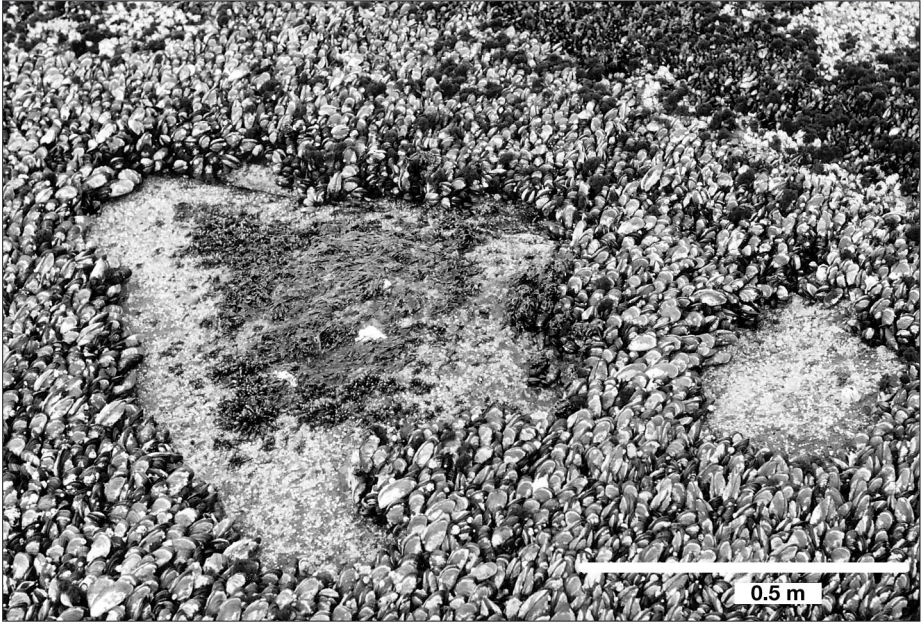
Fig. 11. Natural patches produced at the same time and tidal height at Tatoosh Island, Washington, USA. Mussels (*Mytilus californianus*) constitute the background or reference state. The smaller patch has not been successfully colonized by benthic algae, although barnacles (*Balanus glandula*) are abundant. The larger patch illustrates the transitional "dart board" pattern: a generally barren browse zone adjacent to the mussels, and then rings of more palatable algae appearing towards the center

islands) is a necessary consideration little examined in the context of dynamical models. A gap forming adjacent to one occupied by a poorly dispersing species is apt to be invaded; a comparable gap beyond the dispersal range will remain uninvaded. It seems uncertain how to add gap dispersion to existing models of gap formation and invasion, although the models of individualistic behavior as explored by Durrett and Levin (in press) hold promise.

Life history events in a patchy environment

The interface between within-patch dynamics and the production of dispersing propagules bears consequences for all benthic populations and therefore relates directly to how assemblages are organized. The organic world is

clearly not a homogenized mix of species. Distributional gaps abound, population sizes vary over orders of magnitude in local density, even similar species have different geographical distributions and so forth. The implications for a cohesive and synthetic multispecies or community ecology are daunting and well-recognized (e.g. Smith 1972, Caswell and Cohen 1991). Six biologically based considerations are discussed below: they are important at local scales; they relate directly to considerations of both within- and between-patch dynamics; they are easily forgotten or averaged over when larger spatial scale models of ecological systems are employed. Patch size is considered initially: it influences species composition because species which come to interact with each other are not simply a random draw from some larger pool. Next, because most of the eventual inhabitants are plastic in their growth, and inasmuch as that relates to density, flexibility influences performance, especially body size and per capita reproductive output. Finally, I try to relate the spatial explicitness implied above to current ideas on dispersal, source-sink dynamics, metapopulation structure and recruitment variation.

Patch size. When a gap, patch or ecological opportunity is formed, its relative value is in the "eye" of a potential invader. Whether this is interesting or even observable to an ecologist depends on the study's focus. Pattern vital to a nesting bird is immaterial to a wide-ranging mammal; a barnacle's world view is vastly different from that of the fish which might eat it. Perceived patch size is thus relevant to a potential invader, and such aspects as invadability and persistence as a function of size become important considerations. In some sense, the issue is patch quality as determined by the identity of the invader.

Patches of different sizes could be subject to any or all of a wide variety of influences. Distance from conspecific adults becomes significant if limited dispersal is a factor (e.g. Sousa 1984a). Patches of different sizes should differ in the hydrodynamic forces they experience. Given the documented effect of surface texture or chemistry on recruitment (e.g. Crisp 1974), localized surface variation could be a consideration. Larger patches might simply represent a more likely target, if competent larvae are non-selective. And the nature of the surrounding biota will surely generate significant influences, as witnessed in the browse line/edge effect phenomenon.

Nonetheless, there is evidence that some species select, prefer or survive better in small patches. Jackson (1977) found that small (3.6 cm^2) patches were invaded more rapidly than large patches (3820 cm^2), that few species were involved but that they grew rapidly, covering 80% of the area within

6 months. In contrast, many more than 25 species could be found in larger patches which after 6 months were only 22% covered. The implied small patch strategy was quick identification of the resource, invasion and rapid growth, perhaps facilitated by the limited number of interspecific competitive contacts. In similar fashion, Jernakoff (1983, in Sousa 1985) showed that the barnacle *Tesseropora rosea* settled in greater density in small (25 cm^2) than large (200 cm^2) patches.

There appears to have been less interest in the biological inhabitants of large patches. Sousa (1984a) found no effect of patch size (either 625 cm^2 or 2500cm^2) on the recruitment of most invading algal species or a mussel. Underwood et al. (1983), however, demonstrated that a limpet (*Cellana tramoserica*) persisted longer in larger patches and those with experimentally reduced barnacle cover. And, I have shown (Paine unpubl.) that higher densities of recently recruited barnacles (*Semibalanus cariosus*) can be found along the edges of large patches than in adjacent smaller ones. The proximate cause or causes underlying these patterns remain generally unknown. However, the recruiting larvae, at least of invertebrates, possess the sensory capabilities to judge numerous attributes of the space, and because small and large spaces will differ in properties, especially how long they persist, patch size specializations could be commonplace. To my knowledge, there have been no applications of Diamond's (1975) incidence function (a measure of the relative frequency of occupation of habitats of a given size by a species) to such situations, although it could yield interesting results, especially if the sampling properties of different sized patches and the substantial influence of the surrounding biota were accounted for.

Growth plasticity and population density. On many rocky shores, individuals become isolated and often crowded into discrete and conspicuously bounded patches. For other species, the subpopulation units are less obvious as when the population inhabits a number of intertidal zones, each of which differs in physiological and ecological challenges. Whatever the situation, the consequences of local density and its relationship to performance are important. Here I explore that importance: one thread is that maximal individual performance is at best obliquely related to fitness; a related implication is that judgments on intrinsic habitat quality are apt to be misleading in the absence of manipulation. The historical basis of these interests can probably be traced to questions about factors limiting populations of birds, insects and fish. However, because most non-arthropod marine invertebrates are indeterminate growers (Sebens 1987) size and age are confounded, complicating demographic studies, and individuals can shrink or otherwise

adjust their size or growth in response to alterations in local conditions. It is probably this variation, in addition to a poorly understood planktonic interval, exceptional adult longevity, the difficulty of defining what an individual is and the ubiquity of clonality, which has kept marine invertebrate ecology isolated from the mainstream of animal population biology with its focus on regulation, dynamics and age-specific life history strategies. The examples discussed below have been chosen on the basis of my familiarity with them. I believe, however, that they are representative.

Ebert (1968) examined a sea urchin (*Strongylocentrotus purpuratus*) in three portions of a mosaic environment. Densities varied from 85 to 200 m^{-2}. Where the urchins were sparser, they were larger with modal test diameters of about 7.0 cm vs. 4.6 cm. Reproductive capability, which will scale with volume, varied by a factor of 2.3. Most remarkably, reciprocal transplants of marked urchins showed that the smaller individuals characteristic of dense subpopulations were simply stalled in their growth. When moved to sites with reduced density and possibly more food, their growth rate increased. Larger urchins transplanted into sites characterized by denser populations actually shrank in size. Fig. 12 (overleaf) illustrates Ebert's results. In Panel A (*Postelsia palmaeformis* zone), the modal test diameter of large individuals is 4.64 cm. For the eelgrass area (Panel B) the modal diameter is 5.70 cm and the intercept is 5.14 cm. In the boulder field (Panel C) urchins had a modal diameter of 6.98 cm and an experimentally determined zero growth intercept of 6.39 cm. Ebert interpreted these data to indicate the potential for urchins to track local conditions in an environment variable in quality by site-specific adjustments to and fine-tuning of their body size.

My examination of the turban snail, *Tegula funebralis*, suggests other sources of spatially explicit, individual variation (Paine 1969b). *T. funebralis* recruits to the upper portions of its intertidal distribution and grows for some years at high densities (about 800 m^{-2}). Individuals that remain there tend to be smaller, and only 7% of the population ever develop a gonad. Individuals migrating lower in the intertidal encounter an environment with more food, their density is about half that of the upper zone, they grow substantially faster, and the gonad of the average female is about 4 times greater. However, approximately 25% are consumed per year by a predatory starfish. Individual snails are capable of living 35 to 40 years, and although no data on lifetime reproduction exist, the earlier maturation and greatly enhanced per-individual reproductive effort of the low intertidal individuals in the face of, and perhaps because of, the measurable risk should make them especially important members of the species population.

Sutherland (1970, 1972) studied a limpet (*Acmaea scabra*) on an exposed rocky shore, finding that individuals were denser and smaller lower down (Table 6). Further, at comparative sizes the Zone 1 (higher intertidal) individuals grew more rapidly, had a greater standing stock biomass and were 2.8 times as fecund. By most measures, Zone 1 is more suitable limpet habitat. Sutherland, however, explored these patterns further by experimentally reducing limpet density in Zone 2 to 350 m^{-2}. The partial
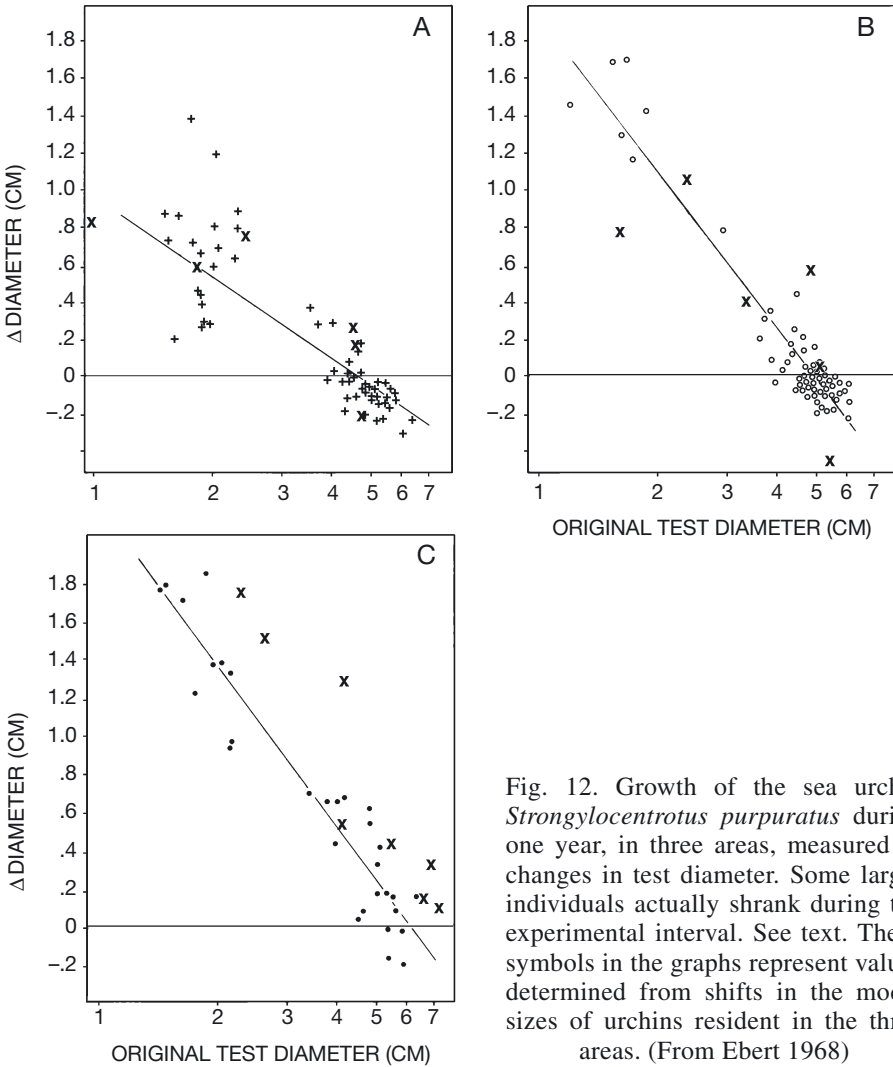
Fig. 12. Growth of the sea urchin *Strongylocentrotus purpuratus* during one year, in three areas, measured as changes in test diameter. Some larger individuals actually shrank during the experimental interval. See text. The **x** symbols in the graphs represent values determined from shifts in the modal sizes of urchins resident in the three areas. (From Ebert 1968)

Table 6. Characteristics and performance (growth and reproduction) of intertidal populations of *Acmaea scabra* in central California, USA (from Sutherland 1970, 1972)

Intertidal level	Density (m^{-2})	Mean size (mm)	Mean biomass (g m^{-2})	Growth rate (mm d^{-1})		Reproduction (kcal m^{-2} yr^{-1})
				4–8 mm	8–12 mm	
Zone 1 (higher)	450	13	14	0.02	0.01	68
Zone 2 (lower)	1350	8	11.5	0.008	0.005	24
Zone 2 experiment	350	–	–	0.06	0.03	–

release from intraspecific competition produced a dramatic result: Zone 2 limpets now grew about 7 times faster than their higher density counterparts. The manipulation was not designed to see how much better than Zone 1 the low zone might be. However, it suggests that snap judgments of habitat quality based on such criteria as density, size attained, growth rate or even the prevalence of such negative attributes as catastrophic mortality (characteristic of Zone 1) will be difficult. Perhaps the most appropriate evaluation would be comparison of standardized or average individuals living freed from the constraints imposed by increasing conspecific density (but see next section). Patterns like the above, arrayed across a variable and mosaic landscape, are a major result of the ecological plasticity associated with indeterminate growth. The spatially localized variability in habitat quality and a species response to it is central to at least two disparate bodies of ecological theory.

Patch characteristics and individual performance. The previous paragraphs suggest that even seemingly homogeneous habitat can in fact be surprisingly variable as a result of local and inexplicable variation in population density. This variation also translates into important differences in individual performance with respect to body size, growth rate, energy reserves, mortality and potential reproductive output. To the extent that such traits or performance criteria provide a satisfactory index to individual fitness contributions, high and spatially localized variation makes an evaluation just that much more difficult. Or the environment could be initially heterogeneous with respect to its intrinsic (meaning free from density effects) quality. Fretwell (1972), writing about a "theory of habitat distributions", has built a bridge between intrinsic quality and density by developing a view of how

perceptive individuals would react to and choose habitats whose intrinsic quality had been compromised by prior inhabitants. Higher quality sites are recognized, colonized and, with increasing density, diminished in attractiveness because crowding diminishes per capita reproduction or survival. At some point secondary and tertiary habitats become equivalent in attractiveness (quality) and are invaded, and so forth. The result is an equalization of individual performance across a range of initially different habitats. The viewpoint assumes a mosaic, non-homogeneous environment, site choice biased by quality, and density-dependent influences. Most of these properties are characteristic of rocky shore assemblages. A negative relationship between body mass and local density seems general, at least for echinoderms (Ebert 1968, Menge 1972, Paine 1976) and developmental plasticity (e.g. Hyman 1951 for flatworms) is the rule. Hence, local adjustment is commonplace. What is lacking is an independent assessment of habitat quality as required in Fretwell's conception.

Unfortunately, assessment of intrinsic site quality may be impossible to achieve in marine benthic systems, even if risk from predation is ignored, in the absence of experimental manipulation. Chapter III discussed a representative set of samples in which habitat quality for competitive dominants was compromised by the activities of consumers to such an extent that the potential dominants were rare, small and restricted spatially. Such species often flourish, revealing their true potential, when the constraints are eliminated. Connell's (1961b) study showed that the barnacle *Chthamalus stellatus* is confined to a more physically stressful portion of its distribution by a superior competitor. Starfish removal experiments (e.g. Paine 1966, 1971a) indicate that mussels tend to be confined to high intertidal bands. If the consumer is highly mobile (e.g. spiny lobsters; Robles 1987) the dominant may be essentially eliminated. Under such circumstances, potential occupancy of higher quality habitats may not be recognized and performance certainly cannot be estimated. On the other hand, predation is rarely absolute: small prey individuals may remain unnoticed, habitat features can provide a partial refuge or massive recruitment events may swamp the consuming capacities of the local predators. Escapes in size are well documented for all habitats (terrestrial plants, Peterkin and Tubbs 1965, Janzen 1976; fish: Werner et al. 1983; marine algae: Lubchenco and Gaines 1981; marine invertebrates: Paine 1976). When it occurs, it allows prey and predator to coexist. These larger individuals living in a more hospitable portion of the environment are, not surprisingly, substantially more fecund than their crowded and smaller counterparts. For instance, Suchanek (1981) has calculated a habitat-based

difference in gonadal tissue of 80-fold for *Mytilus edulis*. Using data in that paper and mean sized *M. californianus* of 6.0 cm (middle intertidal) and 12.0 cm (lower), a minimal individual difference is 15-fold. The performance discrepancy between large (2600 g wet weight) and small (200 g) starfish *Pisaster ochraceus* (Paine 1976, and unpubl.) is a factor of 108 when absolute mass of the gonad is compared. In another echinoderm, the urchin *Diadema antillarum*, Levitan (1989) calculated a difference factor of 20 between populations of large and small-bodied individuals. At least three examples are available from gastropods: I estimated (Paine 1969b, 1971b) a four-fold reproductive output difference in *Tegula funebralis*; Sutherland (1970 and Table 6) found a factor of three in *Acmaea scabra*; Branch (1975), working with *Patella cochlear*, provides evidence for a seven-fold difference in individual output between population densities of about 175 and 750 m^{-2}. In Sebens' (1983) study of the anemone *Anthopleura xanthogrammica*, the calculated number of expected female offspring produced at the density extremes of 3 and 51 m^{-2} differed by a factor of 90. All the above studies are of free spawning invertebrates, but the pattern reappears in some barnacles, where fertilization is internal and proximity of partners essential. Wu (1980) calculates a density related reproductive decrease of approximately two-fold for *Balanus glandula*. Wethey (1984a) has repeated that result: mean-sized individuals from low-density sites have a conical shape and a clutch weight of 2.83 mg; high-density, columnar individuals have a significantly lower clutch weight, 2.24 mg. In contrast, in Strathmann et al. (1981) for the same species, there is evidence for positive density dependence: more crowded individuals are on a per capita basis more productive. Interestingly, Wethey (1984a) also showed for two other barnacle species a positive relation between density and fecundity, suggesting a benefit to crowding. Finally, in the only marine plant example known to me, Ruckelshaus (1994) has estimated that intertidal *Zostera marina* (a marine tracheophyte) produce about 80 times the seed capsules per m^2, and 15 times more seeds per vegetative shoot than their subtidal equivalents.

Given that 70% of all marine invertebrates broadcast their gametes (Thorson 1950), with fertilization occurring externally, and because larger individuals tend to produce more gametes, are they fitter? That important question has been best addressed by Levitan (1989, 1991) with the answer being "probably not". If egg and sperm were long-lived and retained their viability, neither of which is true, spawning efficiency would be much higher. Measures of adult gonad volume as an index of fitness or reproductive success assume perfect or at least equal fertilization prospects which are

independent of adult density. Levitan has shown this to be unlikely, at least for the tropical sea urchin *Diadema antillarum*, a species with no special aggregation-forming behavior at the time of gamete release. His measures suggested that beyond a distance of 5 m from an isolated sperm source, fertilization was a low-probability event, and therefore that adult density could be an important factor. High-density (15 m^{-2}) but small females were estimated to release 0.1×10^6 eggs; low density (0.2 m^{-2}) but larger females release 2.0×10^6 eggs. Estimated fertilization success at high densities was 22% versus 1% at the low densities. While the production of zygotes is essentially equivalent at the population level, which would accord with an interpretation based on Fretwell, the small females are actually producing more zygotes on an individual basis than their larger conspecifics. Levitan's conceptual framework is shown in Fig. 13. If these patterns hold generally for broadcast spawners, the presumed superiority of individuals that are larger, safer, more fecund and even possibly longer-lived must be questioned.
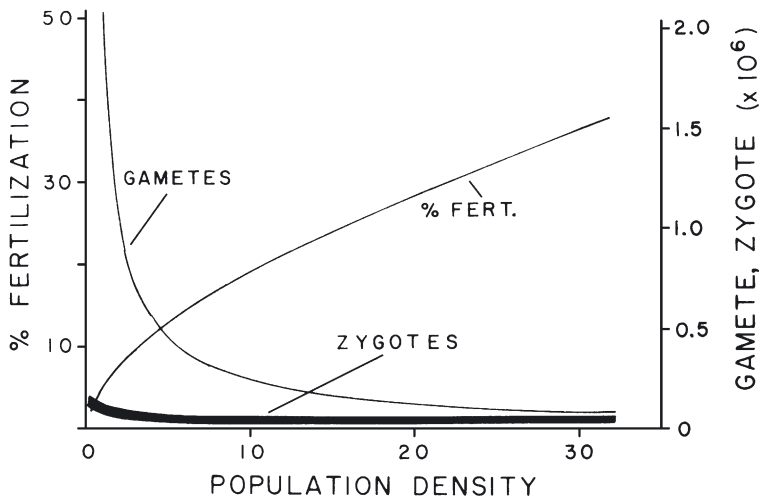

Fig. 13. The tradeoff between gamete production of an average-sized sea urchin (*Diadema antillarum*) characteristic of a given density level (no. m^{-2}) and the percent fertilization of her gametes. The "gamete" curve drops because of decreases in mean individual body volume at increasing density. Percent fertilization increases because at high urchin densities, more males are present and sperm sources therefore more uniformly available. Small and crowded individuals at high densities, on average, produce as many zygotes as much larger individuals at low density. (From Levitan 1991)

Although Levitan's results were not based on contemporaneous studies of patches, being estimates of zygote production at the same site but at different times, they relate directly to two further subjects. The first is whether a patch or localized sub-population is capable of sustaining itself or whether it requires an external subsidy. The second is whether pre- or post-settlement events determine the character and therefore the productivity of post-settlement populations. Broadly stated, the question is under what conditions does supply-side ecology hold?

Source-sink populations. Ecosystems and populations exchange materials and individuals, and it is the relative directionality and balance of the rates which is important to understand. There seems to be no consensus on the significance of such transfers at the ecosystem level, where the concept of import/export dynamics was initially developed by the Odums. The deep sea, without consequential primary production, is an obvious example of a worldwide system powered by an energy subsidy. But the answers in the photic zone are not so clear. Coastal marshes and estuaries export masses of detrital material to offshore shelf waters (Odum and de la Cruz 1967). However, the material is of low nutritive content, and phytoplankton prove to be a more suitable food source for shelf inhabitants. The salt marsh examined by Nixon and Oviatt (1973) suggests a near balance of consumption and production. Estuaries fertilized by sewage effluent, if they are not outright poisoned, can be very productive and will subsidize shelf production (Malone 1977). At the population level the relations are equally ambiguous. Estuaries, because of their high productivity, are renowned as nurseries for fish and invertebrates. But where do the eggs or larvae come from? They are often not produced locally. Even superb studies like Harrison et al. (1988) on organisms (butterflies) which disperse as adults pose problems. That work, originally cast as a metapopulation study, is probably as appropriately considered as a source-sink situation, with a single large and permanent source supplying recruits to a halo of smaller, less suitable and less permanent sites in which extinctions commonly occur. A population perspective on source-sink relationships has been developed by Pulliam (1988). The relevance to probably every assemblage is obvious. Some species are common, others rare. For the latter, do hotspots of occurrence function as subpopulations so that the species is in some sense self-maintaining, or are individuals simply present more or less by accident, a tourist species (Moran and Southwood 1982)? One of the first attempts to evaluate the problem, more from a sampling perspective than a demographic one, was Lloyd's (1967) development of a "mean crowding" index. Crowded but generally rare individuals might

be able to function as a population; scattered but equally dense individuals might not. Pulliam has extended the inquiry. The question is disarmingly simple: in mosaic or patchy environments, are the local residents successful enough to maintain themselves and to export dispersing individuals, or do they require immigrants for maintenance of the local population and continuance at the site? Pulliam's analysis, which assumes that relatively easily monitored and followed birds are the study subject, is hardly reassuring largely because most taxa are less well known than birds yet participate in the same spatial lottery in which regional persistence is the product of exchange between habitat types varying greatly in quality.

Large portions of a species population may be maintained in a sink habitat if the source is highly productive and the sink's annual deficit small. Possible marine examples might be the dense barnacle populations found towards the heads of estuaries (Strathmann et al. 1981), the rather specific conditions for effective reproduction of the crown-of-thorns starfish *Acanthaster planci* despite its broad Indo-Pacific distribution (Birkeland 1982), or stable adult populations of the clam *Mya arenaria* and the effective incubation and retention of their larvae in bays with larval export to less persistent populations (Ayers 1956). Pulliam's calculations suggest that under some circumstances less than 10% of a population need be in the source habitat. One sidelight of such a perspective is that the definition of niche seemingly preferred by ecologists, the n-dimensional or Hutchinsonian hypervolume (Hutchinson 1958), is probably incorrect. If the fundamental niche is defined on the basis of where a population can generate a surplus (a source population), most realized niches will be larger, not smaller than the fundamental niche when mapped onto the real world. Such a view accepts as useful a niche concept, despite its continued success at raising a ruckus among ecologists and despite a logically devastating argument by Connell and Orias (1964) that, from a practical viewpoint, the concept is circular, because niches cannot be evaluated independently of species.

The implications of Pulliam's perspective for species conservation are profound. In particular, focusing on an area where a threatened species is especially abundant may be misleading and an inappropriate guide to a habitat's or patch's overall importance to species' maintenance. In a mosaic environment in which units exchange individuals or propagules, it becomes vital to recognize source populations.

Patchily distributed individuals and metapopulations. Spatial pattern on marine rocky shores is both conspicuous and dynamic. Where it is expressed as a patch or gap, it suggests the availability of transient resources

and species. The community consequences of a shifting relationship between local extinction, resurrection of the resource and successful invasion was basic to the viewpoint advocated by Andrewartha and Birch (1954). Although unpopular and often disregarded at the time, it seems eminently reasonable now. One possible historical reason is that the original controversy centered on aspects of population regulation. However, gaps do form and disappear and local, site-specific extinction seems to be commonplace. Levins' (1969) metapopulation approach provided a vehicle to study the phenomenon, requiring only that the patch populations be independent demographic units that, when connected by dispersal, become interdependent over time. The characteristics of species whose dynamics might be modelled by a metapopulation approach include: a spatially discontinuous distribution; population units of variable abundance, suggesting that either as habitat quality or actual area declines, local extinction becomes more likely; and measurable dispersal capabilities. Because local disappearance can be considered an extinction event, the relevance to conservation biology is obvious. There are also genetic consequences associated with both the size of the founding populations and the genotypes of individuals dispersing from small source populations. Harrison et al. (1988) provide a superior terrestrial example of applying the approach to a butterfly population, and Gotelli (1991) has extended it.

Briefly, Levins suggested that a metapopulation approach would contribute to understanding population abundance at large spatial scales, and as such unite local dynamics and biogeography. The environment was assumed to be homogeneous. When p gives the proportion of occupied sites, i the number of successfully colonized empty sites per time, and e the extinction rate of occupied sites, a single, internal equilibrium for p exists when $i > e$ (Gotelli 1991). Specifically, the change in the proportion of occupied sites is given by

$$\frac{dp}{dt} = ip(1-p) - ep$$

This model is not concerned with patches or subpopulations of different sizes, with variations in intrinsic patch quality or with different magnitudes of dispersal or extinction. All sites are equivalent and equally accessible. Only the global rates change, and with them the proportion of occupied sites. One objection (Hanski 1982), called the "rescue effect", relates the extinction probability to p. Thus when p is large, most sites are occupied and the extinction rate diminishes. Gotelli has extended the approach by invoking a

"propagule rain", a rate of entry which is proportional to the number of unoccupied sites. This is tantamount to invoking a necessary immigration from sources external to the study system (MacArthur and Wilson 1967), a long-lived seed bank (Gotelli 1991), a storage mechanism (Warner and Chesson 1985) or a planktonic bath (Levin and Paine 1974). When the propagule rain is combined with the rescue effect, it predicts a not unreasonable positive correlation between distribution and abundance.

I have identified this class of models because of their importance to conservation biology and because they potentially address patterns and processes readily observable in rocky shore assemblages. Is this supposition realistic or simply amateurish optimism that an approach, founded in a model, can be parameterized, used effectively and even extended in an experimentally tractable system, and therefore yield inferences about substantially more complex and perhaps more important assemblages? I believe the answer to be yes. Spatial discontinuities in distribution are commonplace. Where they are not, they can be added through manipulation of the system, especially if a background or reference assemblage is present. I have in mind mussel (*Mytilus* spp.) beds, but extensive plantations of marine grasses or stands of oysters, giant tunicates (e.g. *Pyura praeputialis*), worms like *Galeolaria caespitosa* or *Gunnarea capensis* or vermetid gastropods would suffice. Paine and Levin (1981) provide one example of how a seascape might be carved into a pattern of patches, Sousa (1984b) and Keough (1984a) others. It would be possible to predetermine the spacing and size of the patches (or sites) and to adjust that to the estimated dispersal capabilities of some target species. Following this routine, important models could be examined and extended in an experimentally tractable system, with their appeal resting on the presence of a known background state and the proven power of collaboration between empiricists and theoreticians.

Dispersal. Dispersal is the process by which individuals extend ranges, invade unoccupied yet acceptable habitat or replenish local populations of conspecifics. It implies capacity for invasion; it is not necessarily a seasonal migration along fixed routes by adults. Despite being a critical life history attribute, it is also the most poorly understood: surprisingly, it has generated a debate over "supply-side ecology" and the relative importance of larval settlement to postlarval population dynamics. Dispersal plays a central role in community ecology because it links populations in geographically separated habitats. Here, I eventually discuss two general questions not so much to provide answers but as a means of relating this important subject to the community composition of rocky shores.

Dispersal in marine environments. It is tempting to believe that all individuals and therefore species have some mechanism for effective spatial spread of their genotype. The dogma arises because of our overall familiarity with birds, insects and even fishes, all of which move easily from place to place. The process is clearly more constrained for terrestrial plants, some of which are unlikely as seeds to disperse more than a short distance from their natal site. The same holds for marine biotas despite examples of spectacular faunal exchanges. Scheltema (1971, 1986) has described teloplanic larvae capable of transoceanic transport and retention of settlement competency. Naylor (1965) provides examples of range extension of 100's of kilometers when competent larvae of Mediterranean species encounter cold water habitats warmed by nuclear power plant effluent. Compilations of reproductive modes and development times of marine invertebrates (e.g. Strathmann 1987) document numerous examples of flexible and often lengthy durations of the planktonic interval. For instance, the starfish *Mediaster aequalis* maintains its competency to settle from the plankton after 1 to 14 months in culture (Birkeland et al. 1971); another starfish, *Pycnopodia helianthoides*, metamorphosed over a period of 90 to 146 days (Strathmann 1978). Thus some species spend a sufficient time in the plankton to be transported enormous distances; for them and the 70 % of marine bottom inhabiting invertebrates having a planktonic interval of some duration (Thorson 1950), the standard dogma on effective dispersal is not an issue, although the spatial pattern, local intensity, and timing of settlement remain important components.

It is with the other 30 % where the dilemma of dispersal, or lack thereof, exists. For many of these a miniature version of the adult hatches from a benthic egg case, or crawls away after an extended interval of parental brooding. For these, no apparent long-distance dispersal mechanisms exist. The adults of certain species, if mobile, could crawl some distance, and a few, if they can become water-borne and are sufficiently buoyant, might be transported for distances more than a few hundred meters. Other, and increasingly exotic, mechanisms have been imagined: for sessile adults, long-distance movement could occur if individuals were attached to the holdfasts or associated debris of drifting algae. Although such transport surely occurs, it seems evolutionarily capricious and ecologically ineffective. Other benthic species liberate demersal larvae which simply crawl away from the parent. Gerrodette's (1981) investigation of the cup coral *Balanophyllia elegans* suggests the limited efficacy of this process; adults transplanted onto settling plates released larvae which moved only a few cm before metamorphosis

and attachment. An occupiable site 4 km distant was not invaded in a 16-year observation interval. The quandary posed by the missing dispersal mechanism is only heightened by this species' 2000 km range unless a continental terraining mechanism is invoked. The antiquity of the Pacific basin also provides a solution: even with directional movement of only 5 cm yr^{-1}, the entire distance could be traversed in 40 million years, which is but a small fraction of the basin's age.

Dispersal ability in marine benthic algae is probably only slightly less variable than in animals, in large part because most can float potentially great distances and during the process release viable spores or germlings. However, the topic has been minimally investigated, and an impression of uniformly effective dispersal based on the release of huge numbers of spores (e.g. 9×10^9 spores by *Laminaria* sp.; Chapman 1984) is misleading. Again, I illustrate poor or limited dispersing ability since it is these species which are most apt to be influenced by patchily distributed acceptable habitat. The most commonly employed investigative technique is to quantify propagule settlement either on natural (e.g. Dayton 1973 and Paine 1979 for the brown alga *Postelsia palmaeformis*) or artificial surfaces (e.g. glass slides for a variety of brown algae; Reed et al. 1988). Many of the species have a limited dispersal ability measured in meters under normal conditions (for reviews see Dayton 1985 and Santelices 1990). There is evidence for episodic long-distance transport (Reed et al. 1988). As an example, the kelp *Macrocystis pyrifera* can release 5×10^5 spores h^{-1} per sporophyll, and a plant has numerous sporophylls. Recruitment distance usually varied from 5 to 40 m, depending on the source stand's density. However, they observed an effective, mass invasion of a site at least 1.6 km from the nearest source during an extreme environmental event. The proposed mechanism was zoospore transport, not drift of fertile plants. But drift does occur. Deysher and Norton (1982) show that in *Sargassum muticum* most colonization occurs within 2 to 3 m of the parent plant, although drifting germlings can be found in the plankton 1.3 km from a source. However, this species appears to have made a single "epic" jump of 1100 km. Calculations indicate that the most plausible mode was wind-aided drift of vegetative fronds.

There are almost no data indicating how effective long-distance dispersal might be, although the study of Sousa (1984a) suggests that it is of limited utility. He cleared patches within mussel beds, excluded benthic grazers, and mapped the location of adult plants adjacent to the patches. For half of the eight species considered, recruitment was dependent on an adult source within l m of the experimental patch. If these four species (*Fucus gardneri*,

Pelvetiopsis limitata, *Mastocarpus papillata*, *Iridaea flaccida*) can be dispersed by a "drifting", fertile adult, Sousa's study provides no evidence for it. One cannot assume, then, that benthic algae are uniformly effective dispersers.

Recruitment variation or supply-side ecology. Recruitment variation and the relative significance of supply-side ecology represent the interaction between dispersal events, aspects of habitat quality and individual performance. Adult performance is important because it is they (in sexually reproducing species as opposed to those acquiring more resource through vegetative growth) who generate and release dispersing larvae. It is the larva's responsibility to find and invade suitable habitats. The fundamental question is whether the traits of adult populations are based on the number and performance of the larvae, prior to the instant of metamorphosis, settlement and the acquisition of postlarval morphology, or whether postlarval (= postsettlement) events determine the adult population's density. There are numerous dimensions to the problem; accurate definition of terms is critical. As Keough and Downes (1982) summarize them, settlement embodies finding and testing a suitable site and then "includes attachment to the substratum and metamorphosis". Recruitment is a measure of post-settlement biology involving survival, growth and most critically, attainment of a size at which the individual can be identified and counted. Stated this way, settlement dynamics reflect the uncertainties associated with planktonic existence and discovery of a possibly suitable site, while recruitment involves all the vagaries and dangers of life on (or in) a surface. The issue remains important because of its ties to local population regulation.

This is an old but continuingly important topic dressed in new clothes. One could claim that Malthus was warning about supply side problems for human populations, to which Swift (1729) already had concocted a gruesome post-recruitment remedy. An appreciation for the dynamic relation between entry to a population, density in relation to resources, and post-entry effects is venerable. In marine systems, it probably began with Hjort (1914) and has been summarized by Sinclair (1988); stock-recruitment or spawner-recruit relationships are central to resource management and have long been recognized as such. The resurrection and rediscovery of spawner-recruit relationships (as in the proverbial wheel), and specific application to marine benthic ecology were stimulated by the analysis of Underwood and Denley (1984), theoretical development by Roughgarden et al. (1988), and application of the catchy phrase "supply-side ecology" by Lewin (1986).

Species do go extinct locally (and increasingly so globally). In either case, the reason must reside in the combined factors of local mortality and emigration being greater than the supply-side forces of settlement or immigration, either by propagules or vegetative growth. Thus the BIDE (B = birth, I = immigration, D = death, E = emigration) models of Pulliam (1988) are relevant. The answer at sources will differ from those at sinks, and will equally be dependent on one's view of habitat suitability and numerous life-history traits. For instance, it seems obvious that the abundance of an annual species (reduced life span and breeding in one year) requires an immediate inter-generational dependence. Because such species are often ruderal or fugitives and characterized by excellent dispersal abilities, the size of the spatial domain necessary for studying the relationship must be prohibitively large. To my knowledge there are no marine studies of what should comprise the most straightforward supply-side circumstance.

Numerous examples do exist, however, for another kind of supply-side dynamic, one where there is no ambiguity. Species close to their range margins may show episodic bursts of abundance, followed by a decline possibly lasting many years. For these, the very presence of a stock and its initial abundance are dependent on pre-recruitment circumstances. Postlarval performance and development of an adult population will be of no general consequence. For example, if spiny lobster (*Palinurus argus*) populations at Bermuda are maintained by larval transport from the Antilles or other Caribbean areas, and because of oceanic currents are incapable of contributing to their own maintenance, this is likely to be a supply-side situation. Foreman (1977) describes a dramatic increase in the local abundance of a sea urchin (*Strongylocentrotus droebachiensis*) in western Canadian waters, attributable to a major recruitment episode in 1969. The same incursion probably included the outer coast of Washington State. In 1974, approximately 10% of the intertidal urchins were *S. droebachiensis*. Over the last decade they have amounted to between 1:1000 and 1:10000 of the local urchin population (Paine pers. obs.). For most species, however, capable of breeding in two or more years and living within their normal distributional limits, the question is not so easily answered as the selected examples discussed below suggest.

Barnacles should provide ideal study material due to their world-wide distribution, known systematics, a lengthy larval interval and a rich literature. Connell (1961a, 1985) considered whether the supply of cyprids of *Semibalanus* (formerly *Balanus*) *balanoides* were capable of consistently saturating the spatial resource at his Scotland site. They were. Wethey

(1984b), studying the same species on the U.S. east coast and in Britain, documents waves of recruits with daily settlement rates varying from few to more than 60 cyprids cm^{-2}. The individuals appearing at this rate, especially in the absence of post-metamorphosis mortality, would saturate the space many times over. Michinton and Scheibling (1981) examined the same species in Nova Scotia at two adjacent study sites stratified by tidal height and found a range of pattern. High intertidal areas characterized by low adult density (0.3 to 7.7 barnacles per 100 cm^2) appeared to be regulated by settlement dynamics. In the mid (7.5 to 121.7 barnacles per 100 cm^2) and low (40.6 to 333.3 barnacles per 100 cm^2) intertidal, where most of the population lived, post-settlement processes, mainly predation, controlled the adult density. Thus within-site conclusions are very much zone dependent, with fringe low-density populations providing convincing evidence for supply-side importance and the denser, lower intertidal individuals being influenced by post-recruitment processes. It would be interesting to know how manipulations like Sutherland's (1970) or measurements like Wethey's (1984a) would affect these conclusions.

Another dimension of the *Semibalanus balanoides* story has been developed by Gaines and Bertness (1992) and Bertness et al. (1991) who show that settlement variation is tightly correlated with the mean flushing time of Narragansett Bay, Rhode Island, USA. Bay barnacles grow to twice the basal diameter and have approximately ten times the reproductive output relative to open coast individuals. Water column food concentrations and current velocities strongly influence local barnacle dynamics, and transplant experiments suggested the differences to be a phenotypic or plastic response. I suspect that these information-dense barnacle details would apply to most marine invertebrates: growth, ultimate size, reproductive output, recruitment and adult mortality rates will be enmeshed in a regional and minimally understood nexus. Questions relating to population regulation should acquire added difficulty for truly long-lived species capable of dominating solid surfaces, for their age or size structure could represent a blend of recruitment cohorts. For these, highly variable juvenile dispersal and recruitment may, or may not, substantially influence the continuity and abundance of adult stocks.

Experimental tests can be invented for distinguishing the relative contributions of pre- or post-settlement circumstances to the structure of the reproductive stock. For benthic populations, like most barnacles, one could conceivably protect the rare, infrequent recruits from potential predators. If protection resulted in no accumulation of a reproductive stock, pre-

settlement processes would most likely control the adults. Conversely, if protection permits adult accumulation, no matter how gradually, then the population is controlled by post-recruitment influences. The reciprocal and complementary manipulation is probably impossible. The reproductive output of individual invertebrates broadcasting their gametes can run into the millions. How does one manipulate planktonic mortality? Could a single individual's eggs, given perfect fertilization efficacy and complete planktonic survival, saturate a site?

Benthic marine asssemblages are highly variable, especially if all members of a species population rather than just the reproductively competent classes are considered. The following two examples suggest the interpretive complications introduced by considering adult population fluctuations relative to mesoscale oceanic conditions. Because both examples involve commercially significant inhabitants of marine sediments rather than solid surfaces, their relevance to rocky shore ecology could be questioned but they are nonetheless instructive. Ayers (1956), working in Massachusetts (USA), constructed a simple model to illustrate how combined mortality and dilution, defined as decreases in population density in the absence of mortality during the larval interval, influenced adult population dynamics of the bivalve *Mya arenaria*. He assumed all eggs released (3×10^6 yr^{-1}) were fertilized and a 14 day or 28 tidal cycle larval interval. Under the assumptions of the model, one site (Barnstable) was estimated to have a dilution rate of 20% per tidal cycle and a mortality coefficient of 0.97. Local stocks should not be able to maintain a stable adult population and, in fact, they don't. Other sites were thought to be stable, with *M. arenaria* populations potentially increasing and thus able to support a commercial harvest. Peterson and Summerson (1992) examined potential recovery rates in a North Carolina, USA, bay scallop (*Ptychodiscus brevis*) population decimated by a red tide. The scallop appears to be a relatively poor disperser, and inhabits a series of interconnected water bodies called "sounds". The initial red-tide-induced decline tended to be perpetuated, as evidenced by three subsequent years of limited harvest. Two kinds of explanations are given. One suggests that reproductive individuals surviving at some low density simply cannot produce enough successful larvae to rebuild the stock rapidly. At low adult densities, some combination of too few adults with the expected huge and natural larval mortality makes the species "recruitment-limited". A complementary explanation evokes a source/sink explanation. One of the sites (Yellow Shoal) seemed to rebound immediately, with recruits and adult densities equal to or greater than historical means. Four other sites were well

below the historical, pre-red-tide densities. Despite the continued presence of reproductive adults, they seem limited in their recovery by the rate of recruit entry.

Both these seminal studies identify the interplay between adult stock density, larval production and mortality. They also explicitly invoke a role for mesoscale phenomena, for some regions to be highly productive and capable of both self-maintenance and export of larvae and others to require such a subsidy. If Thorson's (1946, p. 439) famous graph of bivalve population fluctuation as a function of developmental mode is generally correct, high spatial variability should be expected in all species with dispersing larvae. Under such circumstances, the source/sink viewpoint becomes relevant. Sources, given sufficient adult density to ensure fertilization and zygote production, should not be limited by supply-side considerations. Sinks will always or usually be. In mosaic or stratified environments, sinks will require an input in addition to that of their own productivity. Their adult dynamics will reflect the importance of the delivery of new members and thus, beyond the universal necessity of population replenishment, will be characterized by higher between-year variance in local reproductive stock density. Marginal or sink habitats should often be recruitment-limited; in source or potentially optimal situations, overproduction should be the rule.

An added dimension of how marine plant and invertebrate populations are regulated has been examined by Strathmann et al. (1981). This study considered the consequences of lengthy larval dispersal periods and the potential of long-distance transport. The implications of the opposite situation, no or spatially limited dispersal, will not be considered here, although they are relevant to the concept of local adaptation and philopatry (Shields 1982). Both are important problems given the diversity of reproductive modes and dispersal capabilities. Neither will be resolved without combining recently developed techniques in molecular biology (e.g. the polymerase chain reaction) with local demographic analysis. The study by Strathmann et al. suggests that widely dispersing barnacle larvae, produced by adults who have survived the vicissitudes (meaning post-recruitment selective pressures), may well fall victim to the vagaries of dispersal and be deposited at sites for which they are minimally or poorly adapted. Thus at moderately protected habitats, the preference of the barnacle *Balanus glandula* for low shore settlement sites led to decreased fecundity and fitness. The genetic basis for these behaviors and their consequences were not examined. However, fine-scale genetic patchiness has been documented for *Mytilus edulis* (Milkman and Koehn 1977), where the seasonally varying pattern is caused

by recruitment pulses from different sources. Johnson and Black (1984) came to a different conclusion for an Australian limpet *Siphonaria jeanae* in which very local variation in allelic frequences was attributed to selective mortality of well-mixed larvae either while they were in the plankton or shortly after settlement. The implications of such genetic variation for the performance or fitness of recruited stocks remain essentially unknown. In recruitment-limited populations the accidents of history could well be perpetuated into the breeding population. Where population density is determined by post-recruitment selection, differential winnowing could have an important effect. Given a mosaic environment, such processes could often influence that 70 % of invertebrate species with planktonic larval stages. Is poor recruitment or adult production the result of a genetic mismatch between genotype and habitat, and if this is reflected in adult performance, how does it relate to supply-side ecology? In addition, if the reproductive, adult stock is regulated by some negative density-dependent process, one could imagine cycles of recruitment-linked dynamics.

Whether species are regulated by larval or post-larval circumstances seems ambiguous when cast into a metapopulation or source/sink context. The answer is that it depends on such adult features as density, fertilization efficiency and zygote production, and the possible consequences of inbreeding, or the stochasticity of larval source and transport. The density of breeding adults has been implicated in at least two studies (Karlson and Levitan 1990, Peterson and Summerson 1992). Is this an adult or larval issue? Other work suggests variable adult performance reflected in larval choice along gradients of habitat quality. Again, how should these be judged? The essential attributes of marine population regulation remain the quality and quantity of adult contribution to the next generation, as influenced and perhaps determined by the vagaries of larval mortality and transport. In an environment considered "mosaic" at a variety of spatial scales, any answer seems possible. A source/sink perspective accompanied by judicious application of Fretwell's (1972) views of the interplay between habitat quality and population performance should provide an appealing framework for interpreting the relative contributions of different life history stages.

Trophic interactions

With the exclusion of most plants capable of photosynthesis, organisms must eat one another; life feeds on life. That inexorable necessity continues to

provide naturalists with a feast of exotic observations: carnivorous plants, nematode-eating fungus, cannibalism, role reversals of prey and predator as a function of size, tightly bonded symbioses and so forth are all just part of the menu. Unlike competitive interactions which are often subtle, trophic relationships can be dramatic, observable and commonplace. They also lend themselves to easy quantitation. Boyer (1968, p. 17) describes the Rhind Papyrus dating from about 1650 BC, apparently derived from earlier material, in which these relationships are posed: "seven houses, 49 cats, 343 mice, 2401 ears of spelt, 16807 hekats". The food chain is clear as is the implication of a tie to refugia, numerical pyramids and productivity. The next obvious citation is Darwin (1859, especially the cat-mouse-bee-clover chain) although predation events both singular and multiple (e.g. the frontispiece in May 1973) were commonplace in art well before then. Forbes (1877), Pierce et al. (1912) with the first pictorial web, Elton (1927) and his pyramids, and Lindeman's (1942) trophic-dynamics set the stage for the current food web bandwagon and interest. In some sense understanding the consequence of trophic interactions is essential. At the least it is an unavoidable fact of life. How ecologists have approached the subject frames nicely both by contrast and in philosophy, the differences between "static" and "dynamic" ecology.

Static or descriptive food webs. The subject has been an ecological growth industry since Cohen's seminal book (1978) and initial compilation of food webs. The motivation was clear and compatible with the reigning ecological philosophy: data existed in the absence of mathematical examination, the phenomenon was both real and ecologically significant and in an equilibrial world, deduction of generalized and quantitative web properties would be important. Cohen's book remains a milestone. Subsequent interest stimulated both the collection of new material and the recovery/reanalysis of existing observations. As the data base grew, so did the catalogue of patterns. And much like the history of competition, the flurry of interest generated both new data and eventual opposition.

Another landmark publication in the post-Eltonian era is May (1973), who articulated the essential traits necessary to describe, or better, model food web interactions. The number of species, equivalent to "diversity", was important; so was the pattern of who ate whom, which gave rise to the idea of connectance. Connectance necessitates the identification of "links" between consumer and consumed, and for an assemblage is calculated as the proportion of all possible relations that are realized or recognized. Numerous assumptions plague this approach, the most critical one being what con-

stitutes a "link" (May 1983, Paine 1983, 1988). Specific linkage can be inferred from assessments as varied as immunological cues, scatology or direct observation. The problem is, do these links matter, does one include all known relationships or only those arbitrarily thought to have some ecological consequence? The analyses have no ground rules, so linkage at the individual consumer level and collectively at the assemblage level becomes capricious.

The opposition to the continued development of a static food web "theory" takes many forms, mostly generated by field ecologists concerned about aggregation of species into collective units or the appropriateness of previous studies (Paine 1988) or simply the overwhelming fact of real world complexity (Polis 1991). These concerns are valid. However, in defense of attempts to generalize communities and develop patterns, numerous analyses have been done. At the worst, they will fall by an ecological wayside, becoming part of our history and having done no damage. At the best, they will have both stimulated increased recognition of the importance of linkage determination and substantially improved the taxonomy of who eats whom. These by themselves embody a substantive legacy. But is omnivory really rare, are some of the ratios between top, intermediate and basal species scale invariate, are ecological compartments real or a fiction, are food chains short and can most webs be characterized as having only three or four trophic levels (Pimm 1982, Pimm et al. 1991)? Some of the methodological problems might be mitigated by standardizations as suggested by Cohen et al. (1993) although as admitted, the challenges to and cost of improvements are daunting. The history of food webs suggests that in graphic format they were convenient and artistic simplifications of the study system, often being presented to provide an overview of the assemblage and those particular interactions of special interest to the author(s). They were a pedagogical tool and never intended to provide completeness or portray spatial or temporal variation. In newer form the basic information is given as a matrix of predators and their prey (e.g. Hall and Raffaelli 1991, Martinez 1991). Even with this improvement the formalism of food web theory is incapable of addressing how local disturbances or spatially mosaic environments influence the web's properties. Further, because food webs strictly presented intentionally omit competitive links, only indirect effects propagated by trophic interactions can be considered. Many other kinds of mutualistic relationships and even compartments or modules owe their existence to such cross-links (Paine 1980). Current theory actually inhibits incorporation of most mutualisms though these are increasingly recognized as an

important, even dominant, aspect of nature's fabric. A litmus test for static (descriptive) approaches to food web structure will be the extent to which they'll become accepted as a management tool. Spatially localized applied problems, for instance the decision to add or possibly delete or restrict the activities of certain species, or the single-species focus of much conservation ecology, demand highly specific information. Contrary to the optimism of Pimm et al. (1991, p. 674) that food web theory will be increasingly used in "the management of multispecies fisheries, integrated pest control, and predicting the effects of climate change on ecological communities", I believe it will fail the test. The reasons are straightforward: nature is dynamic, not static; linkage strength cannot be inferred from abundance; competitive and mutualistic relations are excluded from current treatments. Because natural assemblages are linked arrays of individuals and species, documenting and understanding the suspected dynamics should become the critical element.

Dynamics and real food webs. Most if not all natural assemblages are composed of highly interactive populations as shown by a literature of considerable antiquity and increasing breadth. Experimental manipulation is not necessary to reveal the ubiquity of these dynamical consequences. The invasion of a small planktivorous fish (the alewife) into a Connecticut (USA) lake produced sweeping changes in the composition of zooplankton populations, altering density, size structure and species make-up (Brooks and Dodson 1965). Natural variation in the abundance of native species can have a similar broad influence (e.g. the account by Birkeland and Lucas 1990, of coral reef devastation by *Acanthaster planci*). Or wanton, uncontrolled exploitation can lead to local commercial extinction, and instigate a series of multi-trophic-level shifts in abundance. Sherman's (1991) description of shifts in species abundances, replacement of assemblages by alternative "states", and management strategies motivated by yield, all occurring at large ($> 200\,000$ km^2) spatial scales, is a testament to the extent to which humans have the capacity to alter globally the fabric of nature. The consequences of sea otter extirpation throughout most of its original range and the subsequent documentation (Estes and Palmisano 1974, Duggins 1980, Estes and Duggins 1994) remains a convincing result based on opportunistic and primarily observational ecology. The change in African savanna grassland ecosystems due to propagation through the food web of the effects of a disease (rinderpest) (Sinclair 1979, McNaughton 1992) provides a terrestrial counterpart. Rinderpest indirectly affected other grazers and predators, canopy cover, the distribution of grasses, litterfall and the prevalence of fire,

and even nutrient dynamics. Assuming that the above examples truly reflect the commotion and change characteristic of natural systems, in what ways might dynamics be added to real and imaginary food webs?

May (1973) is an appropriate starting place. He identified three key attributes of food webs. The static aspects included the assemblage's diversity, accounted for by the number of entries (S) and the extent of their linkages or connectance (C). Dynamics were introduced by a term called interaction strength (i), a per capita estimate of the effect of species j on species i. In May's models this was varied by setting the community value to a mean of 0 with known variance. Webs with many "weak" or feeble interactions had all strengths clustered close to the mean. As variance increased, spreading the distribution, "strong" interspecific interactions became increasingly likely. May's assemblages with randomly chosen coefficients tended to be stable when the expression $i\sqrt{SC}$ was less than 1, and unstable otherwise. Further, two corollaries were cautiously noted. Stable webs rich in interacting species should be characterized by weak relationships, while if strong connections were the rule, there should be relatively few. Further, one could greatly increase the probability of stability by subdividing the community into "blocks" or what has subsequently become known as compartments or modules. The power of May's approach was its random or unbiased basis; its Achilles heel was the nature of the stable assemblage. The intent, however, was never to provide an accurate portrayal of nature but only to suggest the rich implications of dynamical processes for community structure. The harvest of stimulation has yet to be fully realized.

Part of the appeal of May's presentation is its simplicity and relevance. Although no prescription was offered to guide field ecologists in data gathering (which would have been presumptuous) it is certain that species richness (S) and trophic patterns (C) can be derived abundantly from straightforward field work. Adding the dynamics (i) has been the sticking point and one I discuss next. Interaction strengths and thus elements of a community matrix should be derivable from the field. Experimental manipulation may well be essential, but if the goal is achievable, it frees the field ecologist from simply contributing phenomenology to bolster the theoretician's caricatures and conceptions of nature and moves both parties in the direction of a working partnership. I believe the place to start is with the a_{ij} of a community matrix, these per capita relationships between species.

Various schemes to estimate these from the field have been tried before, especially for competition coefficients. The approach originated with MacArthur and Levins (1967), was more fully developed by MacArthur

(1972) and May (1973) and involved the concepts of a resource spectrum and resource utilization curves. It led to the ideas of limiting similarity and niche overlap but it has never been obvious how to order discrete (or discontinuous) components into a resource spectrum or to know what statistical shape the utilization functions might assume. The value of the competition coefficient (a_{ij}) was often estimated from an overlap index computed for the competing species based on their combined use of some resource. Pianka (1969) and Cody (1974) provide the best examples though numerous others of the same vintage exist. Despite its focus and tie to field data, the approach was gradually discarded, predominantly because the underlying assumptions were untestable, competition was assumed to be the only operative natural force, and it was an equilibrial vision of a distinctly disequilibrial world.

Marine ecologists have become fond of applying the term strong interactions whenever a single species' removal or addition produces a striking effect. Chapter III provides many examples. Such results while dramatic, repeatable and, to me, convincing are little more than phenomenology. They document that something significant has occurred; often some of the mechanistic details (food choice, escapes in size) will have been explored but the results rarely are given as rates of specific interaction as opposed to rates of assemblage change. Focus has been on the end point with the transient dynamics ignored. I (Paine 1980) developed a qualitative "model" of such relationships. Strong interactions are identifiable by both the change in prey population distribution and abundance, *and* a cascade of indirect consequences. The problem lay with documenting weak effects, and my suggested approach was flawed.

I have since attempted a more direct evaluation (Paine 1992), by excluding all large grazers, mainly molluscs and chitons, from low intertidal sites, thus permitting development of a reference state of a competitively superior brown alga (*Alaria marginata*). This treatment is the control (C). Different species of grazers are then added to other sites and enclosed there for the manipulation's duration. The terminal density of brown algal sporelings in these experimental (E) treatments relative to sporeling density in the control, combined with knowledge of the manipulation's duration and consumer density (d), permits an estimate of a per capita influence: $(E - C)/Cd$. The basic rationale is that a consumer capable of restricting the development of a competitively superior prey will be a strong interactor, recognized both by its immediate actions and their conferred indirect consequences. Weak interactions will have no quantitative influence on the potential community dominant and therefore could be an inconsequential component at the

assemblage level. The use of a reference state permits the effects of different species to be calibrated against a common denominator. These effects are readily given as a per capita rate and, if one assumes the communities are at equilibrium, directly correspond to the interaction strengths in May's community matrices.

Three results of the study seem especially pertinent to food web analyses. First, both strong and weak, and positive and negative influences were identified. Second, although all the experimental species are grazers, combining them into a single unit would generate an interaction strength which seriously underestimates both the extremes. Aggregation, then, diminishes recognition of potentially important assemblage members. In fact, the presence of positive and negative interaction values within even more restricted taxa (e.g. limpets and chitons) suggests that aggregation should be avoided when possible. Third, because the basic result is cast in a per capita form, it permits two important aspects of density to be addressed. If, for whatever reason, a strong interactor is locally rare, it should be ecologically insignificant within that assemblage despite its potential influence. And if spatial aggregation characterizes some but not other consumers, the specific per capita effect allows pattern resulting from concentrated attack to be identified. This was true in Paine (1992) when sea urchins (spatially concentrated) and a chiton (scattered), both with comparable regional densities and interaction strengths, were compared. Urchins introduce pattern into the benthic algal community whereas the chiton effect is much less obvious. The importance of rates of change and spatial aggregation has a lengthy history in arthropod based, consumer-victim systems (Hassell 1978, Kareiva 1987), and these should be necessary ingredients in all attempts to consider food chain or web dynamics.

Raffaelli and Hall (in press) based on an earlier study (Raffaelli and Hall 1992) have applied the above approach to the Ythan Estuary (Scotland) food web, comprising 92 species and 5518 possible food chains. Their manipulation was to exclude all consumers (or as many as possible) from a soft bottom assemblage, providing a multispecies reference state or control (C), and to compare these prey densities with those estimated from predator inclusion treatments (E). Duration, density and effect are known or quantified, and are attributable to the actions of a single consumer. Assuming that there are no interactions within the treatments that would modify changes due to direct predation, and that resident density was not altered during the experimental interval by recruitment, estimates of interaction strength, i, should be possible. Raffaelli and Hall found little evidence for either strong, negative per

capita interactions or positive ones. Most interaction strengths were weak, implying that compartments will probably not exist and that aggregation into "trophic species" could be possible.

The future of food web research. Because natural assemblages are rich in species linked in various ways, webs represent an appropriate starting point for analysis. As long as webs are defined solely on the basis of known or inferred feeding links they will be oblivious to whole categories of ecological interactions, especially interference competition and many kinds of indirect effects. Development of a community web theory incorporating these thus is essential.

Can this be done for a natural world whose ecosystems are increasingly altered by invasions and extinctions, and where even the assembly of species lists is seriously hampered by incomplete taxonomy? I think not if the approach is entirely descriptive. As Lawton's (1989) fine review emphasizes, "food webs in nature are nested in time and space"; and most studies simply extract a dimensionally convenient portion. Scale problems will remain an especially vexing issue for descriptive data bases. I suggested earlier that one test of their utility would be an application to applied problems by individuals charged with managing resources or restoring assemblages. I believe food web theory as currently constituted will be ignored. A second measure of acceptance would be where experimentalists were stimulated to examine community dynamics in novel ways. Non-interactive or non-dynamical food web approaches, for instance, have had no effect on how Power and her associates design experiments to examine assemblage dynamics in streams (Power 1985, 1990, Wootton and Power 1993), and there is little mention of the subject in experimental studies of whole lakes (Carpenter and Kitchell 1993) centered on the underlying theme of trophic cascades.

Can experimentalists do much better? For applied issues and scaled down systems, yes. However, yet to be resolved is whether per capita dynamics expressed as rates of population change will be more useful than experimentally determined pair-wise outcomes based on understanding of mechanism. Both approaches have an increasing following, both allow interacting pairs to be united into more complex systems, permit the identification of possible higher order interactions, and share the limitation that 5 species have 10 possible interactions, and as few as 10 have 45. The latter number is probably an insurmountable barrier to simultaneous and satisfactory examination. Experimental approaches seem doomed by their inability to confront complexity adequately, descriptive ones by the absence of

dynamics. Community ecology will make only slow progress until a resolution to this dilemma is found. Better descriptions and mathematical treatment based on realistic parameters, leading to testable predictions, seem essential. Without the latter, the development of food web theory is certain to suffer the same scientific extinction as previous plausible and eventually sterile approaches.

V RETROSPECTIVE

Writing this short book has consolidated a personal viewpoint that community ecology is deceptively demanding. It seems a relatively simple matter to record zonation patterns, log in seasonal presence or absence, and even to sample quantitatively. Ecologists have long mastered these procedures, and when helped by an army of skilled amateurs, as especially with birds, have been able to refine observations and identify distinctive patterns. But how much further research has quantification of these patterns generated? Put another way, has this increasingly explicit description of nature expedited our understanding of how assemblages work, convincingly revealed the operation of significant processes, or developed insights on how they might be conserved or even resurrected? I believe the answer, with some qualifications, to be "no". The quest for such detail has been particularly terrestrial, and has avoided taxa or situations in which the assemblage is characterized by wide variation in size/age structure or in which "individuality" is hard to recognize. Marine benthic assemblages represent both these traits in profusion.

What has come from an accelerated pace of description, much of it motivated by a concern to develop a disheartening roster of anthropogenic extinctions and therefore to document an increased loss of biodiversity? One product is certainly a growing catalogue of tropical insects (e.g. May 1992, Gould 1993). Another would be greatly enhanced lists of all species in particular biotopes as some ecologists attempt to assemble a taxonomically complete description of a food web (e.g. Martinez 1991). Endeavors such as these are necessary but unfortunately cannot provide unambiguous information on how the species coexist, how vulnerable they might be to change, whether they will respond individually or in the collective blocks I have called modules and others have referred to as compartments (Paine 1980, Pimm and Lawton 1980, Yodzis 1982), or what roles they might play in organizing the community.

What the availability of these quantitative lists has achieved is the stimulation of a massive and often creative effort by theoreticians to detect pattern. Such lists are seemingly irresistible research material. Williams' (1964) statistical evaluation of frequency distributions of moths is an early example. Preston's (1948, 1962) development of log normal approaches is another, and of course there are MacArthur's numerous contributions, e.g. the "broken stick" model for the distribution of individuals per species

within an assemblage (1957), geographic patterns of bird abundances (1961, with Klopfer), and especially models of dynamic biogeography (1967, with Wilson). Only the last has survived relatively unscathed. Most of the recent food web catalogues would qualify as patterns seeking explanations and I have discussed my reservations about these earlier. At a more population level, the deep acrimony resulting from the models of niche diversification, limiting similarity and coexistence initially presented by MacArthur and Levins (1967) has probably not served ecology well. One summary view can be found in Simberloff (1982). The efficacy of derivative approaches based on observation has been equally debated (see Strong et al. 1984 for details). Although these have produced a much deeper appreciation of both the need for and difficulty with neutral or null models, the imputed patterns of absence, presence and coexistence would still benefit enormously from explanations which were more mechanistic and less inferential. That is, it would help if the hypotheses were experimentally testable or falsifiable although it should be acknowledged that the protected status of some taxa, site remoteness, or absence of appropriate technique may inhibit or retard scientific examination.

In Chapters III and IV, I provided examples of the insights gained by applying an approach historically distinctive to rocky shore assemblages and largely absent from terrestrial ecology. This "style" has been developed to be appropriate to intertidal inhabitants that are largely indeterminate growers, meaning that local populations are characterized by different and often highly divergent size distributions (Ebert 1968, Paine 1976). In addition, mobile and sessile species often compete for the same space. Although mass per unit area might provide the clearest estimate of space utilization, it does not translate easily into information about density or a species' functional role. The related problem of evaluating the spatial boundaries of an "individual" is equally obtuse. For example, if the individual is territorial, what size spatial domain should be used? Or, how can one equate a limpet and a clone of anemones, or a single *Fucus* with a mat or sheet of green algae? Because the answers remain unknown, analyses of community or of assemblage composition remain essentially untried. Root's (1967) concept of a guild, a suite of similar but not necessarily closely related taxa exploiting some environmental resource in a common fashion, remains an attractive means for both restricting terrestrial comparisons and aggregating species into functional units. For marine systems, however, where the resource in short supply for many species, belonging to many phyla and even kingdoms and often characterized by radically different life histories, is two-dimen-

sional space, the guild concept becomes inoperable. There is also the role played by a lengthy tradition of manipulation which began for most purposes in the early 1930s. Seemingly modest alterations in abundance of one species often produced large changes in the identity and abundance of the associated flora and fauna. The implication that naturally driven variation (e.g. Fauvel 1901) could also generate major shifts in assemblage pattern surely suggested a cautious approach to interpreting and generalizing from point samples. Recognition that the organisms inhabiting rocky shores are in some kind of biological disequilibrium goes back at least to Fischer-Piette (1935). Under such circumstances interpretation or extension of samples or observations employing some static model seemed inappropriate, and they were seldom applied. The point is this: on conspicuously and demonstrably dynamic shorelines change is expected and snapshot impressions, even if taxonomically and descriptively accurate, may provide only a poor predictor of future patterns. I now turn to the best marine example of this disharmony between static and dynamic overviews known to me, one which also conveys an essential applied message.

(1) Human Exclusions from the Rocky Shoreline of Chile

People have, for thousands of years, inhabited the shorelines of central and northern Chile. Geography and climate concentrated them along a slender band between the ocean and exceptionally xeric coastal regions and high mountains. Abundant middens attest to utilization of nearshore marine resources. For instance, the study site about to be discussed has been under human influence since about 700 BC (Montané 1964, Schiappacasse and Niemeyer 1964). The initial ecological surveys (Guiler 1959a, b) were entirely descriptive. Guiler's papers catch the essence of this relatively homogeneous marine assemblage: high zones of barnacles, a band of a small-bodied mussel (*Perumytilus purpuratus*) and lower yet, a region characterized by coralline algae, grazers and starfish. Below this, large laminarialian brown algae begin to appear. There is nothing exceptional to this pattern, and it was one readily accommodated by Stephenson and Stephenson (1972) in their descriptive catalogue of the world's rocky shores. I should add, from personal experience, that Guiler's general descriptions hold from Iquique (20° S) to at least the large island of Chiloe (44° S). Guiler's surveys

provided useful and adequate descriptions, especially considering his inspection of an assemblage certainly foreign to him and characterized by minimal taxonomic resolution. Can one examine his work and infer the underlying dynamics? Not at all, but the evidence has only come from a series of intensely revealing "human exclusion" experiments.

The initial or at least first effective exclusion (Moreno et al. 1984) was carried out from 1978 to 1982 on a 6000 m^2 reserve near Mehuin, Chile (39° S). The exclusion site was representative of a semi-protected rocky shore traditionally exploited by "mariscadores" or shoreline harvesters. Algae and invertebrates are taken both for local consumption and export. Harvesting effort varies with proximity to human population centers but appears ubiquitous and intense at regional scales. Most harvested molluscs are consumed locally but in 1981, for instance, 2115 tons (wet weight) of the dominant intertidal red alga *Iridaea boryana* was shipped from this region to Japan. Intertidal areas external to the reserve tend to have percent covers of *I. boryana* ranging from 40 to 90%; at the same sites the density of the harvested keyhole limpet *Fissurella picta* varies from almost none to 2 m^{-2}. Human exclusion initiated in May 1978 generated a reversal in the reserve of
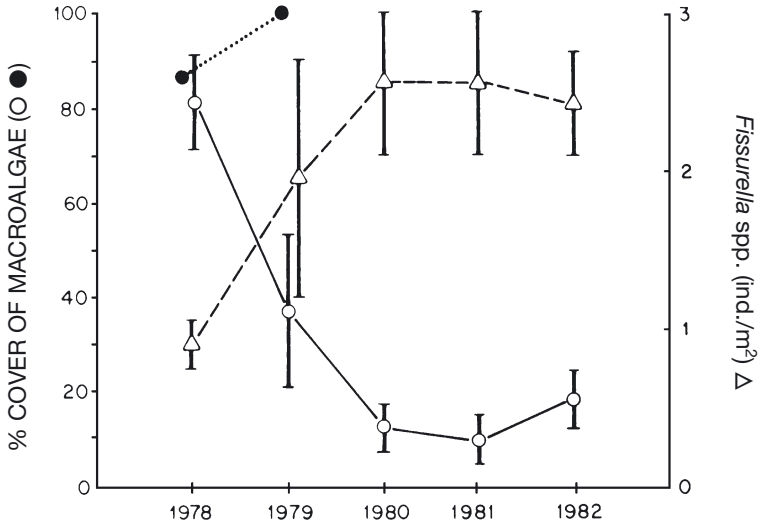

Fig. 14. Changes in the percent cover of macroalgae (mean ±1 SD, n = 3) and herbivore density (mean ± 1 SD, n = 3) subsequent to human exclusion beginning in May 1978 at Mehuin, Chile. ● indicates changes in algal cover on a single herbivore removal rock within the reserve. (From Moreno et al. 1984)

these conditions by November 1981: less than 5% cover of *I. boryana* and an increase in *F. picta* density to 2.8 m^{-2} (Fig. 14). Protection had also changed the limpet population size structure from modes less than 4 cm shell length in exploited areas to occasional 10 cm individuals in the reserve. An irony, probably typical of strongly linked consumer-resource interactions, is that "Probably unbeknownst to them, Chilean fishermen are managing the intertidal zone in a way which produces a cash crop they wouldn't otherwise have" (Moreno et al. 1984, p. 159). Other manipulations of herbivore density (Jara and Moreno 1984) confirm the basis of this pattern.

In 1982 a more ambitious undertaking was initiated at Punta El Lacho, near Las Cruces (33° S), by J. C. Castilla and his coworkers. The exclusion or non-harvested area includes about 500 m of waterfront. Access is restricted by a chain-link fence; control areas of equal dimension, to which human access is unrestricted, are adjacent. Duran and Castilla (1989, p. 561) describe the resultant changes in the non-harvested area.

> Hence, the exclusion of a top predator (humans) in the rocky intertidal resulted in an increase of a key-stone predator: *Concholepas concholepas*, and two species of herbivorous key-hole limpets. In turn, the increase of *C. concholepas* reduced the cover of *Perumytilus purpuratus*, a dominant competitor, favoring settlement of macroalgae in newly available primary space. This state is transient, since macroalgae were subsequently eliminated from the system (most probably due to grazing by key-hole limpets). After five years, the community at the non-harvested area was dominated by barnacles.

Fig. 15 (overleaf) portrays these continuing changes within the exclusion site. Although the list of resident species remains essentially identical through time, their transient dynamics, interactions and spatial distributions continue to be modified. If the abundances of highly mobile birds, fishes and crabs, all known to exploit benthic resources, can themselves adjust to a relatively small spatial scale human exclusion, the shoreline pattern can be anticipated to change further. Could any of these results have been anticipated? I am tempted to answer "yes" if one only sought the outcome of a pair-wise encounter. However, despite detailed "natural history" observations and extensive quantitation gathered by skilled and dedicated biologists, a more synthetic forecast of the ecological outcome of this single-factor manipulation remains impossible. The lesson is not that the details are faulty or even incomplete, but rather that the results of complex dynamics in multispecies assemblages remain well beyond the predictive grasp of ecologists.

The data supporting the results of this unreplicated but demanding manipulation are extensive and convincing. Table 7 indicates the general effect of effective human exclusion. Data before and after, or with and without, humans are available for the large alga *Durvillaea antarctica* (Castilla
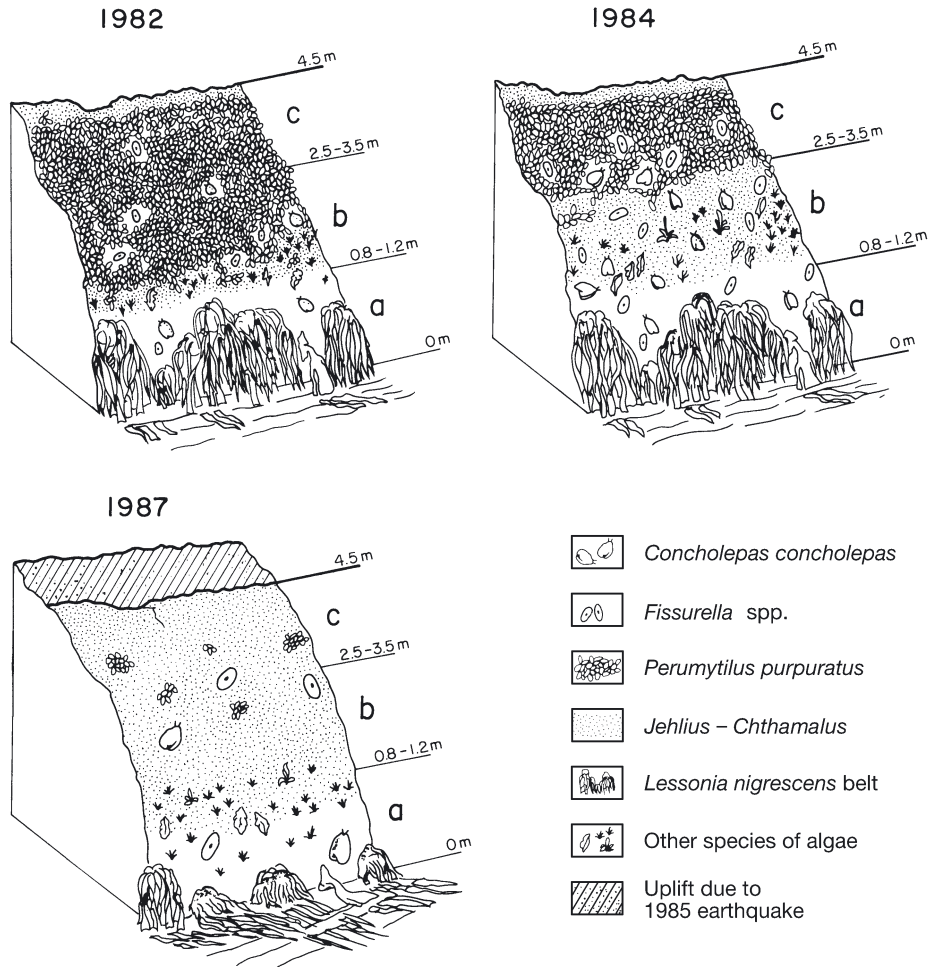

Fig. 15. Three schematic views of biological change on an exposed rocky shore at Las Cruces, Chile, following a human exclusion procedure initiated in December 1982. The 1982 overview represents the "before" condition; the gradual transition from a mussel- to a barnacle-dominated shoreline and increasing body dimension of the mobile consumers (*Fissurella* spp. and *Concholepas conchopelas*) are illustrated. (From Duran and Castilla 1989)

and Bustamante 1989), *Concholepas concholepas*, the carnivorous gastropod whose activities play a major role in organizing the entire assemblage (Castilla and Duran 1985), and keyhole limpets (Oliva and Castilla 1986). A complementary analysis (Duran et al. 1987) on the intensity of human predation on adjacent shores completes the picture: along 1.5 km of harvested shoreline, the mariscadores extract annually about 61 000 *C. concholepas*, over 130 000 keyhole limpets, and almost 6 000 sea urchins. When all gastropod and urchin species are considered, the estimated annual harvest amounts to about 140 individuals per linear meter of shore. The take by skin-divers adds substantially to these figures. The main point is this. There remains a sense of relative homogeneity to the rocky shoreline of central Chile, especially when one factors in variations in surface slope, the presence of sand and wave exposure. I believe one could use intensive observations along one stretch of this shoreline to predict accurately the zonation pattern and even the densities of the major constituents elsewhere. There is surprisingly little qualitative difference between Guiler's 1955 overview and the patterns described by Castilla and coworkers in the 1975 to 1990 interval, *in the presence of human exploiters*. This successful prediction, though, would miss entirely the critically important roles played by humans and *C. concholepas*. One can obviously describe and predict without understanding. If one wished to restore or manage this shoreline, however, the insights on process gained from the human exclusion manipulations would provide essential and necessary information.

Table 7. Standing crop mass (*Duvillaea antarctica*), shell length (*Fissurella* spp.) or density (*Concholepas concholepas*) of four exploited species characteristic of a mid-intertidal zone in central Chile before and after human exclusion

Species	Harvested or control area	Human exclusion site:		Duration of exclusion
		Before	After	
D. antarctica[a]	~100 g m^{-2}	~100 g m^{-2}	200–300 g m^{-2}	52 mo
F. crassa[b]	~ 29 mm	–	39 mm	30 mo
F. limbata[b]	~ 20 mm	–	35 mm	30 mo
C. concholepas[c]	0.4 ind. m^{-2}	0.5 ind. m^{-2}	4.3 ind. m^{-2}	19 mo

[a] Castilla and Bustamante (1989)
[b] Oliva and Castilla (1986) (exposed, mid-intertidal levels)
[c] Castilla and Duran (1985)

Much the same point could be made about the northern sea otter and its influential role in subtidal rocky shore assemblages from at least the Oregon coast, USA, northward. Shorelines with and without otters (Estes and Palmisano 1974) or before and after invasion (Duggins 1980) are conspicuously different in size and density distributions of numerous species, their rate of recruitment, and the rate of primary production and sources of fixed carbon for suspension feeders (Duggins et al. 1989, Estes and Duggins in press). Fig. 16 illustrates these order-of-magnitude differences in measures of kelp (primarily *Laminaria groenlandica*, *L. longipes* and *Alaria fistulosa*) presence, an influence demonstrated to translate into enhanced barnacle and mussel growth rates where otters are present and hence kelp-based detritus, both dissolved and particulate, is especially available. As in coastal Chile, comparative species lists would probably show few if any differences and local extinction is not an issue. However, the structure of the assemblage, as defined in Table 1, because it is reactive to changes in the underlying processes, has been altered substantially by the activities of a high-trophic-level consumer.
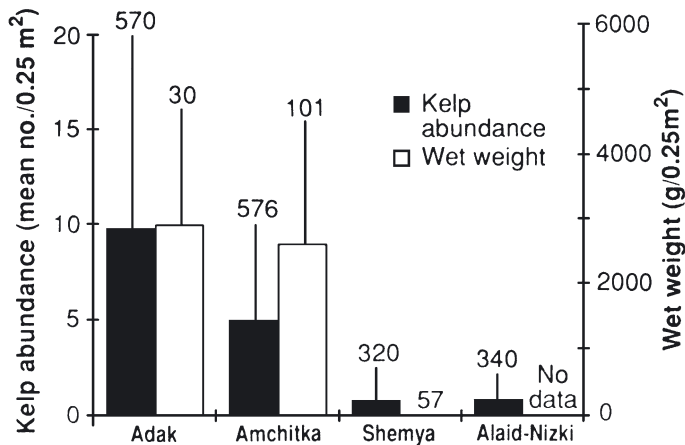

Fig. 16. The influence of sea otters on kelp abundance and biomass at Aleutian Islands with (Adak, Amchitka) and without (Shemya, Alaid-Nizki) resident otter populations. Sample size is given above each error (1 SD) bar. Kelp biomass at Shemya = 0. (From Duggins et al. 1989)

(2) Generalization of the Human Impact

I have no intention of implying that the Chilean rocky shoreline is uniquely over-exploited. In fact, it is not. I considered it because it provides the clearest evidence for the extent of biological changes produced by human activities whether they be recreational or commercial. Evidence is globally widespread that rocky shore assemblages have been degraded, as examination of almost any shore close to urban centers or at sites subject to centuries of human activity indicates. I have seen shores in Japan and the eastern Mediterranean essentially picked bare of all but the smallest invertebrate or benthic alga. Such rampant plundering is not confined to regions of exceptionally great human population density. Hockey and Bosman (1986) identify changes in the molluscan assemblage adjacent to coastal villages in South Africa, with the major modification being in size structure of the exploited species. Density was a less meaningful metric. Protected islands off the California, USA, mainland have abalone (*Haliotis* spp.) densities currently unknown at more accessible and exploited mainland sites. In the vicinity of Seattle, Washington, USA, Carney and Kvitek (1991) documented the disappearance of one invertebrate species, numerical declines of others and anthropogenic threats to still more. Users of the resource ranged from groups of school children to researchers, biological supply houses and consulting firms. Twenty-nine percent of the gatherers were collecting invertebrates as food, twenty-two percent for bait. Underwood and Kennelly's (1990) research proposition is based on similar motivation and concerns: rock platforms near Sydney, Australia, are visited by thousands of individuals who look, stroll, exploit or fish. Their pilot study was aimed at acquiring the knowledge essential to the design of larger scale surveys which would be used to assess the human impact and eventually manage it. Keough et al. (1993) describe the difference in gastropod population size structure and a time-based measure of collectability between sites available to the public in South Australia and those protected by a rifle range. Human, recreational foraging produces pronounced changes in the desirable species.The general implication is that human activities are producing sweeping modifications in the structure of near-shore communities. Since most people live relatively close to the land-sea margin (Steele 1991) and our planet is increasingly characterized by the problems attendant to human overpopulation, the situation is hardly surprising.

Furthermore, believing that such effects will be confined to that small fraction of the biosphere called shoreline (or beach, etc.) is dangerously self-serving and unwarranted. Van der Elst's (1979) reconstruction of the change in the near-shore fish assemblage near Durban, South Africa, as the result of protecting swimmers from oceanic sharks is a startling example. The observed consequence of effective and long-term shark removal is a change in fish populations dominated by teleosts to one in which small sharks and rays predominate. Because larger sharks eat smaller ones, a reasonable mechanism involves proliferation of small shark populations following severe reduction of their major predator. Witman and Sebens (1992) suggest that long-term (ca. 300 years) systematic reduction in near-shore predatory fish stocks (primarily cod) off New England, USA, has led to population increases of crabs and other mobile epibenthos. Because crabs themselves can be important consumers, there are implicit but undocumented indirect consequences. Finally, Springer (1992) has reviewed the evidence that wall-eye pollock play a key role in the organization of the North Pacific ecosystem. The pollock — presently the largest single species commercial fishery in the world — is subject to substantial harvesting pressure. Although it is premature to attribute the 50 to 80 % drop in sealion numbers, and comparable or greater declines in two seal species, murres and kittiwakes to changes in pollock numbers, population size structure and availability, it remains a likely possibility. All of them consume pollock and both estimated pollock numbers and biomass have been declining for at least the last decade. If a cause-effect relationship can eventually be demonstrated, the implications are dismal, for that ecosystem occupies millions of square kilometers and is "open" in every sense of the term. Although I would like to, I cannot agree with Cohen's (1993) optimistic vision of an intensively managed yet beautiful "global garden" a century from now. Human greed, overpopulation and, above all, general disrespect for all other life forms will have exacted its toll. We are dismantling earth's ecosystems at an accelerating pace, and the prospects for sufficiently understanding community assembly rules or the direct and indirect consequences of interspecific interactions seem increasingly bleak.

(3) The Value of "Pristine" Environments

Human activity has probably influenced all environments and species. In this sense no truly pristine situations remain, and all will become increasingly altered by stresses stemming from such direct impacts as exploitation or point-source pollution, or the more subtle and less direct effects of global warming, changes in the concentration of atmospheric gasses, the elevation of sea levels, or the destruction of the ozone layer. Dependent on the relative sensitivity of marine larvae or recently settled spores or other propagules to increased ultraviolet radiation, the latter might be the most significant. It would operate by increasing mortality rates during the poorest known yet potentially most critical life history stages.

There are obvious esthetic and moral reasons for maintaining ecosystems or at least samples of them in as biologically complete a condition as possible. Such concerns underlie the biodiversity issue and certainly power much of the effort to conserve, whether at the scale of local bogs or shores, or systems of natural parks. In many respects scientific study can be nourished by opportunities to examine these preserved or quasi-pristine samples of the real world. Thus, to the extent that disrupted communities are poorer in species and pattern, they will also be less stimulating. More enduring ecological ideas have been generated by examining coral reefs than sewage outfall assemblages.

There is at least one perverse consequence of ecosystems becoming anthropogenically simplified, or at least ecologically homogenized: research may be easier to conduct. Fewer species suggests fewer interactions to be sensitive to. Relative homogeneity becomes important if and when the real world is designated as the "control" to some manipulation. Thus, although I know of no marine examples, I suspect that managed crops (e.g. wheat/corn/ *Pinus radiata*) are probably characterized by substantial reductions in both species richness and habitat dimensionality when compared to the natural assemblages they replaced. Although such assemblages share the features of unnaturalness (artificiality) and ecological simplicity with the "reference states" (Paine 1984) discussed in Chapter IV, they depart in two critical ways. First, the reference state organism should be a native to the system under investigation. Second, it should attain its local dominance by superior competitive abilities, even if full expression of these is contrived through intervention. Neither of these needs to be true in anthropogenically simplified systems. The dominant

organism may well be introduced, in addition it may have to be protected or nurtured chemically.

Finally, the most important feature of quasi-pristine environments is perhaps that in them one might hope to glimpse the full array of ecological interactions, both direct and indirect, that characterize the resident species. Community ecologists have long been interested in emergent properties, especially stability. If all species were equivalent in the strengths of their interactions, a condition I have argued to be highly unlikely, then the deletion of a relatively few species should be of little overall consequence. If large species-specific disparities in interaction strengths exist, if there are critical or keystone species, then the identity of the missing species becomes important. Rocky shore assemblages may harbor a disproportionate fraction of demonstrably critical species, for it seems certain that the addition or elimination of *Pisaster ochraceus*, sea otters, *Concholepas conchopelas*, *Acanthaster planci*, spiny lobsters and certain urchins will lead to sweeping community changes. All these have been shown experimentally to exert, or could be argued to exert, a major influence on assemblage patterns. Some of these species are an economically valuable resource, others are not. Some, under normal conditions, can be relatively uncommon and hence role is decoupled from abundance. The magnitude of change subsequent to either their elimination or re-entry provides an invaluable clue to the importance of interactions to the observable structure of these assemblages. When such species appear only as fossils, or in verbal tradition or even fond memories, it may be nearly impossible to reconstruct the full adaptive environment in which the surviving species evolved. Most species will not be critical species; all, however, will be subject to the process of natural selection. When the full array of interactions becomes unavailable, and possibly replaced by novel and potentially misleading ones, the important bond between a species' evolutionary history and its current ecological interactions is increasingly difficult to interpret. In this sense the scientific loss approaches the esthetic one. We will never understand the manifest complexities in community ecology, never disentangle Darwin's tangled bank, without the benefit of the intuition and biological appreciation garnered by studying nature the way it has evolved, rather than the alternative and dismal shadow associated with accelerating human intervention.

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About the Author and the Book

Professor Robert T. Paine is the recipient of the ECOLOGY INSTITUTE PRIZE 1989 in marine ecology. Born in Cambridge, Massachusetts (USA), in 1933, our Laureate graduated from Harvard College, then went on to the University of Michigan, where he received his Ph.D. He is now Professor of Zoology at the University of Washington. His teaching and research have stimulated, deepened, and widened our concepts of ecology. They draw their main inspiration from his work on rocky intertidal assemblages.
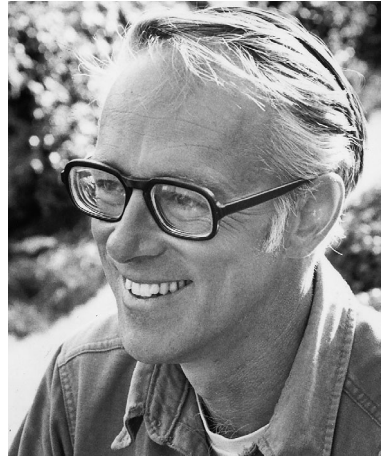
Chaired by Professor Tom Fenchel (University of Copenhagen, Denmark), the ECI Jury selected Bob Paine for his substantial contributions to marine biology and ecology. Paine significantly advanced the understanding of the role of patch

Robert T. Paine

formation and of the properties of food web structure in shaping communities of sedentary organisms. He thus fundamentally changed the way in which we view marine benthic communities. His publications have also served as guidelines for new mathematical descriptions of community processes and they continue to further our understanding of 'landscape dynamics', which are of importance to the development of scientific and conservation ecology.

This book focuses on population biology and community ecology, viewed from the perspectives of a naturalist and experimentalist. Its primary theme is that the facts garnered by observation on or measurement of behaviour, sampling abundance, distribution or habitat features, when explored by appropriate experiments, permit patterns to be explained in terms of their underlying processes.

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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 promising young environmental scientists in Eastern European countries by providing financial assistance for professional travel and scientific equipment. Each ECI Prize Laureate is requested to author a book taking into account ECI's aims and addressing an audience beyond professional boundaries. 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 representatives of modern environmental sciences are offered the possibility of disseminating their personal views on current ecological issues, and of serving the general public who financed their studies in the first place and who depend acutely on definitive ecological knowledge for planning our present and future.