

**PATTERNS AND CAUSES OF INTERTIDAL COMMUNITY
STRUCTURE AROUND THE COAST OF SOUTHERN AFRICA**

by

Rodrigo H. Bustamante

Thesis submitted for the degree of Doctor of Philosophy

Faculty of Science

University of Cape Town

March 1994

The University of Cape Town has been given
the right to reproduce this thesis in whole
or in part. Copyright is held by the author.

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

DECLARATION

This thesis documents original research, carried out in the Zoology Department, University of Cape Town, between 1989 and 1993. It has not been submitted in whole or in part for a degree at any other university. Most of the data presented here are original and any other sources are fully acknowledged. Any uncited interpretations are my own and any assistance I have received is also fully acknowledged.

Signed by candidate

R. H. Bustamante

29.03.94

Date

*To my wife Sol for her continual support and love, to my parents Ester and Ociel
for their love and encouragement to pursue a scientific career.*

TABLE OF CONTENTS

Acknowledgments	5-6
Abstract	7-9
General Introduction	10-20
Chapter 1: <i>Biogeographic Patterns and Trophic Structure of Southern African Rocky Shores</i>	21-51
Chapter 2: <i>The Influences of Physical Factors on the Distribution and Zonation Patterns of the South African Rocky-Shores Communities</i>	52-86
Chapter 3: <i>Patterns of Intertidal Productivity on Rocky Shores Around the Coast of South Africa, and their Relationship to Consumer Biomass</i>	87-113
Chapter 4: <i>The Dependence of Intertidal Consumers on Kelp-Derived Organic Matter on the West Coast of South Africa</i>	114-149
Chapter 5: <i>Maintenance of an Exceptional Grazer Biomass on South African Intertidal Shores: Trophic Subsidy by Subtidal Kelps</i>	150-185
Chapter 6: <i>The Dynamics of an Algal-Limpet-Kelp Interaction: an Ecological and Resource Management Simulation</i>	186-218
Chapter 7: <i>Synthesis</i>	219-232

ACKNOWLEDGMENTS

In the making of science, several conditions converge to produce relevant contributions to knowledge. Of these a challenging work environment and positive human relationships, are in my opinion, among the most important. Of that I had plenty! I am deeply indebted to my supervisor George M. Branch, who 'imported' and introduced me to the wonderful and unique living shores of southern Africa. His sharp, inquisitive and practical way of doing science greatly improved this project. I also thank him for the immense amount of energy, time and sleepless nights devoted to criticizing all stages of this thesis, but over all I thank him for his support, encouragement and friendship.

The final manuscripts of this thesis were greatly improved by the comments and criticisms of many colleagues: Wayne M. Getz introduced me to the 'metaphysiological' realm of modeling ecological systems (Chapter 6); Charles L. Griffiths patiently corrected my first English draft (Chapter 5); Phillip A. R. Hockey also helped my 'Spanglish' and made useful and pertinent comments on the content of my writing (Chapter 1); Colleen L. Moloney helped with the development of the filter-feeder model (Chapter 4); Peter Ryan, and Eva Plagányi made valuable comments on earlier manuscripts (Chapter 6) and Rob Day criticized and improved my statistical analyses (Chapter 5); and Sergio Navarrete did an excellent review of an initial draft (Chapter 5). Many people helped me to collect the samples of primary production taken around the coast, for that I would like to thank Bruce Robertson, Peter Zoutendyk, Arthur Dye, Mike Schleyer, Nick Hanekom, Derek Keats, Michelle Jurd and Christopher MacQuaid for their valuable help (Chapter 3).

The information synthesized in this project is the result of an immense effort to collect biological data across the borders of three countries and over *ca.* 5000 km of shoreline around the southern African coast. In this process, many colleagues and friends assisted in the sampling and data collection. Here I would like to thank Alison and Ricco Sakko for their logistic arrangements, financial support and creation of the Groenrivier Research Hut (Namaqualand). Long, wet days and nights were devoted to field work, during which a number of people gave me invaluable help. For that I would like to thank my wife Sol for her support and still 'unpaid' years of field assistance. I especially thank Lisa Kruger for her help, sincere friendship and patience in my first lessons of 'street survival' English and Sean Eekhout for his help and quick mind in the designing and setting of field experiments...and his tasty cooking! To Margo Branch, Claudio Velásquez, Alice Linton, François Odendaal, Tracy Phillips, Ian Davidson and John Boland, for their hard work and companionship during the extensive, but fun field work! Jorge Alvarado 'cheaply' helped me during the last and frantic stages of the data punching.

I would like to thank John G. Field for his initiative and drive behind the Marine Biology Research Institute (M.B.R.I.), and his wise vision of a Macintosh-dominated computer world! I am also greatly indebted to Carlos Villacastin-Herrero for the superb computer support, advice and friendship. René Navarro patiently helped me to disentangle the huge data matrices used in this project.

I am grateful for the support of my friends, in particular those in J. G. Field's laboratory, Patty Wickens, Jan Korrubel, Roger Krohn, Eva Plagányi, and Sandy Tolosana, for bearing my loud voice and messy behaviour. I also greatly appreciate the advice and feedback of Steve Tugwell, Brian Tibbles, Colin Atwood, and Jean Harris who were always available for my continual questions and problems. I would also like to thank Liz Reynolds for her inspired suggestions and comments during the isotopic analyses.

Financial support for this project was received from the FRD Core Program, and FRD-DEA Joint Venture *Conservation and Exploitation of Rocky Shores*. During the course of this project I was personally funded by the FRD Doctoral Bursary, UCT Foreign Student's Scholarship, UCT Postgraduate Research Grant, UCT Doctoral Travel Grant and the M.B.R.I. Postgraduate Scholarship.

Last but not least, I would like to thank my Chilean mentors, Juan C. Castilla who nine years ago gave me my first 'taste' of the field of intertidal ecology and guided the initial steps of my career as a marine biologist, and my brother Ramiro O. Bustamante who set the example for my scientific endeavour. I also especially thank my friend Ernesto Ortíz who with his bright and controversial mind motivated and challenged all my experimental and quantitative 'appetites', Juan Cancino gave me a balanced guide to experimental ecology, Patricio Bernal encouraged me to pursue a scientific career, and finally, I thank Mario George-Nascimento who through his beatnik and psychedelic eyes discovered my scientific interests 16 years ago.

ABSTRACT

A biogeographic analysis was undertaken using data for intertidal rocky-shore communities obtained from quantitative biological surveys made around the southern African coast. Substantial differences in species composition, abundance and trophic structure were found between 15 different rocky shores along *ca.* 5000 km of coast. These differences allowed the division of South African coast into three major biogeographic provinces. The large-scale variations were due to geographical differences in the physical environment including temperature, nutrients and primary production. Large-scale and local-scale vertical and horizontal zonation of intertidal communities were investigated. Local-scale variations were largely due to the effect of differential wave action, but also included the vertical gradient of desiccation. Gradients of wave action generate divergence of the mid-to-low zone communities, whereas in the upper shore communities converge due to the desiccation gradient. The consistent repetition of the vertical and horizontal patterns of patterns of distribution for both community biomass and species richness lead to the conclusion that the physical processes involved in the creation of local patterns also operate over a large geographical scale.

The patterns of community structure on southern African rocky shores are investigated in relation to *in-situ* primary production and micronutrient concentrations. A conspicuous gradient of intertidal primary production was found. The west coast exhibits significantly higher levels of primary production than the south and east coast. Nutrient concentrations in intertidal waters parallels *in-situ* primary production. It is concluded that nutrients are responsible for the levels of *in-situ* intertidal primary production. The availability of nitrogen on the west and south coasts, and phosphorus on the east coast, are likely to be the factors controlling intertidal primary productivity. The biomass per-unit-area of the intertidal primary consumers was related to levels of *in-situ* productivity. The levels of biomass achieved and the large-scale variation of community biomass are strongly influenced by the gradients of productivity, while local-scale variation is dictated by wave action.

Trophic linkages between the intertidal and subtidal ecosystems were explored for the west coast intertidal rocky-shore communities. The extent of the dependence of intertidal consumers to subtidal macrophyte production is explored using double stable isotopes analyses. The results demonstrated that intertidal invertebrate grazers and filter-feeders depend to a large extent on the subtidal production of kelp as their main sources of organic carbon and nitrogen. In particular, the bulk of the particulate organic matter on intertidal waters is kelp-derived detritus. This is the major source of food for intertidal filter-feeders. The combined effects of a steady food supply (kelp detritus) and water turnover are likely to be sufficient to explain the observed abundance of filter-feeders on exposed rocky-shore communities. Two extremely abundant and specialized limpet species also depend on subtidal kelp as their main source of carbon and nitrogen. It is clearly evident that for west coast intertidal communities, the subtidal primary production is likely to determine the levels of secondary production of the intertidal ecosystem (i.e. a bottom-up effect).

Semi-exposed and sheltered shores of the west coast are dominated by two unusually exceptionally abundant limpet species, *Patella argenvillei* and *P. granatina*. How these populations are maintained was investigated in the light of the apparently limited food supply. Highly specialized feeding behaviour was found. Both limpet species feed on the intertidal *in-situ* algal production and on fronds of subtidal kelps. Both species feed on the same food sources, but clear differentiation on habitat, timing and feeding mode were found. If access to kelp is experimentally denied, both limpet populations experience an increased mortality and a significant reduction of individual body mass. The results led to the conclusion that the high abundance of these limpet populations can only be sustained if they are trophically subsidized by the subtidal kelp production. This is direct evidence of magnification of intertidal secondary production by subtidal primary production. The net effect is that this trophic subsidy by subtidal kelps magnified the limpet carrying capacity, and only the availability of space sets the upper limits to their biomass.

An individual-based model is used for the simulation of the dynamics of an algal-kelp-limpet system. A metaphysiological approach is used under the assumption that this biotic interaction can be treated as a predator-prey system. The model predicted the standing stock of limpets, and is used to a) investigate the extent of dependence on either the *in-situ* algal production or subtidal kelp input, and b) to predict limpet standing stocks under various harvesting regimes for a hypothetical limpet fishery. It is discussed how sound ecological processes can be employed to complement traditional resource management policies.

GENERAL INTRODUCTION

Since the early 1970s, ecology has increasingly focused on small-scale events and become experimental in approach. Most of the big questions about community structure and organization remained elusive, inducing scientists to concentrate on particular problems that could be solved. In answer to this deficiency, more recent research work has simultaneously addressed large- and small-scale ecological patterns and processes over large geographical areas. This approach has helped scientists to gain insights about the relationships between micro- and macroscopic ecological phenomena and general processes that determine the landscape of biotic communities (Brown and Maurer 1989).

Whether ecological communities exhibit a patterned structure or consist of a random collection of species has long been a central issue of ecological studies. However, there is enough evidence (empirical and theoretical) to conclude that there are some assembly rules that govern community patterns (Drake 1990). These rules are normally hard to uncover because of our inability to "see" overall large-scale patterns and, more importantly, past events that have shaped extant biological communities. Nevertheless, insight into the potential rules can be gained, using both comparative and experimental approaches, by focusing in the common mechanisms involved in community assembly (Cale *et al.* 1989).

In ecological communities, variation in space and time is the rule. However, despite this variation, their organization and structure often exhibit consistent trends along a changing environment (Whittaker 1975; Brown 1984). Both physical and biological factors operate on ecological communities over a range of spatial scales, and the degree of influence of a given environmental factor depends on the spatial scale over which it operates (Menge and Olson 1990). Several models and/or generalizations have been proposed to explain variation and organization of assemblages of species in natural communities. However, they have often been too particular, operating at a very local scale, and most of them are based on the assumption that biotic interactions are the main

factors driving the structure of communities (e.g. Hairston, Smith, and Slobodkin 1960; Paine 1966; Cody and Diamond 1975; May 1975; Caswell 1976; Menge and Sutherland 1976; Connell 1978; Lubchenco 1978; Inouye *et al.* 1980; Menge and Sutherland 1987). Although many of these models were originally proposed for terrestrial systems, an increasing proportion of them have been derived for marine habitats, specifically intertidal rocky shores.

The early history of intertidal ecology consisted of detailed accounts of small- and large-scale patterns of intertidal communities (e.g. Lewis 1964; Stephenson and Stephenson 1972). Since these early works on patterns and structure, intertidal rocky shores have been successfully used to test the mechanistic effects of competition and predation on their biotic communities, most studies dealing with temperate habitats (e.g. Connell 1961; Paine 1966; Dayton 1971; Underwood 1978; Menge 1976; Lubchenco and Menge 1978; Underwood 1980). Much of this intertidal work was done in wave-exposed habitats, giving little importance to less glamorous semi-exposed and protected areas where different suites of species exist (Dayton 1984). Consequently, many of the generalizations that have arisen from these works have limited applicability, since organisms are regulated by different processes in different habitats, and even within a particular habitat type, communities do not always contain clear-cut competitive dominants and/or important predators (Underwood and Denley 1984).

Some of the generalization (at least for intertidal communities) arisen by those pioneer works have been less applicable than other, this has stimulated the need for comparative studies that investigate variations of community patterns over spatial scales ranging from meters to thousands of kilometers (Mann and Lazier 1991). A recent review on community structure and interaction webs of shallow hard-bottom marine communities stresses the need for a comparative approach for the inspection of large- and small-scale community variations, to develop a conceptual framework which deals with the relative importance of ecological (biotic) and environmental (abiotic) factors influencing community structure (Menge and Farrell 1989).

The starting point for the development of general principles about community dynamics depends on quantitative descriptions of natural patterns (Whittaker 1975). In this context, a great deal of research has been done on the rocky shores of southern Africa (e.g. Stephenson 1936, 1939, 1943, 1944, 1947; Stephenson *et al.* 1940; Brown and Jarman 1978; Branch and Branch 1981; Branch and Griffiths 1988; Field and Griffiths 1991; Emanuel *et al.* 1992). However, most of these studies are purely descriptive, and often they have failed to adopt standardized procedures for quantification, so that their results cannot be easily used in comparative studies and syntheses.

The geographical position of the southern African coast makes it ideal for comparative studies of the marine biota (Fig. 1). This was early recognized by T. A. Stephenson, whose works on zonation patterns and biogeography are still cited in rocky-shore studies. The southern African coast is bathed by two current systems: the warm (Indian Ocean) Agulhas Current is derived from the Moçambique Current and flows southward, bathing the east coast; at the southern tip of Africa it meets the cool (Atlantic Ocean) Benguela Current which flows northwards up the west coast, introducing upwelled deep cold waters (Fig. 1). This creates a oceanographic scenario in which radically different temperatures are recorded on the east and west coasts, in addition to other differences in the dynamics of the two water masses (e.g. upwelling, nutrient levels, light penetration). Despite the large body of coastal research done on southern African shores, little attention has been paid to the west coast. Most recent intertidal studies have been done around the populated areas such as the Cape Peninsula (e.g. Branch and Branch 1981; McQuaid 1981; McQuaid and Branch 1984, 1985; Bosman 1987), and no modern quantitative studies have been conducted on the Namaqualand coast (Fig. 1).

Using a standardized sampling technique and data analyses, in this study I examine the biological composition of, and some abiotic processes relevant to, the structuring of rocky intertidal communities around southern Africa. My approach is initially comparative and covers a large geographic scale, whereas the later parts of the study are

empirical and/or theoretical and conducted on a small scale to test concepts emerging from the large-scale studies. The comparisons were designed to establish geographic patterns between rocky shore communities over a broad scale, and to detect large- and small-scale environmental factors which appears to structure these communities. In general, I explore and synthesize the main patterns and apparent causes of the trophic functioning of the intertidal rocky shores around southern Africa, and then concentrate more particularly on the mechanisms I hypothesize that are responsible for the structure of west coast intertidal communities and the reason they differ from those on the east coast.

The thesis consists of seven Chapters.

In Chapter 1, using modern quantitative analyses, I establish primary and secondary biogeographic patterns of community structure around the coast of southern Africa. In order to discern different biogeographic provinces, I use both quantitative binary (presence/absence) and biomass data collected at 15 different localities around the coast, between southern Namibia on the west coast and southern Moçambique in the east (Fig. 1). I compare the trophic functional structure of the different provinces, as well as localized differences related to wave action. I also assess the patterns of biomass dominance over large geographical areas, and at sites experiencing contrasts of wave action. Finally, I present a series of working hypotheses to account for differences between communities in different regions and experiencing different amounts of wave action, and these hypotheses are explored and evaluated in later Chapters.

In Chapter 2, I establish common vertical and horizontal zonation patterns for the intertidal biota of rocky shores. For that, I use biomass and species richness measured at 14 different geographical localities around southern Africa, and I conclude that similar vertical and horizontal distribution patterns do exist independently of biogeographic differences. I then choose two specific and comparable geographical localities, one on the Atlantic and one on the Indian Ocean, to evaluate quantitatively the importance of three selected environmental factors that appear to have strong influences on local zonation patterns. I conclude that small-scale variations within localities are greater than between

different biogeographical regions, and that most local variations can be accounted for by gradients of wave action and shore elevation.

In Chapter 3, I record measurements of *in-situ* intertidal primary production and nutrients around the entire coast. Analyzing data cooperatively collected by several research groups, I demonstrate the existence of a strong gradient of primary production around the coast. Using statistical inference, I explore the sources of variation of intertidal primary production, nutrient concentration and the biomass of different functional-form groups of macroalgae around the coast. Finally, I correlate primary productivity with the biomass of intertidal primary consumers, and discuss the role of productivity in modifying community structure in different geographical regions.

In Chapter 4, I treat more particularly the poorly-known west coast intertidal system and establish some trophic relations between the abundance of intertidal consumers and subtidal primary production. Specifically, using stable isotope techniques, I establish a strong trophic linkage between selected groups of intertidal consumers (notably filter-feeders and grazers), and subtidal kelp production. I determine the nature of particulate organic matter and its abundance, and statistically infer their variation through time, tidal phase, and degree of wave exposure. I then evaluate the importance of water turnover on exposed and sheltered shores and on the supply of particulate organic matter to intertidal filter-feeders. Finally, I model the effects of food supply and water turnover on the maintenance of filter-feeder standing stocks.

In Chapter 5, I became even more specific, and experimentally investigate the relationship between two extremely abundant congeneric west-coast limpet species and the input of subtidal kelp fronds into the intertidal system. Using geographical distribution data, I establish the correlation between the distribution ranges of the limpets and kelp, and also investigate their zonation patterns and the feeding behaviour of the two limpet species. In the last part of this Chapter, I test experimentally the effects of kelp exclusion on the survivorship and individual body mass of these two key intertidal

grazers. I and then discuss the ecological implication of the demonstrated link between subtidal and intertidal ecosystems.

In Chapter 6, I apply an individual-based stand-growth model to a single west-coast intertidal limpet to simulate the trophic maintenance of its standing stocks. I treat the relationship between kelp, intertidal algae and limpets as a predator-prey system. For that, I evaluate experimentally the dynamics of the *in-situ* production of epilithic microalgae and measure the input of kelp into the intertidal system. I then determine consumption rates of individual limpets feeding on both epilithic microalgae and kelp fronds. I construct a steady-state metaphysiological model for the simultaneous forecast of both epilithic microalgae and limpet standing-stocks. I verify whether the model is able to reproduce empirical results derived from (a) the experimental exclusion of kelp and (b) observations of natural limpet and algal standing stocks (Chapters 3 and 5). I use this ecological modeling approach to explore the management of a hypothetical commercial limpet fishery, developing a set of fishing policies based on maximum sustainable yields. Finally I discuss the use of this novel ecological modeling of populations as a complement to more traditional fishery management strategies.

I conclude this thesis with Chapter 7, in which I synthesize the results derived from all aspects of the research, providing general conclusions about the patterns and causes of intertidal community structure of the intertidal rocky shores of southern Africa.

References

- Bosman, A. L. 1987. Avian determinants of rocky intertidal community structure in South Africa. Ph. D. Dissertation University of Cape Town, Cape Town.
- Branch G. M., and M. Branch 1981. The living shores of southern Africa. C. Struik, Cape Town, South Africa.
- Branch G. M., and C. L. Griffiths. 1988. The Benguela ecosystem. Part V. The coastal zone. *Oceanography Marine Biology Annual Review* **26**: 395-486.
- Brown, A. C., and N. Jarman. 1978. Coastal marine habitats. Pages 1239-1277 in M. J. A. Wegner editor. *Biogeography and Ecology of Southern Africa*. Junk, The Hague, Netherlands.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* **124**: 255-279.
- Brown, J. H. and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. *Science* **243**: 1145-243.
- Cale, W. G., G. M. Henebry, and J. A. Yeakley. 1989. Inferring processes from pattern in natural communities. *BioScience* **39**: 600-605.
- Caswell, H. L. 1976. Community structure: a neutral model analysis. *Ecological Monographs* **46**: 327-354.
- Cody, M. L., and J. M. Diamond. 1975. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge.

- Connell, J. H. 1961. The effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* **31**: 61-104.
- Connell, J. H. 1978. Diversity in tropical rain forest and coral reefs. *Science* **199**: 1302-1310.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: provision and subsequent utilization of space in rocky intertidal community. *Ecological Monographs* **41**: 351-389.
- Dayton, P. K. 1984. Processes structuring some marine communities: are they general? Pages 151-180 *In* D. R. Strong, Jr, D. Simberloff, L. G. Abele and A. Thistle editors. *Ecological Communities. Conceptual issues and the evidence*. Princeton University Press, New Jersey.
- Drake, J. A. 1990. Communities as assembled structures: do rules govern patterns? *Trends in Ecology and Evolution* **5**: 159-164.
- Emanuel, B. P., R. H. Bustamante, G. M. Branch, S. Eekhout, F. J. Odendaal. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of Africa. *South African Journal of Marine Science* **12**: 341-368.
- Field, J. G., and C. L. Griffiths. 1991. Littoral and sublittoral ecosystems of southern Africa. Pages 323-346. *In* A. C. Mathieson, P. H. Nienhuis editors. *Ecosystems of the World 24. Intertidal and Littoral Ecosystems*. Elsevier Science Publisher, Amsterdam, The Netherlands.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *The American Naturalist* **94**: 421-425.

- Inouye, R. S., G. S. Beyers, and J. H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* **61**: 1344-1351.
- Lewis, J. R. 1964. *The Ecology of the Rocky Shores*. The English University Press Ltd., London.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of food herbivore preference and algal competitive abilities. *The American Naturalist* **112**: 23-39.
- Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* **48**: 67-94.
- Mann, K. H., and J. R. N. Lazier. 1991. *Dynamics of Marine Ecosystems*. Blackwell Scientific Publications, Oxford.
- May, R. M. 1975. Patterns of species abundance and diversity. Pages 81-204 in M. L. Cody and J. M. Diamond editors. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts.
- McQuaid, C. D. 1981. Spatial and temporal variations in rocky intertidal communities. Ph.D. thesis, University of Cape Town.
- McQuaid, C. D., and G. M. Branch. 1984. The influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Marine Ecology Progress Series* **19**: 145-151.
- McQuaid, C. D., and G. M. Branch. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series* **22**: 153-161.

- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* **46**: 355-393.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *The American Naturalist* **110**: 351-369.
- Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**: 730-757.
- Menge, B. A., and T. M. Farrell. 1989. Community structure and interactions webs in shallow marine hard-bottom communities: test of an environmental stress model. *Advances in Ecological Research* **19**: 189-262.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends in Ecology and Evolution* **5**: 52-67.
- Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* **100**: 65-75.
- Stephenson T. A. 1936. The marine ecology of the South African coast, with special reference to the habits of limpets. *Proceedings Linnean Society of London* **148**: 74-79.
- Stephenson T. A. 1939. The constitution of the intertidal fauna and flora of South Africa, I. *Journal of the Linnean Society of London* **40**: 487-536.
- Stephenson T. A. 1943. The causes of vertical and horizontal distribution of organism between tide-marks in South Africa. *Proceedings of the Linnean Society of London* **154**: 219-213.

Stephenson T. A. 1944. The constitution of the intertidal fauna and flora of South Africa, II. *Annals of the Natal Museum* **10**: 261-358.

Stephenson T. A. 1947. The constitution of the intertidal fauna and flora of South Africa, III. *Annals of the Natal Museum* **11**: 207-324.

Stephenson T. A., A. Stephenson, and C. A. du Toit. 1940. The South African intertidal zone and its relation to currents, VIII. Lamberts Bay and the West coast. *Annals of the Natal Museum* **9**: 345-380.

Stephenson T. A., and A. Stephenson. 1972. *Life between tidemarks on rocky shores*. Freeman, San Francisco, USA.

Underwood, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia (Berlin)* **33**: 185-202.

Underwood, A. J. 1980. The effects of grazing by gastropods and physical factors on the upper limits and distribution of intertidal macroalgae. *Oecologia (Berlin)* **46**: 201-213.

Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151-180 in D. R. Strong, Jr, D. Simberloff, L. G. Abele and A. Thistle editors. *Ecological Communities. Conceptual issues and the evidence*. Princeton University Press, New Jersey.

Whittaker, R. H. 1975. *Communities and Ecosystems*, Second edition. The Macmillan Company, New York.

Chapter 1

Biogeographic Patterns and Trophic Structure of Southern African Rocky Shores

Summary: In this Chapter I revise the biogeographic delimitation, and large-scale pattern of community structure of the intertidal rocky shores of southern Africa. I use binary (presence/absence) and per-species biomass data collected at 15 different localities, encompassing the shores of southern Namibia, South Africa and southern Moçambique. The multivariate analyses performed here revealed that the shores of southern Africa (south of 25°) can be divided into three main biogeographic provinces; the west coast or *Namaqualand* province, the south coast or *Agulhas* province and the east coast or *Natal* province. The biomass structure of the intertidal rocky shores communities of southern Africa varied at a large scale, corresponding to biogeographic differences, while local-scale variation accorded with the intensity of wave action. The biomass per-unit-area of the west coast communities was in average significantly greater than on average biomass of the south and east provinces. At a local scale, the community biomass on exposed shores was an order of magnitude greater than on sheltered shores within all biogeographic provinces. Semi-exposed shores exhibited intermediate average biomass. The trophic structure of these communities varied significantly with wave action; i.e. autotrophs, filter-feeders and invertebrate predators prevailed on wave exposed shores whereas grazers were more abundant on sheltered and semi-exposed shores. At the geographic level of analysis, the trophic structure did not change, but the abundance of specific functional groups did. The patterns of biomass dominance revealed that exposed shores were consistently dominated by far fewer species than semi-exposed and sheltered shores, independently of biogeographic differences. These results also revealed that, within all biogeographic provinces, semi-exposed and sheltered shores were more diverse than exposed shores. The patterns of dominance showed that the west coast intertidal communities have high level of biomass, but are consistently species-poor. Several working hypotheses that could explain the large and small-scale patterns of structure are presented.

Introduction

Two major water masses meet at the southern tip of Africa - the Atlantic ocean in the west, and the Indian ocean in the east - giving rise to a hydrographically complex area. The west coast is influenced by the upwelled cold Benguela current, and the east coast by the warm Agulhas current, itself under the influence of the tropical Indian Ocean (Shannon 1985).

The oceanographic characteristics of this region make it ideal for comparative ecological and biogeographic studies of the marine biota. Biogeography can be described simply as the study of the geographical distribution of organisms (Myers and Guiller 1988). The apparent simplicity of this definition is deceptive, for it hides the importance of historical events and processes (including geological and biological evolution) which may profoundly influence modern biogeographic patterns.

The work described in this Chapter concentrates on ecological biogeography (as defined by Myers and Guiller 1988) and the identification of patterns, rather than the elucidating the processes which influence those patterns. Biogeographic patterns can be recognized at three levels: a) primary patterns, i.e., all those non-random spatial distributions of species which are responses to large-scale environmental phenomena (underlying controlling processes); b) secondary patterns which are inferred from a nested set of attributes of a collection of species or taxa, e.g. diversity, richness, endemism, etc.; and c) tertiary patterns that describe the relationship between secondary and non-biotic data, e.g. species-area relationships (Myers and Guiller 1988). As a starting point, the main focus of this Chapter is the determination of non-random geographical distribution patterns of the biota of intertidal rocky shores in southern Africa.

During the past 50 years, several studies of intertidal and littoral biota have dealt with the description and composition of the southern African species and their geographical distributions (Stephenson 1936, 1939, 1943, 1944, 1947; Stephenson *et al* 1940; Brown and Jarman 1978; Branch and Branch 1981; Field and Griffiths 1991; Emanuel *et al.* 1992). Biogeographically, three major provinces have been proposed for the southern African region; a) the cold-temperate west coast, b) the warm-temperate south coast, and c) the subtropical east coast (Stephenson and Stephenson 1972). Until now, studies addressing the biogeographic affinities of littoral taxa have consistently followed the Stephenson's biogeographic delimitation. All of them have been descriptive or narrative, mainly based on qualitative data (e.g. Ekman 1953; Brown and Jarman 1978; Field and Griffiths 1991). The existence of and limits to these three biogeographic provinces have been questioned by several authors, usually on the basis of analyses of distribution patterns of discrete taxonomic groups. It has been questioned, for example, whether the west coast is a warm rather than cold-temperate province (Ekman 1953). The boundary between the west and south coast provinces apparently differs depending on the suite of species analyzed (see Day 1967 for polychaetes; Griffiths 1974 for amphipods; Gosliner 1987 for opisthobranchs; Thandar 1989 for echinodermata; and Williams 1992 for octocorals). This debate becomes rather semantic, since different taxonomic groups have colonized the region from different centres of dispersion, and they have intrinsically different ecological and physiological adaptations. In the above mentioned studies, and in the majority of the biogeographic analyses (e.g. Brown and Jarman 1978; Gosliner 1987; Williams 1992) boundaries between biogeographic regions have been based on each author's *ad-hoc* criteria, or 'inferred' from the species distributions. Analysis of multispecies distribution patterns requires objective and repetitive criteria, independent of the ecology of specific groups or taxa. Such independence and objectivity are met in modern multivariate techniques that provide statistical methods for the study of the joint inter-relationship of variables in data sets (Whittaker 1973; Pielou 1979 1983; McCoy and Heck 1987; James and McCulloch 1990). These analytical methods have demonstrated their value in the elucidation of marine biogeographic patterns based on

quantitative binary data (Murray and Littler 1981; Joosten and van den Hoek 1986; Roberts *et al.* 1992; Stegenga and Bolton 1992; Clarke 1993).

The majority of the intertidal ecological research in the southern African region has been undertaken on South African shores. Despite detailed localized knowledge of the South Africa rocky intertidal communities, there have been no quantitative comparative studies at a subregional scale. Descriptions of the zonation patterns and species composition of the southern African intertidal rocky shores have been documented in a number of qualitative works (e.g. Penrith and Kensley 1970a, b; Stephenson and Stephenson 1972; Brown and Jarman 1978). However, the majority of these (mostly) South African studies were small-scale (spatial and temporal), and quantitative evaluations have been confined to a few points along the coast (McLachlan *et al.* 1981; McQuaid and Branch 1985; Hugget and Griffiths 1986; Branch and Griffiths 1988; Field and Griffiths 1991). From these studies, several structuring factors, both biotic and abiotic, have been postulated. In particular, the role of wave action has been elegantly demonstrated as an important, if not the most important, abiotic factor in structuring South African intertidal communities (McQuaid 1981; McQuaid and Branch 1984, 1985; Field and Griffiths 1991; Emanuel *et al.* 1992). This is in agreement with research findings elsewhere, which show that wave-induced stress acts as structuring force and mediates biological interactions (Dayton 1971; Menge and Sutherland 1976; Denny 1988; Menge and Olson 1990).

Functional descriptions and analyses of natural communities have been a fundamental part of ecological research from the beginning of this century (i.e. Elton 1927; May 1973; Terborgh and Robinson 1986). More recently, functional groups or guilds have increasingly been used as means of understanding the trophic structure of marine communities (e.g. McQuaid and Branch 1985; Menge and Sutherland 1987; Menge and Olson 1990; Hixon and Menge 1991). The advantage of using functional groups or 'ecological equivalents' (Schoener 1988) is that they provide a common ecological base

for comparing sets of taxonomically unrelated species (e.g. barnacles and mussels are both filter feeders and are both functionally similar in being sessile).

This Chapter deals with primary and secondary biogeographic patterns and community structure around the coast of southern Africa between Lüderitz in Namibia and Inhaca Island in Moçambique (see Fig. 1). Analyses are based on quantitative binary (presence/absence) data and biomass data for rocky intertidal species (invertebrates and algae) gathered from 15 different localities around the coast. The Chapter is divided into three parts. The first part attempts to elucidate the biogeographic patterns of the intertidal rocky shores, based on the presence or absence of intertidal species. The second part describes the trophic structure of the intertidal communities that characterize the different biogeographic regions, particularly in relation to the degree of wave action. The third part compares the biomass dominance patterns of intertidal communities present on sheltered and exposed shores in the main biogeographic regions.

Specifically, the Chapter addresses the following questions:

- a) do southern African rocky intertidal communities reflect any primary biogeographic pattern?
- b) does this pattern conform to biogeographic provinces previously proposed for the region?
- c) are there any quantitative differences in the trophic structure of communities in different biogeographic provinces?
- d) do different functional groups have different distribution patterns around the coast?
- e) are there any differences in biomass dominance patterns between the different communities around the coast?

I hypothesize the following general patterns:

- i) There will be distinctive biogeographic regions around the coast which can be recognized by species composition.
- ii) Intertidal community biomass will decrease from west to east as productivity declines, and exposed shores will support a higher biomass than sheltered shores.
- iii) The biomass of communities of the west coast will be dominated by fewer species than the south-east intertidal communities.
- iv) Exposed shores will be similarly dominated by few species in relation to sheltered shores.
- v) Within exposed shores, there will be no differences in the dominance between the west, south and east coast; but within sheltered shores, the west coast shores will be more dominated by a smaller numbers of species relative to the south-east coasts.

Materials and methods

Sampling procedures

Surveys of intertidal rocky shores communities were undertaken in 1989-1992 at 15 different localities (Fig. 1). At each locality surveys were made in two or three different sites which covered the range of coastal geomorphology and wave action. These sites were subjectively separated into three different categories; a) *exposed rocky headlands*, normally rocky shores on the seaward side of headlands, b) *semi-exposed rocky shores*, open rocky shores in the lee of kelp forests, and c) *sheltered boulder bays*, protected from the wave action and devoid of kelp forests. All three site-types were present along the Atlantic west coast, but on the south and east coasts only types a) and c) were present (kelp forest being absent). At each site, surveys were conducted along transects that were set perpendicularly to the shoreline from mean low water spring tide (MLWS) to mean high water spring tide (MHWS) (Fig. 2). Four replicate transects were chosen, taking care to avoid tidal pools and gullies. Along each transect, eight to 12 quadrats of 0.5 m² were randomly stratified according to the intertidal zones described by Branch and Branch (1981). The quadrats consisted of a grid with 171 intersection points over a surface of 0.5 m². Within each quadrat, coverage of the major sessile fauna and flora was measured by point intersection counts, and the density of all mobile invertebrate fauna, including epifauna (e.g. limpets on mussels) was recorded. At the same time, species richness of all macro-fauna and flora visible within the quadrats was also recorded. This method underestimates the total species richness but provides information that is comparable between sites.

Along two of the four transects per site, two or three destructive samples of 0.075 m² were taken of all space dominant species in each of the intertidal "zones" (i.e., limpets, barnacles, foliose algae, mussels, etc.) in order to evaluate the whole wet biomass per

species present in each quadrat. Subsamples of each species were taken in order to obtain conversions between wet, dry and ash free dry weight (AFDW) expressed in grams. The data are expressed in terms of their AFDW biomass per m^{-2} . Complete data sets for species richness, including the cryptic infauna in sessile beds (mussels, colonial polychaetes, barnacles, oysters etc.) were obtained for all 15 localities surveyed. Biomass data were obtained for all sites except Inhaca Island (Mozambique).

Data analysis

Different statistical procedures were applied to the data, using either binary data (presence/absence) or AFDW per species or genus. However, due to taxonomic uncertainty, some groups have been treated as a single unit (e.g. crustose and articulated corallines, pycnogonids, sipunculids and hydrozoans, see Appendix I).

Multivariate techniques were applied to either binary or AFDW data arranged in rectangular matrices where cases=species and samples=localities or sites. Classification of the different samples was performed using a hierarchical clustering method based on the Bray-Curtis similarity index applied to these species-sample matrices (Bray-Curtis 1957), and using a group average linkage (Field *et al* 1982; Clarke and Warwick *in prep.*; Carr *in prep.*). In addition to the classification techniques, the data were also subjected to a non-metric multi-dimensional scaling (MDS, Kruskal and Wish 1978) based on the Bray-Curtis similarity of the species-samples matrix. The ordination yielded a graphic representation in two or three dimensions of the similarity between the different samples, in this case geographical localities, based upon the binary presence/absence data for species.

The statistical significance between biogeographic units identified using the above analyses and the main effects of wave action on intertidal biomass (AFDW) were tested using a nested design of a Generalized Linear Model (GLM) with *a posteriori* contrast between the biogeographic units (SAS 1986). All biomass data were log transformed prior to the analyses.

The trophic structure of the different intertidal communities was described by dividing the species into functional groups using the AFDW data. Species were pooled in the following trophic groups: a) *autotrophs*, b) *filter-feeders*, c) *grazing herbivores*, and d) *predators*. The main effects of wave action at each locality were tested using one-way ANOVA with *a posteriori* comparison of the average biomasses (Bonferroni inequality test SAS 1986).

Univariate methods were also applied to the species biomass in different samples or group of samples. Ranked species abundance or k-dominance curves (Lamshead *et al.* 1983) were constructed using the biomass (AFDW) per species on a logarithmic scale (Clarke and Warwick *in prep.*). I compared the biomass contributions of different species to two large geographic regions a) the west coast which included seven localities from Lüderitz to Paternoster, and b) the seven localities on the south and east coast between Cape Infanta and Cape Vidal (see Fig. 1). The data for both large-scale geographic regions were sub-divided according to the wave action categories (i.e. exposed, semi-exposed and sheltered).

To detect which species were responsible for the different dominance patterns within community types experiencing different degree of wave action, an analysis of the contribution by individual species to the overall similarity measure (Bray-Curtis) SIMPER (Similarity Percentages, Clarke 1993) was performed. For this purpose the data for the west coast was separated into sheltered, semi-exposed and exposed shores, and those for the south and east coasts into sheltered and exposed shores. In each group, an average Bray-Curtis similarity \bar{S} and the standard deviation SD for the group, and the per-species average \bar{S}_i , standard deviation $SD(S_i)$ and the percentile $\% \bar{S}_i$ contribution to \bar{S} were calculated. Similarly, the per-species average biomass \bar{Y} ($\pm sd$) and the respective percentile $\% \bar{Y}$ contribution to the total biomass were also calculated. Using the ratio $\bar{S}_i / SD(S_i)$ it was possible to check how consistently each species contributed in an intra-group comparison. Finally, a ranking of importance for the 'top 10' most important species for each group was constructed based on the \bar{S}_i value. I have excluded from this

analysis those species with a biomass smaller than 0.75% of the total community biomass.

All multivariate and univariate community analyses were done using the Plymouth Routines In Multivariate Ecological Research, PRIMER v3.1a (Carr *in prep.*).

Results

Biogeographic Patterns

A total of 231 intertidal species of algae and invertebrates was recorded around the southern African coast: details of species presence or absence at each of the 15 localities sampled are presented in Appendix I.

At the subregional level, species composition of the east coast communities differed by more than the 70% from those of the south and west coasts (Fig. 3). As similarities between localities increased (*ca.* 50.0%), three distinct groups of localities were clearly defined. The seven localities of the cool temperate west coast clustered together forming the Namaqualand province, with an average similarity of 66.7% (*sd*=4.1%). A second cluster was formed by all five localities on the warm temperate south coast. This cluster conforms to the Agulhas biogeographic province, and had an average similarity of 62.4% (*sd*=3.9%). A distinctive and smaller cluster included all three localities on the subtropical east coasts, conforming to the Natal biogeographic province, with an average similarity of 49.8% (*sd*=10.6%). However, within this cluster Inhaca Island split at about 55%, reflecting a more tropical component (Fig. 3).

Figure 4 shows the two-dimensional plot produced by non-metric multidimensional scaling (MDS), using the same Bray-Curtis similarity matrix. MDS analysis gives essentially the same picture as the dendrogram, but illustrates how distinct (by Euclidean distance, Field *et al.* 1982) the localities are in 2-D space. The localities on the west coast were ordered geographically in a correct sequence from north to south (see Fig. 1). Sites on the south coast were not ordered sequentially, but formed a distinct and independent group, with a transition zone between the south (Dwesa) and the east province (Ballito Bay). A more diffuse east coast province appears due to the smaller number of localities sampled (Fig. 4).

Thus, there were three clear distinctive groups of localities identifiable on the basis of their rocky intertidal species composition. These groups can be equated to different biogeographic regions (or provinces) i.e., the Namaqua, Agulhas and Natal provinces (Emanuel *et al.* 1992).

Intertidal Biomass Patterns

There were major differences in the faunal and floral biomasses supported per unit area on exposed as compared with sheltered shores in all three regions (Fig. 5). The average and maximum biomass on exposed shores was more than twice that of sheltered shores. The biomass supported on semi-exposed shores in the west coast was intermediate between that of sheltered and exposed shores (Fig. 5). Intertidal communities on the west coast had average biomasses significantly greater than of those of the south and east-coast groups, on both exposed and sheltered shores (Bonferroni *t*-test, $p < 0.05$). The regional variation in biomass was significantly explained by the differences between the biogeographic provinces (ANOVA, $p < 0.0001$), and the local variation was explained largely by wave action (ANOVA, $p < 0.0001$). The *a posteriori* contrast of the overall average biomass of the different provinces shows that the West province is significant different from both the South ($p < 0.0001$), and the East ($p < 0.0002$) provinces. However, there was no difference between the South and the East provinces ($p > 0.1881$) (Table 1).

Trophic Structure

The functional classification based on the feeding mode of all 231 intertidal species (autotrophs, filter feeders, herbivores and predators) shows that filter feeders achieved the highest biomass values (up to 3300 g m^{-2}), dominating the exposed shores, but being much less abundant on sheltered shores (Fig. 6). On the west coast localities, the average biomasses achieved by autotrophs, filter feeders and predatory species on exposed shores were in most cases significantly higher than those of sheltered shores. This pattern tended to agree with that found at the south and east localities (Fig. 6). The only cases in which sheltered and semi-exposed shores exhibited greater average biomasses than exposed

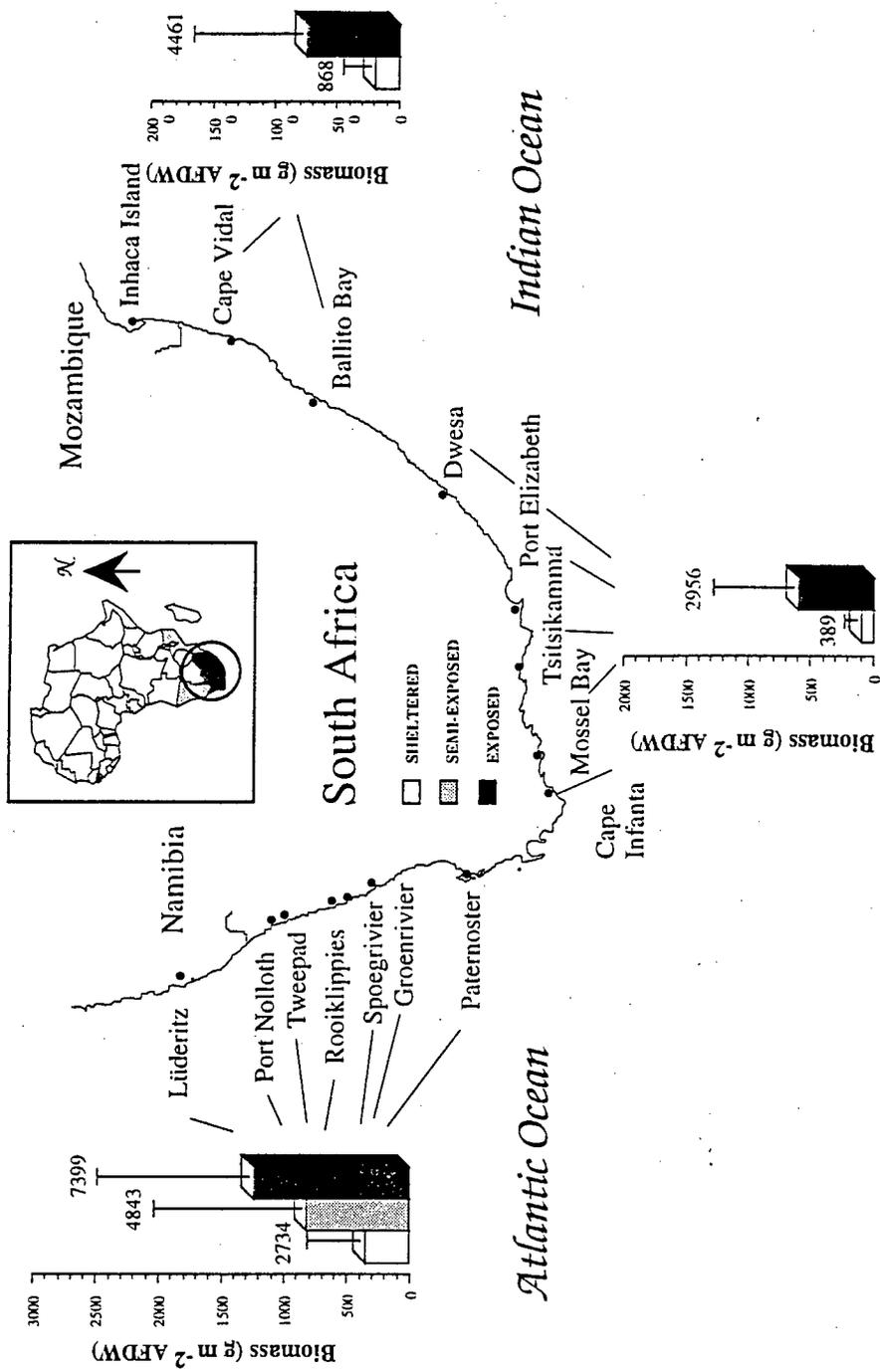


Figure 5. Average AFDW biomass (\pm SD) of intertidal communities as a function of wave action. Numbers above bars indicate the maximum values.

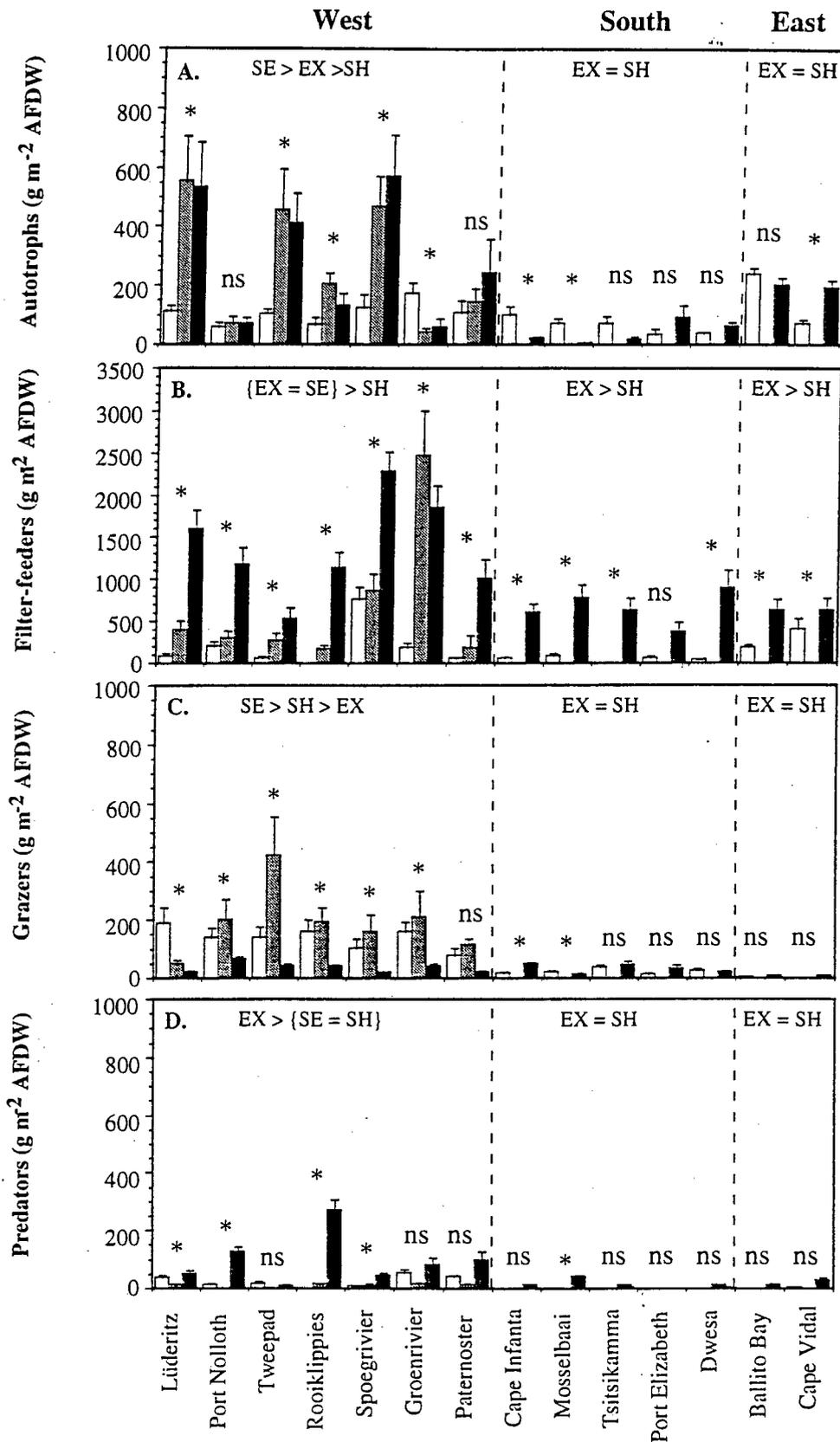


Figure 6. Average (\pm SE) biomass of the 4 functional groups of the southern African rocky intertidal communities separated by locality and wave action. Sheltered (SH = \square), semi-exposed (SE = \square) and exposed (EX = \blacksquare) shores. Localities are ordered from North-West (left) to North-East (right). Asterisks and ns represent the significance of the main effects of wave action in a one-way ANOVA applied to the biomass per locality (* = $p < 0.05$; ns = $p > 0.05$).

shores were the grazers on the west (Fig. 6c) and at two localities, the autotrophs in the south coast (Fig. 6a).

As a function of wave action, trends in biomass within each biogeographic province showed distinct patterns for different functional groups: a) autotrophs in West province were significantly (ANOVA, $p < 0.05$) more abundant on semi-exposed and exposed shores than in sheltered habitats, but this difference was not apparent (ANOVA, $p > 0.05$) in the Agulhas and Natal provinces; b) filter feeders biomass was significantly (ANOVA, $p < 0.05$) greater on exposed and semi-exposed shores than on sheltered shores in all biogeographic provinces; c) in the West province, grazers were significantly (ANOVA, $p < 0.05$) more abundant on semi-exposed and sheltered shores than on exposed shores, but this pattern was not repeated in the other biogeographic provinces (ANOVA, $p > 0.05$); d) predatory species in the West province were significantly (ANOVA, $p < 0.05$) more abundant on exposed shores than on semi-exposed and sheltered shores, but there were no differences in predator biomass related to wave action in either the Agulhas or Natal provinces.

Patterns of Intertidal Dominance

Figure 7 shows the curves of the ranked order of importance of the different intertidal species (in a log x -axis), plotted against their cumulative biomass (% y -axis) for all localities of the west coast (Fig. 7a) and the combined localities of the south and east coasts (Fig. 7b). A steep dominance curve means that a few species account for a great proportion of the biomass, i.e., the community is highly dominated by those species. A flat curve indicates less domination, with a larger number of species contributing to the biomass (greater diversity). There were clear differences in the slopes and forms of the dominance curves depending on wave exposure (Fig. 7). Exposed shores were dominated by fewer species than semi-exposed or sheltered shores. On the exposed shores of the west coast, three species made up more than 75% of the total community biomass; 75% of the biomass was accounted by seven species on exposed south and east

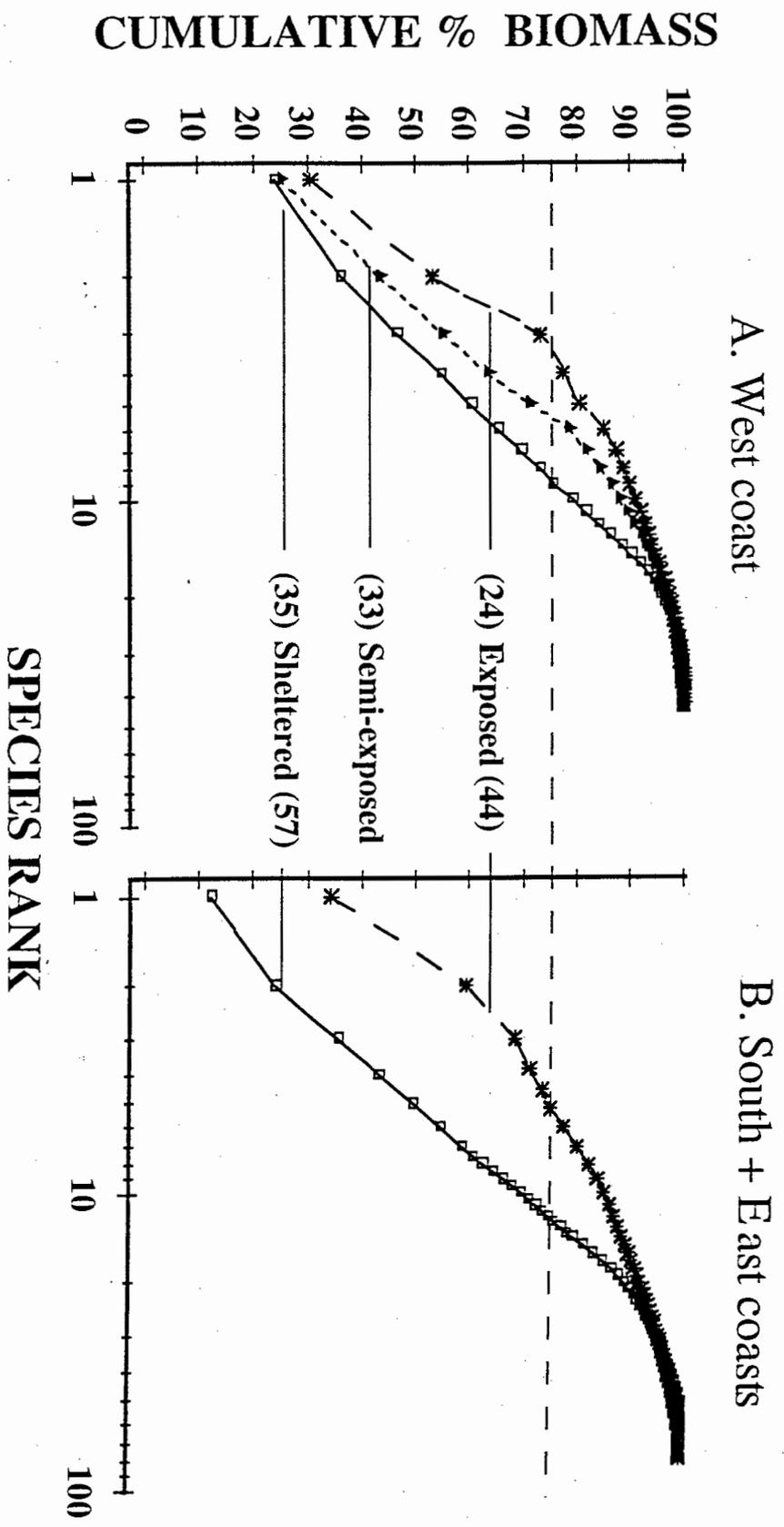


Figure 7. Dominance curves of three rocky intertidal community-types that characterizes the west and the two that characterizes the east coasts of southern Africa. Numbers in brackets indicate the total number of species recorded during biomass surveys of in each community. All species with a biomass contribution smaller than 0.75% of the total community biomass were not included (n=193).

coasts. On sheltered shores, nine species made up 75 % of the biomass on the west coast, against 16 species in the south and east coasts. Semi-exposed shores on the west coast had a dominance pattern intermediate between exposed and sheltered shores (Fig. 7a).

The 'top 10' intertidal species that characterized communities in the different west and south-east provinces are listed in Table 2. The ranking importance of these species was determined according the average score of individual species (\bar{S}_i) in the overall group's similarity (\bar{S}). Sheltered habitats on the west coast (Namaqua) had an average similarity of 48.24 % (± 11.88). The patellid limpet *Patella granatina* accounted for 41.85% of the group similarity and 25.44% of the total community biomass (Table 2A). Their populations form dense monospecific stands that can achieve average AFDW biomasses of 189.43 g m⁻². The other nine 'top' species accounted for 44.86% of the total community similarity. Of these, the most important were the kelps *Ecklonia maxima* and *Laminaria pallida*, the red alga *Porphyra capensis*, the colonial polychaete worm *Gunnarea capensis*, and the limpet *Patella granularis*. Together these four species accounted for the 34.88% of the biomass and 28.62% of the group's similarity (Table 2A). Semi-exposed habitats on the west coast had an average similarity of 36.79% (± 15.15) and were dominated by dense monospecific stands of the limpet *Patella argenvillei* which form a conspicuous fringe in the low shore. Their populations had an average AFDW biomass of 346.86 g m⁻² (± 347.71), representing 26.23% of the total biomass and 26.15% of the group similarity. Of the remaining nine major species, the red algae *Champia lumbricalis* was the second most important, averaging 253.14 g m⁻² (± 253.14) and accounting for 18.42% of the group's biomass. None of the remaining eight of the 'top 10' species accounted for more than the 12% of the total biomass (Table 2A). Exposed shores on the west coast had a group similarity of 39.86% (± 16.50), and were dominated by the mussels *Aulacomya ater* and *Mytilus galloprovincialis* which accounted respectively for 23.05% and 31.16% of the total community biomass. The red algae *Champia lumbricalis* was the third most important species, with an average biomass

Table 2. The ranking of importance of the 'Top 10' intertidal species that characterize the rocky shores of the (A.) West and (B.) South and East coasts. \bar{S} is the average similarity within each exposure; %Si is the percentile contribution of each species to \bar{S} ; and Si and SD(Si) are the average and standard deviation of each species to the \bar{S} , while Si/SD(Si) is the ratio between them. \bar{Y} , sd and %Y indicate the average, standard deviation and percentile contribution per-species to the total community biomass (AFDW).

Ranking	Names	% \bar{S}_i	\bar{S}_i	SD(\bar{S}_i)	\bar{S}_i /SD(\bar{S}_i)	\bar{Y} (gm-2)	sd	% Y
A. West Coast.								
Sheltered		$\bar{S} = 48.24\%$			SD= 11.88%			
1	<i>Patella granatina</i>	41.85	20.20	6.22	3.25	189.43	56.73	25.44
2	<i>Ecklonia/Laminaria</i>	9.48	4.60	3.47	1.32	64.57	46.34	8.67
3	<i>Porphyra capensis</i>	8.34	4.00	5.65	0.71	94.29	105.66	12.66
4	<i>Gunnarea capensis</i>	6.99	3.40	4.33	0.78	82.86	97.91	11.13
5	<i>Patella granularis</i>	3.81	1.80	0.58	3.18	18.00	7.21	2.42
6	Anemones	3.73	1.80	1.89	0.95	28.00	23.18	3.76
7	<i>Aeodes orbitosa</i>	3.65	1.80	0.54	3.23	21.14	14.28	2.84
8	<i>Chordariopsis capensis</i>	3.42	1.70	0.86	1.93	19.71	12.41	2.65
9	Articulate corallines	2.84	1.40	1.10	1.24	26.57	32.37	3.57
10	<i>Gymnogongrus</i>	2.60	1.30	3.09	0.41	45.14	62.46	6.06
	Others (14 spp.)	13.29				Total=744.59		
Semi-Exposed		$\bar{S} = 36.79\%$			SD= 15.15%			
1	<i>Patella argenvillei</i>	26.15	9.60	9.35	1.03	346.86	347.71	25.23
2	<i>Champia lumbricalis</i>	21.26	7.80	8.79	0.89	253.14	265.28	18.42
3	<i>Ecklonia/Laminaria</i>	9.49	3.50	5.12	0.68	116.00	138.36	8.44
4	<i>Aulacomya ater</i>	9.34	3.40	4.57	0.75	101.71	97.93	7.40
5	<i>Gunnarea capensis</i>	6.94	2.60	4.70	0.54	108.00	120.24	7.86
6	<i>Gigartina spp.</i>	4.21	1.50	0.85	1.83	32.57	25.32	2.37
7	<i>Patella granularis</i>	3.37	1.20	0.44	2.85	17.71	3.15	1.29
8	<i>Plocamium spp.</i>	2.50	0.90	1.29	0.71	35.71	42.68	2.60
9	<i>Mytilus galloprovincialis</i>	2.47	0.90	0.92	0.99	163.14	365.37	11.87
10	<i>Porphyra capensis</i>	2.01	0.70	1.62	0.46	45.43	76.29	3.31
	Others (23 spp.)	12.27				Total=1374.57		
Exposed		$\bar{S} = 39.86\%$			SD= 16.65%			
1	<i>Aulacomya ater</i>	32.63	13.00	14.30	0.91	530.29	410.46	23.05
2	<i>Mytilus galloprovincialis</i>	22.97	9.20	11.88	0.77	716.86	811.28	31.16
3	<i>Champia lumbricalis</i>	19.09	7.60	7.43	1.02	353.43	298.88	15.36
4	Anemones	6.65	2.70	1.98	1.34	108.00	79.29	4.69
5	<i>Plocamium spp.</i>	4.37	1.70	4.08	0.43	180.29	255.76	7.84
6	<i>Ecklonia/Laminaria</i>	3.30	1.30	2.25	0.58	105.43	129.49	4.58
7	<i>Patella argenvillei</i>	1.81	0.70	0.19	3.84	30.86	34.19	1.34
8	Nereid polychaets	1.80	0.70	0.74	0.96	28.57	22.68	1.24
9	<i>Gunnarea capensis</i>	1.05	0.40	0.45	0.93	19.43	17.12	0.84
10	<i>Patella granularis</i>	1.04	0.40	0.27	1.51	14.29	8.28	0.62
	Others (25 spp.)	5.29				Total=2300.88		

Table 2. (cont.)

Ranking	Names	%Si	Si	SD(Si)	Si/SD(Si)	Y (gm-2)	sd	%Y
B. South + East Coast								
Sheltered					$\bar{S} = 26.95\%$	$SD = 14.57\%$		
1	Articulate corallines	36.04	9.70	5.38	1.80	56.29	26.27	15.14
2	<i>Gelidium spp.</i>	11.10	3.00	2.69	1.11	54.86	78.76	14.76
3	<i>Pomatoleios kraussii</i>	10.50	2.80	4.96	0.57	30.29	36.76	8.15
4	<i>Tetraclita serrata</i>	5.75	1.50	1.77	0.88	18.57	25.79	5.00
5	<i>Patella oculus</i>	5.22	1.40	1.49	0.94	8.00	5.54	2.15
6	<i>Patella longicosta</i>	4.79	1.30	1.45	0.89	11.71	15.03	3.15
7	<i>Perna perna</i>	3.79	1.00	1.79	0.57	19.43	27.29	5.23
8	<i>Oxystele sinensis</i>	2.33	0.60	0.84	0.75	4.29	3.90	1.15
9	<i>Chtamalus dentatus</i>	2.13	0.60	1.04	0.55	23.71	44.44	6.38
10	<i>Siphonaria spp.</i>	2.03	0.50	0.49	1.11	3.14	1.95	0.84
	Others (34 spp.)	16.32				Total=371.74		
Exposed					$\bar{S} = 44.13\%$	$SD = 10.08\%$		
1	<i>Perna perna</i>	66.28	29.20	6.71	4.36	595.14	192.01	33.87
2	<i>Octomeris angulosa</i>	9.34	4.10	5.23	0.79	159.71	171.94	9.09
3	<i>Pyura stolonifera</i>	8.12	3.60	6.34	0.56	435.43	781.44	24.78
4	<i>Chtamalus dentatus</i>	2.38	1.00	1.45	0.72	35.71	32.83	2.03
5	Articulate corallines	1.98	0.90	0.80	1.09	30.00	23.94	1.71
6	<i>Gelidium spp.</i>	1.74	0.80	1.18	0.65	51.14	73.20	2.91
7	<i>Tetraclita serrata</i>	1.65	0.70	0.99	0.73	44.29	56.31	2.52
8	Anemones	0.98	0.40	0.49	0.87	13.14	9.86	0.75
9	<i>Patella cochlear</i>	0.85	0.40	1.14	0.33	20.86	30.70	1.19
10	<i>Crassostrea cucullata</i>	0.58	0.30	0.92	0.28	55.14	106.32	3.14
	Others (47 spp.)	7.00				Total=1757.13		

of 353.43 g m⁻² and representing 15.36% of the total biomass and the 19.09% of the group similarity (Table 2A).

Articulate coralline algae dominated the low fringe of sheltered shores on the south and east coasts, where they averaged a biomass of 56.29 g m⁻², accounting for 15.14% of the total community biomass; they accounted for 36.04% of the group's similarity. In this habitat, the next most important taxon was the red algae *Gelidium* spp. which made up 14.76% of the total biomass. Although they had levels of average biomass comparable to the corallines, they accounted for only 11.10% of the similarity (Table 2B.). The other 34 species not listed in Table 2B account for the 16.32% of the group similarity and 38.05% of the total community biomass. Exposed shores on the south and east coasts, as on the west coast, were dominated by the mussels. The mussel *Perna perna* contributed 66.28% to the community similarity and had an average biomass of 595.14 g m⁻², making up 33.87% of the total community biomass. In terms of biomass the next most important was the ascidian *Pyura stolonifera*. This species made up 24.78% of the biomass, but only contributed 8.12% to the group similarity (Table 3B.). None of the remaining seven of the 'top 10' species contributed more of the 3% to the similarity or the 3% of the community biomass. The other 47 species (not listed in Table 2B) together contributed only 7% of the group similarity.

Discussion

There were substantial geographic differences in the species composition of the rocky shores biota around the southern African coast. These quantitative differences justify the division of the region into three biogeographic provinces; the West, South and East provinces, proposed by earlier qualitative analyses (Stephenson 1936, 1939, 1943, 1944, 1947; Stephenson *et al* 1940; Brown and Jarman 1978; Branch and Branch 1981; Field and Griffiths 1991).

Emanuel *et al.* (1992) have produced an definitive zoogeographic analysis, based on analyses of literature records for all well-researched invertebrate taxa and including data for intertidal and subtidal biota (to 15 m depth). They concluded that there are four major zoogeographic provinces in southern Africa. On the east coast there is a subtropical Natal Province, extending from southern Moçambique to just south of Durban. The warm temperate Agulhas Province stretches from Dwesa to Cape Point. On the west coast there are two provinces. In the south, the cool temperate south west coast province extends from Cape Point to Lüderitz, and is named the Namaqua Province. The cool temperate Namib province extends from Lüderitz to the Cunene River.

The work presented in this Chapter differs from that of Emanuel *et al.* (1992) in that it relies on quantitative data obtained from equal-sized samples at all sites, rather than using records from the literature and from earlier non quantitative works. The strength of the present study is thus its more rigorously quantitative approach, eliminating bias due to different sampling intensities in different regions. Its weakness is that the sampling methodology is unlikely to detect many of the rare species. Emanuel *et al.* (1992) include data from all species known to occur on the coast of southern Africa. Despite the differences in methodology, the two approaches yield very similar results.

Based on the rocky intertidal biota, two clear biogeographic contributions can be extracted from the present work. First, the confirmation of the existence of a clear and distinctive West coast biogeographic province. The west coast localities show the most consistent similarity between them (*ca.* 67%, see Fig. 3) and they form a compact and homogeneous cluster (Fig. 4). Similar results have been reported for rocky intertidal fish species (Prochazka and Griffiths 1992). Much of the controversy related to the boundaries, definitions and existence of West and South provinces, has been raised when specific taxonomic groups have been investigated (e.g. Griffiths 1974; Gosliner 1987; Thandar 1989; Williams 1992). The West coast province defined in this work comes from a multitaxa data set, and fits almost exactly with the definition of the Cool Temperate South West or *Namaqua* province, named by Ekman (1953) and subsequently analytically defined by Emanuel *et al.* (1992).

The second biogeographic contribution of this work comes from the quantitative confirmation of a South or Agulhas province, as defined by Stephenson (1944). The extent of this province has been redefined several times in different works. One extreme is the 'mega' Cape province defined by Williams (1992) based on Octocorallia. Williams concluded that it is impossible to separate the South and West provinces. The opposite extreme is the recognition of a 'reduced South coast' (Cape Agulhas to Port Elizabeth) defined by Thandar (1989). However, agreeing with our findings, recent quantitative analyses have consistently defined the South coast as an independent province (e.g. Stegenga and Bolton 1992; Emanuel *et al.* 1992).

The above biogeographic patterns remain speculative if no underlying causative processes are inferred or identified (Rosen 1988). Nevertheless, the consistency and repetition of the patterns provides a solid base for the characterization of geographical areas and their communities (Myers and Guiller 1988).

A comparative scenario can be developed when general attributes or structural secondary patterns can be identified within the biogeographic units defined above. The

first general macro-pattern is that the observed changes in the rocky intertidal landscape (biomass) around southern Africa, are significantly explained by differences at regional (biogeographic) and local (wave action) scales (Table 1). There are striking differences in biomass between the West, South and East provinces. On both sheltered and exposed shores, the West coast supports a significantly greater average biomass than the two other provinces (see Fig 5). It is also clear that the biomass of intertidal communities increases with wave action. Grazers are the only functional group to depart from this generalization: their biomass is significantly higher on sheltered and semi-exposed shores (Fig. 6c), particularly on the west coast.

Exposed shores support a higher average biomass than sheltered shores, particularly on the west coast (Fig. 5). This occurs pattern at most localities (Fig. 6). Exposed shores are dominated by filter-feeding species (Fig. 6b). This finding is consistent with those reported for the Cape Peninsula (Fig. 1), where the filter-feeder biomass on exposed shores was an order of magnitude greater than that of sheltered shores (McQuaid and Branch 1985, Table 2). Menge and Sutherland (1987) have proposed a general community structure model in which they incorporate the role of the wave action in moderating the outcome of biological interactions (principally predation and competition). One of the predictions of this, and subsequent works (e.g. Menge and Olson 1990), is that in stressful environments, mobile organisms (mostly consumers) are more likely to be environmentally constrained. The disadvantage of such conceptual frameworks, is that they predict relative importance of particular biological interactions rather than examining the emergent properties of the community as a whole (e.g. Yodzis 1986; Sebens 1987; Menge and Sutherland 1987). None of these models makes predictions about the abundance and distribution of the community components (from single species to trophic levels). Menge and Olson (1990), adopting a broader perspective and working on the effect of scale and environmental factors in regulating community structure, predict that at intermediate to low environmental stress the abundance of mobile consumers would increase while "basal species" (sessile space occupiers) decrease (see Menge and Olson 1990, Fig. 1). On the other hand in stressful habitats, basal species dominate and the

abundance of consumers should decrease. The trophic structure of the southern African communities does not fit the above predictions. For example, although basal species conform to Menge and Olson (1990) predictions, secondary consumers (predatory species) do not, being consistently more abundant in exposed shores where there is a high physical stress (Fig. 6). However, on exposed shores the majority of the predatory species are commonly found living within the matrix provided by the basal species (mussels) and seldom in the open rock. If sheltered shores are considered as a benign habitat, only the communities present in the West province fit Menge and Olson's (1990) predictions for primary consumers, i.e. high abundance of herbivores in sheltered habitats and low abundance in exposed habitats. In the South and East the biomass pattern is reversed or absent (see Fig. 6b).

The use of dominance analysis for comparing different aspects of marine community structure does not seem to have established itself in routine ecological research (Warwick 1993), although its use in the detection of environmental impact (i.e., pollution, disturbance) on marine systems has increased in the last few years (e.g. Lamshead *et al.* 1983; Warwick *et al.* 1987; Clarke 1990; Warwick 1993). It is evident from the biomass dominance analyses, that wave action (as physical disturbance) has an important role in structuring southern African intertidal communities at a local-scale. However, there are other factors that have local and regional influences in community structure, and a more detailed analyses of the roles of environmental stressing factors (gradients), given in relation to zonation, in the following Chapter.

On all coasts, the biomass of exposed shores is dominated by few a species, notably of filter feeders, whereas on sheltered shores a larger number of species contribute to the bulk of the biomass which is dominated by algae and grazing herbivores (Fig. 7, Table 2). Semi-exposed shores of the West coast are intermediate. On the west coast, physical stress clearly modifies the biomass structure. For example, the 75% of the intertidal biomass is explained by three, six and nine species in exposed, semi-exposed and sheltered shores, respectively (Fig 7a). On the South and East coast these figures are

from seven and 16 species for sheltered shores respectively (Fig. 7b). The patterns of species richness also differs geographically. South and East coast intertidal communities contained on average almost twice as many species as those of the West coast communities (Fig. 7). The net effect is that west coast communities reach higher biomass levels but with fewer species (Figs. 5 and 7) than those of the South and East coasts. These patterns can be related to the high productivity of the upwelled west coast (Brown 1992; Pitcher *et al.* 1992) which will support a large biomass per-unit-area. Part of the reason of that the East and South coast have a richer fauna may be historical in that they derive many of their species from the rich Indo-Pacific radiation (Kohn 1990; Vermeij 1978, 1992).

The use of similarity analysis has proved useful in determining the contribution of individual species to both inter- and intra-community comparisons (Clarke 1993; Agard *et al.* 1993). Large-scale biogeographic patterns are normally examined using presence/absence data that define the geographic ranges of individual species. However, such data are of limited value in examining community structure and its variation within regions. For example, the community structure of wave-beaten and sheltered shores is radically different when examined in terms of biomass (Fig. 6), even although these two habitats draw on the same regional pool of species (Table 2).

Furthermore, the use of average biomass values to decide which species most usefully define a community is of little value if standard deviations are large. A species whose biomass is highly variable from site to site is of little use in clarifying a community. This problem is well illustrated in data from exposed shores of the west coast (Table 2A), where the alien mussel *M. galloprovincialis* had the greatest average biomass, but was less useful in predicting community structure than the indigenous mussel *Aulacomya ater* (Table 2A). In order to look for 'consistency' within a community (and also between communities of different geographical localities, and point not treated here), is the use of the ratio between the species average contribution to the overall community similarity (\bar{S}_i) and its standard deviation ($SD(S_i)$) of the species (Clarke 1993). On the west coast, the

most consistent species, across wave exposures, was the limpet *P. granularis*, which possessed high values of $\overline{Si}/SD(Si)$ in sheltered (3.18), semi-exposed (2.85) and exposed situations (1.51). This means the *P. granularis* was 'evenly' represented from site to site, and always with little variation. Similarly, on the south-east coast the articulate corallines were the most consistent group across wave exposures, with high ratios $SD(Si)$ in both sheltered (1.8) and exposed (1.09) shores.

The aim of this work was to describe geographic patterns in the community structure of the southern African intertidal rocky shores. Underlying these patterns, historical processes are normally invoked as in the majority of biogeographical studies (Myers and Guiller 1988). However, several physical features (physical and productivity gradients) may powerfully influence variation of these patterns. These include nutrient inputs, export and import to or from adjacent systems (subtidal and/or terrestrial), wave action, desiccation and heat stress.

Based on the present results, several hypotheses can be erected as to processes underlying observed differences between communities. Table 3 shows the main patterns revealed for different functional groups, and summarizes potential explanatory hypotheses. At a large geographical scale, high biomass of autotrophs on the west coast can be explained by the enhancing effects of upwelling of nutrient rich waters, mostly found along the west coast of southern Africa. At the local scale, it is known that grazers control autotrophs, thus the effect of increasing wave action would decrease the controlling effect by grazers on intertidal autotrophs. On the west coast, the high intertidal primary production plus the inputs of subtidal kelp, in the forms of detritus and drifting fronds, would enhance the abundance of the filter-feeders, grazers and predatory species. Locally, wave exposed environments would have high concentration food particles and water turnover that would favor growth and survival of filter-feeders, which will control the abundance of grazers by competition for space and physical disturbance (Table 3). The high productivity of the west coast would be felt on the abundance of the invertebrate

predatory species, being more abundant where the preys (mostly sessile invertebrates) occurs, i.e. exposed shores.

In the following Chapters, some of these hypotheses are explored at smaller and local scales in order to identify some of the underlying causes and processes that structure intertidal communities. This aspect of this thesis concentrates mainly on the west coast of southern Africa.

Table 3. General hypotheses for the observed abundance patterns for the different functional groups.
(W=west, S= south and E= east coasts. EX= exposed, SE= semi-exposed and SH= sheltered shores).

Functional group	Biomass Pattern	Hypothesis
Autotrophs	$W > \{S = E\}$	Greater Primary production (GPP) on the west coast.
	$SE > EX > SH$	Grazer activity restricted in exposed environments.
Filter feeders	$W > \{S = E\}$	GPP plus detrital input by subtidal kelp forest in the west coast.
	$\{EX = SE\} > SH$	Exposed shores have greater water turnover and favor growth and recruitment.
Grazers	$W > \{S = E\}$	Greater algal production plus subsidy by drift kelp.
	$EX < SH < SE$	Grazer abundance limited by physical disturbance and space competition.
(1) Predators (invertebrates)	$W > \{S = E\}$	High secondary production on west coast
	$EX > \{SE = SH\}$	Filter-feeder beds provide food and refugia

(1) Including anemones which were considered as 'sit-and-wait' predators.

References

- Branch G. M., and M. Branch 1981. The living shores of southern Africa. C. Struik, Cape Town, South Africa.
- Branch G. M., and C. L. Griffiths. 1988. The Benguela ecosystem. Part V. The coastal zone. *Oceanography Marine Biology Annual Review* **26**: 395-486.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest community of southern Wisconsin. *Ecological Monographs* **27**: 325-349.
- Brown, A. C., and N. Jarman. 1978. Coastal marine habitats. Pages 1239-1277 in M. J. A. Wegner editor. *Biogeography and Ecology of Southern Africa*. Junk, The Hage, The Netherlands.
- Brown, P. C. 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. *South African Journal of Marine Sciences* **12**: 515-525.
- Carr, M. (*in prep.*). User guide to PRIMER v3.1a. Routines in multivariate ecological research. Plymouth Marine Laboratory, United Kingdom.
- Clarke, K. R. 1990. Comparison of dominance curves. *Journal of Experimental Marine Biology and Ecology* **138**: 143-157.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of ecology* **18**: 117-143.
- Clarke, K. R., and R. M. Warwick. (*in prep.*). Statistical analysis and interpretation of marine community data. Plymouth Marine Laboratory, United Kingdom.

- Denny, M. W. 1988. *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton, New Jersey, USA.
- Day, J. H. 1967. *A monograph of the polychaeta of southern Africa. Volume 2*, The British Museum of Natural History, London, United Kingdom.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: provision and subsequent utilization of space in rocky intertidal community. *Ecological Monographs* 41: 351-389.
- Ekman, S. 1953. *Zoogeography of the sea*. Sidwick and Jackson limited, London, United Kingdom.
- Elton, C. S. 1927. *Animal Ecology*. Sidwick and Jackson, London, United Kingdom.
- Emanuel, B. P., R. H. Bustamante, G. M. Branch, S. Eekhout, F. J. Odendaal. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of Africa. *South African Journal of Marine Science* 12: 341-368.
- Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.
- Field, J. G., and C. L. Griffiths. 1991. Littoral and sublittoral ecosystems of southern Africa. Pages 323-346 in A. C. Mathieson, P. H. Nienhuis editors. *Ecosystems of the World 24. Intertidal and Littoral Ecosystems*. Elsevier Science Publisher, Amsterdam, The Netherlands.
- Gosliner, T. 1987. Biogeography of the opisthobranch gastropod fauna of southern Africa. *American Malacological Bulletin* 5: 243-258.
- Griffiths, C. L. 1974. *The gammaridean and caprellid Amphipoda of southern Africa*. Ph. D. thesis, Univ. of Cape Town.

- Hixon, M. A, and B. A. Menge. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology* **39**: 178-200.
- Hugget, J, and C. L. Griffiths. 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. *Marine Ecology Progress series* **29**: 189-197.
- James, F. C. and C. E. McCulloch. 1990. Multivariate analysis in ecology and Systematics: panacea or pandora's box? *Annual Review of Ecology and Systematics* **21**: 129-166.
- Joosten, A. M. T. and C. van den Hoek. 1986. World-wide relationships between the red seaweed floras: a multivariate approach. *Botanica Marina* **29**: 195-214.
- Kohn, A. J. 1990. Biogeography and evolution of Indo-Pacific marine mollusca: patterns, progress, problems and prospect. *Bulletin of Marine Science* **47**: 2-9.
- Kruskal, J. B., and M. Wish. 1978. *Multidimensional scaling*. Sage Publications, Beverly Hills, California, USA.
- Lambhead, P. J. D., H. M. Platt, and K M. Shaw. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History* **17**: 859-874.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, New Jersey, USA..
- McCoy, E. D. and K. Heck, Jr. 1987. Some observations on the use of taxonomic similarity in large scale biogeography. *Journal of Biogeography* **14** : 79-87.

- McLachlan, A., H. W. Lombard, and S. Louwrens. 1981. Trophic structure and biomass distribution on two east Cape rocky shores. *South African Journal of Zoology* **16**: 85-89.
- McQuaid, C. D. 1981. Spatial and temporal variations in rocky intertidal communities. Ph.D. thesis, University of Cape Town.
- McQuaid, C. D., and G. M. Branch. 1984. The influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Marine Ecology Progress Series* **19**: 145-151.
- McQuaid, C. D., and G. M. Branch. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series* **22**: 153-161.
- Menge, B. A., and J. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *The American Naturalist* **110**: 351-369.
- Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**: 730-757.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends in Ecology and Evolution* **5**: 52-67.
- Murray, S. N., and M. M. Littler. 1981. Biogeographical analysis of intertidal macrophyte floras of southern California. *Journal of Biogeography* **8**: 339-351.
- Myers A. A., and P. S. Giller. 1988. Analytical biogeography. An integrated approach to the study of animal and plant distributions. Chapman and Hall, London, United Kingdom.

- Penrith, M. L. and B. F. Kensley. 1970a. The constitution of the intertidal fauna of rocky shores of South West Africa. Part I. Lüderitzbucht. *Cimbebasia* 1: 191-239.
- Penrith, M. L. and B. F. Kensley. 1970b. The constitution of the intertidal fauna of rocky shores of South West Africa. Part II. Rocky Point. *Cimbebasia* 1: 243-268.
- Pielou, E. C. 1979. *Biogeography*. J. Wiley and Sons, New York, USA.
- Pielou, E. C. 1983. Spatial and temporal change in biogeography: gradual or abrupt? Pages 29-55 in R. W. Sims, J. H. Price and P. E. S. Whalley editors. *Evolution, time and space: the emergence of the biosphere*. Academic Press, London, United Kingdom.
- Pitcher, G. C., P. C. Brown, and B. A. Mitchell-Innes. 1992. Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. *South African Journal of Marine Sciences* 12: 439-456.
- Prochazka, K, and C. L. Griffiths. 1992. The intertidal fish fauna of the west coast of South Africa - species, community and biogeographic patterns. *South African Journal of Zoology* 27: 115-120.
- Roberts, C. M., A. R. Dawson Shepherd, and R. F. G. Ormond. 1992. Large-scale variation in assemblage structure of red sea butterflyfishes and angelfishes. *Journal of Biogeography*. 19: 239-250.
- Rosen, B. R. 1988. Biogeographic patterns: a perceptual overview. Pages 23-56 in A. A. Myers and P. S. Giller editors. *Analytical biogeography. An integrated approach to the study of animal and plant distributions*. Chapman and Hall, London, United Kingdom.
- SAS. 1986. SAS[®] System for linear models, 1986 Edition. SAS Institute Inc., Cary, NC, USA.

- Schoener, T. W. 1988. Ecological interactions. Pages 255-297 in A. Myers and P. S. Giller editors. Analytical biogeography. An integrated approach to the study of animal and plant distributions. Chapman and Hall, London, United Kingdom.
- Sebens, K. P. 1987. Competition for space: effects of disturbance and indeterminate competitive success. *Theoretical population Biology* **32**: 430-441.
- Shannon L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, Physical features and processes. *Oceanography Marine Biology Annual Review* **23**: 105-182.
- Stegenga, H., and J. J. Bolton. 1992. Ceramiaceae (Rhodophyta) of the Cape province, South Africa: distribution in relation to concepts of marine provinces. *Botanica Marina* **35**: 99-107.
- Stephenson T. A. 1936. The marine ecology of the South African coast, with special reference to the habits of limpets. *Proceedings Linnean Society of London* **148**: 74-79.
- Stephenson T. A. 1939. The constitution of the intertidal fauna and flora of South Africa, I. *Journal of the Linnean Society of London* **40**: 487-536.
- Stephenson T. A. 1943. The causes of vertical and horizontal distribution of organism between tide-marks in South Africa. *Proceedings of the Linnean Society of London* **154**: 219-213.
- Stephenson T. A. 1944. The constitution of the intertidal fauna and flora of South Africa, II. *Annals of the Natal Museum* **10**: 261-358.
- Stephenson T. A. 1947. The constitution of the intertidal fauna and flora of South Africa, III. *Annals of the Natal Museum* **11**: 207-324.

- Stephenson T. A., A. Stephenson, and C. A. du Toit. 1940. The South African intertidal zone and its relation to currents, VIII. Lamberts Bay and the West coast. *Annals of the Natal Museum* **9**: 345-380.
- Stephenson T. A., and A. Stephenson. 1972. *Life between tidemarks on rocky shores*. Freeman, San Francisco, USA.
- Terborgh, J., and S. Robinson. 1986. Guilds and their utility in ecology. Pages 65-90 in J. Kikkawa and D. J. Anderson editors. *Community ecology. Patterns and process*. Blackwell Scientific Publications.
- Thandar, A. S. 1989. Zoogeography of the southern African echinoderm fauna. *South African Journal of Zoology*. **24**: 311-318.
- Vermeij, G. J. 1978. *Biogeography and Adaptation. Patterns of Marine Life*. Harvard University Press, London.
- Vermeij, G. J. 1992. Trans-equatorial connections between biotas in the eastern Atlantic. *Marine Biology* **112**: 343-348.
- Warwick. R. M. 1993. Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology* **18**: 63-80.
- Warwick. R. M., T. H. Pearson, and Rushwahyuni. 1987. Detection of pollution on marine macrobenthos: further evaluation of the species abundance/biomass method. *Marine Biology* **95**: 193-200.
- Williams, G. C. 1992. Biogeography of the octocorallian coelenterate fauna of southern Africa. *Biological Journal of the Linnean Society* **46**: 351-401.
- Whittaker, R. H. 1973. Ordination and classification of communities. *Handbook of vegetation science*. 5. W. Junk, The Hage.

Yodzis, P. 1986. Competition, mortality, and community structure. Pages 480-491 *in* J.

Diamond, and T. J. Case editors. *Community Ecology*. Harper and Row, New York,

USA.

1

3

2

172 112 15 +6 +10 +2 17 +4 10 +1 113 12 17

Appendix I. List of species found on the intertidal rocky-shores of southern Africa (1=present, 0=absent).

Species name	Lüderitz	P. Nolloth	Tweepad	Brazil	Speoigrivier	Groenrivier	Paternoster	C. Infanta	M. Bay	Tsitsikamma	P. Elizibeth	Dvesa	B. Bay	C. Vidal	Inhaca Is.
1 Crustose corallines	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2 Articulate corallines	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3 <i>Perna perna</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 <i>Octomeris angulosa</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5 <i>Pyura stolonifera</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
6 <i>Patella cochlear</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7 <i>Ralfsia</i> sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
8 <i>Gelidium abbotiorum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9 <i>Gelidium pristoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 <i>Gelidium cartilagineum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 <i>Parechinus angulosus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12 <i>Patella argenvillei</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13 <i>Caulacanthus ustulatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
14 <i>Siphonaria capensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15 <i>Siphonaria aspera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16 <i>Siphonaria concinna</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 <i>Siphonaria tenuicostata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18 <i>Siphonaria carbo</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19 <i>Patella granularis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20 <i>Tetracitla serrata</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
21 <i>Tetracitla squamosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22 <i>Ponatoleios kraussii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23 <i>Austromegabalanus cylindricus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24 <i>Notomegabalanus algicola</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
25 <i>Chthamalus dentatus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26 <i>Hildenbrandia</i> spp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27 <i>Oxysteles variegata</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
28 <i>Oxysteles impervia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29 <i>Patella longicosta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30 <i>Patella oculis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31 <i>Oxysteles sinensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32 <i>Oxysteles tigrina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33 <i>Laurencia natalensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34 <i>Laurencia glomerata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35 <i>Littorina afric. knysnaensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
36 <i>Littorina afr. africana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37 <i>Littorina kraussii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38 <i>Littorina scabra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

172 +12 +5 +6 +10 +2 17 +4 10 +1 113 12 17

→ +12 +13 +12 +11 +10 +7 +7 +6 +5 +4 +2 +1

(cont.)

Species name	Lüderitz	P. Nolloth	Tweepad	Brazil	Spoe-grivier	Groenrivier	Paternoster	C. Infanta	M. Bay	Tsitsikamma	P. Elizabeth	Dwesa	B. Bay	C. Vidal	Inhaca Is.
41 <i>Patella barbara</i>	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0
42 Sponges	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1
43 <i>Anothoe stimpsonii</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44 <i>Anthopleura michaelsoni</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0
45 <i>Actinia equina</i>	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
46 <i>Pseudactinia</i> spp.	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
47 <i>Bunodactis reynaudii</i>	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0
48 <i>Patella minata</i>	0	1	1	1	1	1	0	0	0	1	0	1	0	0	0
49 <i>Nicella squamosa</i>	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
50 <i>Nicella dubia</i>	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0
51 <i>Nicella cingulata</i>	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0
52 <i>Burupena</i> spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
53 <i>Grateloupia filicina</i>	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
54 <i>Helcton dunkeri</i>	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0
55 <i>Helcion pruinosis</i>	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0
56 <i>Helcion pectunculus</i>	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
57 <i>Enteromorpha</i>	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0
58 <i>Turbo cidaris</i>	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0
59 <i>Turbo sarmaticus</i>	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
60 <i>Turbo coronatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61 <i>Gunnarea capensis</i>	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0
62 <i>Ecklonia radiata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
63 <i>Ecklonia maxima</i>	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0
64 <i>Laminaria pallida</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
65 Turfs- Green, Brown, Black	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
66 <i>Bryopsis</i> spp.	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1
67 <i>Cellaria capensis</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
68 <i>Patella concolor</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
69 <i>Ulva</i> spp.	1	1	1	1	1	1	1	1	1	0	0	1	1	0	0
70 <i>Haliotis spadicea</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
71 <i>Haliotis midae</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
72 <i>Codium fragile</i>	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
73 <i>Codium lucasii</i>	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
74 <i>Saccostrea cucullata</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
75 <i>Sirostrea margaritacea</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
76 <i>Caulerpa holmsetii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
77 <i>Caulerpa racemosa</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
78 <i>Caulerpa filiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
79 <i>Hypnea viridis</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0

(cont.)

Species name	Lüderitz	P. Naloth	Tweepad	Brazil	Speoerivier	Groenrivier	Palernoster	C. Infanta	M. Bay	Tsitsikamma	P. Elizabeth	Dwesa	B. Bay	C. Vidal	Inhaca Is.
80 <i>Hypnea spicifera</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
81 <i>Fissurella mutabilis</i>	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0
82 <i>Fissurella natalensis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
83 <i>Patirella exigua</i>	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0
84 <i>Petalonia</i>	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
85 <i>Nerita albicilla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86 <i>Nerita polita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87 <i>Nerita plicata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88 <i>Nerita textile</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89 <i>Ectocarpus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90 <i>Colpomenia</i>	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0
91 <i>Plocamium cornutum</i>	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0
92 <i>Cliton nigrovirescens</i>	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0
93 <i>Sargassum heterophyllum</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
94 <i>Sargassum longifolium</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
95 <i>Splyridia hypnoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96 <i>Morula granulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97 <i>Patella obtecta</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
98 <i>Gynnogongrus</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
99 <i>Chemidoris delphinis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100 <i>Halimeda cuneata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101 <i>Halopteris sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102 <i>Diclyota dichotoma</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
103 <i>Thais capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104 <i>Purpura panama</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105 <i>Eriphia smithii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106 <i>Splachnidium rugosum</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
107 <i>Champia compressa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108 <i>Acrosorium</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
109 <i>Georginia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110 <i>Tricolia neritina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111 <i>Tricolia capensis</i>	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0
112 <i>Padina comersonii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113 <i>Cucumeria spp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114 <i>Cryptopolysoa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115 <i>Hydrozoa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116 <i>Thais savignyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117 <i>Margareta triplex</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118 <i>Aulacomya ater</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
119 <i>Champia lumbricalis</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0

(cont.)

Species name	Lüderitz	P. Nolloth	Tweepad	Brazil	Spoegrivier	Groentivier	Paternoster	C. Infanta	M. Bay	Tsitsikamma	P. Elizabeth	Dwesa	B. Bay	C. Vidal	Inhaca Is.
121 <i>Chordariopsis capensis</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
122 <i>Iridaea capensis</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
123 <i>Aeodes orbitosa</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
124 <i>Cladophora</i> spp.	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0
125 <i>Mytilus galloprovincialis</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
126 <i>Gigartina striata</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
127 <i>Gigartina radula</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
128 <i>Neuroglossum binderianum</i>	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
129 <i>Bairiocrapa prolifera</i>	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1
130 <i>Patelloida profunda</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
131 <i>Crepidula porcellana</i>	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0
132 <i>Pseudonereis variegata</i>	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0
133 <i>Patella granatina</i>	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
134 <i>Gracilaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135 <i>Nodilitorina natalensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
136 <i>Oxysteles tabularis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
137 <i>Venerupis corrugatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138 <i>Thecalia concamerata</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
139 <i>Cyclograpsus punctatus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
140 <i>Plagusia chabrus</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
141 <i>Patella pica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
142 <i>Acanthochiton gamoi</i>	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1
143 <i>Ischnochiton</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
144 <i>Chaetomorpha</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
145 <i>Verrucaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
146 <i>Trematocarpus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
147 <i>Dendropoma corallinaceus</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
148 <i>Chaetangium ericiniem</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
149 <i>Chaetangium ovale</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
150 <i>Pterosiphonia cloiophylla</i>	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
151 <i>Hyale</i> spp.	1	0	1	1	1	1	0	0	1	1	0	1	0	0	0
152 <i>Paridotea</i> sp.	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
153 <i>Paridotea rubra</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
154 <i>Dynamenella</i> spp.	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0
155 <i>Myriogloea</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
156 <i>Polysiphonia corymbifera</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
157 <i>Scytosiphon</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
158 <i>Nemastoma</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
159 <i>Ophiactis</i> spp.	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0
160 <i>Centroceras clavatum</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

(cont.)

Species name	Lüderitz	P. Nolloth	Tweepad	Brazil	Spoegrivier	Gronrivier	Paternoster	C. Infanta	M. Bay	Tsitsikamma	P. Elizabeth	Dwesa	B. Bay	C. Vidal	Inhaca Is.
162 <i>Seminylus algosus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
163 <i>Ptilunoides perlatus</i>	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
164 <i>Carpoblepharis flaccida</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
165 <i>Eatonella nigra</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
166 <i>Henricia ornata</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
167 <i>Leptilonotus semitectus</i>	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0
168 <i>Aristothonium</i>	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
169 <i>Choromytilus meridionalis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
170 <i>Lysianassa</i> spp.	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0
171 <i>Synidotea hirripes</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
172 <i>Tanyostylum brevipes</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
173 <i>Timarete capensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
174 <i>Onithochiton literatus</i>	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1
175 <i>Pycnogonida</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
176 <i>Octopus</i> spp.	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
177 <i>Sipunculida</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
178 <i>Clavatulula sinuata</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
179 <i>Lumbrineris</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
180 <i>Exosphaeroma</i> spp.	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
181 <i>Cymodoella pustulata</i>	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
182 <i>Cymodoella sublevis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
183 <i>Golfingia capensis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
184 <i>Marphysa depressa</i>	0	1	0	0	1	0	1	0	1	1	0	0	1	0	0
185 <i>Terebella pterochaeta</i>	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0
186 <i>Onchidella</i> sp.	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
187 <i>Gibbula</i> sp.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
188 <i>Platynereis dumerilii</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
189 <i>Carradoria</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
190 <i>Clitonella sinuata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
191 <i>Paranoera capensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
192 <i>Calliopiella michaelseni</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
193 <i>Subria vitata</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
194 <i>Desis formidabilis</i>	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
195 <i>Ectocarpus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
196 <i>Parisoctadus stimpsoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
197 <i>Nereis</i> spp.	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
198 <i>Planocera gilchristi</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
199 <i>Leptanthura laevigata</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
200 <i>Perinereis capensis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
201 <i>Clibanarius virescens</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

(cont.)

Species name	Lüderitz	P. Nolloth	Tweepad	Brazil	Spoegrivier	Gruenrivier	Paternoster	C. Infanta	M. Bay	Tsitsikamma	P. Elizabeth	Dwesa	B. Bay	C. Vidal	Inhaca Is.	
202 <i>Eunice aphroditis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
203 <i>Syllis</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
204 <i>Euphrosine capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
205 <i>Gregariella simplicifilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
206 <i>Euchymene</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
207 <i>Ampithoe falsa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
208 <i>Pentacta doliolum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
209 <i>Patella aphanes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
210 <i>Dehaanius dentatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
211 <i>Chaetopteura pertusus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
212 <i>Arca</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
213 Zoathidea 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
214 Zoathidea 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
215 Zoathidea 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
216 Zoathidea 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
217 Zoathidea 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
218 <i>Planaxis sulcatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
219 <i>Cerithium</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
220 <i>Conus algoensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
221 <i>Conus ebraeus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
222 <i>Fusinus ocelliferus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
223 <i>Calcinus laevimanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
224 <i>Grapsus fourmanoiri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
225 <i>Septifer bilocularis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
226 <i>Mancinella aloccina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
227 <i>Idanthysus pennatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
228 <i>Pinctada capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
229 <i>Microcosmus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
230 <i>Thais</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
231 <i>Parviperna dentifera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total=	63	72	65	60	65	76	57	55	52	78	53	83	69	69	66	

Chapter 2

*The Influences of Physical Factors in the Distribution and Zonation
Patterns of South African Rocky -Shore Communities*

Summary: In this Chapter, I initially establish at a broad geographic scale, the vertical and horizontal distribution patterns of both community biomass and species richness. For that, I use the data of the biological surveys presented in Chapter 1. I compare the general trends of distribution for seven west and seven southeast intertidal rocky shore communities. There were consistent distribution patterns for both community biomass and species richness. Independently of geographical scale, biomass and species richness showed similar distributions in equivalent habitats. The consistency of these vertical and horizontal patterns casts light on the fact that the processes which create these patterns operate and vary in a similar way over large geographical scales. In particular, I assess at local-scale the relative importance of wave force, rock temperature and shore elevation on the structuring and spatial variability of community biomass. Using a multivariate approach, I relate the local zonation patterns to these environmental variables. The results of the direct gradient analyses revealed that differences in wave action generate divergence of mid-to-low shore communities, while the interaction between rock temperature and shore elevation (both accounting for desiccation) produces convergence of high shore communities. There was a significantly positive relationship between wave action and the per-unit-area community biomass, and an inverse relationship between shore elevation and biomass. The potential role that waves may play by enhancing overall intertidal productivity is discussed.

Introduction

All species occurs in a characteristic limited range of habitats; and within their range, they tend to be most abundant at their particular environmental optimum (Whittaker 1975). It has been consistently shown that the biota exhibit trends along environmental gradients, regardless of the particularities of their habitat (Menge and Olson 1990). These 'gradients' do not necessarily have physical reality as continua in either space or time, but are a useful abstraction for exploring the distributions of organisms (Austin 1985). Whittaker (1967) developed the first quantitative approach to ecological *gradient analysis* to assist the interpretation of spatial community composition in terms of species' responses to environmental variations. There are two kinds of gradient analyses: a) *indirect* gradient analyses, in which environmental gradients are inferred from the community data (latent variables), and b) *direct* gradient analyses, in which each species' abundance is described as a function of measured environmental variables. The latter analytical technique can either be exploratory, i.e. to examine how community composition varies with the environment, or confirmatory, i.e. a means of testing the effects of particular environmental variable taking into account the effects of other variables (ter Braak and Prentice 1988).

Underwood (1986) has stated that only field experiments can determine the causal mechanisms that creates the patterns of species distribution. However, any efficient experimental design will require extensive preliminary analyses of distributional data, and numerical descriptive analyses may play an important role in determining which experimental hypotheses are going to be tested in the field (James and McCulloch 1990; Santos 1993). More particularly, numerical multivariate analyses have been long used in ecology (for review see James and McCulloch 1990), and applied to a range of different marine communities, including soft bottom benthic macrofauna (e.g. McLachlan *et al.* 1984; Austen 1989; van der Meer 1991; van Nes and Smit 1993), nekton and fish

assemblages (e.g. Weinstein *et al.* 1983; Rakocinski *et al.* 1992), subtidal assemblages (e.g. Field *et al.* 1982; Kautsky and van der Mareel 1990; Castric-Fey and Chassé 1991; Santos 1993), and intertidal rocky communities (e.g. Field and McFarlane 1968; Field and Robb 1970; Kooistra *et al.* 1989; Fuji and Nomura 1990). All these works have explored the importance of the joint relationship between community data and environmental factors. Such analytical methods are increasingly used in marine ecology because they offers succinct summaries of large data sets, especially in the exploratory stages of an investigation. The exploration of large data sets can be a very creative part of the scientific work that can suggest causes; at a later stage these can be formulated into new research hypotheses and causal models (James and McCulloch 1990).

The body of ecological evidence relating to the structure and regulation of marine communities (especially intertidal ecosystems) has largely concentrated on how particular species respond differentially to the effects of ecological processes such as disturbance, predation, competition, or recruitment (e.g., Connell 1961; Paine 1966; Underwood and Denley 1984; Lubchenco 1986). Only recently, research has been developed around the effects of the environment on the regulation and structuring of whole marine benthic communities or species assemblages (Menge and Sutherland 1987; Menge and Farrell 1989; Menge and Olson 1990; McGuinness 1990). However, intertidal ecologists have long recognized that two of the most important local physical forces structuring intertidal rocky shores are gradients of desiccation, which produce a vertical zonation, and the differential effects of wave forces that generate a horizontal zonation (Stephenson and Stephenson 1972; Dayton 1971; Menge and Sutherland 1987; Sousa 1979a,b; Underwood *et al.* 1983; Dayton 1984; Menge and Farrell 1989; Menge and Olson 1990). These studies suggest that community structure (abundance and diversity of species) depends on a complex interplay between large-scale processes (e.g. environmental stress and productivity) and small-scale processes (strong biotic interactions). One of the main conclusions reached by studies that have revised patterns in intertidal communities, is the need for further comparative studies that simultaneously evaluate the contribution of environmental stresses at large- and local-scales to variations in community structure

(Dayton and Tegner 1984; Foster *et al.* 1988; Menge and Sutherland 1987; Menge and Olson 1990). However, the comparison of particular environmental factors, such as temperature and wave action, are of little value when made between disjunct localities because local climatic conditions can override the observed differences. A more fruitful comparison would be within different localities (i.e. exposed vs. sheltered or high- vs. low-shore), because the comparisons are made simultaneously under comparable conditions.

The rocky intertidal biota of southern Africa are among the most varied in the world. The array of oceanographic conditions and the particular physical and biological dynamics of its shores have forged characteristic communities in different biogeographic regions (see Chapter 1). These rocky shores have been the focus of extensive local ecological research, centered on the identification of forces structuring rocky shore communities. The majority of these works have dealt with the identification of particular factors, including several biotic influences (Branch 1985; Branch *et al.* 1987; Bosman and Hockey 1988; van Zyl and Robertson 1991), abiotic factors (Field and McFarlane 1968; Field and Robb 1970; MacQuaid and Branch 1984; MacQuaid and Branch 1985; Hugget and Griffiths 1986; Bosman *et al.* 1987; Branch *et al.* 1988; McQuaid and Dower 1990; Field and Griffiths 1991), or a combination of abiotic and biotic factors (MacQuaid *et al.* 1985; Griffiths and Hockey 1987). Griffiths and Branch (1991) have revised the known causes of vertical zonation of the macrofauna of rocky shores in False Bay (see Fig.1). They concluded that physical factors control the abundance and vertical zonation of the dominant species, whereas the subordinates are biological controlled. Among the physical factors, they recognized that wave action and desiccation are perhaps the most important. Despite the general acceptance of the importance of these factors, in South Africa and elsewhere (e.g., Lewis 1976; Underwood 1981; Foster *et al.* 1988; Menge and Olson 1990; McGuinness 1990), their variation among sites, and comparisons at local and meso-geographical scales are seldom documented. The nature and the magnitude of small-scale (local) differences of intertidal communities, within and between localities,

must be considered before general models for community structure and regulation can be sensibly erected.

The effects of the environment (leading to physiological and/or mechanical stress) have been incorporated into general community models as independent variables (Hairston, Smith and Slobodkin 1960; Connell 1975; Menge and Sutherland 1976 1987). To correctly evaluate these models, it is ideal as a first stage, to quantify independently the main environmental gradients and the community variation along them, at different spatial scales (Menge and Sutherland 1987), and then to synthesize the main environmental factors (and their interactions) that influence that variation.

In this Chapter, my purpose is three-fold: a) to describe, evaluate, and compare at broad geographical scales, the existence of trends of biomass zonation and species richness of the rocky intertidal communities at seven localities in the west coast compared with seven other localities in the south and east coasts of southern African, b) assess the relative importance of physical factors such as wave force, shore elevation and rock temperature, on species abundance and distribution at two specific localities; i.e. Groenrivier in the west and Port Elizabeth on the south coast, to explore in detail the spatial distribution of organisms in two geographically disjunct rocky intertidal communities, and c) to relate zonation patterns of intertidal species to environmental variables at a local-scale. This Chapter is descriptive in nature and relies on direct gradient analyses to detect and explore patterns in community structure and their correlation with physical variables.

Materials and methods

The sites

The data on biomass zonation used in this Chapter were collected at 14 different localities around the southern African coasts (Lüderitz, Port Nolloth, Tweepad, Rooiklippias, Spoegrivier, Groenrivier, Paternoster, Cape Infanta, Mosselbaai, Tsitsikamma, Port Elizabeth, Dwesa, Ballito Bay and Cape Vidal, see Fig. 1 in Chapter 1). More particularly, I compare data from the intertidal rocky shores of Groenrivier (30°48'S - 17°30'W) on the west coast and from Port Elizabeth (34°00'S - 26°37'W) on the south-east coast (Fig. 1). At these localities, respectively three and two sites were selected to represent grades of wave action - i.e. *sheltered* boulder bays, *semi-exposed* rocky shores (lee side of kelp forests, only in the west coast) and *exposed* rocky headlands. The sites were selected to ensure comparability in orientation, slope (between 15° to 45° inclination) and substrate type (sandstone). Both localities exhibit a similar semi-diurnal tidal regime and tidal amplitude, the latter being 2.21 m and 2.40 m for Groenrivier and Port Elizabeth, respectively (SAN 1993).

Data acquisition

The average (± 1 S.E.) values of community biomass per unit area for all sites described in Chapter 1, were used to describe general biomass patterns in relation to rocky intertidal zonation (vertical and horizontal). Standard intertidal community surveys (see details in the Material and Methods section of Chapter 1) were carried out at each locality. In general, at each sites, four replicate transects 15 to 30 m long were laid down perpendicularly to the sea, and along them, between 8 and 12 quadrats (0.5 m² each) were randomly placed, and the biomass contribution per-species (converted to g m⁻² of ash free dry weight, AFDW), density, species richness (total number of species per unit area) and trophic structure were recorded. Only the most important species were included

in the biomass analyses, although the presence of small cryptic species was also recorded. At Groenrivier and Port Elizabeth, three simple environmental variables were recorded at the same surveyed areas. At the position of each individual quadrat (within which biomass had been sampled), measurements were made of (a) shore elevation (height) above the Mean Low Water Spring tide (MLWS), (b) rock and air temperatures, and (c) wave force. Shore elevation was measured using a modified water-level device (see Appendix I) which recorded the difference in height between sampled quadrats and the zero level (MLWS). Wave force (measured in N m^{-2}) was defined as the force exerted by waves over a hollow hemi-spherical drogue, divided by the cross-sectional area of the drogue. The forces were measured with dynamometers, using a modified version of the Jones and Demetropoulos (1968) apparatus, described and tested by Palumbi (1984). At each quadrat, a series of three parallel dynamometers were fastened to the rock surface perpendicularly to the direction of waves (Fig. 2A). The dynamometers were left *in situ* for a period of three days and the wave forces exerted on the dynamometers during each tidal cycle were recorded. In order to make comparison between the subjectively ranked sites, the absolute average value, or the variation of wave forces are frequently not critical for wave-swept organism, but their maximal values or extremes in a given period (Denny 1988; Denny and Gaines 1990). However, simultaneous measurements and the use of identical drogues are absolutely essential.

Simultaneously at Groenrivier and Port Elizabeth, rock temperatures were measured within each quadrat during low tide, every hour for three consecutive days. Using epoxy glue, a 30 Ga Type T thermocouple were attached to the rock surface (Fig. 2B). Temperatures detected with these thermocouples were recorded by a Bat-12 Bailey Instruments Inc.) digital thermocouple reader.

Data analysis

A total of 101 algae and invertebrate taxa was recorded at the two localities, although it must be recognized that the sampling methodology will fail to detect many of the less abundant species. For the biomass and multivariate analyses, only taxa that contributed >

0.01% to the total biomass were included - i.e. 38 and 34 taxa for Groenrivier and Port Elizabeth respectively. Nevertheless, the community biomass data used in this Chapter comprises more than the >71% of the recorded species richness and > 95% of the total biomass recorded during the surveys. In the biomass analyses, a total of 140 samples=quadrats (or 70 m²) were included, and all statistical analyses were performed on the averages per sample (quadrats). The contribution of the different species to the community biomass varied by five orders of magnitude (from 0.2 g to *ca.* 1700 g m⁻²). Consequently, in the analyses the biomass data were standardized and logarithmically transformed [$\log_{10}(x+1)$]. The ordinal environmental variables (elevation, temperature and wave action) were entered as continuous variables.

To detect trends in vertical distribution of biomass and total number of species, curves were fitted to the plots by using the locally weighted least squared error method. This curve fit has no data restrictions and has no parameters associated with it. The result of this curve fit is to plot a best fit smooth curve through the center of the data, or 50% smoothing. This is an extremely robust fitting technique and, unlike standard regression methods, is nearly insensitive to outliers (Press *et al.* 1986).

Linear regressions and univariate non-parametric analyses of variance (ANOVA by ranks) with *a-posteriori* mean comparisons of main effects (Bonferroni *t*-test) were performed for the comparison of shore elevation, rock temperature and wave exposure between and within localities. All ANOVAs and regressions were performed using Generalized Linear Models, GLM (SAS[®] 1986).

To explore the joint relationship between the biomass of rocky intertidal species assemblages and the selected environmental variables, a multivariate (ordination) direct gradient analysis was performed. Canonical Correspondence Analysis (CCA) was used to correlate the benthic community with the abiotic variables (ter Braak 1986; Palmer 1993). Direct gradient analysis was carried out using the average biomass per species at each height interval, for Groenrivier and Port Elizabeth independently. The environmental variables used in the analyses were the maximum wave force, maximum rock temperature

and shore elevation. The computer package CANOCO v2.1 (ter Braak 1986) was used to perform CCA (ter Braak and Prentice 1988).

Results

Biotic and abiotic distribution patterns

Biomass

Two different zonation patterns of community biomass-per-unit-area were detected, and could be related to differences in wave exposure. On sheltered shores of the west coast, the community biomass reached a maximum on the low shore, decreasing exponentially as elevation increased (Fig. 3A). On sheltered south-east shores, biomass was lower, so that although biomass decreased up the shore this pattern was less obvious (Fig. 4A). Maximal values up to 2000 (± 445) g m⁻² were recorded on the west coast, and up to 700 (± 135) g m⁻² on the south-east coast. From 50 cm upwards, in both west and south-east intertidal communities, the average biomass never exceeded 450 (± 58) g m⁻², and the upper maximum limit of the community was around the 250 cm above MLWS (Figs. 3A and 4A).

A second general pattern was found consistently in semi-exposed and exposed shores on west and south-east coasts. By contrast with the sheltered shores, peak biomass was concentrated on the mid shore (50 to 100 cm), followed by steady decrease above this; intermediate levels were recorded low on the shore (Figs. 3B, C and 4B). The maximum biomass values on the west coast were 2675 (± 168) and 3726 (± 150) g m⁻² for semi-exposed and exposed shores respectively, while the biomass on south-east exposed shores never exceeded 2500 g m⁻² (Figs. 3 and 4). On the west coast, the upward extent of the intertidal communities of the semi- and exposed shores was significantly different than of the sheltered shores (ANOVA, $p < 0.001$). Thus, the upper limit of the semi- and exposed shores (350 cm) was significantly greater than the sheltered shores (247 cm, Bonferroni t -test, $p < 0.05$) (Fig. 3). Similarly, in the south and east coasts, exposed shores had a significantly higher upper limit (350 cm) than sheltered shores (259 cm,

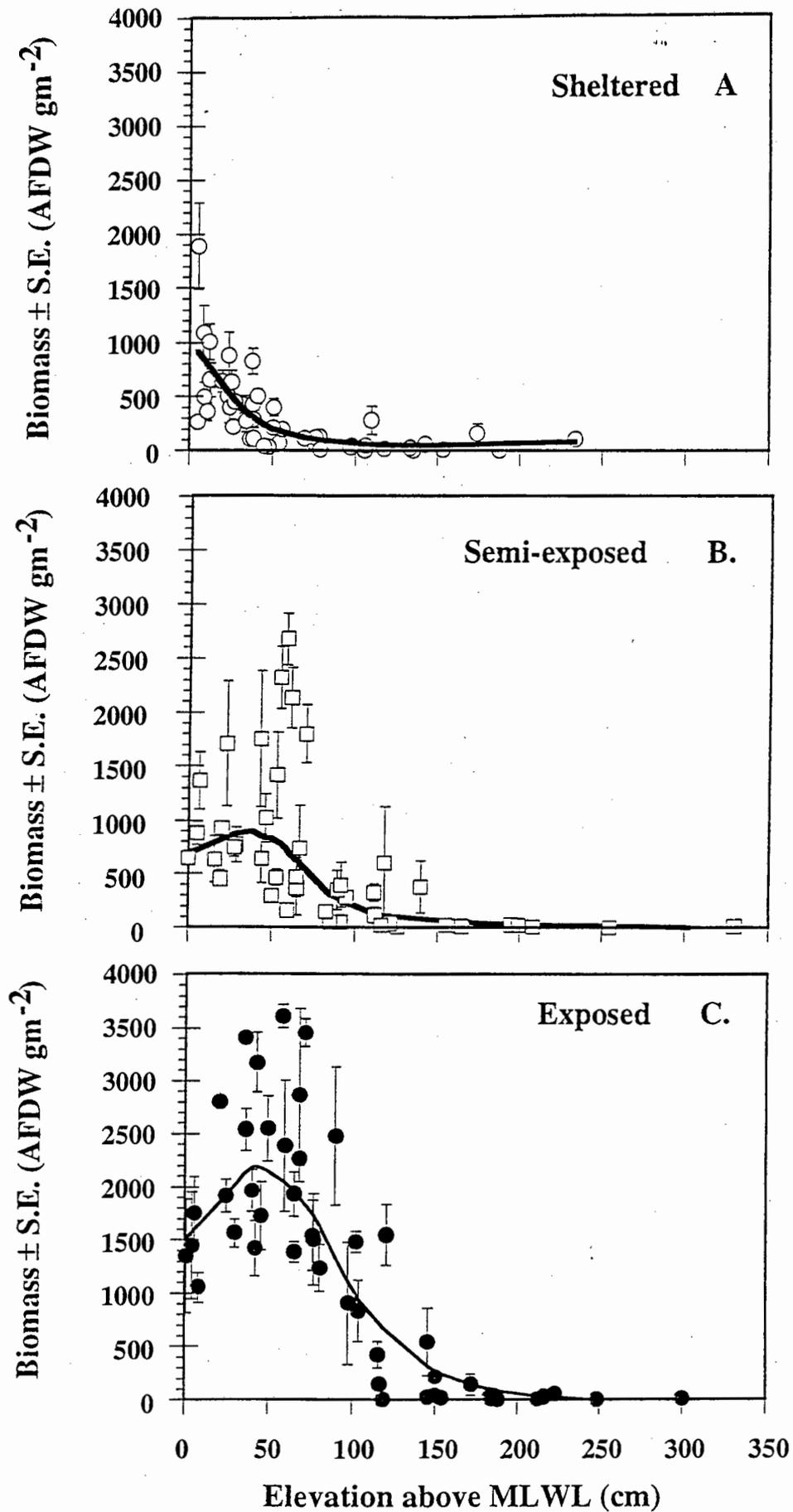


Figure 3. Vertical zonation of the average (\pm S.E.) biomass in seven localities on the west coasts of southern Africa, in three subjectively defined wave exposures. The biomass trend from low to high shore is indicated by the weight fitted lines with a 50% smoothing.

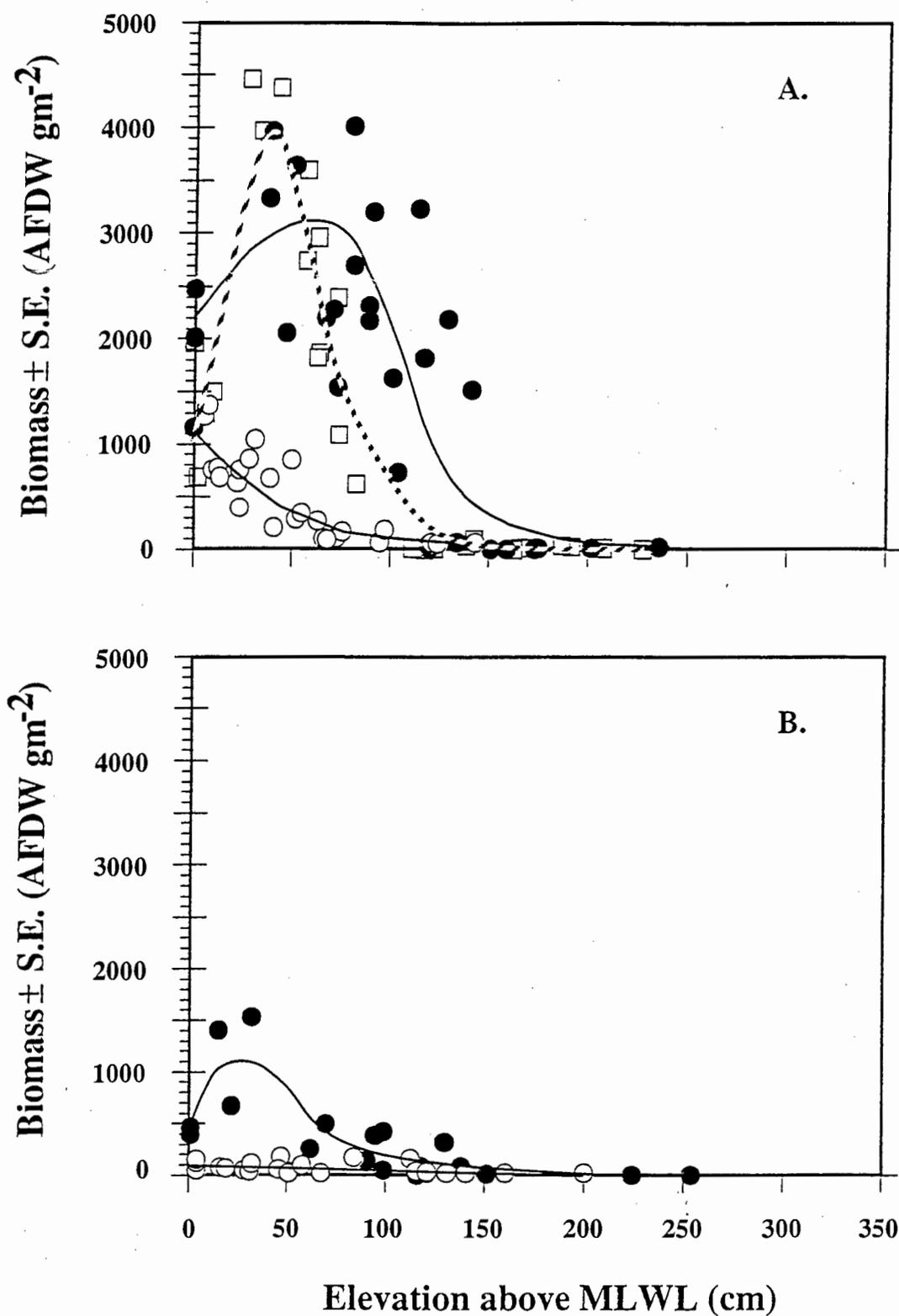


Figure 5. Vertical zonation of the biomass at the localities of Groenrivier (A.) and Port Elizabeth (B.). Symbols are ● =exposed, □ =semi-exposed and ○ =sheltered shores. The biomass trend from low to high shore is indicated by the weight fitted lines with a 50% smoothing.

Bonferroni *t*-test, $p < 0.05$) (Fig. 4). Above 150 cm, the community biomass varied over similar average ranges (between 74 g and 420 g m⁻²) regardless of exposure and geographic differences.

The overall biomass was consistently higher on the west coast than the south-east coasts, and also higher at wave exposed sites than sheltered sites (Figs. 3 and 4).

The trends of the vertical biomass zonation at the specific localities of Groenrivier and Port Elizabeth are shown in Figure 5. At both localities, semi-exposed and exposed shores had intermediate levels of biomass on the low shore (< 30 cm), and maximum biomass in the mid shore (50-100 cm) (Fig. 5), and closely follow those described above for the west and south-east coasts as a whole. Similarly, on sheltered shores the biomass was concentrated in the low shore, followed by a sharp up-shore decrease at Groenrivier (Fig. 5A), while at Port Elizabeth the biomass decreased gradually as elevation increased (Fig. 5B). The average community biomass was significantly greater at Groenrivier than at Port Elizabeth (Fig. 5), at both exposed shores and sheltered shores (ANOVA, $p < 0.001$; Bonferroni *t*-test, $p < 0.05$).

Species richness

On the west coast the maximum number of species per unit area was 20 m⁻² the highest values being reached in the mid intertidal (50-100 cm above MLWL tide) of semi-exposed and exposed shores (Figs. 6B, C). Sheltered shores achieved a maximum of only 14 m⁻², being achieved low on the shore (Fig. 6A). Very similar patterns were found at exposed and sheltered shores of the south-east coast (Fig. 7), except that species richness was higher there than on the west coast. The vertical distribution of species per-unit-area thus parallel the patterns described for biomass.

More specific examination of the two sites at which physical measurements were made, Groenrivier and Port Elizabeth, revealed similar vertical distribution patterns of species richness per-unit-area (Fig. 8). At exposed and semi-exposed shores, the peak of species richness occurred in the mid shore (≈ 50 cm above MLWS), whereas at sheltered

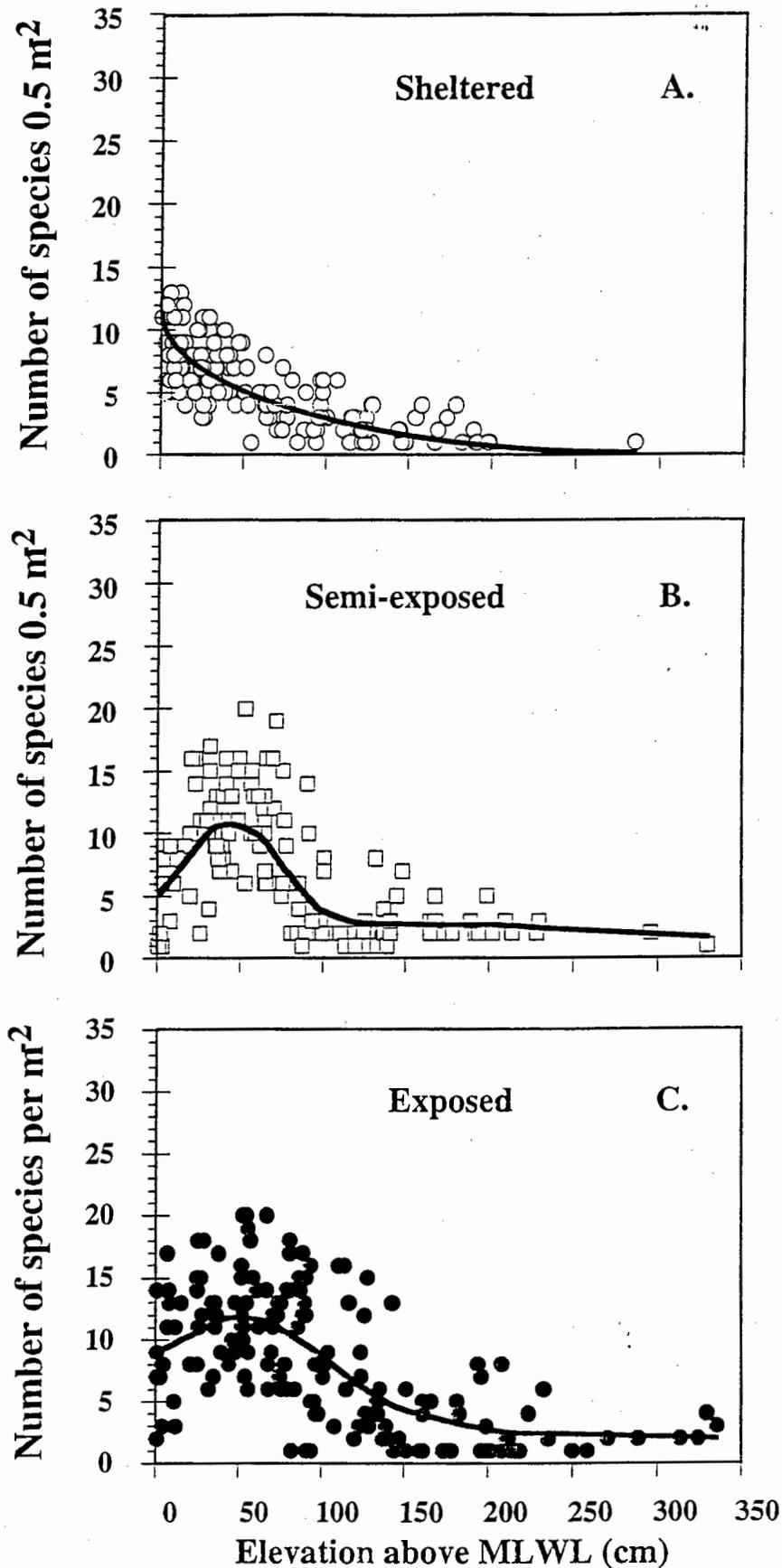


Figure 6. Vertical zonation of the total number of species per unit area in seven localities on the west coasts of southern Africa, in three subjectively defined wave exposures. The trend of the number of species from low to high shore is indicated by the weight fitted lines with a 50% smoothing.

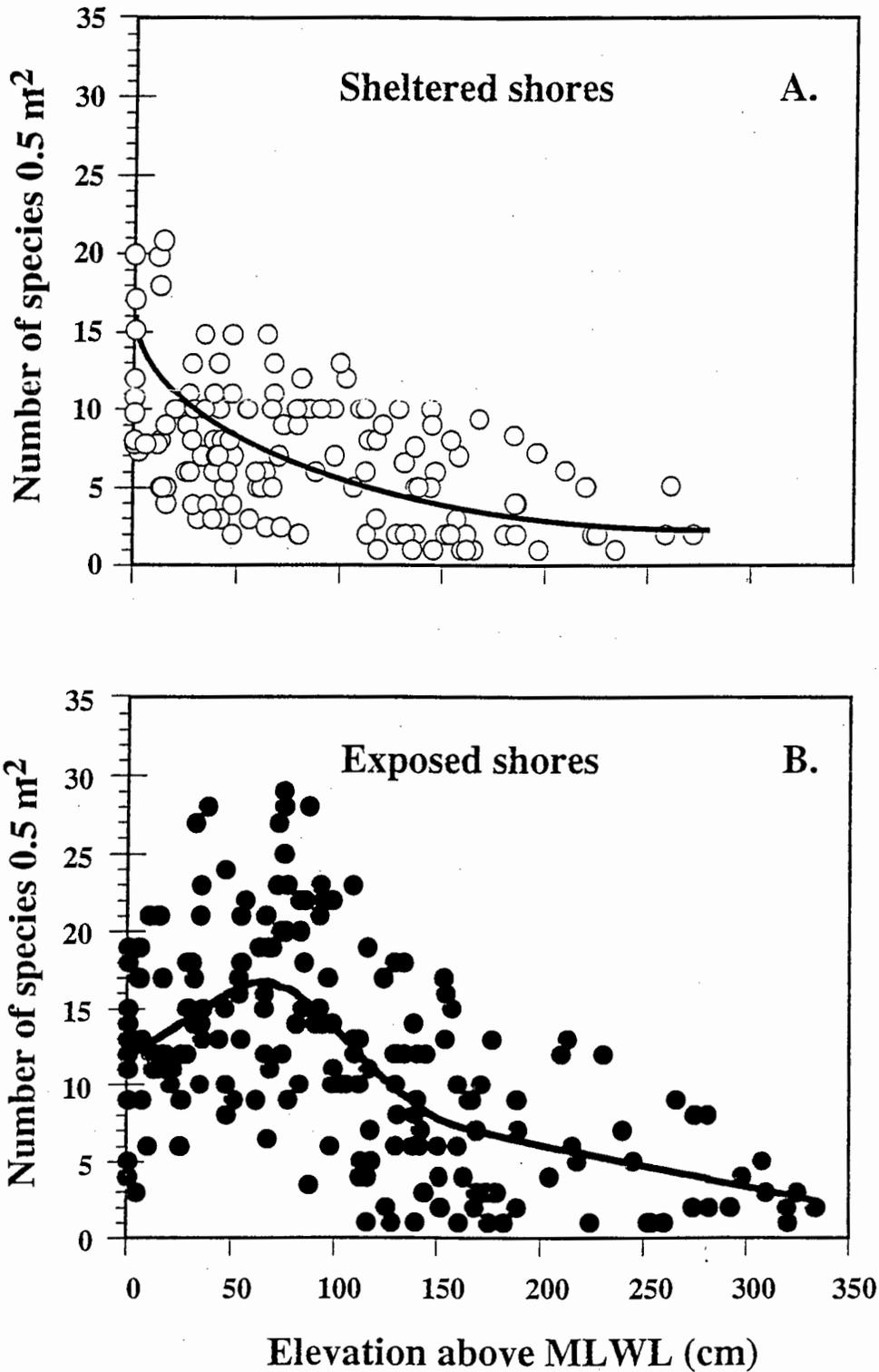


Figure 7. Vertical zonation of the total number of species per unit area t in seven localities on the south-east coasts of southern Africa, in two subjectively defined wave exposures. The trend of the number of species from low to high shore is indicated by the weight fitted lines with a 50% smoothing.

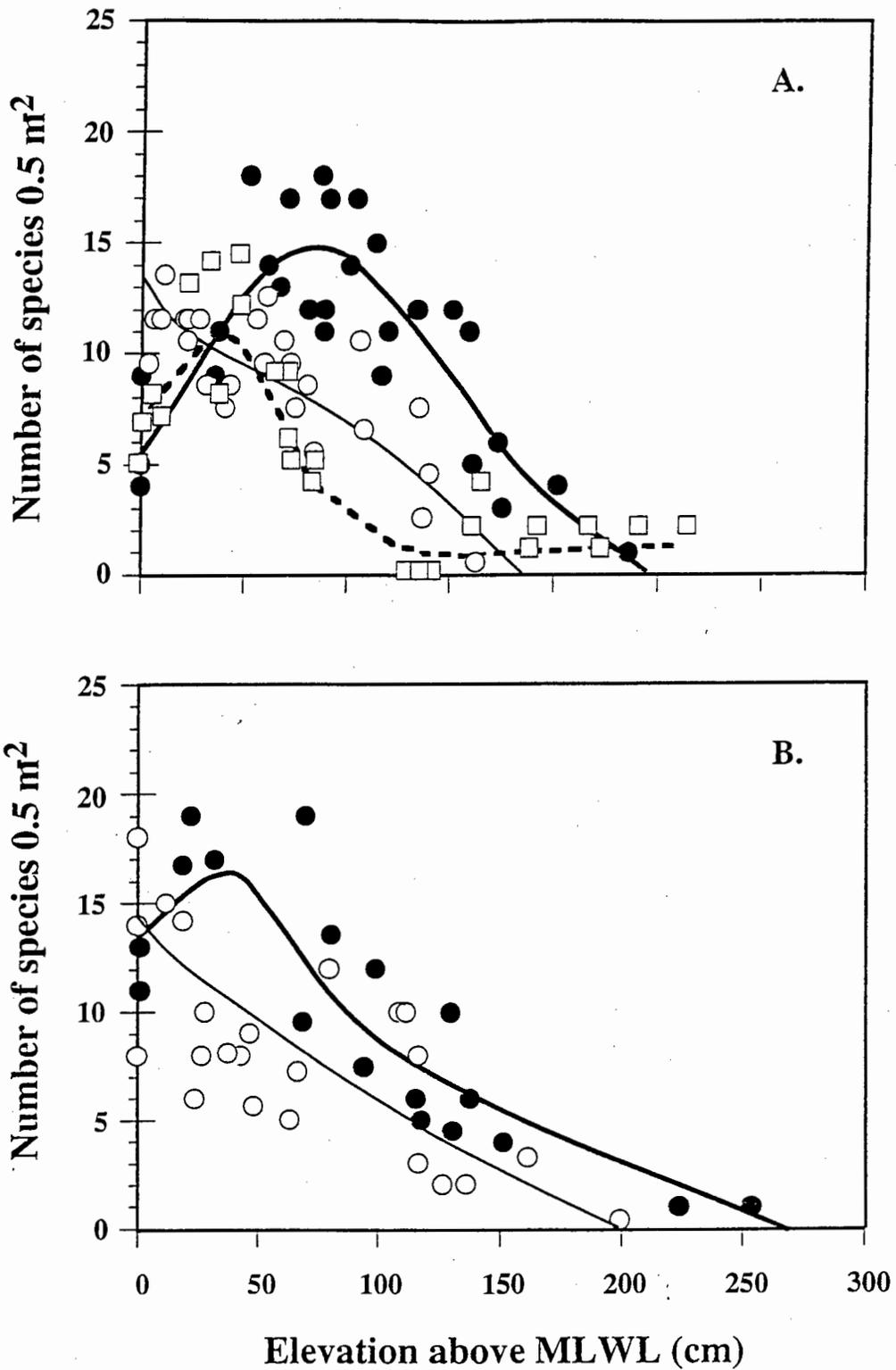


Figure 8. Vertical zonation of the total number of species per unit area at the localities of Groenrivier (A.) and Port Elizabeth (B.). Symbols are ● =exposed, □ =semi-exposed and ○ =sheltered shores. The trend of the number of species from low to high shore is indicated by the weight fitted lines with a 50% smoothing.

shores, the species richness decreased exponentially from low to high shore. The number of species was also higher at exposed than sheltered shores (Fig. 8).

Abiotic factors

The abiotic factors measured at Groenrivier and Port Elizabeth are depicted in Figures 9A and 9B, in which the maximum values of wave action and rock temperature are plotted in relation to the shore elevation. On average, the maximum values of wave force recorded on exposed sites at Groenrivier (15000 N m^{-2}) were significantly greater (ANOVA, $p < 0.0001$) than those of sheltered shores (1500 N m^{-2}). Similarly, exposed sites at Port Elizabeth (10500 N m^{-2}) had significant greater wave forces (ANOVA, $p < 0.0001$) than sheltered shores (1100 N m^{-2}). The vertical distribution of wave force at exposed sites followed a similar trend to that of community biomass and species richness (see Figs. 3-5 and 6-8), i.e. medium forces on the low shore (0 to 20 cm), and a peak on the mid shore, decreasing towards the high shore as elevation increased. The values at exposed shores were consistently higher at all shore elevations than those measured at sheltered sites (Fig. 9A), although the differences between exposed and sheltered shores became less obvious in the high shore. On sheltered shores there was no obvious vertical trend in the wave force distribution as elevation increased (Fig. 9A). The subjectively selected semi-exposed shores of Groenrivier occupied an intermediate position between the sheltered and exposed shores, with maximum wave forces of 7000 N m^{-2} (Fig. 9A).

There was a positive relation between the maximum rock temperatures and shore elevation at all sites (see Fig. 9B), i.e. in the low shore, rocks had a temperature close to that of sea water, rising as elevation increased, achieving values up to 45°C . The average distribution of the rock temperature was marginally different (ANOVA, $p < 0.049$) between the localities of Groenrivier ($23.1^\circ \pm 8.54$) and Port Elizabeth ($30.9^\circ \pm 9.25$), but no differences were found between their respective wave force habitats (ANOVA, $p > 0.810$). No great significance can be attached to these differences, however, since prevailing weather conditions would have strong influences on differences between regions. Within regions, temperature did differ on shores experiencing different grades of

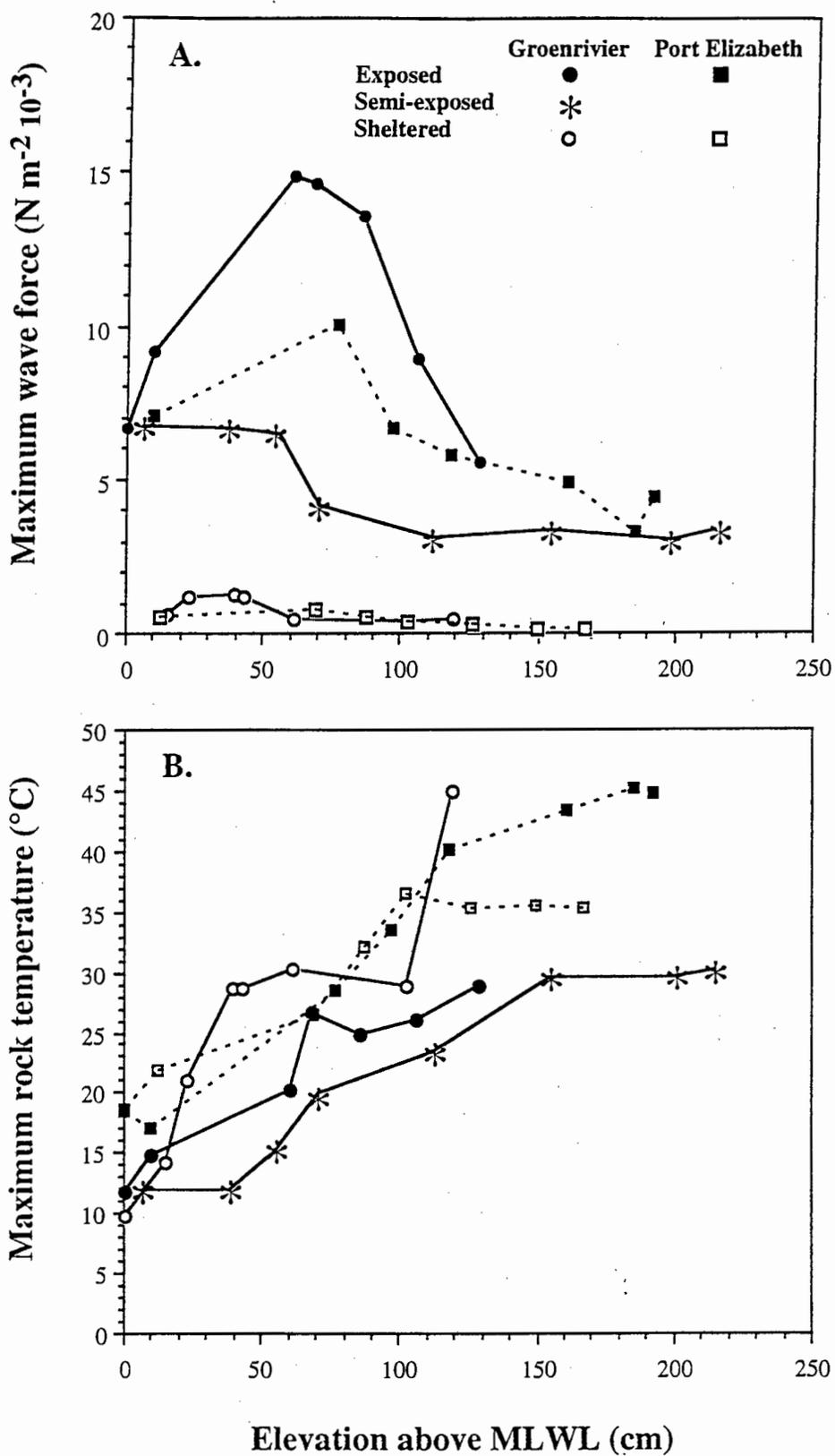


Figure 9. Maximum values recorded of **A.** Wave force, and **B.** Rock temperature in relation to tidal elevation on exposed, semi-exposed, and sheltered habitats at Groenrivier and Port Elizabeth.

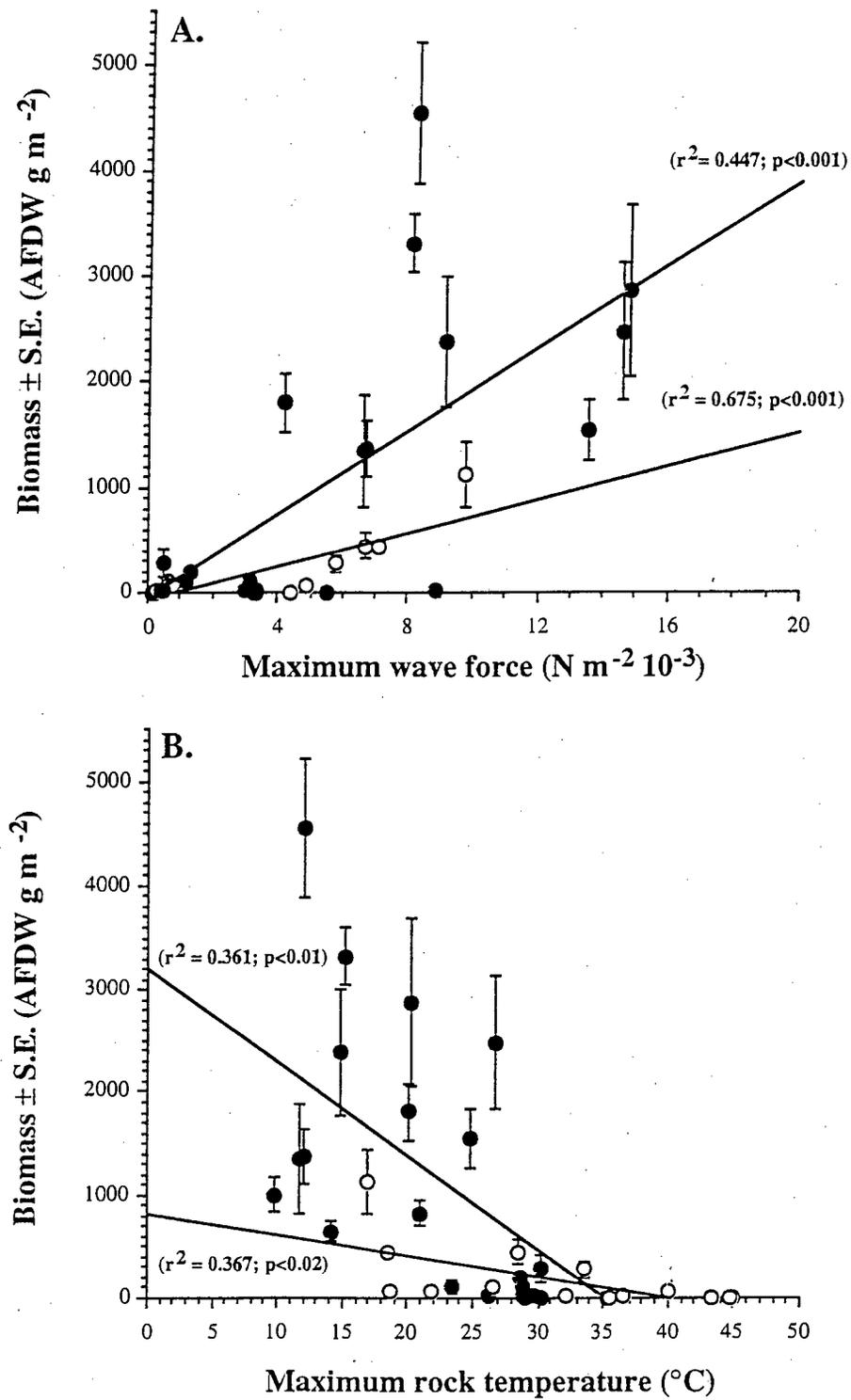


Figure 10. Relationship between average intertidal community biomass and maximum wave force (A) and maximum rock temperature (B) at the localities of Groenrivier (●) and Port Elizabeth (○).

wave action, but no consistent pattern emerged (Fig. 9B). At Groenrivier, semi-exposed shores were cooler than sheltered or exposed shores, which did not differ significantly (ANOVA, $p > 0.05$). At Port Elizabeth no significant differences were found between sheltered and exposed shores (Fig. 9B).

Relationships between physical factors and biota

The relationship between the average (\pm S.E.) biomass and the maximum wave force (Fig. 10A) and the maximum rock temperature (Fig. 10B) is shown for each locality. The biomass per unit area was positively correlated with wave action at both Groenrivier ($r=0.669$; $p < 0.01$) and Port Elizabeth ($r=0.822$; $p < 0.001$) (Fig. 10A). Conversely, the average community biomass-per-unit-area was negatively correlated with the rock temperature, at both Groenrivier ($r=-0.601$; $p < 0.01$) and Port Elizabeth ($r=-0.606$; $p < 0.02$) (Fig. 10B). There is an obvious inverse relationship between wave force and rock temperature, both being related to tidal elevation. This situation preclude the use of each of this factors in isolation.

Community structure and species composition

The occurrence and biomass contribution of each taxon to the different intertidal communities, separated by wave exposure, are listed in Tables 1 and 2, for Groenrivier and Port Elizabeth respectively.

On sheltered sites at Groenrivier, 68% of the total community biomass was represented by 5 taxa (Table 1). These were the kelps *Ecklonia maxima* and *Laminaria pallida* (combined 15.01%), the limpet *Patella granatina* (18.59%), which forms dense monospecific stands in the low to mid shore, and dense colonies of the polychaete *Gunnarea capensis* (17.85%); high on the shore the red alga *Porphyra capensis* (17.2%) formed dense patches. However, the most frequent species likely to be found in the samples was the limpet *Patella granularis* (12.15% frequency). The next most frequent species were the sea anemone *Bunodactys reynaudii* and two species of the scavenging

Table 1. Species frequency of occurrence per quadrat (%), average biomass, standard deviation (SD), standard error (SE), percent biomass and minimum and maximum values of biomass (g m⁻² AFDW), for the different wave-exposures habitats at Groenrivier. Only species contributing > 0.01% to the AFDW biomass are listed.

Species	SHELTERED						SEMI-EXPOSED						EXPOSED										
	Abrev.	Mass	SD	SE	% Mass	Min. Max.	Freq. %	Mass	SD	SE	% Mass	Min. Max.	Freq. %	Mass	SD	SE	% Mass	Min. Max.					
Algae																							
Articulate corallines	Artcor	5.52	25.11	18.31	5.79	2.27	5.56	66.38	1.66	14.14	7.70	4.45	0.36	6.86	22.20	4.12	4.88	1.85	0.56	0.22	2.60	8.88	
Gelidium spp.	Gelspp	3.31	190.54	241.97	98.78	17.19	21.52	620.00	0.55	1.48	1.48	1.48	0.04										
Porphyra capensis	Porphy								0.55	4.86	4.86	4.86	0.12										
Ceramium spp.	Cerami	0.55	3.46	3.46	3.46	0.31			4.42	12.26	10.59	3.75	0.31	3.70	36.78								
Gymnogongrus spp.	Gynspp	1.10	12.85	10.90	7.71	1.16	5.14	20.56	2.21	21.80	28.50	14.25	0.56	5.12	64.36	0.37	5.32	5.32	5.32	0.24			
Gigartina spp.	Gigaspp	1.66	3.84	1.51	0.87	0.35	2.34	5.36	0.55	25.44	25.44	25.44	0.65			0.37	2.38	2.38	2.38	0.11			
Iridaea capensis	Iridaea	1.66	31.91	37.16	21.45	2.88	6.10	74.50	2.21	34.66	32.72	16.36	0.89	7.32	72.92	1.50	27.30	30.81	15.41	1.23	3.18	69.40	
Splachnidium rugosum	Chlum	6.63	10.10	6.36	1.84	0.91	1.76	19.52	3.31	3.72	2.04	0.83	0.10	1.42	5.58	1.87	1.53	1.57	0.70	0.07	0.26	4.16	
Aeodes orbicosa	Aeodes	0.55	5.66	5.66	5.66	0.51			1.66	37.52	19.26	11.12	0.96	23.62	59.50	2.62	107.83	150.55	56.90	4.87	4.66	435.92	
Canthacanthus istulianus	Canbac	6.63	166.40	119.13	34.39	15.01	3.78	336.86	0.55	4.12	4.12	4.12	0.11										
Ecklonia/Laminaria	EckLam	2.76	14.78	19.84	8.87	1.33	5.12	50.24	2.21	22.57	38.39	19.20	0.58	3.38	80.16								
Chordarcepis cupensis	Chorda	3.87	5.01	3.49	1.32	0.45	2.76	12.60															
Ulva spp.	Ulva	1.10	9.62	6.34	4.48	0.87	5.14	14.10															
Codium fragile	Codium	1.66	9.36	9.45	5.46	0.84	3.40	20.26															
Cladophora spp.	Cladoph															0.37	0.98	0.98	0.98	0.04			
Grazers																							
Patella granatina	Pgranat	8.84	206.04	154.14	38.53	18.59	10.64	530.76															
Patella argenvillei	Pargv	12.15	36.47	35.60	7.59	3.29	1.18	125.74	2.21	1171.42	579.55	289.77	29.93	448.50	1864.24	0.75	2.47	3.10	2.19	0.11	0.28	4.66	
Patella granularis	Pgranul	1.10	2.78	0.40	0.28	0.25	2.50	3.06	17.13	18.11	14.26	2.56	0.46	2.26	53.98	16.10	12.67	9.87	1.51	0.57	0.46	44.76	
Patella barbata	Pbarb																						
Patella miniata	Pmini																						
Patella coclear	Pcocl																						
Siphonaria spp.	Siphsp								2.21	68.08	36.13	18.07	1.74	23.08	104.08	0.75	2.08	1.58	1.12	0.09	0.96	3.20	
Crepidula porcellana	Crepid	0.55	1.72	1.72	1.72	0.16			1.66	5.00	3.07	1.77	0.13	3.02	8.54	0.37	5.12	5.12	5.12	0.23			
Oxysyde spp.	Oxyspp	2.21	4.37	1.07	0.53	0.39	2.86	5.12	6.08	8.83	9.58	2.89	0.23	1.70	34.34	0.37	2.54	2.54	2.54	0.11			
Oxysteles tigrina	Oxytig	0.55	3.48	3.48	3.48	0.31																	
Helicon spp.	Helisp	2.21	2.12	1.09	0.54	0.19	1.44	3.74	4.97	10.00	7.39	2.46	0.26	2.00	22.86	3.75	3.00	2.66	0.84	0.14	1.32	10.08	
Predators																							
Nucella spp.	Nucell	9.94	11.98	13.48	3.18	1.08	0.46	60.88	2.76	2.44	1.09	0.49	0.06	0.98	3.82	8.61	7.46	6.39	1.33	0.34	0.42	25.02	
Burnupena spp.	Burnsp	9.94	52.21	52.43	12.36	4.71	2.72	162.68	4.42	7.17	4.47	1.58	0.18	1.42	14.30	8.24	5.51	4.46	0.95	0.25	0.36	15.38	
Bufolectus reynaudii	Bunod								7.18	10.48	5.45	1.51	0.27	2.46	20.96	13.86	42.15	71.80	11.80	1.90	0.18	318.46	
Pseudoneis variegata	Pseusp								4.42	15.04	8.57	3.03	0.38	2.62	28.58	7.12	6.23	5.44	1.25	0.28	0.96	20.02	
Filter-feeders																							
Gunnarea cupensis	Gunnar	7.18	197.84	170.77	47.36	17.85	22.12	575.26	8.84	1389.43	1257.11	314.28	35.50	17.16	4821.88	3.75	148.37	315.16	99.66	6.70	9.84	1029.96	
Octomeris angulosa	Octom								0.55	7.94	7.94	7.94	0.20			0.37	4.12	4.12	4.12	0.19			
Tetraclita serrata	Tetracl																						
Notomegalanus alsticula	Notob								11.05	981.10	1290.85	288.64	25.07	24.08	4207.52	7.87	1705.04	1124.62	245.41	77.02	4.66	4396.22	
Mytilus galloprovincialis	Mytilus	1.10	54.18	25.54	18.06	4.89	36.12	72.24	6.08	18.46	18.14	5.47	0.47	3.92	67.36	11.24	42.59	44.64	8.15	1.92	0.82	193.04	
Aulacomyza ater	Auter	7.18	46.48	42.64	11.83	4.19	7.44	174.38															
Total mass= 1108.31																	Total mass= 3913.85			Total= 2213.81			

whelks *Burnupena* spp. (*B. cincta* and *B. catharctha*), both present in 9.94% of the samples.

In the semi-exposed habitats more than 90% of the total community biomass was accounted for 3 species, while a further 24 different taxa contributed the remaining 10% (Table 2). Of the three dominants, the limpet *Patella argenvillei* (29.93%) forms a conspicuous monospecific band of ca. 2 m width on the low shore, and in the mid shore, large colonies of the polychaete *Gunnarea capensis* (35.5%) form a complex mosaic landscape together with the alien mussel *Mytilus galloprovincialis* (25.07%). The most frequently encountered species in the samples were *P. granularis* (17.13%) and *M. galloprovincialis* (11.05%).

In the exposed sites *M. galloprovincialis* (77.02%) dominated much of the entire mid-low shore, forming dense mussel beds, which house a number of cryptic species and are interspersed *Gunnarea capensis* (6.70%) and overgrown by epibiont algae (<5%, Table 1). The most frequent species were again the limpet *P. granularis* (16.10%), sea anemone *Bunodactis reynaudii* (13.86%) and the indigenous mussel *Aulacomya ater* (11.24%).

The community biomass of sheltered sites at Port Elizabeth was dominated by the colonial polychaete *Pomatoleios kraussii* (42.22%), several forms of articulate coralline algae (14.71%), several species of the red algae *Gelidium* spp. (7.66%), together with two limpet, *Patella barbara* and *P. oculus*, and the encrusting *Hildenbrandia* sp. (Table 2). All these species were concentrated low on the shore. The mid and high shore was characterized by the presence of numerous mobile grazers and predatory gastropods but they contributed little to the overall biomass. The most frequent species, however, were grazers - i.e. two species of winkle (*Oxystele variegata* and *O. impervia* with 10.95%), the pulmonate limpets *Siphonaria* spp. (8.76%) and the limpets *Patella oculus* and *Helcion* spp. (both with 8.03%) (Table 2).

On the exposed sites at Port Elizabeth more than 50% of the community biomass was also dominated by filter feeders, in this case the mussel *Perna perna* (36.34%) the

Table 2. Species frequency of occurrence per quadrat (%), average biomass, standard deviation (SD), standard error (SE), percent biomass and minimum and maximum values of biomass (g m⁻² AFDW), for the different wave-exposure habitats at Port Elizabeth. Only species contributing > 0.01% to the AFDW biomass are listed.

Species	SHEET/RED						EXPOSED								
	Abrev.	Freq. %	Biomass	SD	SE	Mass %	Mln.	Mux.	Fre. %	Biomass	SD	SE	Mass %	Mln.	Max.
Algae															
Articulate corallines		2.92	34.75	39.25	19.63	14.71	1.66	80.72	4.82	59.79	96.94	34.27	6.12	0.58	276.96
<i>Gelidium</i> spp.		4.38	17.95	13.82	5.64	7.60	1.32	39.66	4.22	31.30	26.47	10.00	3.20	4.38	83.26
<i>Hildenbrandia</i> sp.		5.84	16.45	13.40	4.74	6.97	3.90	41.32	0.60	14.08	14.08	14.08	1.44		
<i>Laurencia</i> spp.									1.20	85.77	114.37	80.87	8.78	4.90	166.64
<i>Sargassum</i> spp.		4.38	3.54	3.05	1.24	1.50	0.60	6.88	0.60	3.98	3.98	3.98	0.41		
Grazers															
<i>Panella barbata</i>		0.73	10.34	10.34	10.34	4.38			2.41	1.81	1.41	0.70	0.19	0.60	3.24
<i>Panella oculata</i>		8.03	10.49	4.92	1.48	4.44	5.20	23.62	2.41	0.83	0.45	0.22	0.08	0.48	1.42
<i>Panella longicosta</i>		2.19	5.25	5.61	3.24	2.22	1.70	11.72	3.61	5.36	7.41	3.02	0.55	0.38	17.06
<i>Panella granularis</i>		2.19	2.33	2.03	1.17	0.99	1.10	4.68	8.43	9.47	10.78	2.88	0.97	0.06	39.82
<i>Panella argenvillei</i>									1.20	21.73	15.37	10.87	2.22	10.86	32.60
<i>Panella cochlear</i>									3.01	59.81	70.08	31.34	6.12	5.88	168.90
<i>Helcion</i> spp.		8.03	1.58	1.38	0.42	0.67	0.68	5.12	0.60	0.40	0.40	0.40	0.04		
<i>Siphonaria</i> spp.		8.76	1.08	1.15	0.33	0.46	0.10	4.14	6.02	3.93	3.27	1.03	0.40	0.60	10.36
Chitons		2.19	0.22	0.19	0.11	0.09	0.08	0.44	2.41	1.13	0.77	0.39	0.12	0.46	1.80
<i>Turbo</i> spp.		5.11	3.80	2.77	1.05	1.61	0.62	7.46	0.60	0.72	0.72	0.72	0.07		
<i>Oxystele tigrina</i>		7.30	1.87	1.14	0.36	0.79	0.60	4.50	0.60	1.88	1.88	1.88	0.19		
<i>Oxystele</i> spp.		10.95	4.25	2.76	0.71	1.80	0.38	10.46	5.42	2.18	2.94	0.98	0.22	0.68	9.78
<i>Oxystele sinensis</i>		3.65	5.01	4.00	1.79	2.12	1.74	11.64	1.81	2.34	1.64	0.95	0.24	0.46	3.50
<i>Littorina</i> spp.		3.65	2.28	1.44	0.64	0.97	0.30	4.32	2.41	2.75	0.93	0.46	0.28	2.00	3.96
<i>Paracalappa angulosa</i>									1.81	4.07	3.30	1.90	0.42	2.08	7.88
<i>Purpura</i> spp.									4.22	0.11	0.05	0.02	0.01	0.08	0.22
Predators															
<i>Burnupia</i> spp.		2.92	0.39	0.15	0.08	0.17	0.26	0.52	6.63	1.54	2.69	0.81	0.16	0.04	9.28
<i>Pseudonebris variegata</i>		1.46	4.10	3.48	2.46	1.74	1.64	6.56	4.82	1.17	2.00	0.71	0.12	0.02	5.90
<i>Nucella</i> spp.		2.92	0.51	0.22	0.11	0.22	0.32	0.76	1.81	0.26	0.00	0.00	0.03	0.26	0.26
Filter-feeders															
<i>Gammarus caespitosus</i>									3.61	26.16	26.36	10.76	2.68	3.82	76.58
<i>Cucumaria</i> spp.									2.41	2.49	2.96	1.48	0.25	0.32	6.78
<i>Pomatoceros kraussii</i>		2.92	99.71	36.77	18.39	42.22	56.98	142.42	2.41	89.02	51.19	25.60	9.11	42.72	156.68
<i>Perna perna</i>									6.02	355.12	496.05	156.87	36.34	2.54	1361.28
<i>Octomeris angulosa</i>									3.01	20.02	28.50	12.75	2.05	2.94	70.66
<i>Thecacia concamerata</i>		0.73	0.30	0.30	0.30	0.13									
<i>Tetractia serrata</i>		4.38	5.44	7.46	3.04	2.30	0.30	19.50	5.42	99.78	81.77	27.26	10.21	1.40	225.44
<i>Chthamalus dentatus</i>		2.19	0.32	0.24	0.14	0.14	0.12	0.58	4.82	66.75	63.95	22.61	6.83	2.22	152.28
<i>Plagusia chabris</i>		2.19	4.21	2.76	1.59	1.78	1.80	7.22	0.60	1.44	1.44	1.44	0.15		
Total=			236.19						977.18						

barnacle *Tetraclita serrata* (10.21%) and the colonial polychaete *Pomatoleios kraussii* (9.11%), all concentrated in the low to mid shore. However, the most common species in the samples were *Patella granularis* (8.43%), *Burnupena* spp. (6.63%) and *Siphonaria* spp. and *Perna perna* (with 6.02% each) (Table 2).

Direct gradient analysis

The graphical results of the canonical correspondence analyses for the rocky communities associated with the environmental factors are presented in Figures 11 and 12. These figures display the combined 2D-biplot of species (abbreviations), samples (numbers) and the environmental vectors (arrows), where the length and direction of the arrows indicate the relative importance and direction of each vector. At Groenrivier, the ordination along the x and y axes explained 43.9% and 30.6% of the total community variance respectively (Table 3A). Similarly, in the ordination for Port Elizabeth the same axes accounted for 36.4% and 29.5% of the total community variance with respect to the environmental variables (Table 3A). For both localities the first two canonical axes of the species ordination were significantly linked to the environmental variables (Monte Carlo permutation test, $p < 0.01$), and thus indicate significant differences in the species composition among sites.

The sample separation along the x -axis clearly illustrates the vertical gradient (zonation) of the community, where the low shore is indicated by smaller numbers (0, 1, 2) in the right side of x -axis, while the larger numbers (5, 6 and 7) in the left side of the x -axis indicate the high shore (Figs. 11 and 12). Along the y -axes, the samples taken within each of the different wave exposures group together, with the exposed sites at the bottom of the y -axis and sheltered sites at the top of the same axis. The semi-exposed sites occupied an intermediate position between sheltered and exposed (Fig. 11). The y -axis in both ordinations, clearly indicated a wave force gradient (see Figs. 11 and 12).

A summary of the weighted correlation coefficients between the x - y axes of the ordination and the environmental variables for each locality is given in Table 3A. At

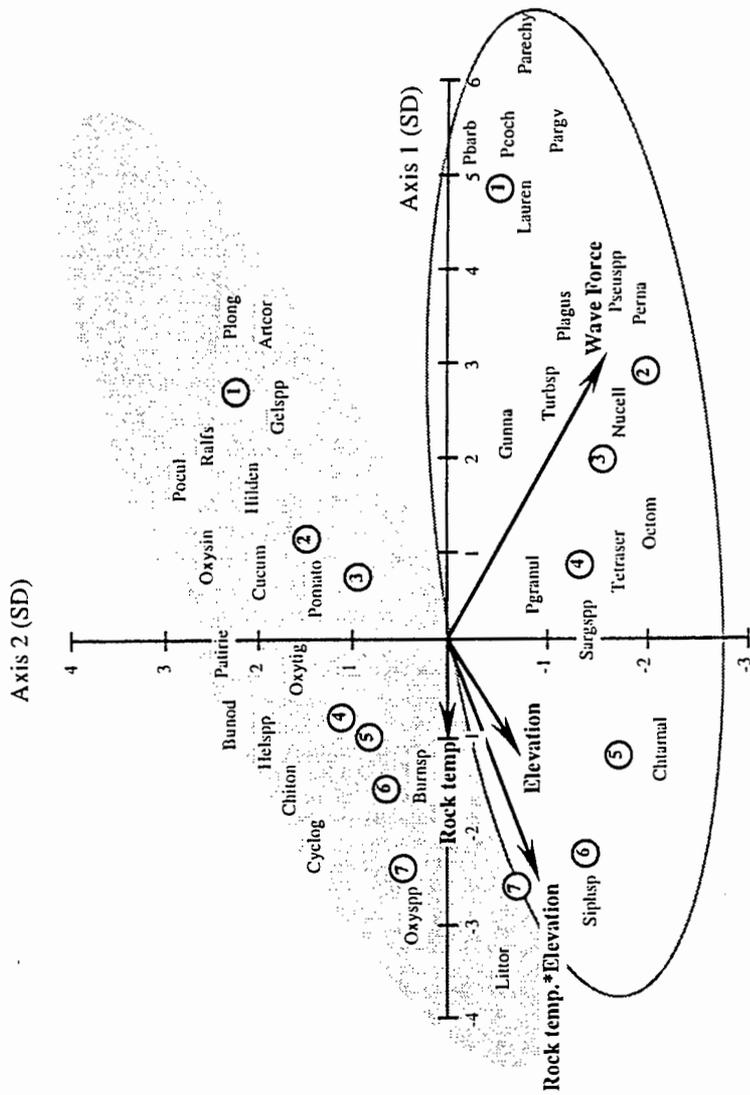
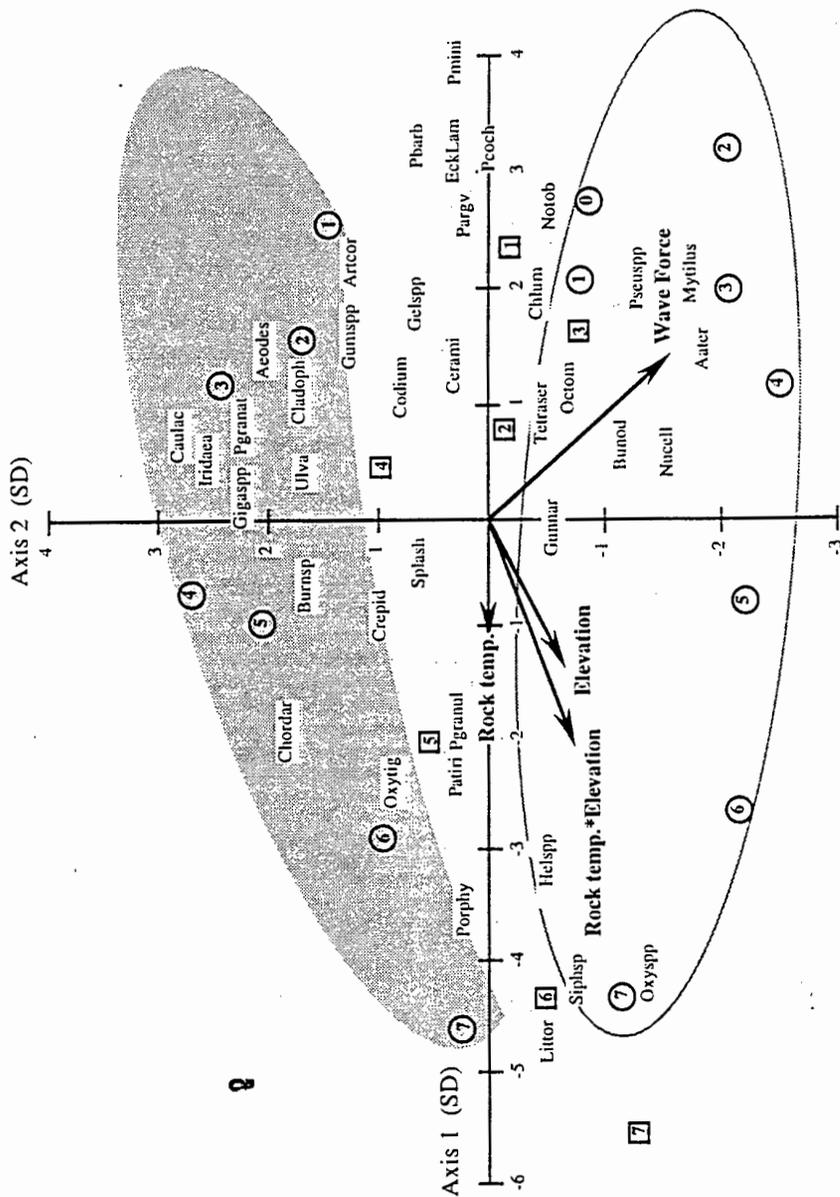


Figure 12. Ordination diagram based on canonical correspondence analysis of the rocky intertidal communities at Port Elizabeth with respect to three environmental variables (wave force, rock temperature and elevation). Increasing numbers indicate the sampling stations from low to high shore in the different communities. ○ , exposed and ○ , sheltered shores. Arrows show the magnitude (length) and direction of the environmental vectors. Full species/ taxa names corresponding to abbreviations can be found on Table 2.



Groenrivier the x -axis was significantly correlated with all environmental factors, the highest correlation being obtained with the interaction between elevation and rock temperature ($r=-0.812$; $p<0.005$, Table 3B). Similarly, at Port Elizabeth the highest and most significant correlation was between the x -axis and the interaction between elevation and rock temperature ($r=-0.888$; $p<0.0005$, Table 3). Conversely, the y -axis was only significantly correlated with maximum wave force, at both Groenrivier and Port Elizabeth ($r=-0.665$; $p<0.001$ and $r=-0.842$; $p<0.001$ respectively, see Table 3B). In short, the relative magnitude (length) of the different environmental vectors (arrows in Figs. 11 and 12) indicates that maximum wave force, and the interaction between elevation and rock temperature were the most important environmental factors in the ordination of the communities of both Groenrivier and Port Elizabeth.

In all samples taken in the high shores of both localities, the genera *Littorina*, *Oxysteles* and *Siphonaria* were equally represented, independently of wave exposure or geographic differences (Figs. 11 and 12). This indicates that the composition of the species assemblages in the upper shore converge. Conversely, the species composition on the low shores diverged consistently, depending primarily on the effects of the wave exposure. The convergence of community samples is also evident in the way that the upper shore samples are positioned closely in the ordination, whereas the lower shore samples are distanced from one another (Figs. 11 and 12). The exposed shores were clearly characterized by the presence of filter-feeders, especially the mussels *A. ater* and *M. galloprovincialis* at Groenrivier (Fig. 11), and the mussel *P. perna* and the barnacles *T. serrata* and *O. angulosa* at Port Elizabeth (Fig. 12), all of which tend to be positioned near to the end of the wave force vector.

Table 3. (A) Eigenvalues and percentage of variance accounted for the four axes of the CCA ordination of samples and species scores. (B) Weighted correlation coefficients between the environmental variables and the first 2 axes of the CCA ordination.
Degrees of freedom = ((No. samples - No. factors) - 1)

		Groenrivier		Port Elizabeth	
Axes	Eigenvalue % Variance	Eigenvalue % Variance	Eigenvalue % Variance		
1	0.805	43.9	0.816	36.4	
2	0.559	30.6	0.661	29.5	
3	0.306	16.7	0.472	21.0	
4	0.162	8.8	0.293	13.1	

		Groenrivier n=21		Port Elizabeth n=14	
	X-axis	Y-axis	X-axis	Y-axis	p
Wave force	0.605	-0.665	0.502	-0.842	<0.001
Rock temperature	-0.727	-0.095	-0.822	-0.441	>0.05
Shore elevation	-0.711	-0.504	-0.834	-0.398	<0.001
R. temp.*Sh. elev.	-0.812	-0.390	-0.888	-0.454	<0.0005

Discussion

The patterns of vertical distribution of intertidal species assemblages have been intensely studied since the early works on zonation (e.g., Stephenson 1943; Lewis 1964 1976; Stephenson and Stephenson 1972; Moore 1975; Underwood 1978). In contrast, there is little published information on horizontal zonation patterns (Menge and Farrell 1989). In particular, the quantitative responses of intertidal communities to horizontal gradients have not been fully explored (Foster 1988).

The biomass data for the southern African rocky intertidal communities show consistent patterns in both vertical and horizontal distributions over large and local geographical scales (Figs. 3-5). These findings reveal two vertical patterns that can be consistently detected over a large geographical scale. The first shows that exposed shores exhibit much greater overall biomass than protected shores, an issue addressed in Chapter 1, and demonstrated for the Cape Peninsula (Fig. 1) cold-temperate shores by McQuaid and Branch (1984). However, the 'spread' of the biota from low to high shore indicates that the major concentration of biomass on semi-exposed and exposed sites occurs consistently in the low-to-mid shore (Figs. 3-5). This contrasts with sheltered sites, where the greatest community biomass is concentrated in the low shore. To my knowledge, there is no fully equivalent data set available in the literature to compare with the above patterns. However, biomass patterns can be inferred from descriptive works (as Menge and Farrell 1989) and from estimations of relative abundance or percent coverage. The vertical patterns on exposed shores found in this work seems generally comparable with those described for equivalent temperate regions in the south and north eastern Pacific (Santelices *et al* 1977; Foster *et al.* 1988; Menge and Farrell 1989) and north western Atlantic (Menge 1976; Lubchenco and Menge 1978), where the low shore appears to support intermediate levels of biomass due to the dominance of few species of encrusting algae and mobile consumer species. There is strong evidence showing that in

the low-to-mid zones of rocky shores biological interactions (either predation or competition) have important influences on community structure, with consumers controlling the abundance of space-occupying species in the low shore while the mid-shore level is dominated by sessile species (mussels and/or barnacles). However, a different vertical distribution pattern has been described for exposed rocky shore in False Bay (McQuaid and Branch 1985), where large colonies of sessile filter-feeding invertebrates and understory algal turf constitute the majority of the low shore biomass. This situation indicates that consumers are not effective in controlling space occupying-species. Descriptions of part of the British Isles (Lewis 1964; Newell 1979) and south Australia (Stephenson and Stephenson 1972) suggested similar patterns. Unfortunately, there is no information about the species richness of these communities nor degree of wave exposure experienced at the above-mentioned localities, thus precluding any direct comparison. Although this conjecture cannot be evaluated at the present, the implication is that the classical generalization related to the importance of biological interactions in determining the community structure on rocky shores, may well need to be re-assessed taking into account the effects of the environmental stress modulating these interactions.

The patterns presented in this Chapter clearly showed that, as with biomass, the species richness (number of species per unit area) also displays consistent vertical and horizontal distribution patterns independent of geographical localities (Figs. 6-8). Many of the studies of intertidal ecology of the last several years have emphasized the role of scale in the maintenance and production of species diversity (e.g. Dayton 1971; Underwood and Fairweather 1985; Petraitis *et al.* 1989; Menge and Olson 1990). However, most of the comparative studies for patterns of species richness have failed to make comparison between shores with similar small-scale physical environments (McGuinness 1990). Similarly, most of the studies of intertidal diversity do not include (or do not mention) species occupying secondary substrata (e.g. McGuinness 1990), leading to conclusions that are applicable only to the diversity of species occupying primary rock-space. For example, the removal of mussels (space dominant species) leads to the augmentation of the diversity of species using rock as a primary substrata (e.g.

Harger 1970; Paine 1971, 1974; Suchanek 1978; Paine *et al.* 1985); while decreasing the diversity of the epifaunal and infaunal species associated within the mussel bed (Lohse 1993). In the present study, the consistency of the patterns on species richness is greatly strengthened by the fact that all localities were compared within equivalent physical environments (Figs. 6-8) and all species living on secondary substrata were included.

The significance of these findings is that they confirm the prediction of Dayton and Tegner (1984), that many of the processes involved in the creation of patterns of species richness and biomass act and vary at a local scale (i.e. at the scale of sites within shores), though they may also operate at large geographical scales.

The relative importance of the determinants of the zonation patterns (vertical and horizontal) for intertidal rocky shore communities varies with scale (Dayton and Tegner 1984; McGuinness 1990). In this work, I considered in more detail two particular localities where differences in community structure are generated by coastal geomorphology (headlands, boulder bays, etc.) and, hence, differential wave forces (Fig. 9A). The magnitude of these local differences in wave forces will certainly be greater than any that can be experienced between different geographical regions (Figs. 9 and 10). Furthermore, the simple local effect of vertical environmental gradients (rock temperature, elevation and their interaction) on the spatial distribution of the species assemblages were consistently similar within localities and only marginally different between the disjunct geographical localities (Fig. 9B). This implies that the physiological stress imposed by tidal excursions on intertidal organisms operate in a similar way at local and meso-geographical scales.

Wave action is considered as one stressing factor which induces physical disturbance. Hence, it is expected to cause random, localized, mortality (Petraitis *et al.* 1989; MacGuinness 1990). However, my findings show that there is a positive relationship between the biomass-per-unit-area and the maximum drag force exerted by waves (Fig. 10A). This relationship agrees with results reported by Leigh *et al.* (1987) for the

northeastern Pacific, were at wave-beaten sites, the sea palm *Polstelsia palmaeformis* produce extraordinary quantities of dry matter per unit area. In sum, they conclude that wave energy enhances the production of intertidal systems. This is an important consideration that need to be taken into account when deciding which factors (and their respective interactions) need to be incorporated into environmental stress models for community regulation (e.g. Menge and Olson 1990).

The results of the direct gradient analysis presented in this Chapter support, with quantitative evidence, the traditional assumption that gradients of emersion and magnitude of wave force are the most important local determinants influencing rocky intertidal communities (Menge and Farrell 1989). The analyses used three simple environmental factors and a single interaction, and explained more than 65% and 74% of the variance of the community biomass recorded at two disjunct geographical localities (Table 3A).

The first gradient in the ordination diagrams (Figs. 11 and 12), was related to the main direction of variation along the x -axis, equivalent to an emersion (or desiccation) gradient, as indicated by the arrows representing the rock temperature, elevation and their interaction. The x -axis in both ordinations was significantly correlated (Table 3B) with these variables, especially their combined effect on the species ordination (Figs. 11 and 12). In addition, the overall community biomass (regardless of wave exposure) was negatively correlated with the rock temperature (Fig. 10A). Field and Robb (1970), using a quantitative indirect gradient analysis, have previously shown that this vertical gradient is significantly correlated to the biomass of intertidal species assemblages of the rocky shores of False Bay (see Fig. 1). Although their analyses were done using different statistical techniques and sampling procedures, and on a much more limited geographical scale, their results coincide with the findings of this work. Unfortunately, there are few equivalent multivariate community analyses for rocky intertidal shores, the majority of such studies having been devoted to soft bottom ecosystems or subtidal ecosystems (e.g., McLachlan *et al.* 1984; Gray *et al.* 1988; Dawson *et al.* 1992; Warwick and Clarke 1993; van Nes and Smit 1993). However, in all intertidal rocky shores that

have been analyzed in this manner, shore elevation plays an important role in explaining the changes in species composition (e.g., Kaandorp 1986; Koistra et al. 1989; Takada and Kikuchi 1990).

The second major gradient in our analyses was related with the differences in wave force exerted on the rocky shores. The main variation of the wave force gradient occurred along the y-axis, which was only correlated with wave force (Table 3B). Samples taken from exposed sites were consistently ordered low on the y-axis and variations in wave action yielded three (Fig. 11) or two (Fig. 12) distinct species assemblages. The previously observed fact that sessile filter feeders are more abundant on exposed shores (McQuaid and Branch 1984 1985; McQuaid *et al.* 1985) was also clearly detected in this analysis. On wave-exposed shores, filter-feeder species were dominant, contributing > 67% of the community biomass at both cold- and warm-temperate sites (Tables 1 and 2). At Groenrivier (Fig. 11) the mussels *A. ater* and *M. galloprovincialis* and at Port Elizabeth (Fig. 12) the mussel *P. perna* and the barnacles *T. serrata* and *O. granulosa* were the dominant space-occupying species, and prevailed where the highest wave forces were measured (Fig. 9). This was obvious in the ordinations (Figs. 11 and 12) where samples taken from the mid shore (2 to 4, which correspond to 50-120 cm above MLWS) were all placed close to the end of the wave force vectors (Figs. 11 and 12). Additionally, mussel beds provide a suitable microhabitat for a number of co-occurring species that are seldom found living on the bare rock. In the ordinations, cryptic species like the nereid mussel worm (*Pseudonereis variegata*), the predatory whelks (*Nucella* spp.), and predatory anemones (*Bunodactys reynaudii*), were all placed close to the mussel species (Figs. 11 and 12). All of those species either shelter among, or feed on, mussels.

The convergence of the upper shore and the divergence of the lower shore species assemblages was clearly depicted in the gradient analyses (Figs. 11 and 12). Convergence suggests that the ecological response of the mid to upper shore communities to the constraints of this environment is in many ways similar, as has been suggested by

previous studies (Stephenson and Stephenson 1972; Menge and Lubchenco 1981; Lubchenco et al. 1984; McGuinness 1990). However, the consistent divergence of intertidal species assemblages in the lower shore, according to differential wave force regimes have not been clearly defined for cold and warm-temperate intertidal systems. The implication is that low-shore communities are dictated largely by differences in wave action, whereas high shore communities are influenced by the uniform stress of high temperature and desiccation.

In a similar study using a multivariate approach, Fuji and Nomura (1990) investigated the relationships between community structure and environmental factors (i.e. categories of degree of wave force, height above datum and microtopography) for the rocky shore macrobenthos of southern Hokkaido, Japan. Their analyses did not include algae. Their main conclusion was that community structure of the macrofauna is primarily influenced by microtopographic characteristics, while the effects of wave force and shore elevation were not apparent. However, their work only reflects the effects of their sampling procedure. That is, at a particular site, they sampled with different intensity (some microhabitats were under-represented) all possible distinct microhabitats - i.e. nip, bench, ledge, slope and boulders (Fuji and Nomura 1990 Table 1). Besides, in their analyses each particular microtopographic category was subjected to a broad range of wave force categories (which were not determined by direct *in situ* measurements), to that wave force could not be used as a discriminatory environmental variable. Consequently, their conclusion that differences in microhabitat explain most of the variation in intertidal community structure, overriding the effects of other important environmental factors, is associated to their methodology more than anything else.

In relation to the main objectives of this study, distinctive community structures were detected at a local-scale, whose differences are strongly related to local environmental variation. At this level of exploratory analysis, biotic interactions are of little importance. As in terrestrial ecology, the apparent gradual changes of the landscape that are normally not easy to isolate, but they can be operationally described as discontinuous pattern

variation (Whittaker 1970) - i.e. certain taxa occurred on discrete habitats with relative perceptible contours (defined by the position of the samples in Figs. 11 and 12). As in those terrestrial gradients, the intertidal ones can be analytically describe as very sharp, consequently zonation patterns are clearly observed. Within those vertical 'zones', the different taxa were consistently ordered horizontally along the shore in all sampled sites. It does, however, seems clear that there are frequently striking differences in the physical environment and the communities among sites within any geographical region - i.e. large mussel beds in exposed sites, mobile consumers and foliose algae in sheltered sites etc. The present work shows that such differences may result from the small-scale variation in the physical environment, such as the tidal gradient and wave exposure (explored in this Chapter), and as well as other mechanical disturbances like ice scour, river runoffs, etc. (not covered here), that will 'set the stage' for the subsequent biological interactions between the survivors of the environmental constraints (Menge and Olson 1990).

The main conclusions of this work reinforce some of the hypotheses erected in Chapter 1 (see Table 3, Chapter 1) which are all related to large- and small scale patterns. In this Chapter I have quantitatively described small-scale local distribution patterns and I have statistically inferred the role of simple environmental factors in structuring rocky intertidal communities in a similar manner at two disjunct geographical localities. The main conclusions are:

- a) There are consistent patterns of vertical and horizontal zonation of the intertidal biota, in terms of both biomass-per-unit-area and species richness.
- b) These patterns are valid over a large geographical scale.
- c) The relationships between community structure and the local environmental factors included in this analysis, operate similarly in different geographical regions.
- d) The biomass-per-unit-area of rocky intertidal biota is positively related to degree of wave action and inversely related to rock temperature.

e) The vertical zonation of the rocky intertidal species is associated with an interaction between shore elevation and rock temperature, while the horizontal zonation is strongly correlated with the degree of wave action.

f) The community characterizing the upper shore, converges in species biomass and richness, whereas significant divergence was found in the low shore and could be explained by differences in wave action.

By the very nature of the analyses in this Chapter, they can yield patterns and correlations but no direct evidence of the causative factors. Two of the strongest relationships that emerge are the high biomass on the west coast shores relative to south-east coasts, and the fact that biomass (particularly of filter-feeders) is higher on exposed shores than sheltered shores. These two aspects are presented in more detail in the next two Chapters. In particular, the following Chapter documents direct measurements of productivity around the coast to test whether productivity may underpin contrast in the biomass of the west, south and east coast.

References

- Austen, M. C. 1989. Factors affecting estuarine meiobenthic assemblage structure: a multifactorial microcosm experiment. *Journal of Experimental Marine Biology and Ecology* **130**: 167-187.
- Austin, M. P. 1985. Continuum concept, ordination methods, and niche theory. *Annals Review of Ecology and Systematics*. **16**: 36-61.
- Bosman, A. L., P. A. R. Hockey, and W. R. Siegfried. 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. *Oecologia (Berlin)* **72**: 226-232.
- Bosman, A. L., and P. A. R. Hockey. 1988. Life-history patterns of populations of the limpet *Patella granularis*.: The dominant roles of food supply and mortality rate. *Oecologia (Berlin)* **75**: 412-419.
- Branch, G. M. 1985a. Limpets: their role in littoral and sublittoral community dynamics. Pages 97-116 in P. G. Moore, D. Seed editors. *The Ecology of Rocky Coasts*. Hodder and Stoughton Educational, England.
- Branch, G. M. 1985b. Competition: its role in ecology and evolution in intertidal communities. Pages 97-104 in E. S. Vrba editor. *Species and speciation*. Transvaal Museum Monograph **4**, Transvaal Museum, Pretoria.
- Branch, G. M., A. Barkai, P. A. R. Hockey, and L. Hutchings. 1987. Biological interactions: causes or effects of variability in the Benguela ecosystem? *South African Journal of Marine Sciences* **5**: 425-445.

- Castric-Fey, A., and C. Chassé. 1991. Factor analysis in the ecology of rocky subtidal areas near Brest (West Brittany, France). *Journal of the Marine Biology Association of the United Kingdom* **71**: 515-536.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**: 710-723.
- Connell, J. H. 1975. Some mechanism producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. M. Diamond, editors. *Ecology and Evolution of Communities*. Belknap, Cambridge.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: provision and subsequent utilization of space in rocky intertidal community. *Ecological Monographs* **41**: 351-389.
- Dayton P. K. 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs* **54**: 253-289.
- Dayton P. K., and M. J. Tegner. 1984. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. Pages 457-481 in: P. W. Price, C. N. Slobodchikoff and W. S. Gaud editors. *A New Ecology: Novel Approaches to Interactive Systems*, Wiley, New York.
- Denny, M. W. 1988. *Biology and the Mechanics of the Wave-swept Environment*. Princeton University Press, Princeton, New Jersey, USA.
- Denny, M. W., and S. D. Gaines. 1990. On the prediction of maximal intertidal wave forces. *Limnology and Oceanography* **35**: 1-15.
- Dawson-Shepherd, A., R. M. Warwick, K. R. Clarke, and B. E. Brown. 1992. An analysis of fish response to coral mining in the Maldives. *Environmental Biology and Fisheries* **33**: 367-380.

- Field, J. G., and G. M. McFarlane. 1968. Numerical methods in marine ecology 1. A quantitative "similarity" analysis of rocky shores in False Bay, South Africa. *Zoologica Africana* **3**: 119-137.
- Field, J. G., and F. T. Robb. 1970. Numerical methods in marine ecology 2. Gradient analysis of rocky shores samples from False Bay. *Zoologica Africana* **5**: 191-210.
- Field, J. G., and C. L. Griffiths. 1991. Littoral and sublittoral ecosystems of southern Africa. Pages 323-346 in A. C. Mathieson, P. H. Nienhuis editors. *Ecosystems of the World 24. Intertidal and Littoral Ecosystems*. Elsevier Science Publisher, Amsterdam, The Netherlands.
- Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for multispecies distribution patterns. *Marine Ecology Progress Series* **8**: 37-52.
- Foster, M.S., A. P. De Vogelaere, C. Harrold, J. S. Pearse and A. B. Thum. 1988. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. *Memoirs of the California Academy of Sciences Number 9*, California Academy of Sciences, San Francisco.
- Fuji, A, and H. Nomura. 1990. Community structure of the rocky shore macrobenthos in southern Hokkaido, Japan. *Marine Biology* **107**: 471-477.
- Gray, J. S., M. Aschan, M. R. Carr, K. R. Clarke, R. H. Green, T. H. Pearson, R. Rosenberg, and R. M. Warwick. 1988. An analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Marine Ecology Progress Series* **66**: 285-299.
- Griffiths, C. L., and P. A. R. Hockey. 1987. A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. *South African Journal of Marine Sciences* **5**: 547-556.

Griffiths, C. L., and G. M. Branch. 1991. The macrofauna of rocky shores in False Bay. *Transaction of the Royal Society of South Africa* **47**: 575-594.

Hairston, N. G., and L. B. Slobodkin. 1960. Community structure, population control, and the American Naturalist **44**: 421-425.

Hugget, J., and C. L. Grimm. 1966. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. *Marine Ecology Progress series* **29**: 189-197.

James, F. C. and C. E. McCulloch. 1990. Multivariate analysis in ecology and Systematics: panacea or pandora's box? *Annual Review of Ecology and Systematics* **21**: 129-166.

Jones, W. E., and A. Demetropoulos. 1968. Exposure to wave action: measurement of an important ecological parameter on rocky shores on Anglesey. *Journal of Experimental Marine Biology and Ecology* **2**: 46-63.

Kaandorp, J. A. 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: a quantitative survey. *Marine Biology* **92**: 255-265.

Kautsky, H., and E. van der Maarel. 1990. Multivariate approaches to variation in phytobenthic communities and environmental vectors in the Baltic Sea. *Marine Ecology Progress series* **60**: 169-184.

Kooistra, W. H. C., A. M. T. Joosten, and C. van den Hoek. 1989. Zonation patterns in intertidal pools and their possible causes: a multivariate approach. *Botanica Marina* **32**: 9-26.

Leigh, E. G., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave energy and intertidal productivity. *Proceedings of the National Academy of Science, USA* **84**: 1314-1318.

- Lewis, J. R. 1964. *The Ecology of the Rocky Shores*. The English University Press Ltd., London.
- Lewis, J. R. 1976. The role of physical and biological factors in the distribution and stability of rocky shore communities. Pages 417-423 *in*: B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden editors. *Biology of Benthic Organisms*. Pergamon Press, New York.
- Lohse, D. P. The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology and Ecology* **166**: 1-17.
- Lubchenco, J. 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. Pages 537-555 *in*: J. Diamond, and T. Case editors. *Community Ecology*. Harper and Row, New York.
- Lubchenco, J, and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* **48**: 67-94.
- Lubchenco, J, B. A. Menge, S. D. Garrity, P. J. Lubchenco, L. R. Askenas, S. D. Gaines, R. Emlet, J. Lucas, and S. Strauss. 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Tabogilla Island, Bay of Panama). *Journal of Experimental Marine Biology and Ecology* **78**: 23-73.
- McGuinness, K. A. 1990. Physical variability, diversity gradients and the ecology of temperate and tropical reefs. *Australian Journal of Ecology* **15**: 465-476.
- McLachlan, A., A. C. Cockroft, and D. E. Malan. 1984. Benthic faunal response to a high energy gradient. *Marine Ecology Progress series* **16**: 51-63.
- McQuaid, C. D., and G. M. Branch. 1984. The influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Marine Ecology Progress Series* **19**: 145-151.

- McQuaid, C. D., and G. M. Branch. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series* **22**: 153-161.
- McQuaid, C. D., G. M. Branch, and A. A. Crowe. 1985. Biotic and abiotic influences on rocky intertidal biomass and richness in the southern Benguela region. *South African Journal of Zoology* **20**: 115-122.
- McQuaid, C. D., and K. M. Dower. 1990. Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. *Oecologia* **84**: 142-144.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* **46**: 355-393.
- Menge, B. A., and J. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *The American Naturalist* **110**: 351-369.
- Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**: 730-757.
- Menge, B. A., and T. M. Farrell. 1989. Community structure and interactions webs in shallow marine hard-bottom communities: test of an environmental stress model. *Advances in Ecological Research* **19**: 189-262.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends in Ecology and Evolution* **5**: 52-67.
- Moore, P. G. 1975. The role of habitat selection in determining the local distribution of animals in the sea. *Marine Behavioural Physiology* **3**: 97-100.

- Newell, R. C. 1979. *Biology of Intertidal Animals*. Marine Ecological Surveys Ltd., Faversham, Kent.
- Rakocinski, C. F., D. M. Baltz, and J. W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress series* **80**: 135-148.
- Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* **100**: 65-75.
- Paine, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* **52**: 1096-1106.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93-120.
- Paine, R. T., J. C. Castillo, and J. Cancino. 1985. Perturbation and recovery patterns of starfish dominated intertidal assemblages in Chile, New Zealand and Washington. *The American Naturalist* **125**: 679-691.
- Press, W. H., B. P. Flannery, S. A. Tenkolsky, and W. T. Vetterling. 1986. Numerical recipes software library. *The art of scientific computing*. Cambridge University Press, Cambridge.
- Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* **74**: 2215-2230.
- Palumbi S. R. 1984. Measuring intertidal wave forces. *Journal of Experimental Marine Biology and Ecology* **81**: 171-179.
- Petraitis, P. S., R. E. Latham, and R. A. Niesebaum. 1989. The maintenance of species diversity by disturbance. *The Quarterly Review of Biology* **64**: 393-418.

- SAN. 1993. South African Tide Tables. Hydrographer South African Navy, Maritime Headquarters, Tokay.
- Santelices, B, J. Cancino, S. Montalva, R. Pinto, y E. González. 1977. Estudios ecológicos en la zona costera afectada por contaminación del "Northern Breeze" II. Comunidades de playas de rocas. *Medio Ambiente* **2**: 65-83.
- Santos, R. 1993. A multivariate study of biotic and abiotic relationships in a subtidal algal stand. *Marine Ecology Progress series* **94**: 181-190.
- SAS. 1986. SAS[©] System for linear models, 1986 Edition. SAS Institute Inc., Cary, NC, USA.
- Sousa, W. P. 1979a. Disturbance in marine boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**: 1225-1239.
- Sousa, W. P. 1979b. Experimental investigations of disturbance and ecological succession in rocky intertidal communities. *Ecological Monographs* **49**: 227-254.
- Stephenson T. A. 1943. The causes of vertical and horizontal distribution of organism between tide-marks in South Africa. *Proceedings of the Linnean Society of London* **154**: 219-213.
- Stephenson T. A., and A. Stephenson. 1972. *Life between tidemarks on rocky shores*. Freeman, San Francisco, USA.
- Takada, Y., and T. Kikuchi. 1990. Mobile molluscan communities in boulder shores and the comparison with other intertidal habitats in Amakusa. *Publications from the Amakusa Marine Biological Laboratory, Kyushu University* **10**: 145-168.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

ter Braak, C. J. F. 1987. CANOCO- a FORTRAN Program for canonical community ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis, Principal Components Analysis and Redundance Analysis (Version 2.1). Agriculture Mathematics group, Wageningen.

ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Research* **18**: 271-317.

Underwood, A. J. 1978. The refutation of critical levels as determinants of the structure of intertidal communities on British shores. *Journal of Experimental Marine Biology and Ecology* **33**: 261-276.

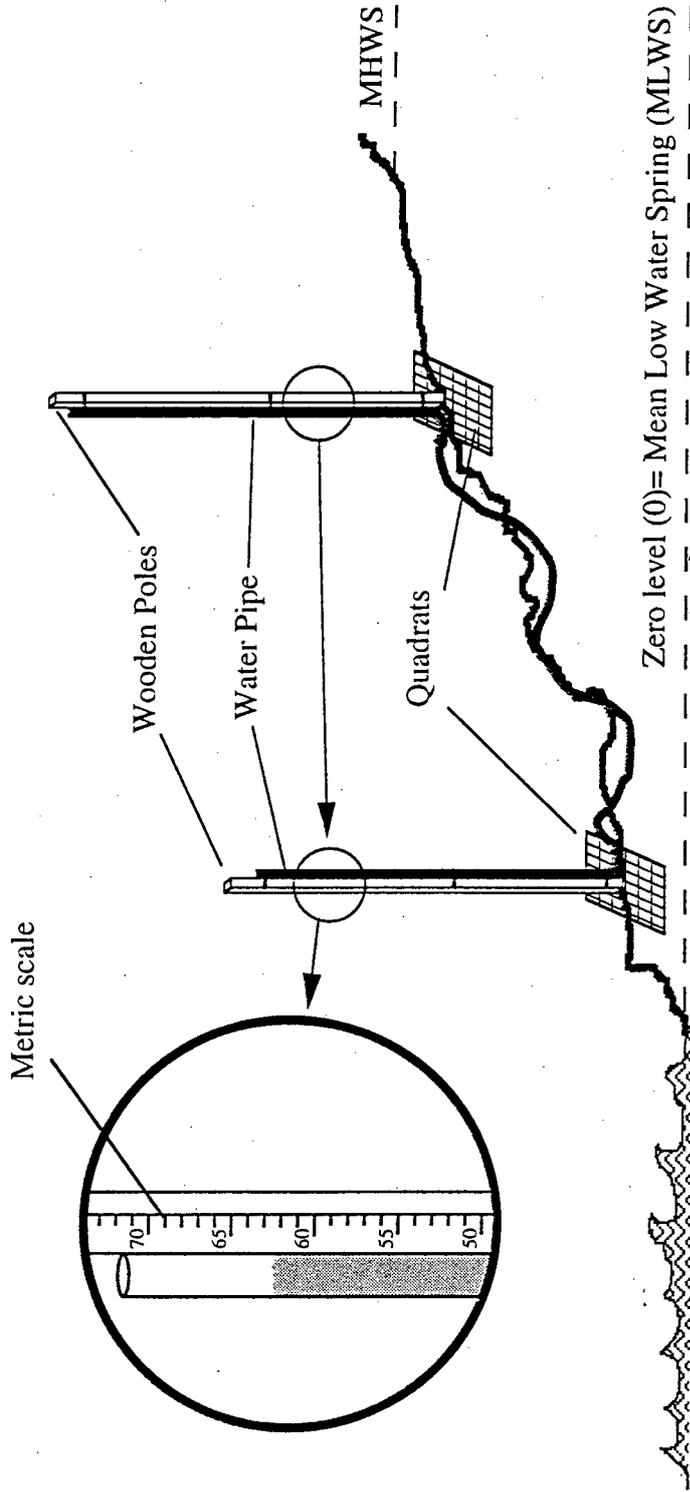
Underwood, A. J. 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology* **51**: 57-85.

Underwood, A. J. 1986. The analysis of competition by field experiments. Pages 240-268 *in*: J. Kikkawa, and D. J. Anderson editors. *Community ecology - patterns and processes*. Blackwell, Melbourne.

Underwood, A. J., and E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of the mid-shore rocky intertidal communities in New South Wales. *Oecologia* **56**: 202-219.

Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151-180 *in* D. R. Strong, Jr, D. Simberloff, L. G. Abele and A. Thistle editors. *Ecological Communities. Conceptual issues and the evidence*. Princeton University Press, New Jersey.

- Underwood, A. J., and P. G. Fairweather. 1985. Intertidal communities: do they have different ecologies or different ecologists? *Proceedings of the Ecological Society of Australia* **14**: 7-16.
- van der Meer, J. 1991. Exploring macrobenthos-environment relationship by canonical correlation analyses. *Journal of Experimental Marine Biology and Ecology* **148**: 105-120.
- van Nes, E. H., and H. Smit. 1993. Multivariate analysis of macrozoobenthos in lake Volkerak-Zoommeer (The Netherlands): changes in an estuary before and after closure. *Archiv für Hydrobiologie* **127**: 185-203.
- van Zyl, P., and B. L. Robertson. 1991. Seasonal and species-environmental succession on an eastern Cape rocky shore. *South African Journal of Science* **87**: 327-330.
- Warwick, R. M., and K. R. Clarke. 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Marine Ecology Progress Series* **92**: 221-231.
- Weinstein, M. P., and H. A. Brooks. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. *Marine Ecology Progress series* **12**: 15-27.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Reviews* **42**: 207-264.
- Whittaker, R. H. 1975. *Communities and Ecosystems*, Second edition. The Macmillan Company, New York.



Appendix I. Diagram of the water level device for the measurement of shore elevation. The difference in height (cm) between surveyed quadrats was the difference between the water levels read against the metric scale fixed on each wooden pole, placed in the middle of the quadrats.

Chapter 3

Patterns of Intertidal Productivity on Rocky Shores Around the Coast of South Africa, and their Relationship to Consumer Biomass

Summary: Nutrient status is an important factor that may influence the production rate and structure of many marine and terrestrial plant assemblages. Enhanced nutrient concentration strongly influences the abundance and organization of primary producers, hence possibly influencing the upper levels of a given food chain (a bottom-up effect). The large-scale patterns of rocky intertidal community structure presented in Chapter 1 may be the results of large-scale patterns of productivity around the South African rocky coasts. In this Chapter I examine the levels of *in-situ* intertidal production of epilithic microalgae, intertidal nutrient concentrations, and standing stocks of different functional-form groups of macroalgae around the South African coast.

Clear gradients of *in-situ* intertidal primary production and nutrient concentration exist around the South African coast, higher values being recorded on the west and the lowest on the east coast. Primary production was correlated with nutrient availability and could also be related to the nearshore phytoplankton production. A clear change of the dominance patterns of different functional-forms of macroalgae was also found around the coast, with foliose algae prevalent on the west coast and coralline algae on the east coast. However, overall standing stocks did not reflect the productivity gradient.

Positive relationships exist between the average biomass of intertidal invertebrate consumers (grazers and filter-feeders) and intertidal productivity, although only the grazers were directly 'connected' to *in-situ* production. The maximum body size of a widely distributed limpet, *Patella granularis*, was also positively correlated with level of *in-situ* primary production.

The maximal values of biomass attained by intertidal filter-feeders were not related to intertidal primary production, and were relatively constant around the coast. However, at a local scale, filter-feeder biomass was strongly influenced by local wave action. This implies the local-scale water movements over-ride any effects that large-scale gradients of primary production may have on filter-feeders.

Introduction

The role of variation in primary productivity has been a neglected factor in many past studies of community organization on intertidal rocky shores (Menge and Olson 1990; Menge 1992). In freshwater ecosystems, by contrast, the influences of variation in primary production and nutrients levels on trophic food webs have been extensively investigated and integrated into studies of ecosystem functioning (e.g. Carpenter and Kitchell 1984, 1987; Stanley *et al.* 1990; Hill *et al.* 1992; Wootton and Power 1993). Only in the past ten years has the role of primary productivity been incorporated, at least in a nominal form, into models of structure and functioning of marine benthic communities (e.g. Menge and Sutherland 1987; Hatcher 1990; Menge and Olson 1990; Menge 1992).

In those few studies where levels of primary production have been measured on intertidal rocky shores, the aim was to use it as an index of food availability for competing consumers, succession and diversity of microflora assemblages, and small-scale distribution patterns, (e.g. Castenholz 1963; Nicotri 1977; Branch and Branch 1980; McQuaid 1981; Underwood 1984c; MacLulich 1986a, b, 1987; Hill and Hawkins 1990, 1991). However, variation in productivity at a large geographical scale and its interrelations with different components of rocky-shore communities has largely been neglected. Several studies of South African rocky shores have been centered on the nutrients status and primary productivity of the system, but have also been restricted to local geographical scale and to interactions with particular species (e.g. Bosman 1988; Bosman and Hockey 1988; Dye and White 1991; Lasiak and White 1993).

A well documented productivity gradient exists in the pelagic ecosystem around southern Africa, due to the existence of strong upwelling on the west coast and its virtual absence on the east coast (e.g. Shannon 1985; Brown and Cochrane 1991; Brown *et al.* 1991; Moloney 1992). In a synthetic review of most of the published productivity data

for the Benguela and Agulhas ecosystems, Brown (1992) demonstrated quantitatively the existence of a clear productivity gradient inshore of the 200 m isobath. The west coast is highly productive (up to 16.5 mg Chl-*a* m⁻³), while intermediate levels (about 5.0 mg Chl-*a* m⁻³) occur in the so-called Cape or southern Benguela; off the south-east coast, chlorophyll concentrations are an order of magnitude lower than the west coast (< 2.0 mg Chl-*a* m⁻³). However, this pattern disappears offshore (i.e. beyond the 200 m isobath), where the overall range of chlorophyll concentration is between 0.5 to 3.0 mg Chl-*a* m⁻³ (Brown 1992).

In a small-scale study at False Bay (Fig. 1), Cliff (1982a, b) analyzed chlorophyll, nutrients, bacteria, and organic detritus concentrations from the intertidal zone to about 150 m offshore. He found that intertidal waters exhibited low values and no seasonal pattern in most nutrients concentration, and were consistently depleted of chlorophyll as compared with the water samples of the deeper nearshore system (Cliff 1982a). These results are in line with those reported by Demers *et al.* (1989), who found consistently low values in nutrients, and also lower values of phytoplankton, in the nearshore compared with offshore waters. Several hypotheses of biogenic origin have been proposed in order to explain these patterns, among them the efficient grazing activity of benthic filter-feeders which may reduce the phytoplankton biomass in the littoral zone (Demers *et al.* 1989). Similarly, low inshore nutrient concentrations (principally nitrogen) have been explained by the effect of shallow-water and intertidal macrophyte communities acting as a nitrogen sink (Raine and Patching 1980).

In Chapter 1 I presented several patterns of community structure for the rocky shore around southern African. Among them, a gradient of consumer biomass emerged as the most conspicuous one. Notably, there is a markedly higher grazer biomass on the west coast, declining towards the east coast; a similar pattern was found in filter-feeders (see Fig. 6, Chapter 1).

In this Chapter I use monthly chlorophyll-*a* accumulation as an index of intertidal *in-situ* primary production to explore large-scale patterns in epilithic micro- and macroalgal

production around the South African coasts. I also correlate this productivity index with nutrient concentrations in intertidal waters. In a less intense sampling procedure, I document macroalgal standing stocks and their geographical variation for three different functional groups of algae.

I then rely on data presented in Chapter 1 to correlate patterns of community structure with the primary production recorded for rocky shores. In particular, the local abundance (i.e. average and maximum biomass patterns) of the filter-feeder guild (see Chapter 1) will be correlated with both intertidal (empirically determined) and nearshore primary productivity patterns (obtained from published data). Similarly, the local abundance of the grazer guild will be related to intertidal epilithic primary production. Using the widely-distributed patellid limpet *Patella granularis* as an indicator species, the correlation between epilithic microalgal production and the maximum size attained by this limpet was also investigated.

The overall aim was to determine geographic patterns (gradients) of intertidal primary production and then to seek possible correlations which may suggest the degree to which primary production influences consumers - i.e. filter-feeders and grazers. More detailed considerations of the processes involved in the maintenance of filter-feeder and grazer biomasses, and experimental and mathematical tests of the relationships revealed here are given in Chapter 4-6.

Materials and Methods

Study sites and data analyses

The data included in this Chapter were collected at 14 different localities around the southern African rocky shores (Fig. 1). A summary of all samples taken at each locality is given in Table 1. Samples were collected by different researchers at different sites, the responsibility being indicated in Table 1, but most samples and all analyses of results were undertaken by myself. Each monitored locality had similar coastal morphology, i.e. moderately exposed rocky platforms of no more than 15° of slope, facing directly into the waves.

Statistical analyses, including analysis of variance (ANOVA), *a-posteriori* tests, regression and correlations, and all were performed with SAS® v.5.0 (SAS 1986).

Chlorophyll-a determination

The monthly *in-situ* production of epilithic micro and macroalgae was determined at 11 different rocky intertidal localities from March 1991 to June 1992 (Table 1). At a height midway between mid-tide and low spring tide, four randomly selected plots of about 0.5 m² each were cleared of all biological growth and their perimeters painted with antifouling paint to stop invasion by vagrant grazers. Every month, for a period of 16 months, eight sterile clear acrylic plates of 25 cm² each were glued down within each plot simultaneously at all localities. The plates were roughened by sand-blasting both surfaces to create a heterogeneous surface. After the plates had been in position for a month, they were lifted from the substratum, washed to remove all sand and loose inorganic material, wrapped in aluminum foil and stored at -20°C. Monthly measurements of the total chlorophyll-*a* contents extracted from the algae settled on each acrylic plates were undertaken by spectrophotometric techniques, using hot methanol as the extraction solvent for plant pigments (HMSO 1986). For each month, four plates were taken

Table 1 Summary of sampling sites. +=samples taken, -=not sampled. Responsibility indicates the research group responsible for the collection of samples.

	Sites	Chlorophyll-a	Algae standing-stock	Nutrients	Responsibility
West coast	Rooiklippies	+	+	+	UCT
	Groenrivier	+	+	+	UCT
	Kommetjie	+	+	+	UCT
	Holbaaipunt	+	-	-	UWC
South coast	De Hoop	+	+	+	EMATEK
	Tsitsikamma	-	+	-	NPB
	Maitlands	+	+	-	UPE
	Cape Recife	+	+	+	UPE
	Schoenmakerskop	+	-	+	UPE
	Port Alfred	+	-	-	RU
East coast	Dwesa	-	+	-	UNITRA
	Ngabara	+	-	-	UNITRA
	Pennington	+	+	+	ORI
	Umdoni	+	+	+	ORI
		12	10	8	

UCT= R. H. Bustamante, S. Eekhout and G. M. Branch, U. of Cape Town; UWC= D. Keats and M. Jurd, U. of Western Cape; EMATEK= P. Zoutendyk, Earth Marine Atmospheric Science and Technology; NPB= N. Hanekom, National Parks Board; UPE= B. Robertson, U. of Port Elizabeth; RU= C. MacQuaid, Rhodes University; UNITRA= A. Dye, U. of Transkei; ORI= M. Schleyer, Oceanographic Research Institute.

randomly from each individual plot at each locality, all plant material was scrapped off the surface and placed in a pre weighted foil dish and the respective algal wet weights measured. The plant material and the individual acrylic plates were transferred into glass containers and covered with 40 ml of analytical reagent methanol. The samples were agitated briefly with forceps to ensure that they were in complete contact with the solvent. The glass container with the sample was carefully covered to prevent loss of methanol and then immersed in a water bath held at a temperature just above the boiling point of methanol (65-70°C). The sample was allowed to boil for about 3 minutes, removed from the source of heat, the container stoppered, and the solution allowed to stand in the dark for about 5 minutes until cooled to room temperature. Once cooled, the methanol extract was pipetted out and, still in the dark, transferred to a 50 cc centrifuge stoppered tube, and then centrifuged at 3500 rv/min for seven minutes. The clear extract was then decanted from the tubes (without disturbing the sediments), and placed in a 1.0 cm pathlength clear cuvette for spectrophotometric readings. Measures of the absorbance of the extract at wave lengths of 665 nm (maximum absorbance of chlorophyll-*a*) and 750 nm (compensation for 'background turbidity') were taken using a Beckman Duo®-50 spectrophotometer, and chlorophyll-*a* concentration (in $\mu\text{g cm}^{-2}$) was calculated using the equation

$$[\text{Chl} - a] = \frac{A \cdot V \cdot 13.9}{a \cdot 1.0},$$

where A = Absorbance at 665 nm - Absorbance at 750 nm, V = Volume of solvent, 13.9 = spectrophotometric constant (Jeffrey and Humphrey 1975), a = Area of acrylic plate (cm^2), and 1.0 = cell pathlength (cm).

Macroalgal standing stock

The standing stock of macroalgae was measured at 10 different rocky intertidal localities around the South African coast from March 1991 to June 1992 (Table 1). Four randomly selected transects, set perpendicularly to the sea from MLWS to MHWS, were permanently marked, and along them between nine and twelve 0.25 m² quadrats were

randomly placed, covering the full intertidal zonation. Every three months, for a period of 12 months, all macroalgal material in each quadrat was scraped-off, washed to remove all sand and inorganic material, sorted by algal species, and wet weight measured. Subsequently, all algal mass was expressed in grams per square meter of dry matter. The relationship between the algal wet mass (WM) and its dry mass (DM) was described by the significant linear function $DM = 0.2535 * WM$ ($n=470$, $r^2=0.86$, $p<0.0001$), with the intercept forced through zero ($a=0$). The algal species was classified into three functional groups according to their respective form: a) filamentous or foliose and corticated forms (referred to thereafter as 'foliose algae'; b), articulated and crustose corallines forms ('corallines'); and c) non-coralline turfs ('turfs').

Nutrients

Every month, six to twelve 50 ml water samples were taken intertidally at eight localities during spring low-tide for the determination of micronutrients (Table 1). The water samples were filtered using Whatman glass-microfibre filters (GF/F), poured into high-density polyethylene tubes and then wrapped in aluminum foil and stored vertically frozen at -20°C .

The concentrations of nitrite- and nitrate-bound nitrogen ($\text{NO}_2\text{-N}$, $\text{NO}_3\text{-N}$), phosphate-bound phosphorus ($\text{PO}_4\text{-P}$) and silicate-bound silica ($\text{SiO}_3\text{-Si}$) were automatically determined using a Technicon Automated Autoanalyzer II (Mostert 1983; 1988). Nutrient concentration was expressed in $\mu\text{moles per liter}$ ($\mu\text{moles l}^{-1}$).

Patterns of community structure

Data for two main functional groups of consumers, filter-feeders and grazers were extracted from the biomass community patterns described in Chapter 1, to relate abundance of these functional groups to intertidal productivity. Specifically, both mean and maximum values of biomass per unit area (g AFDW m^{-2}), are expressed relative to the distance around the coast of each surveyed locality from Lüderitz (Namibia, Fig. 1). All distances were measured linearly on a 1:2500000 scale map. The sampling

procedures to obtain biomass have already been described in Chapters 1 and 2. Maximal body size achieved by the limpet *Patella granularis*, which occurs right around the coast (see Fig. 1, Chapter 1), was also determined at each surveyed site. All individual *P. granularis* present in quadrats on each transect were measured with a vernier micrometer with precision of 0.5 mm. Mean maximal size was determined by averaging the 100 biggest animals recorded for each site. Methods used for laying the transects are given in more detail in Chapters 1 and 2.

Results

Intertidal Productivity

Chlorophyll-a as productivity index

The monthly production (± 1 SD) at each locality (grouped into the three coastal zones) is shown in Figure 2. Considerable monthly and seasonal variations in the microalgal production occurred at most localities. Although the west coast localities showed great variation, the average production was high. Even the minimum achieved never dropped below $10 \mu\text{g Chl-}a \text{ m}^{-2} \text{ m}^{-1}$, whereas at the south and more obviously at the east coast localities, the majority of the monthly average values were below $10 \mu\text{g Chl-}a \text{ m}^{-2} \text{ m}^{-1}$ (Fig. 2).

The major source of variation on microalgal productivity was due to radical differences between biogeographic provinces, between seasons and sites within provinces, i.e. west, south and east coasts, and due to seasonal changes (ANOVA, $p < 0.0001$, Table 2). Conversely, within each locality little variation existed between the production plots (ANOVA, $p = 0.2590$, Table 2).

The average monthly production at each site is expressed in Figure 3. The average production of the west coast localities, i.e. $28.8 \pm 23.0 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ mo}^{-1}$, was significantly higher (Tukey t -test $p < 0.05$) than that of south and east coasts. Similarly, the monthly average at the south coast localities ($15.2 \pm 18.0 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ mo}^{-1}$) was significantly higher (Tukey t -test, $p < 0.05$) than the east coast ($3.9 \pm 3.9 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ mo}^{-1}$). The localities of De Hoop and Port Alfred (Fig. 1) had production levels only slightly lower than to those of the west coast, exhibiting mean values of about 30 and 20 $\mu\text{g Chl-}a \text{ cm}^{-2} \text{ mo}^{-1}$ respectively, but even their combined monthly average was still significantly lower (Tukey t -test, $p < 0.05$) than that of the west coast (Fig. 3).

Table 2. ANOVA for monthly values of chlorophyll-a ($\mu\text{g cm}^{-2}$).

Source of variation	r^2		C.V.		F	P
	df	SS	MS	%		
Seasons	3	14347605.65	4782535.22	43.94	20.40	0.0001
Provinces	2	219691256.77	109845628.39		468.53	0.0001
Sites(Provinces)	9	142708744.77	15856527.20		67.63	0.0001
Plots(Sites)	39	10396281.83	266571.33		1.14	0.259
Error	2149	503823818.98	234445.70			

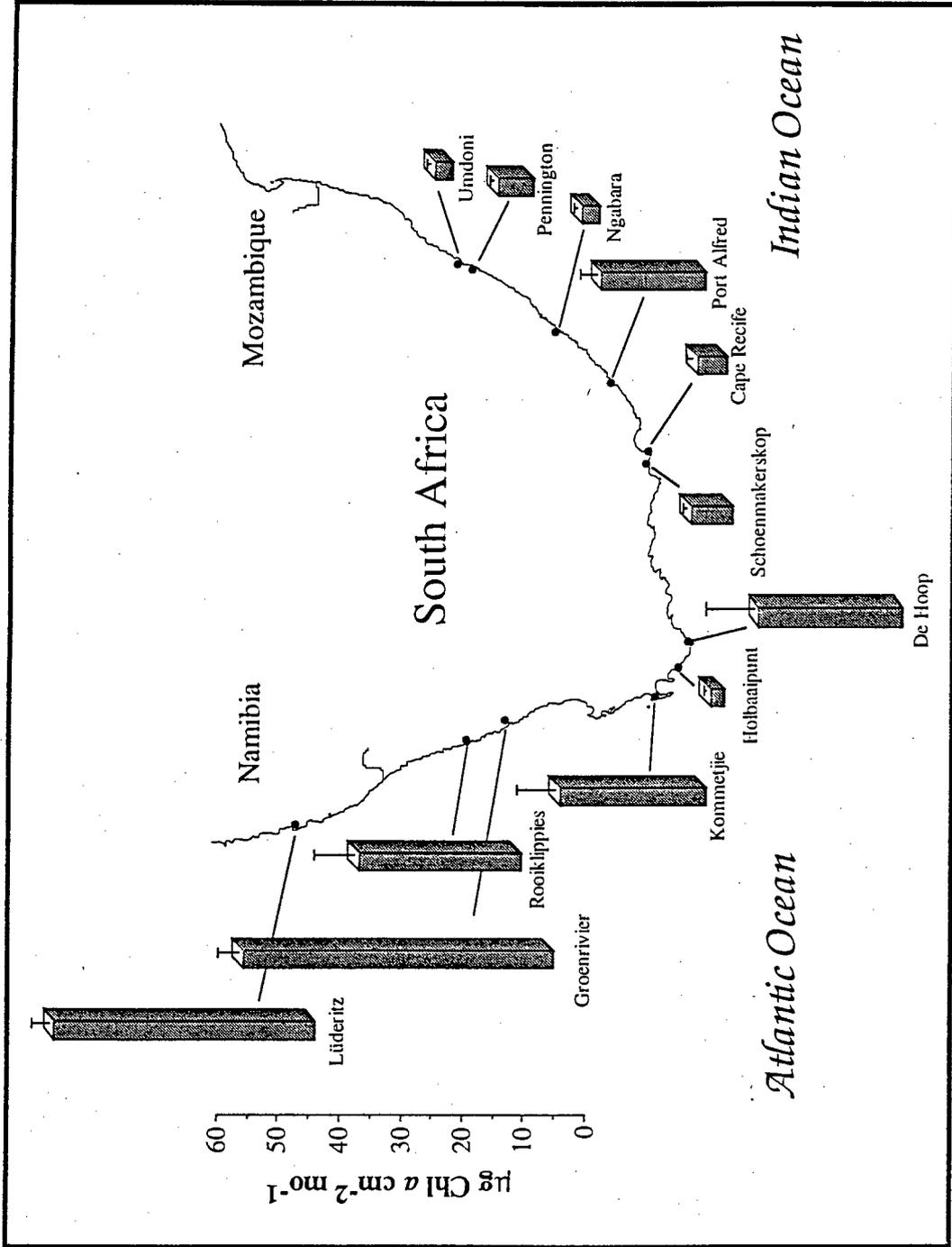


Figure 3. Average monthly production of Chlorophyll-*a* (\pm SE) at 12 localities around southern Africa. The value for Lüderitz represents the average of a single month (March 1991) which is not included in the statistical and seasonal analyses.

Notwithstanding the apparently random monthly variations in the Chlorophyll-*a* production at each of the monitored localities (Fig. 2), there was a clear seasonal trend when the monthly values are pooled into seasons and into three coastal biogeographic provinces (Fig. 4). The localities of the west coast exhibited a clear peak production in the spring-summer and a decline in autumn-winter, whereas the reverse pattern was found in the south coast. Values were consistently low in the east coast province (Fig. 4). When the variability of the monthly production of chlorophyll-*a* was analyzed per biogeographic province (Table 3), it was found that these seasonal trends were significant on the west (ANOVA, $p < 0.0001$) and at the south coasts (ANOVA, $p < 0.0001$), whereas no significant (ANOVA, $p > 0.18$) trend was found on the east coast (Table 3). Differences between localities and seasons, and the interaction between these two factors, explained more than 50% of the variance on the west and south provinces, while in the east province differences between sites and the interaction with seasonal variation explained more than 40% of the total variance (Table 3). Variations within localities were not significant on the west or east coasts ($p > 0.1$, Table 3) but were significant in the south (ANOVA, $p < 0.0001$, Table 3). Variations between plates (within plots) were never significant on any of the coasts (Table 3).

Macroalgal standing stock

The monthly average standing stock of macroalgae found at the west coast localities showed a clear biomass dominance by filamentous, foliose and corticated forms ('foliose algae') over articulated and crustose corallines and non-corallines turfs, these three functional groups averaging about 300, 42 and $< 5 \text{ g m}^{-2}$ respectively (Fig. 5). A different pattern was found at the south coast localities, where corallines were more abundant than foliose algae, exhibiting averages about 62 and 5 g m^{-2} respectively, and there was an increase in turfs, with averages up to 25 g m^{-2} (Fig. 5). Similarly, at the east coast localities, corallines were much more abundant than foliose forms, with averages of about 384 and 35 g m^{-2} respectively, and a large proportion of the macroalgal biomass was attributable to turfs, with values up to 250 g m^{-2} (Fig. 5). The overall average

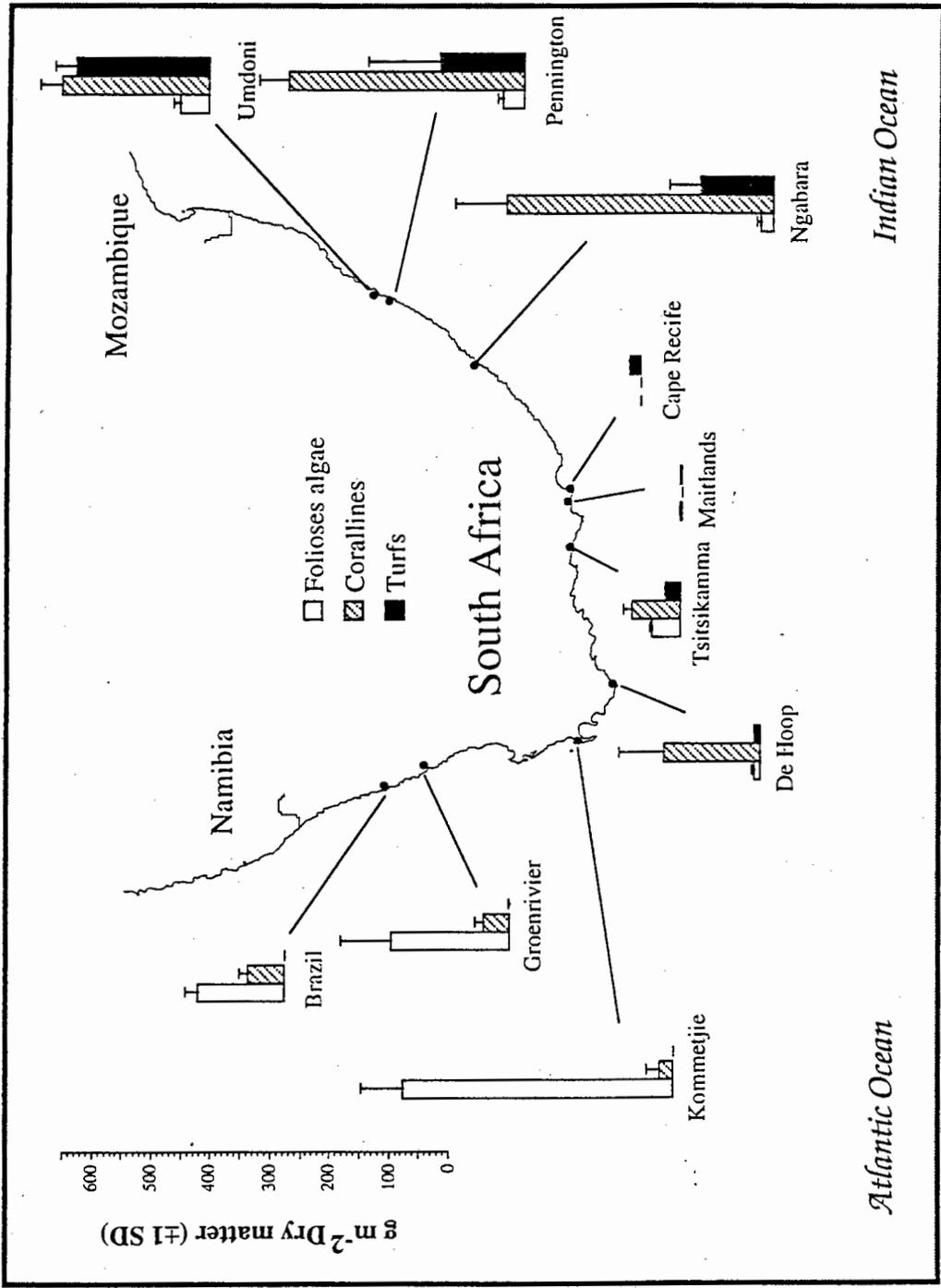


Figure 5. Macroalgal standing stock around the South African shores. Bars represent the monthly average (± 1 standard deviation) dry biomass for each of three functional-form groups of algae.

macroalgal standing stocks found for the west and east provinces were not significantly different (Tukey *t*-test, $p > 0.5$), while that of the south province was significantly smaller than that of either the west or the east coast localities (Tukey *t*-tests, $p < 0.005$).

Intertidal Nutrients

The overall average nutrient concentrations in water samples taken from the rocky intertidal zones is shown in Figure 6. There was a strong gradient of total nutrient concentration around the South African coasts, with higher average values in the west, intermediate values in the south, and the lowest concentrations in the east coast province (Fig. 6). This trend is significant for all four nutrients, i.e. nitrites, nitrates, phosphates and silicates (ANOVA, $p < 0.0001$, Table 4). One south coast site (De Hoop) had unusually high phosphate values that interrupted the trend. The major source of variation in the average nutrient concentrations was that produced by differences between biogeographic provinces (ANOVA, $p < 0.0001$, Table 4). Monthly variations, as well as the interaction between months and province, were significant for nitrates, phosphates and silicates (ANOVA, $p < 0.0001$). Variations between localities within a given biogeographic province were significant only for phosphates and silicates ($p < 0.0001$, Table 4), while no significant differences were found between the different samples within localities (ANOVA, $p > 0.2$, Table 4).

Significant linear relationships existed between all four nutrients and the intertidal production index (ANOVA, $p < 0.002$, Table 5), indicating that the *in-situ* microalgal production is significantly correlated with the concentration of nutrients in the intertidal water.

Table 5. Relationships between the monthly Chl-a and nutrient concentrations.

Chlorophyll-a					
	<i>b</i>	r ²	df	F	<i>p</i>
Nitrites	0.024	0.610	59	93.910	0.0001
Nitrates	0.251	0.550	59	74.575	0.0001
Phosphates	0.105	0.658	59	115.247	0.0001
Silicates	0.299	0.498	59	59.519	0.0020

Patterns of community structure

Grazer biomass decreased significantly from west to east (Fig. 7A). Both the average biomass for the whole-shore ($r=-0.709$, $p<0.01$) and the maximum grazer biomass recorded for a quadrat ($r=-0.828$, $p<0.01$) were correlated negatively with distance around the coast from west to east (Fig. 7A). The maximal values of grazer biomass found on the west, south and east coasts were significantly different (one-way ANOVA, $p<0.0001$).

Filter-feeders, on the other hand, showed two different patterns when their biomass levels were related to distance around the coast (Fig. 7B). The whole-shore average biomass exhibited a significant negative correlation with distance ($r=-0.525$, $p<0.05$), but the maximum filter-feeder biomass recorded per square meter remained unchanged around the coast, there being no correlation with distance around the coast (Fig. 7B). As a consequence, the maximal biomass values of filter-feeders species in the east, south and west were not significantly different (one-way ANOVA, $p>0.29$), despite two outlying high values on the west coast.

Maximal sizes attained by the limpet *P. granularis* decreased from west to east, and also were negatively correlated with distance around the coast ($r=-0.778$, $p<0.001$) (Fig. 8).

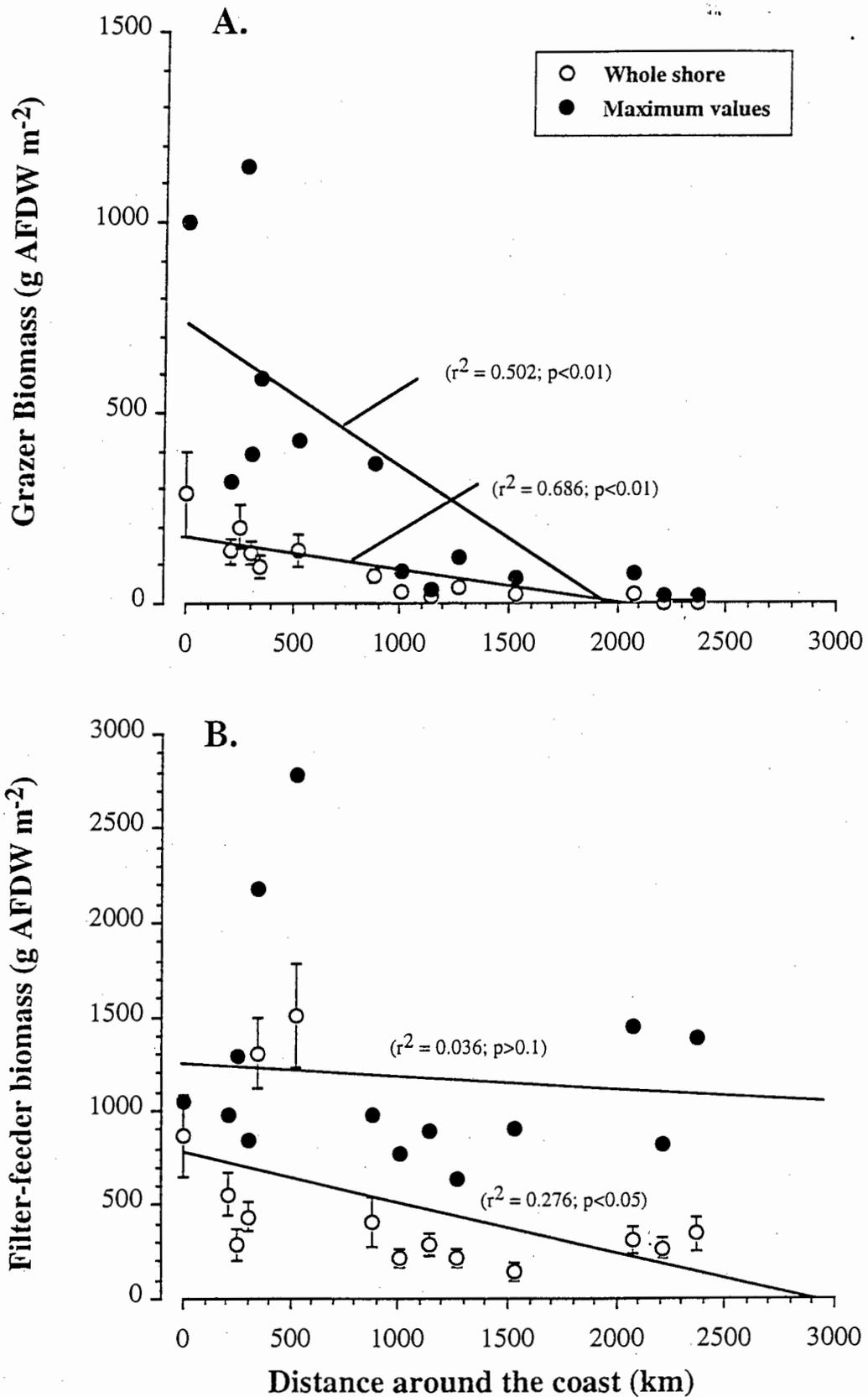


Figure 7. Relationships between biomass (mean \pm 1 SD and maximum values) and distance around southern African shores, for grazer (A), and filter-feeder biomass (B). The zero distance corresponds to Lüderitz (Namibia). Trends are indicated by a least squares fitted lines.

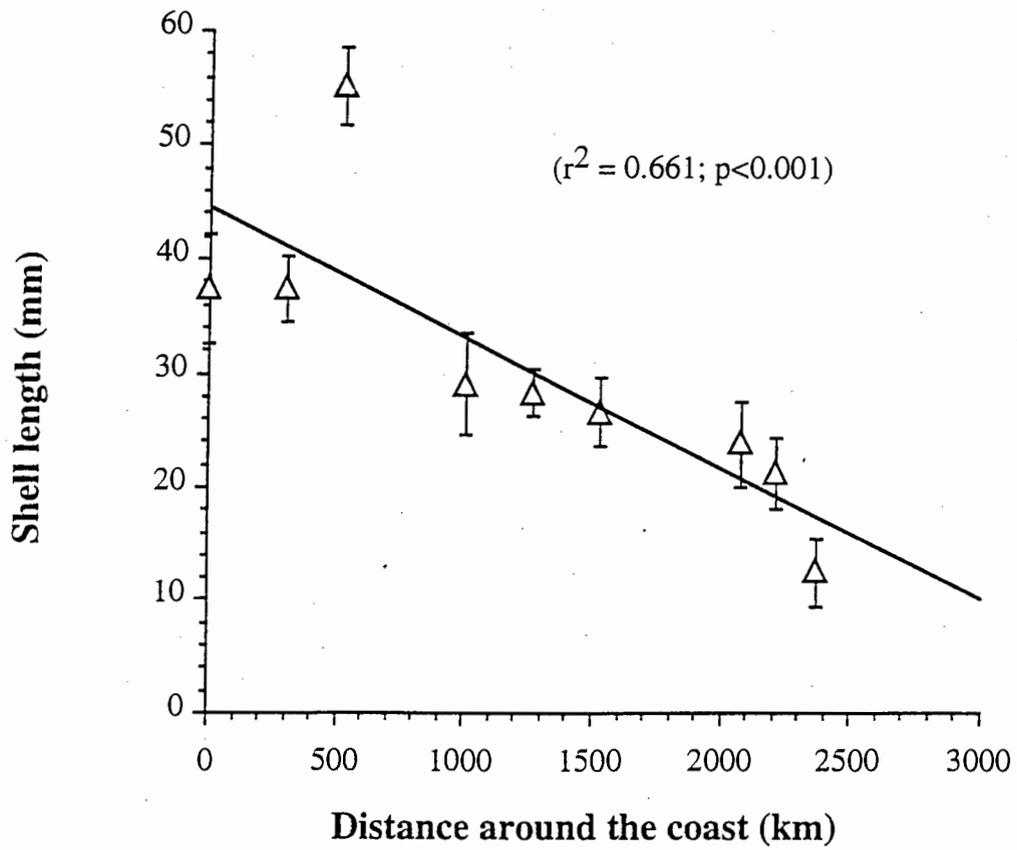


Figure 8. Average (± 1 SD) of the 100 biggest *P. granularis* recorded at 9 localities around the southern African coast. Zero distance was set at Lüderitz (Namibia).

Discussion

The results presented in this Chapter demonstrate quantitatively the existence of a strong gradient of intertidal primary productivity around the southern African rocky shores, highest values being recorded on the west coast, decreasing progressively towards the south and east coast (Figs. 2 and 3). This gradient has a clear seasonal component when the localities were 'lumped' into biogeographic provinces, even although this was not consistently evident when individual localities were inspected (Fig. 2 and 4). Different seasonal patterns existed between the provinces, with summer-spring peaks on the west coast, winter-autumn peak on the south coast, and a lack of seasonality on the east coast. These results are consistent with inshore seasonal productivity patterns reported for phytoplankton by Brown (1992). The levels of intertidal epilithic productivity (measured as monthly chlorophyll-*a* accumulations), were significantly correlated with the nutrient status of intertidal waters (Table 5). Thus, the availability of nutrients is likely to be a major factor regulating the growth rates of intertidal epilithic algae. Although the data were insufficient to indicate a causal mechanism, it is well known that high nutrient concentrations enhance primary production (e.g. Hutchinson 1955; de Boer 1982; Bosman 1987). In addition, the gradient of intertidal epilithic production was significantly and positively correlated ($r=0.896$; $p<0.001$) with the nearshore phytoplankton production reported by Brown (1992). Epilithic intertidal algae and nearshore phytoplankton are likely to be similarly influenced by nutrient levels, given that nearshore waters are well mixed by tidal and wind-driven water exchanges (Legendre *et al.* 1986). The concepts applied to phytoplankton dynamics are thus likely to be equally applicable to attached benthic plants (Mann and Lazier 1991).

The use of functional groups for the analysis of macroalgal distribution patterns has long been established in the literature on benthic ecology (e.g. Littler and Littler 1980 1984; Hay 1981; Steneck and Watling 1982; Littler and Arnold 1982). Using functional

aggregations of algae species with similar forms, vertical gradients of abundance and spatial distribution have been described several times. Algal abundance generally decreases in a logarithmic fashion, from maximum levels in the lower intertidal and shallow subtidal zones towards a minimal level in the upper intertidal shore (e.g. Nicotri 1977; Raffaelli 1979; Underwood 1984a, b; Hawkins and Hartnoll 1983; Steneck *et al.* 1991). However, horizontal gradients of abundance at a larger geographical scale are seldom reported. Macroalgal standing stock has been used as a 'productivity potential' index (*sensu* Steneck and Dethier unpubl. manuscript), indicating the upper limit of net primary productivity possible in a given environment. The data presented in this Chapter demonstrate that the average standing stock of macroalgae per-unit-area in the west coast did not differ from that of the east coast, but the standing stock of the south coast was significantly lower than either west or east coast averages (Fig. 5). These findings stand in contrast to the gradient of primary production (Fig. 3) found around the southern African coasts. Clearly in this case standing stock is a poor indicator of productivity potential. This is scarcely surprising: macroalgal standing stock represents the fraction of algae that accumulates after physical and biological disturbances (Hay 1981; Littler and Littler 1980; Bosman *et al.* 1987), and mere abundance per-unit-area need not necessarily relate directly to *in-situ* productivity.

Several attempts have been made to relate the functional form of algae to two basic regulating factors, i.e. herbivory and nutrients levels (e.g. Littler and Littler 1980, 1984, 1988). The basic model, originally proposed for a tropical environment, suggested that the relative dominance of four different functional groups of organisms (i.e. coral, coralline algae, fleshy macroalgae, and microfilamentous algae) compete vigorously for space and light, and each of these groups can predominate under specific conditions of nutrients and herbivory pressure. The macroalgal patterns presented in this Chapter (Fig. 5) do not entirely agree with some of the predicted patterns that flows from this model. For example, one of the predictions refers to the dominance of foliose and late successional algal forms in areas of high productivity and low grazing pressure (Littler and Littler 1988). The west coast, an area of established high productivity, is indeed

dominated by foliose forms of algae (Fig. 5). However, if invertebrate grazer biomass can be used as an index of potential herbivory, the west coast does not conform the above prediction because grazer biomass is extremely high (Fig. 7). On the other hand, the shift from foliose algae to corallines and turfs, from west to east coasts (Fig. 5) does agree with the functional form model of Littler and Littler (1980), because on the south and east coast nutrients are low (Fig. 6) and, although invertebrate grazer biomass is low, there is high diversity and abundance of herbivorous fish (van der Elst 1990; Burger 1990; Y. Lechanteur pers. comm.).

In the above mentioned functional model the factors potentially controlling growth and dominance of intertidal primary producers are the levels of nutrients in the surrounding waters and levels of herbivory, although the relative importance of each factor is not clear. At the local scale, biotic interaction may determine the algae 'landscape' and abundance (e.g. Underwood and Jernakoff 1981; Steneck and Watling 1982; Hawkins and Hartnoll 1983; Branch 1985; Vadas 1985; Hill and Hawkins 1991), while it appears that at large spatial scale, over hundred or thousands of kilometers, nutrients levels would control the primary productivity (Mann and Lazier 1991; DeAngelis 1992).

In principle, any one of the essential nutrient elements can limit growth of aquatic plants. Nevertheless, in a very large number of aquatic cases, either nitrogen (N) or phosphorus (P) appear to be limiting (see Table 1 in Howarth 1988, and Table 3.2 in DeAngelis 1992). There many case studies, mostly concerning pelagic and coastal lagoon ecosystems, that indicate that primary production can be limited by either N or P. However, several lines of evidence lead one to conclude that net primary production in many marine ecosystems is limited primarily by N, and only in particular cases by P (Mann 1988; Howarth 1988).

The present results demonstrate a clear gradient of nutrients levels around the southern African coasts (Fig. 6). However, simple 'standing stocks' of nutrients do not cast any light on the large-scale control of primary production. One can explore evidence of 'potential' nutrient limitation using the Redfield ratio between N and P (Redfield 1958).

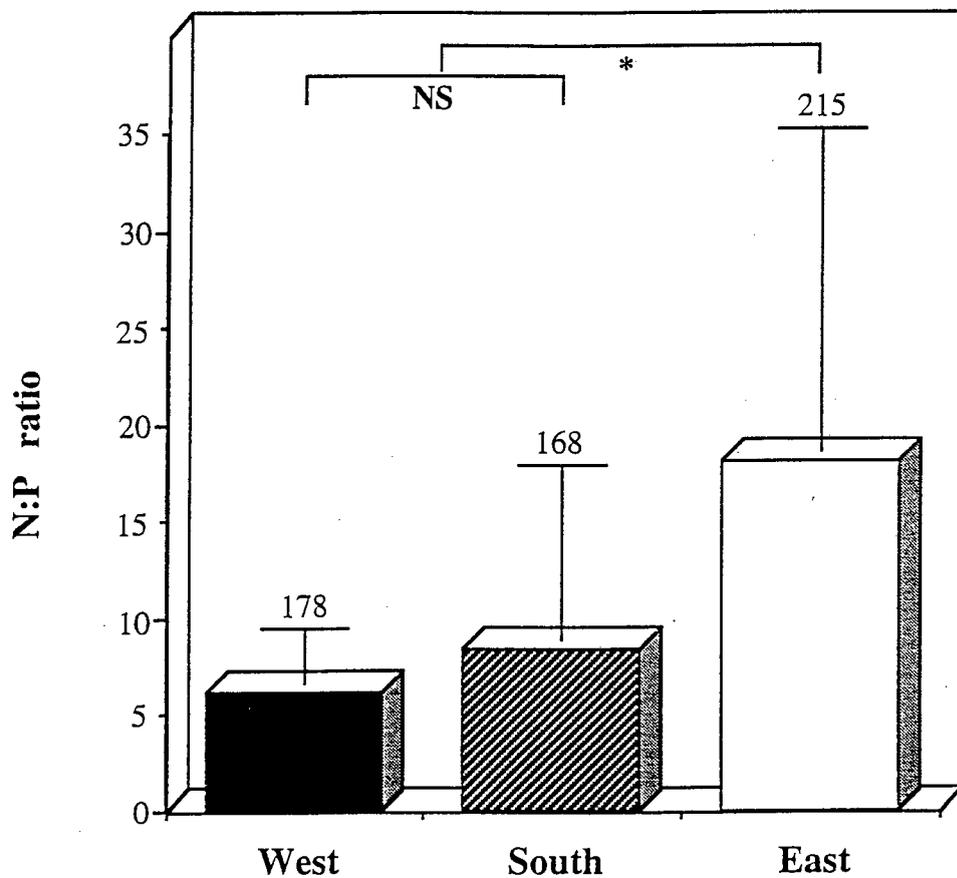


Figure 9. Nitrogen to phosphate ratio (N:P) on samples of intertidal water. Error bars indicate 1 standard deviation of the mean, and values above the number of samples. Statistics indicate $*=p<0.05$, $NS=p>0.05$ in *a-posteriori* comparison of means (Tukey *t*-test).

This is based on the uptake ratios for carbon, nitrogen and phosphorus (principally) by ocean plankton, which are (by atom) 106 C:16 N:1P. In this context, significant differences (ANOVA, $p < 0.05$) between the average N:P ratios were found when the nutrient data were amalgamated into the three biogeographic provinces (Fig. 9). The average N:P ratio for the west and south provinces were not significantly different (Tukey *t*-test, $p > 0.05$) and were always below the expected 16:1 ratio proposed by Redfield (1958) (Fig. 9). Conversely, on the east coast the N:P ratio was significantly greater than that of the south and west provinces (Tukey *t*-test, $p < 0.05$), and well above the expected 16:1, with an average of *ca.* 20:1 (Fig. 9). This suggest that on the east coast phosphorus could be limiting the intertidal productivity, while in the south and west provinces, nitrogen is more likely to be limiting.

The results presented here show that the average levels of biomass of intertidal primary consumers (grazers and filter-feeders) declines from west to east in parallel with decline in intertidal productivity and nutrient levels (Figs. 3, 6 and 7). Indeed, there are strong direct correlations between their average biomass and the average level of primary production (Figs. 10A and 11A), which are in turn related to nutrient levels (Table 5). The traditional notion of trophic functioning of biological communities is that the abundance of primary consumers in a given food chain should be positively correlated with *in-situ* productivity (Leibold 1989; Menge and Olson 1990; Power 1992). Augmentation of the basal levels of a food chain (primary producers) should thus be reflected by corresponding increases in the abundance of the next trophic level (consumers, e.g. Power 1992, Fig. 3). This situation is, however, predicted only if the primary consumers are not held in check by secondary consumers (predators).

In the present case, the herbivore grazer biomass appear to be directly influenced by the *in-situ* microalgal production. On a large geographical scale, this pattern is comparable to Bosman and Hockey (1986) demonstration that invertebrate grazers biomass and production can be enhanced by high algal productivity associated with guano input on west coast bird islands. The argument that primary productivity directly

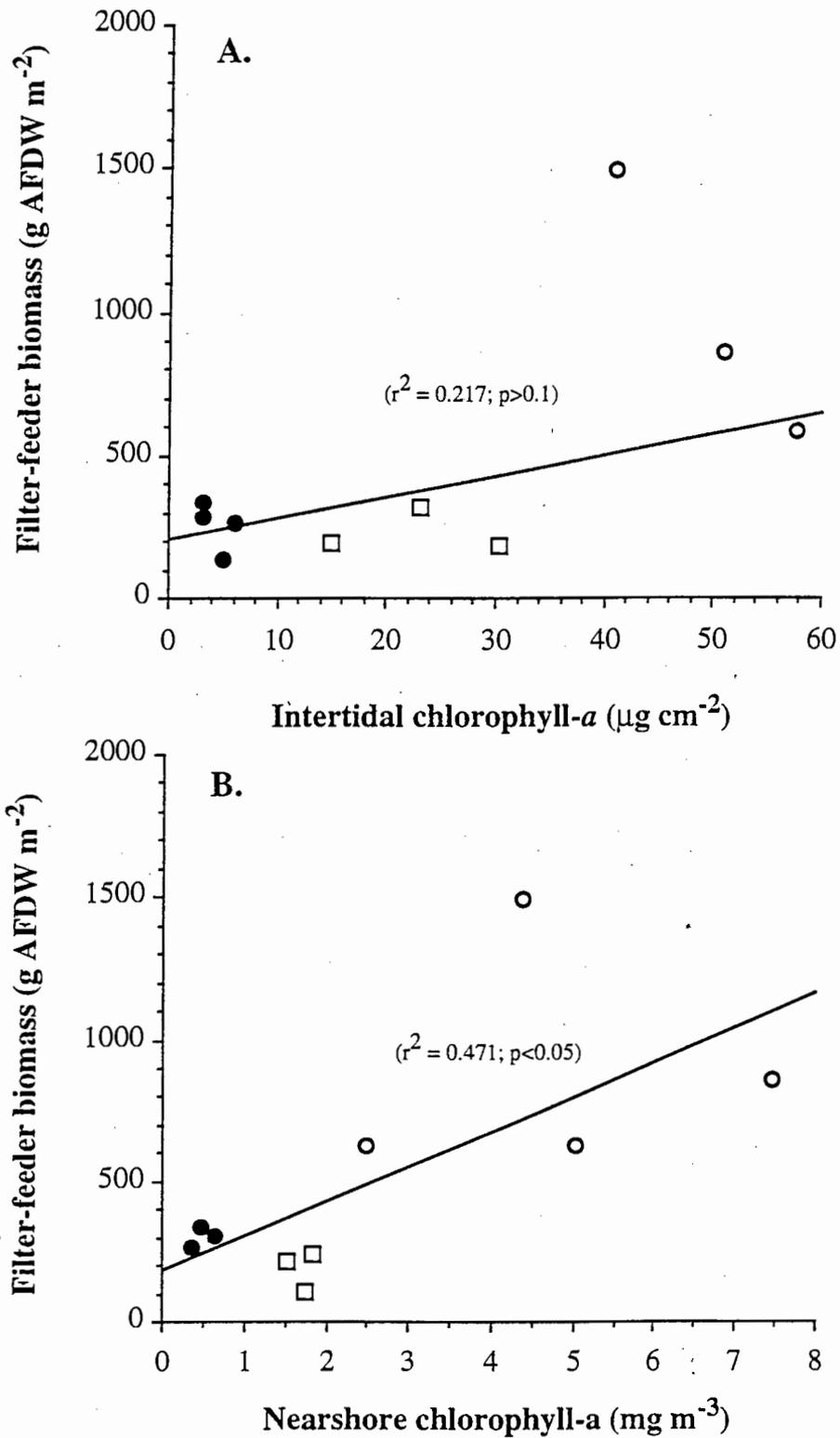


Figure 10. Relationships between filter-feeder biomass and (A.) intertidal productivity, and (B.) nearshore productivity (data from Brown *et al.* 1991, and Brown 1992). West=○, south=□, and east=● coast localities.

influences grazer dynamics is reinforced by the fact that the maximum size achieved by *Patella granularis* is directly correlated with primary production (Fig. 11B). As maximum size is correlated with growth rate (Branch 1975), both size and growth are linked with productivity. Thus, enhanced primary production (due to coastal upwelling), may raise the upper limits of herbivore carrying capacity (Fig. 11A) and also has an influence on individual body size (Fig. 11B). Correlation is, of course, not proof. However, the mere existence of this broad geographic correlation between grazer biomass and intertidal productivity is a strong suggestion of a bottom-up controlling effect (Power 1992; Menge 1992), and in the next two Chapters the factors responsible for the maintenance of a high primary consumer biomass on the west coast will be tested.

Although the average biomass of filter-feeders also correlates with intertidal productivity around the coast, this relationship is certainly indirect, due to the fact that filter-feeders depend on 'importation' of phytoplankton and suspended particulate organic matter (e.g. Stuart 1982; Stuart and Klumpp 1984). For this reason, their biomass is much more likely to be affected by local wave action (see Fig. 6, Chapter 1), which influences the rate of turnover of particulate matter in the intertidal zone, than by large scale productivity gradients around the coast. This argument is reinforced by the fact that the differences in filter-feeder biomass between wave-exposed and sheltered shores are far greater than any west-east gradient in their biomass, that might be related to productivity. This implies local-scale water movement is of immense importance for filter-feeders (an issue developed in Chapter 4). In addition, space is likely to set an upper limit to filter-feeder biomass. Maximum levels of filter-feeders (mainly mussels) biomass does not change around the coast (Fig. 7B), and a likely explanation is that they are at fixed ceiling set by spatial constraints rather than by the productivity or turnover of food supply.

These findings impinge on two important trophic considerations for rocky intertidal systems. The first is that the energy transfer in intertidal food webs, from the producer to primary consumer level, can be divided into two different compartments according to the

main food source: the herbivore and filter- or suspension-feeders pathways (Fig. 12). Intertidal herbivore species are directly supplied by the *in-situ* intertidal primary production. The correlations presented in this Chapter imply that invertebrates herbivore biomass is powerfully influenced by this production, but do not test whether *in-situ* algal production is sufficient as a source of energy to explain the levels of herbivore biomass sustained on the west coast (see Chapters 5 and 6).

The second trophic consideration is that the energy used by filter- and suspension-feeders (the greatest biomass component within the intertidal rocky communities) is, to a large extent, 'imported' as a subsidy from the adjacent pelagic and subtidal ecosystems (Fig. 12; and see MacQuaid and Branch 1985). This is another issue that will be explored further in the following Chapter. As a consequence maximal values achieved by filter-feeders are not related to intertidal productivity (Figs. 7 and 10), but are more likely to be limited by space availability (due to biotic interactions and the effects of wave action). Average (whole-shore) values for filter-feeder biomass are correlated with the gradient of productivity around the coast (Fig. 3), and may be correlated with offshore production and by the degree to which water turnover supply food (Jørgensen 1990).

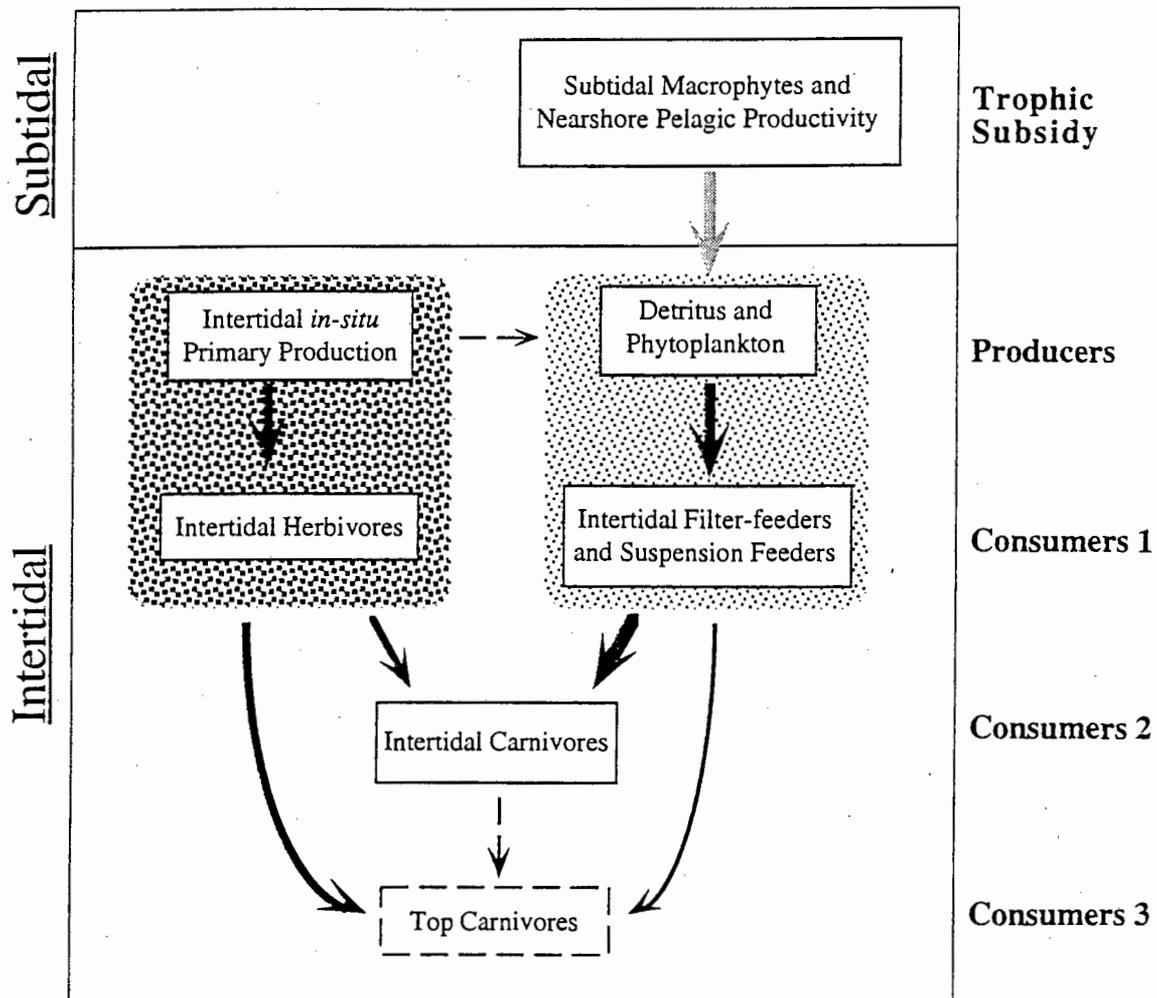


Figure 12. Diagram of the main pathways of energy-matter transfer on a hypothetical rocky intertidal food web. Herbivores  and filter-feeders  pathways. Arrows thickness and pattern indicate the relative importance of the transfer between the different trophic compartments.

References

- Bosman, A. L. 1987. Avian determinants of rocky intertidal community structure in South Africa. Ph. D. Dissertation University of Cape Town, Cape Town.
- Bosman A. L. 1988. The influence of primary production rate on the dynamics of *Patella granularis*, an intertidal limpet. P.S.Z.N.I. Marine Ecology **9**: 181-198.
- Bosman A. L., and P. A. R. Hockey. 1988a. Life-history patterns of populations of the limpet *Patella granularis*.: the dominant roles of food supply and mortality rate. Oecologia (Berlin) **75**: 412-419.
- Bosman A. L., and P. A. R. Hockey. 1986. Seabird guano as a determinant of rocky intertidal community structure. Marine Ecology Progress Series **32**: 247-257.
- Branch, G. M. 1975. Mechanisms reducing intraspecific competition in *Patella* spp: migration, differentiation and territorial behaviour. Journal of Animal Ecology **44**: 575-600.
- Branch, G. M. 1985. Limpets: their role in littoral and sublittoral community dynamics. Pages 97-116 in P. G. Moore, D. Seed editors. The Ecology of Rocky Coasts. Hodder and Stoughton Educational, England.
- Branch, G. M., and M. L. Branch. 1980. Experimental analysis of intraspecific competition in an intertidal gastropod *Littorina unifasciata*. Australian Journal of Marine and Freshwater Research **32**: 573-89.
- Brown, P. C. 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. South African Journal of Marine Sciences **12**: 515-525.

- Brown, P. C., and K. L. Cochrane. 1991. Chlorophyll-*a* distribution in the southern Benguela, possible effects of global warming on phytoplankton and its implication for pelagic fish. *South African Journal of Science* **87**: 233-242.
- Brown, P. C., S. J. Painting, and K. L. Cochrane. 1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *South African Journal of Marine Science* **11**: 5137-564.
- Burger, L. F. 1990. The distribution patterns and community structure of the Tsitsikamma rocky littoral ichthyofauna. M. Sc. Thesis, Rhodes University, Grahamstown, South Africa.
- Carpenter, S. R., and J. K. Kitchell. 1984. Plankton community structure and limnetic primary production. *The American Naturalist* **124**: 159-172.
- Carpenter, S. R., and J. K. Kitchell. 1987. The temporal scale of variance in limnetic primary production. *The American Naturalist* **129**: 417-433.
- Castenholz, R. W. 1963. An experimental study of the vertical distribution of littoral marine diatoms. *Limnology and Oceanography* **8**: 450-462.
- Cliff, G. 1982a. Seasonal variation in the contribution of phytoplankton, bacteria, detritus and inorganic nutrients to a rocky shore ecosystem. *Transactions of the Royal Society of South Africa* **44**: 523-538.
- Cliff, G. 1982b. Dissolved and particulate matter in the surface waters of False Bay and its influence on a rocky shore. *Transactions of the Royal Society of South Africa* **44**: 539-549.
- DeAngelis, D. L. 1992. *Dynamics of Nutrient Cycling and Food Webs*. Chapman and Hall, London.

- de Boer, J. A. 1982. Nutrients. Pages 356-365 in C. S. Loban and M. J. Wynn editors. The Biology of Seaweeds. Blackwell, Oxford.
- Demers, S, J. C. Therriault, E Bouget, and D. Desilets. 1989. Small-scale gradients of phytoplankton productivity in the littoral fringe. *Marine Biology* **100**: 393-399.
- Dye, A. H., and D. R. A. White. 1991. Intertidal microalgal production and molluscan herbivory in relation to season and elevation on two rocky shores in the east coast of southern Africa. *South African Journal of Marine Sciences* **11**: 483-844.
- Hatcher, B. G. 1990. Coral reef primary productivity: a hierarchy of pattern and process. *Trends in Ecology and Evolution* **5**: 149-155.
- Hawkins, S. H., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review* **21**: 195-289.
- Hay, M. E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* **62**: 739-750.
- Hill, A. S., and S. J. Hawkins. 1990. An investigation of methods for sampling microbial films on rocky shores. *Journal of the Marine Biology Association of the United Kingdom* **70**: 77-88.
- Hill, A. S., and S. J. Hawkins. 1991. Seasonal and spatial variation of epilithic microalgal distribution and abundance and its ingestion by *Patella vulgata* on a moderately exposed rocky shore. *Journal of the Marine Biology Association of the United Kingdom* **71**: 403-423.
- Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 504-512.

- HMSO. 1986. The determination of chlorophyll *a* in aquatic environments. Pages 6-13 *in*: Methods for the examination of water and associated materials, vol. 4., section 2. HMSO.
- Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecology and Systematics* **19**: 89-110.
- Hutchinson, G. E. 1955. The biogeochemistry of vertebrate excretion, *Bulletin of American Museum of Natural History* **96**: 134-151.
- Jeffrey, S. W., and G. F. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*₁ and *c*₂ in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanze*. **167**: 191-194.
- Jørgensen, C. B. 1990. Bivalve Filter Feeding: Hydrodynamics, Bionergetics, Physiology and Ecology. Olsen and Olsen, Fredensborg.
- Lasiak, T. A., and D. R. A. White. 1993. Microalgal food resources and competitive interactions among the intertidal limpets *Cellana capensis* (Gmelin, 1791) and *Siphonaria concinna* (Sowerby 1824). *South African Journal of Marine Sciences* **13**: 97-108.
- Legendre, L., S. Demers, and S. Lefaivre. 1986. Biological production at marine ergoclines. Pages 1-54 *in*: J. C. J. Nihoul editor. *Marine Interfaces Ecohydrodynamics*. Elsevier, Amsterdam.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist* **134**: 922-949.
- Littler, M. M., and K. E. Arnold. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. *Journal of Phycology* **18**: 307-311.

- Littler, M. M., and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgal functional form groups model. *The American Naturalist* **116**: 25-44.
- Littler, M. M., and D. S. Littler. 1984. Relationships between macroalgal functional form groups and substrata stability in subtropical rocky-intertidal systems. *Journal of Experimental Marine Biology and Ecology* **74**: 13-34.
- Littler, M. M., and D. S. Littler. 1988. Structure and role of algae in tropical reef. Pages 29-56 in C. A. Lembi and J. R. Waaland editors. *Algae and Human Affairs*. Cambridge University Press, Cambridge.
- MacLulich, J. H. 1986a. Colonization of bare rock surfaces by microflora in a rocky intertidal habitat. *Marine Ecology Progress Series* **32**: 91-96.
- MacLulich, J. H. 1986b. Experimental evaluation of methods for sampling and assaying intertidal epilithic microalgae. *Marine Ecology Progress Series* **34**: 275-280.
- MacLulich, J. H. 1987. Variation in the density and variety of intertidal epilithic microflora. *Marine Ecology Progress Series* **40**: 285-293.
- Mann, K. H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems *Limnology and Oceanography* **33**: 910-930.
- Mann, K. H., and J. R. N. Lazier. 1991. *Dynamics of Marine Ecosystems*. Blackwell Scientific Publications, Oxford.
- McQuaid, C. D. 1981. The establishment and maintenance of vertical size gradients in populations of *Littorina africana knysnaensis* (Phillipi) on a exposed shore. *Journal of Experimental Marine Biology and Ecology* **54**: 77-89.
- Menge B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* **73**: 755-765.

- Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**: 730-757.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends in Ecology and Evolution* **5**: 52-67.
- Moloney, C. L. 1992. Simulation studies of trophic flows and nutrient cycles in Benguela upwelling foodwebs. *South African Journal of Marine Science* **12**: 457-476.
- Mostert, S. A. 1983. Procedures used in South Africa for the automatic photometric determination of micronutrients in sea water. *South African Journal of Marine Science* **1**: 189-198.
- Mostert, S. A. 1988. Notes on improvements and modifications to the automatic methods for determining micronutrients in sea water. *South African Journal of Marine Science* **7**: 295-298.
- Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. *Ecology* **58**: 1020-1032.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* **73**: 733-746.
- Raffaelli, D. G. 1979. The grazer-alga interaction in the intertidal zone on New Zealand rocky shores. *Journal of Experimental Marine Biology and Ecology* **38**: 81-100.
- Raine, R. C., and J. W. Patching. 1980. Aspects of carbon and nitrogen cycling in a shallow marine environment. *Journal of Experimental Marine Biology and Ecology* **47**: 127-140.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* **46**: 205-222.

- SAS. 1986. SAS[®] System for linear models, 1986 Edition. SAS Institute Inc., Cary, NC, USA.
- Shannon L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela. Physical features and processes. *Oceanography Marine Biology Annual Review* **23**: 105-182.
- Stanley, E. H., R. A. Short, J. W. Harrison, R. Hall, and R. C. Wiedfield. 1990. Variation in nutrient limitation of lotic and lentic algal communities in Texas (USA) river. *Hydrobiologia* **206**: 61-71.
- Steneck. R. S., and M. N. Dethier. Unpublished Manuscript. A functional approach to the structure of algal dominated communities.
- Steneck. R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Marine Biology* **68**: 299-319.
- Steneck. R. S., S. D. Hacker, and M. N. Dethier. 1991. Mechanisms of competitive dominance between crustose coralline algae: an herbivore-mediated competitive reversal. *Ecology* **72**: 938-950.
- Stuart, V. 1982. Absorbed ratio, respiratory cost and resultant scope for growth in the mussel *Aulacomya ater* (Molina) fed on a diet of kelp detritus of different ages. *Marine Biology Letters* **3**: 289-306.
- Stuart, V., and D. W. Klumpp. 1984. Evidence for food-resource partitioning by kelp-bed filter-feeders. *Marine Ecology Progress Series* **16**: 27-37.
- Underwood, A. J. 1984a. The vertical distribution and seasonal abundance of intertidal microalgae on a rocky shore in New South Wales. *Journal of Experimental Marine Biology and Ecology* **78**: 199-220.

- Underwood, A. J. 1984b. Vertical and seasonal patterns in competition between intertidal gastropods. *Oecologia* **64**: 211-222.
- Underwood, A. J. 1984c. Microalgal food and the growth of the intertidal gastropods *Nerita atramentosa* Reeve and *Bembicium nanum* (Lamarck) at four heights on a shore. *Journal of Experimental Marine Biology and Ecology* **79**: 277-291.
- Underwood, A. J., and P. Jernakoff. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low shore intertidal algal community. *Oecologia* **48**: 221-233.
- Vadas, R. L. 1985. Herbivory: Pages 531-572 in M. M. Littler and D. S. Littler editors. *Ecological Field Methods: Macroalgae*. Cambridge University Press, Cambridge.
- van der Elst, R. 1990. *A Guide to the Common Sea Fishes of Southern Africa*. Struik Publishers, Cape Town.
- Wootton, T. J., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences* **90**: 1384-1387.

Chapter 4

*The Dependence of Intertidal Consumers on Kelp-Derived Organic
Matter on the West Coast of South Africa*

Summary: In this Chapter I explore the trophic relationships between intertidal and subtidal ecosystems for a west coast rocky shore community. I select a number of intertidal primary consumers, principally grazers and filter-feeders, and investigate their trophic connections with *in-situ* intertidal production and/or subtidal kelp production. Using two stable isotopes (nitrogen and carbon), I examine the degree to which filter-feeders are trophically connected to kelp detritus and pelagic phytoplankton. Similarly, I establish the extent of the trophic connection between several intertidal grazers and the intertidal production or subtidal kelps. The filter-feeders use kelp-derived detritus as their main source of organic carbon and nitrogen. Similarly, two highly specialized grazers also use subtidal kelps as their main source of carbon and nitrogen, although more generalized intertidal grazers rely mainly on intertidal algal production.

I determined the and extent to which kelp detritus contributes to the total particulate organic matter (POM) on exposed and sheltered habitats and during different tidal phases. Kelp-derived detritus represented more than 65% of the POM, being consistently high all year round and during both high and low tides, but was particularly high on exposed shores. Phytoplankton was seldom found and contributed no more than 6% of the total intertidal POM. I conclude that kelp-derived detritus represents a steady source of food for filter-feeders, upon which they can rely all year round. A short-term experiment revealed that the water turnover on exposed shores was about seven times greater than on sheltered shores; the consequent increasing in the supply of food may explain why filter-feeders biomass is high on wave exposed shores.

Finally, a steady-state model was built to simulate mussel standing stocks as function of food supply and water turnover. The model predicts significantly lower mussel biomass on sheltered than exposed shores. I conclude that replenishment of food by waves action , is sufficient to explain the observed differences on filter-feeder biomass between exposed and sheltered shores.

Introduction

Forests of large brown algae, the kelps, fringe the rocky shores of temperate and high-latitude regions throughout the world, frequently associated with cold water upwelled systems (Kain 1979; Mann 1982; Dayton 1985; Schiel and Foster 1986; Johnson and Mann 1988). Along the west coast of southern Africa, extensive forests of the kelps *Ecklonia maxima* and *Laminaria pallida* are commonly found (Velimirov *et al.* 1977; Field *et al.* 1977). This particular kelp bed ecosystem is among the world's most intensively studied regarding its nutrient dynamics and its role in energy flow through the shallow rocky subtidal food web (e.g., Field *et al.* 1977; Newell *et al.* 1980; Wickens and Field 1986). In the course of this research, several important and well documented processes relevant to food web theory have been identified, including the significance of microheterotrophs in regeneration of nutrients (e.g., Steele 1974; Fenchel and Blackburn 1979; Newell *et al.* 1988; Painting *et al.* 1992), new steps in the planktonic food web such as the "bacterial loop" and the virally induced lysis of marine microbial communities as (e.g., Azam *et al.* 1983; Moloney 1992; Thingstad *et al.* 1993), and the role of macrophyte-derived detritus as a source of organic carbon and nitrogen for subtidal consumers (Stuart *et al.* 1982; Seiderer and Newell 1985; Mann 1988; Fielding and Davis 1989). Unfortunately, no similar development has occurred for the food web dynamics of rocky intertidal ecosystems.

The enormous production of kelp beds rivals the most productive terrestrial ecosystems on earth (Witman 1988). There is well documented evidence that most of this production enters the detritus food web, as kelp blades are eroded and fragmented by the action of waves (Field *et al.* 1977; Newell and Field 1983; Newell 1984; Mann 1988). In the kelp-beds of the southern Benguela system, suspension feeders (mainly filter-feeders) are the dominant faunistic component (Velimirov *et al.* 1977; Field *et al.* 1977; Branch and Griffiths 1988). Several of these suspension feeders are able to digest the

carbohydrates contained in kelp-derived detritus (Seiderer *et al.* 1982), and much of their tissue carbon and nitrogen is probably derived from the detritus (Stuart *et al.* 1982; Fielding and Davis 1989). The fate of kelp biomass and particulate detritus is well studied for the subtidal food web (e.g., Newell 1984; Branch and Griffiths 1988), and for the sandy beaches (Koop *et al.* 1982a, b). However, the potential role of kelp-derived matter in adjacent rocky intertidal ecosystems has not yet been explored.

Although there have been many recent reviews dealing with some of the processes and potential mechanisms involved in the structuring and regulation of intertidal rocky communities in different parts of the world (Menge and Sutherland 1987; Foster *et al.* 1988; Menge and Farrel 1989; Menge and Olson 1990), there have been few quantitative studies on material flow through intertidal rocky-shore food webs (except that of Field 1983). Mann (1972; 1982) has suggested that much algal material is used by coastal invertebrates and is readily digested without further transformation. Furthermore, after comparing various freshwater, estuarine and coastal marine systems, he concludes that macrophytic detritus appears to be utilized very effectively in coastal food chains leading to shellfish production (Mann 1988). Thus, an open question is whether the subsidy of the intertidal zone by inputs from the nearshore and subtidal production (phytoplankton, dissolved and, specifically, particulate organic matter derived from macrophytes) does have a controlling 'bottom-up' effect that structures and regulates intertidal rocky-shore communities. A further open question is the extent to which intertidal consumers can utilize subtidal kelp.

The fact that most elements have two or more stable (non-radioactive) isotopes offers tremendous potential for new ecological research or as tool for solving old questions (Rundel *et al.* 1989). Each trophic level has a distinctive 'signal' (the ratio of natural abundance of given isotopes) and the difference in signals between trophic levels or organisms (i.e. isotopic fractionation) provides great insight into trophic processes within a food web. The natural abundance of isotopes has emerged as a powerful means of tracing ecosystem energetic and estimating the dependence of organisms on specific diets

and habitats. In some cases, it is the only tool available for distinguishing and tracing different sources of food (Gearing 1991). For example, with a few measurements of the isotopic composition of organic tissues of aquatic plants and animals, it is possible to establish a chemical outline of food web structure (Fry 1991). A dual-isotope approach is often useful and desirable in studies of trophic structure, for example, when different kinds of plants are important sources of nutrition for consumers (Peterson and Fry 1987; Rundel *et al.* 1989; Fry 1991).

In the preceding Chapters, I have quantitatively described several large- and small-scale community patterns evident for intertidal rocky shores around southern Africa (Chapter 1), with specially reference to differences between the east and west coast communities (Chapter 2). In Chapter 3 a description was given of a gradient in intertidal primary production around the coast and its relationship with some of the more important consumers. Right around the whole of the southern African coast, exposed shores tend to be dominated by sessile, space-occupying filter-feeders. This pattern is consistently repeated in other intertidal systems of the world. For example, mussels and barnacles (both filter-feeders) are the space-dominant species on the mid-low intertidal of exposed rocky shores of North-East Pacific (Paine 1966, 1974; Harger 1972; Paine and Levin 1981; Foster *et al.* 1988), the North-West Atlantic (Lubchenco and Menge 1978; Menge and Farrell 1989), the British Isles (Lewis 1964), New Zealand (Paine 1971), the Baltic sea (Wallentinus 1991), and south-eastern Pacific (Santelices *et al.* 1977; Castilla 1981; Paine *et al.* 1985). Conversely, the levels of dominance achieved by grazers (mostly patellids limpets) on the mid-low zones of semi-exposed and sheltered shores of the temperate west coast of southern Africa appear to be unique (Chapter 1 and 2). Nowhere else do intertidal invertebrate grazer attain a comparable biomass (see Chapter 5).

What are the facts that produce almost universal patterns of dominance of exposed shores by sessile filter-feeding consumers? Why do sheltered shores on the west coast of southern Africa harbour such high grazer biomasses? How are these high biomasses of consumers maintained? These are the overall questions addressed in this dissertation. In

this Chapter, however, I concentrate on more specific questions, some already advanced in Chapter 1, that may explain large-scale patterns in community structure around the coast (Table 3, Chapter 1). The dominance of filter-feeders on exposed shores may be due to many factors, including (i) high recruitment, (ii) better survival due to low predation pressure, which is constrained by wave action, or (iii) better conditions for growth and survival due to greater food input - arising from higher food concentration and/or greater water turnover in areas of high wave action. Similarly, the high biomass of grazers on sheltered shores may be due to (iv) greater availability of food, (v) the absence of physical stress (wave action), which may inhibit grazing or reduce survival on exposed shores, or (vi) reduced spatial competition with filter-feeders on sheltered shores.

The intention of this Chapter is not to explore all this possible hypotheses. Rather, I concentrate on trophic processes that I have implied in hypothesis (iii) for filter-feeder domination of exposed shores, and hypothesis (iv) explaining the high biomass of grazers on semi-exposed/sheltered shores. I attempt to establish the trophic connection between macrophyte-derived materials and trophic guilds of intertidal consumers. Because rocky shores are too open to manipulate nutrients or particles feasibly, I have used observational and comparative approaches.

Using stable isotope analyses, I first establish the trophic link between subtidal kelp and intertidal consumers, and assess the degree to which grazers and filter-feeders may derive their food from macrophytic particulate material. For that, I chose grazer and filter-feeder species that are the most abundant in term of their biomass and which dominate exposed and sheltered shores of the west coast (see Table 2A, Chapter 1). I also include some less-abundant, but trophically distinctive, intertidal and subtidal grazers and predators. I then quantify the availability and turnover of particulate matter on exposed and sheltered shores on the west coast and model whether any differences between these contrasting systems significantly affect filter-feeder populations.

Material and Methods

Stable Isotopes Ratios

The rationale of stable isotope analysis lies in the fact that most elements of biological importance have at least two stable isotopes. The difference between any two stable isotopes (e.g. those of carbon or nitrogen) generates a ratio reflecting the relative abundance of the two stable isotopes (Ehrlinger *et al.* 1986). These differences are normally very small and they are expressed relative to a standard. The unit of isotopic ratio is the delta value (δ) and is expressed as the deviation per mil (‰) from an arbitrary standard. The implication of this chemical phenomenon is that each biological organism incorporates isotopes of a given element (e.g. carbon) at a specific ratio (signature), that in turn reflects the ratio of isotopes present in its diet (DeNiro and Epstein 1978, 1981). This phenomenon has helped researchers to trace the food sources of specific animals or entire ecosystems.

In this Chapter, samples from target animals, algae and POM were collected from the Groenrivier rocky intertidal to determine their stable isotopes ratios ($^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$). The target grazer species included the limpets *Patella granatina*, *P. argenvillei*, which are the most abundant grazers on sheltered and semi-exposed shores respectively and are known to consume kelp as part of their diet (see Chapter 5). Another limpet, *P. granularis* was included because it is abundant but has more generalized feeding habits (Bosman 1988). Data for the subtidal abalone *Haliotis midae* are also presented for comparative reasons, due to the fact that it is also known that they feed on kelps (Barkai and Griffiths 1986; Tarr 1989). The filter-feeders analyzed were the mussels *Mytilus galloprovincialis*, *Aulacomya ater* and the polychaete *Gunnarea capensis*. These three species comprise more than 50% of the community biomass on exposed shores. Table 1 summarizes the species examined, their trophic functional group, the elements for which isotopes ratios were determined, and sample sizes (number of determinations). For a

Table 1. List of species and trophic groups, isotopes ratios, sample size and the sources of data included in the stable isotopes analyses.

Species	Trophic group	Carbon		Nitrogen		n
		(1)	not provided	(2)	not provided	
Phytoplankton	Producer					
<i>Ecklonia maxima</i>	Producer	+	7	+		5
Detritus	Producer	+	4	+		4
<i>Laminaria pallida</i>	Producer	+	9	+		6
<i>Porphyra capensis</i>	Producer	+	6	+		8
Ulva/Enteromorpha mix	Producer	+	4	+		3
Epilithic Diatoms	Producer	+	4	+		3
<i>Ralfsia verrucosa</i>	Producer	+	3	+		3
<i>Patella longicosta</i>	Grazer	+	5	+		3
<i>Patella argenvillei</i>	Grazer	+	6	+		6
<i>Patella granatina</i>	Grazer	+	6	+		5
<i>Haliotis midae</i>	Grazer	(3)	1	(3)		1
<i>Patella granularis</i>	Grazer	(3)	1	(3)		1
<i>Mytilus galloprovincialis</i>	Filter-feeder	+	5	+		6
<i>Gunnarea capensis</i>	Filter-feeder	+	5	+		5
<i>Aulacomya ater</i>	Filter-feeder	+	5	+		4
<i>Burnupena spp.</i>	Scavenger	(3)	1	(3)		1
<i>Jasus lalandii</i>	Predator	(3)	1	(3)		1

+ = This study.

1 = Monteiro et al. (1991).

2 = Owens (1987); Minawada and Wada (1984).

3 = Sealy et al. (1987).

comparative purpose, values for some other co-occurring species were taken from previously published work, as shown in Table 1.

Each sample was washed in distilled water, freeze dried, and homogenized at liquid nitrogen temperatures in a freezer mill. Small quantities of each sample (approximately 7 mg for animal tissue, 14 mg for algae and <4 mg for POM) were weighed into quartz combustion tubes. Samples of mussels and polychaetes consisted of pooled whole bodies of about 3-5 animals; limpet samples comprised the bodies of whole individuals. Copper oxide, copper metal and silver foil were added to each quartz tube, which was heat sealed after evacuation to below 10^{-2} torr. Samples were then combusted for five hours at 800°C and cooled over 17 h in a closed furnace (Coleman and Fry 1991).

Carbon dioxide and nitrogen gases were extracted from the samples by cryogenic distillation on a vacuum line, as described by Sealy and van der Merwe (1986) and Boutton (1991). Yields of nitrogen and carbon dioxide were measured manometrically. Nitrogen was collected in a quartz tube by freezing onto purified coconut charcoal at liquid nitrogen temperature. Carbon dioxide was separated from water vapour by melting frozen carbon dioxide using an ethanol/dry-ice slurry, collected in a Pyrex tube, and cooled to liquid nitrogen temperature. Isotope ratios of both CO_2 and N_2 were measured on a VG Micromass 602E 90° double-collector mass spectrometer. When only small amounts of nitrogen were obtained from a sample, the entire gas sample was first frozen into a carbon "cold finger" before being passed into the spectrometer itself. However, this increases the chance that isotopic fractionation will occur. Consequently, to improve the accuracy of stable isotope analysis, quantitative measurements were made at all stages in the processing of samples, to ensure that the differential loss of isotopes associated with this fractionation was minimal (Boutton 1991).

Reference gas for CO_2 was calibrated against 6 National Bureau of Standards isotopic reference materials (NBS 16, 17, 18, 19, 20, 21) to relate it to the extant Chicago PDB (Pee Dee Belemnite Carbonate marine limestone standard). Nitrogen reference gas was calibrated against atmospheric nitrogen and IAEA standards N.1 and N.2. The $\delta^{15}\text{N}$

measurements are reported relative to atmospheric nitrogen (Sealy and van der Merwe 1986; Sholto-Douglas 1992).

The equation :

$$\delta X = \frac{(R_{sample} - R_{standard})}{R_{standard}} \times 1000 \text{‰},$$

was used to express isotope ratios, where $\delta X = \delta^{13}\text{C}$ or $\delta^{15}\text{N}$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

For each animal sample, the percentage contribution of photosynthesized carbon or organic nitrogen to each animal sample derived from kelp-carbon or kelp-nitrogen was calculated using a simple mixing model for a two-source system (McConnaughey and McRoy 1979), where,

$$\% \text{Kelp - Carbon} = \frac{[\delta^{13}\text{C}_{sample} - \delta^{13}\text{C}_{source_2} - I]}{[\delta^{13}\text{C}_{source_1} - \delta^{13}\text{C}_{source_2}]} \times 100, \text{ and}$$

$$\% \text{Kelp - Nitrogen} = \frac{[\delta^{15}\text{N}_{sample} - \delta^{15}\text{N}_{source_2} - I]}{[\delta^{15}\text{N}_{source_1} - \delta^{15}\text{N}_{source_2}]} \times 100,$$

where I is the average post-photosynthetic fractionation of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ per trophic level. The value of I for any particular animal can seldom be known exactly and is usually approximated, but in the case of the grazers analyzed here, I use the particular situation of the territorial limpet *Patella longicosta* to obtain a natural fractionation values (I) for carbon and nitrogen. Adult *P. longicosta* feed virtually exclusively on the encrusting brown alga *Ralfsia verrucosa*, which grows inside the limpets' territories (Branch 1971, 1975; Branch *et al.* 1992). So, the differences between

$$\delta^{13}\text{C} (\text{Alga}) - \delta^{13}\text{C} (\text{Limpet}),$$

$$\text{or } \delta^{15}\text{N} (\text{Alga}) - \delta^{15}\text{N} (\text{Limpet}),$$

were used as a direct measurement of natural fractionation between the autotroph and the grazer trophic step. It was assumed that these δ increases were applicable to all grazer species included in this study. For filter-feeder species, the fractionation values of 1 ‰ for $\delta^{13}\text{C}$ (De Niro and Epstein 1978; Rau *et al.* 1983; Fry and Sherr 1984; Sholto-Douglas *et al.* 1991), and 4 ‰ for $\delta^{15}\text{N}$ (Minawada and Wada 1984) were used.

Particulate Matter

Between May 1989 and May 1990 monthly samples of sea water were taken simultaneously at exposed and sheltered intertidal rocky shores at the locality of Groenrivier (see Fig. 1, Chapter 2 for localities). To determine the concentration of particles available in the intertidal zone, six 250 cc samples of sea water were collected at each site, during both low and high tides, and filtered through 2.5 cm GF/F glass microfibre filters. The mesh structure of the GF/F filters does not select specific particle size, but normally all particles greater than 0.45 μm are retained. Once the filtering process was completed, the filters were wrapped in aluminum foil and stored at -20°C for further analysis. In the laboratory, the filters were optically analyzed with a stereoscopic microscope for the identification of the different types of particles, at a range of x40 to x120 magnifications. The different types of particulate matter were grouped into six main categories defined by their nature and origin. These categories were: a) kelp-derived particles (from *Ecklonia maxima* and *Laminaria pallida*), b) faecal pellets and pseudofaeces (mostly from mussels), c) other non-kelp macroalgal fragments, d) animal-derived material (mostly parts of the exoskeletons of crustaceans and molluscs), e) fragments of terrestrial plants (wood and leaf fragments), and f) phytoplankton (mostly large-celled diatoms). Due to their small size, it was impossible to physically separate the different particle types. Consequently, their individual biomass contributions could not be determined. However, by scanning the fiberglass filters with the microscope at a constant magnification of x80, it was possible to obtain an index of their relative abundance. This was accomplished by counting each particle type in four independent counts using a 10 X 10 graticule grid placed over each filter. After scoring, each filter was then oven dried at

50°C for 48 h, weighed, combusted at 450 °C for at least 6 h, and again weighed with a precision of five decimal points. Finally, the total concentrations of particulate organic matter (POM) and particulate inorganic matter (PIM) were expressed as ash free dry weight (AFDW) in grams per liter (g l^{-1}). All statistical analyses were performed using the procedures GLM of SAS[©] v.5.1 (SAS 1986).

Water turnover

A known volume of a solution of the organic dye rhodamine (diluted in sea water) was released into the sea, and its dilution over time used as an indirect indicator of sea water turnover. At the locality of Groenrivier, 3 hours after low tide, a solution of 100 g of rhodamine diluted on 25 l of sea water was released simultaneously at a sheltered and a exposed rocky sites. Water samples were taken immediately after the release, and every minute during the first 10 minutes. Subsequently, water samples were taken at 5 and then 10 minute intervals for the following 2.5 hours. At each sampling interval, four 50 ml water samples were taken around the release point, bottled, placed into a cool bag and taken to the laboratory for their analysis using standard spectrophotometric techniques. By scanning a solution of 1.0 mg l^{-1} of rhodamine diluted in sea water over a range of wave lengths between 400 and 640 nm, it was determined that rhodamine has a unique and distinctive absorption peak of visible light at 554 nm. Sea water (used as a background blank) did not exhibit any absorption peak at 554 nm. All spectrophotometric analyses were done using a Beckman DU[®]-50 spectrophotometer. The accuracy of the spectrophotometer readings was four decimal points, a reading of 0.0001 optical density corresponding to a rhodamine concentration of 0.001 mg l^{-1} . Consequently, any optical density values below this were considered equivalent to zero rhodamine in the sea water.

Filter-feeder model

In order to test theoretically if quantity and turnover of food can account for the observed differences in the field of filter-feeder biomass between exposed and sheltered

shores, I built a simple steady-state simulation model for prediction of the mussel standing stock (measured in g m^{-2} of dry flesh mass). The model predict the population growth and not individual growth. Using the empirical data presented here, I simulated two rocky shore habitats subjected to different degrees of wave action (see Chapter 2). For that, I modeled the biomass of the alien mussel *Mytilus galloprovincialis*, which accounts for >77% of the total biomass and >95% of the filter-feeder biomass on exposed rocky shores on the west coast of South Africa (see Table 2, Chapter 2). The model uses as inputs the average food concentrations (detritus and phytoplankton in g m^{-3}) measured on exposed and sheltered shores, the food replenishment consequent upon water turnover (in $\text{g m}^{-3} \text{ day}^{-1}$), maximum mussel growth efficiency (conversion of food mass into body mass, K_I), ingestion rate for an average individual mussel of 50 mm shell length (expressed in $\text{g m}^{-3} \text{ day}^{-1}$), and a mortality coefficient (fix proportion).

The model is based on the biomass data of food availability for filter-feeders, and water turnover presented in this Chapter. The model predicts the dry flesh biomass that can be sustained (in grams per square meter). Food was divided into kelp-derived detritus and phytoplankton, while water turnover represents the rate of food replaced (in grams per cubic meter per day) over a particular area on a given rocky shore. This was calculated from the data obtained from the water turnover experiment. The observed average food standing stocks - i.e. for kelp-derived detritus and phytoplankton, for exposed and sheltered shores - are taken from the results of particle monitoring described above.

The mussel standing stock (S_s) changes according to

$$S_s = S_{s_i} + Gr - Mo,$$

where the initial standing stock S_{s_i} is seeded in the simulation (200 g m^{-2}) and altered by the balance between growth (Gr) and mortality (Mo). The former depends upon food assimilated. The mortality of a given S_{s_i} is

$$Mo = S_{s_i} * M,$$

where M is the daily mortality rate (i.e. 0.059 d^{-1} , derived from an annual figure given in Bayne 1976).

Similarly, growth of a give Ss_i

$$Gr = I * K_I,$$

in which I is the ingestion rate for the whole population and K_I is the maximum gross growth efficiency, or the efficiency (%) with which food is converted into body mass, which was taken to be 35% (Griffiths and Griffiths 1987). I assume that the assimilation efficiency for kelp detritus and phytoplankton is the same. The ingestion rate I is assumed to follow a Holling type II functional response where

$$I = \frac{F_s * I_r}{k + F_s},$$

I_r being the ingestion rate of an average individual mussel of 50 mm shell length, i.e. 0.019 g d^{-1} (Bayne 1979), k the saturation constant, i.e. 2.4 g m^{-3} (van Haren and Kooijman 1993); and the food supply (concentration) F_s is

$$F_s = \sum f_{i+n} * \Delta t,$$

or combined variation of kelp detritus plus phytoplankton through time, in which $\sum f_{i+n}$ is the sum of the different food supply - i.e. detritus plus phytoplankton standing stocks -, and Δt is rate of change of food supply.

Results

Isotopic ratios

The average (± 1 SD) of $\delta^{13}\text{C}$ (Fig. 1A) and $\delta^{15}\text{N}$ (Fig. 1B) values found in 15 taxa belonging to four trophic functional groups are depicted in Figure 1. The average $\delta^{13}\text{C}$ values varied between -6.07‰ and -20.1‰ (Fig. 1A). There was no obvious trend towards trophic enrichment in ^{13}C (i.e., less negative $\delta^{13}\text{C}$, from lower to upper trophic levels). However, the $\delta^{13}\text{C}$ values recorded are typical for marine species and they all fall within the range previously reported for the same or similar species in the Benguela system (Sealy and van de Merwe 1986; Sealy *et al.* 1987; Sholto-Douglas 1992). The isotopic ratio of phytoplankton (taken from Monteiro *et al.* 1991) was the most depleted with a value of -20‰ , while in the upper range of the carbon isotope scale, the limpet *P. longicosta* and the encrusting phaeophyte *R. verrucosa* show substantially enriched ratios, with values of -6.07‰ and -7.48‰ respectively. These two last species represent the almost perfect system for the detection of natural $\delta^{13}\text{C}$ fractionation (since *P. longicosta* adults feed almost exclusively on *R. verrucosa*), and yielded a fractionation value of 1.41‰ (Fig.1A).

The different primary producers - i.e., phytoplankton, kelp-derived materials, micro and macroalgae - showed distinctive isotopic signals. The kelps *E. maxima* and *L. pallida* exhibited average $\delta^{13}\text{C}$ values of -12‰ and -14.1‰ respectively, while the samples of the rhodophyta *P. capensis*, the combined samples of the chlorophyte genera *Ulva/Enteromorpha* and the epilithic diatoms shown $\delta^{13}\text{C}$ values of -16.8‰ , -16.9‰ and -18.9‰ respectively (Fig.1A). Detritus (which is known to be dominated by kelp - see below) fell between the values for the two kelp species. The combined average $\delta^{13}\text{C}$ value for the two species of kelp was significant greater than that of the combined value for diatoms, *Ulva/Enteromorpha* and *P. capensis* (Tukey *t*-test, $p < 0.0001$). The three types of consumers (grazers, filter-feeders and carnivores) possessed average $\delta^{13}\text{C}$ values significantly different from one another (ANOVA, $p < 0.005$). Ignoring *P.*

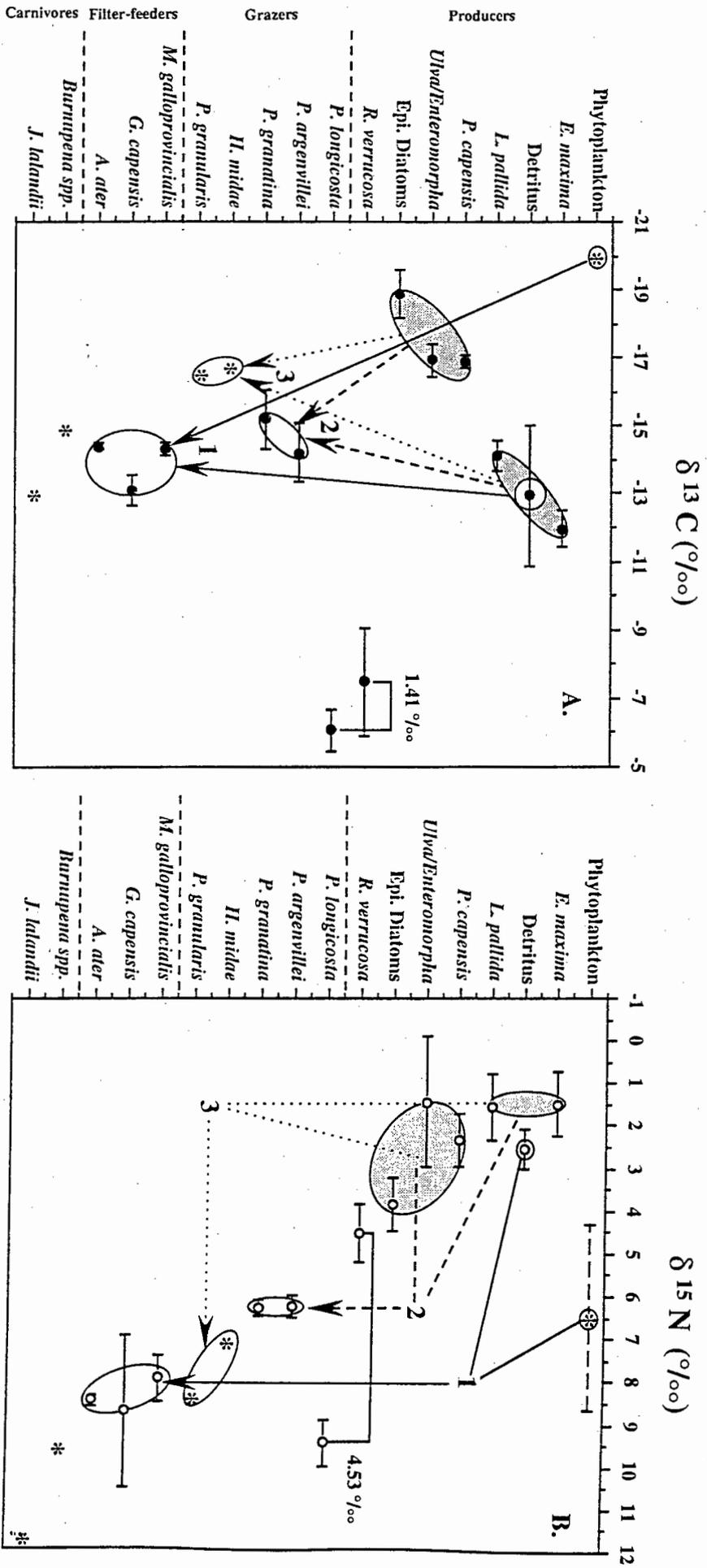


Figure 1. Mean \pm 1 standard deviation of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values found in the tissues of several animal and plants of the rocky intertidal communities on the west coast of South Africa. Oval indicate groups of species from which an overall average value was considered. Asterisks indicate those values taken from previous works.

longicosta, the $\delta^{13}\text{C}$ range within the consumers, which included grazers, filter-feeders and carnivores, was between -17.6‰ and -12.8‰ , the rock lobster *Jasus lalandii* being the most enriched of all (Fig. 1A). The combined average of the isotopic ratios of the filter-feeder species was significantly more enriched than of grazers (Tukey *t*-test, $p < 0.0001$). However, the combined $\delta^{13}\text{C}$ value for the carnivores species *Burnupena* spp. and *J. lalandii*, was not significantly different from that of filter-feeders (Tukey *t*-test, $p > 0.05$).

The average (± 1 SD) values of $\delta^{15}\text{N}$ for the same suite of intertidal seaweeds and animals are depicted in Figure 1B. At present, there is no available $\delta^{15}\text{N}$ value for local intertidal phytoplankton, and the values presented in Fig. 1B are the average reported by Owen (1987) and the range taken from Minagawa and Wada (1984). Excluding the $\delta^{15}\text{N}$ value for phytoplankton, there was a clear trend towards trophic enrichment in ^{15}N moving up through the intertidal food web, i.e. low values of $\delta^{15}\text{N}$ for intertidal producers (micro and macroalgae), with consumers (grazers, filter-feeders and predators) showing increasingly higher $\delta^{15}\text{N}$ values. The average $\delta^{15}\text{N}$ values were significantly different between trophic groups (ANOVA, $p < 0.001$). As in the $\delta^{13}\text{C}$ distribution (Fig. 1A), the *P. longicosta*-*R. verrucosa* association show a clear trophic fractionation, with a value of $+4.53\text{‰}$. Excluding phytoplankton, the producer group (macroalgae, detritus and diatoms) ranged from $+1.5\text{‰}$ to $+4.5\text{‰}$, and the combined isotopic ratio of the two species of kelps was significantly lower than that of combined micro and macroalgae (Tukey *t*-test, $p < 0.0001$). The $\delta^{15}\text{N}$ values for the primary consumers (grazers and filter-feeders) was between $+6.1\text{‰}$ to $+9.4\text{‰}$, and as was the case for the $\delta^{13}\text{C}$ distributions, the combined isotopic value for grazers (excluding *P. longicosta*) was significantly lower (Tukey *t*-test, $p < 0.0001$) than the combined value for filter-feeders (Fig. 1B). The carnivores exhibited the most enriched values of ^{15}N of all intertidal samples (Fig. 1B), and their combined value was significantly higher than of filter-feeders and grazers (Tukey *t*-test, $p < 0.001$).

Isotopic linkage between the sources of $^{13}\text{C}/^{15}\text{N}$ and the intertidal consumers

The solid and dashed arrows in Figure 1A connect the average $\delta^{13}\text{C}$ values found in any given two plant carbon sources (producers, shaded ovals) relative to different groups of fauna (consumers, white ovals). The arrows numbered 1, show the position of the carbon ratio found in filter-feeders (the mussels *M. galloprovincialis*, *A. ater* and the colonial polychaete *G. capensis*) in relation to two carbon sources, i.e. kelp-derived detritus and phytoplankton. The carbon isotopic 'signature' of filter-feeders falls between the two plant sources, but was closer to the kelp detritus than the phytoplankton source. Similarly, arrows numbered 2 show the position of the $\delta^{13}\text{C}$ values for the intertidal grazers *P. argenvillei* and *P. granatina* in relation to two other carbon sources, i.e. the fronds of the two species of kelps, and intertidal algae (epilithic diatoms, *P. capensis* and *Ulva/Enteromorpha*). Again, the average ^{13}C ratios for these two intertidal grazers falls well between the two carbon sources, but there is more affinity with that of the kelps than of the intertidal algae (Fig 1A). When two other more generalized grazer species are considered (*H. midae* and *P. granularis*), their $\delta^{13}\text{C}$ values are closer to the mixture of intertidal micro-macroalgae than of the kelp products (arrows 3, Fig 3A).

The differences between the ^{15}N ratios of the two main types of food (source) and the animal (consumer) samples are represented by the lines and arrows in Figure 1B. These lines again connect the average values of $\delta^{15}\text{N}$ for various groups of intertidal producers (shaded ovals) and their respective consumers (clear ovals). The isotopic position of the filter-feeders in relation to the ^{15}N ratio of the kelp-derived detritus (solid lines 1, Fig. 1B) shows a fractionation value of 5.6‰ , close to the value of 4‰ that would be predicted if they are deriving most of their food from this source. Thus the isotopic values of the filter-feeders are strongly influenced by the kelp detritus and only slightly by that of phytoplankton. Within the herbivore grazers, the fractionation value between the generalist grazers *P. granularis* and *H. midae* and the average value of the mixture of epilithic diatoms and macroalgae (dashed line 3, Fig. 2b) was of 4.4‰ . This fractionation is very close to that found between the limpet *P. longicosta* and its food *R.*

verrucosa, namely 4.48‰ (Fig. 1B, solid line). Similarly, the dashed line 2, which connects the average values of $\delta^{15}\text{N}$ for the limpets *P. argenvillei* and *P. granatina* with that of the kelps, shows a fractionation value of 4.8‰ (Fig 1B). This implies that the two more generalized grazers obtain much of their food from micro and macroalgae rather than kelp, whereas the reverse is true for *P. granatina* and *P. argenvillei*.

The results of the two-sources mixing model are presented in Figure 2. For the three filter-feeders, the mixing model predicts that on average more than 50% of the carbon and 65% of the nitrogen can be conservatively explained by the contribution of kelp-derived detritus (Fig. 2). Similarly, within the grazers, kelp fronds are the main contributor of organic N and C found in the tissues of the two limpets *P. argenvillei* and *P. granatina*, contributing more than 69% to the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, while the remaining 31% can be explained by a mixed diet of epilithic micro and macroalgae. In contrast, within the remaining herbivorous grazers, the mixing model shows that the abalone *H. midae* should receive a lower isotopic contribution from the kelp fronds than from the mixed diet; less than 35% and 20% of the organic N and C respectively (Fig. 2). The intertidal limpet *P. granularis* received no more than 25% of the organic nitrogen and less than 5% of the photosynthesized carbon from kelp fronds, whereas intertidal macroalgae and epilithic diatoms appeared as its main source of both nitrogen (>80%) and carbon (>70%).

The Abundance and Variations of the Particulate Organic Matter (POM)

The monthly average concentration (± 1 SE) of the total POM and the average percent contribution of particulate kelp detritus to the total POM at exposed shores are shown in the Figure 3. There were no obvious seasonal trends in either POM concentration or percentage kelp contribution during either high or low tides.

At high tide (Fig 3A), the overall monthly average POM was $13.53 \pm 0.6 \text{ mg l}^{-1}$ while the overall kelp contribution to the total POM was $68.9 \pm 4.8\%$. The monthly average concentration of POM were significantly correlated with those of particulate kelp

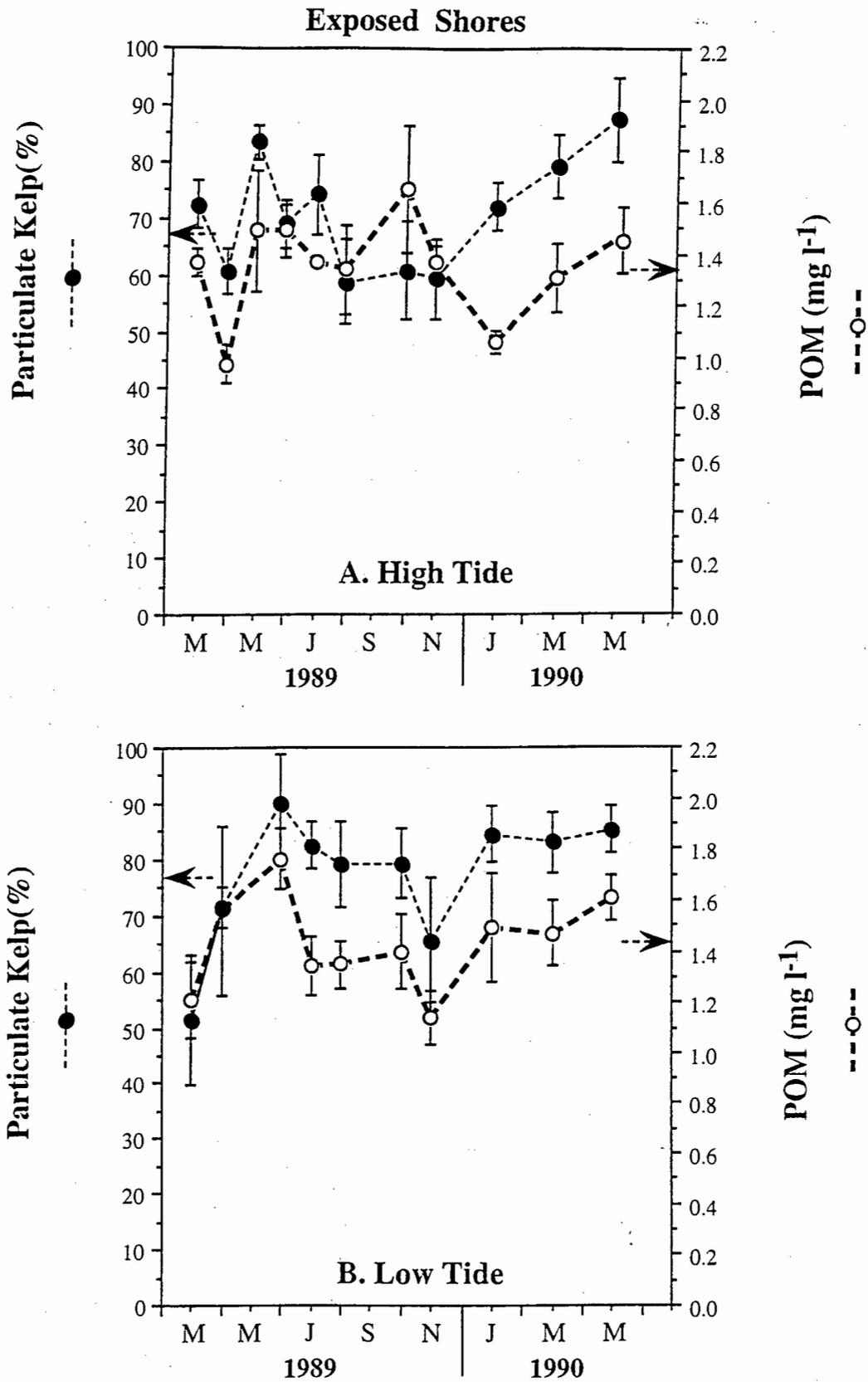


Figure 3. Monthly average (± 1 SE) of particulate kelp detritus and total POM concentration on exposed shores at Groenrivier during both high tide (A.) and low tide (B.). Arrows are indicating the running mean of the time series.

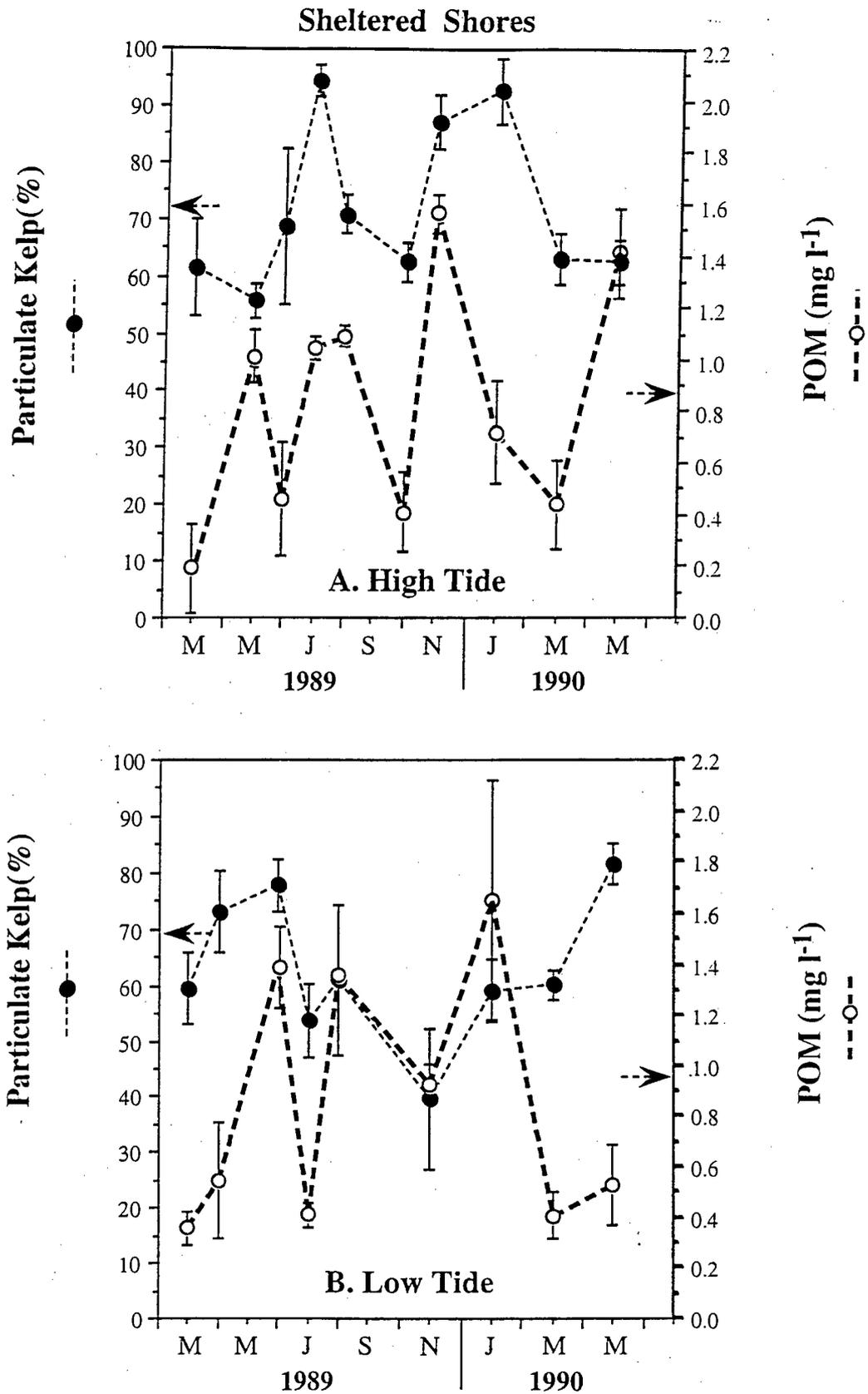


Figure 4. Monthly average (± 1 SE) of particulate kelp detritus and total POM concentration on sheltered shores at Groenrivier during both high tide (A.) and low tide (B.). Arrows are indicating the running mean of the time series.

(Spearman $r_s=0.48$; $p<0.038$, $n=42$). During low tide the average POM was 14.33 ± 0.5 mg l^{-1} , kelp contributing $75.5\pm 4.5\%$ of the total POM (Fig. 3B). As during high tide, a significant correlation (Spearman $r_s=0.78$; $p<0.006$, $n=40$) was found between POM and particulate kelp.

At sheltered shores (Fig. 4) the average POM concentration at high tide was 8.29 ± 1.47 mg l^{-1} , and similar average of 9.56 ± 1.62 mg l^{-1} was recorded during the low tide. The contribution of kelp detritus to the total POM was similar to that of exposed shores, being $71.3\pm 5.1\%$ during high tide and $70.0\pm 3.7\%$ during low tide. However, there were no significant correlations between the total POM and the concentration of kelp detritus during either high tide (Spearman $r_s=0.42$; $p>0.075$, $n=40$) or low tide (Spearman $r_s=0.34$; $p>0.059$, $n=35$).

A non-parametric factorial ANOVA (Table 2) indicated that temporal variability and tidal phase, as well as the interactions between tide and exposure or month and exposure were not significant in explaining the variance of the POM (ANOVA, $p>0.1$). The only significant factor was wave exposure (ANOVA, $p<0.01$). An *a-posteriori* comparison showed that the POM concentration at exposed shores was significantly greater than that of sheltered shores (Tukey's *t*-test, $p<0.05$).

The Nature of the Intertidal POM

The average relative abundance of the total particulate inorganic matter (PIM), the main components of POM and the total POM is summarized for exposed and sheltered shores in Tables 3 and 4 respectively. The PIM consisted of small silt particles (mostly quartz and granite fragments) that on average accounted for no more than 4-12% of the total particulate matter. By contrast, the average POM accounted for more than 89% of the total particles, at both exposed and sheltered shores and during both tidal periods. The ratio POM:PIM was consistently of about 9:1 in favor of the organic matter (Tables 3 and 4).

Table 2. ANOVA by Ranks using the total POM as response variable and the sampling time, wave exposure and tidal cycle as explanatory factors.

		r ² =0.656		CV=52.17%	
Factors	df	SS	MS	F	p
Months	10	913.94	91.39	0.80	0.63
Exposure	1	1144.89	1144.89	10.01	0.01
Tide	1	296.45	296.45	2.59	0.13
Month*Exposure	11	1342.74	134.27	1.17	0.37
Exposure*Tide	1	19.34	19.34	0.17	0.69
Error	16	1829.00	114.36		
Corrected Total	39	5326.50			

Table 3. Monthly average percentages (± 1 SE) of total PIM, total POM, and main particle types of POM on exposed rocky shores at Groenrivier.

High Tide	Year	n	Total PIM		Kelp		Pellets		Other algae		Animal		Wood		Diatoms		Total POM		SE
			SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE		
March	89	6	43.97	5.39	50.10	5.09	1.30	0.78	3.38	1.43	1.25	1.25	56.02	8.56	
April	89	6	18.64	12.90	61.91	2.93	15.33	8.33	2.88	2.78	0.09	0.00	.	1.20	0.02	.	81.41	14.04	
May	89	5	6.65	0.99	90.59	1.50	.	.	2.18	0.94	0.57	0.57	93.34	3.00	
June	89	6	4.57	2.63	93.25	2.19	.	.	1.14	0.66	1.04	1.04	95.43	3.89	
July	89	6	3.35	1.94	74.99	7.36	13.31	6.73	7.78	4.53	0.57	0.57	96.65	19.20	
August	89	6	.	.	47.08	7.35	48.23	4.32	4.69	4.69	100.00	16.35	
October	89	6	.	.	61.35	9.10	30.38	8.80	8.26	5.66	100.00	23.56	
November	89	6	.	.	60.00	7.00	35.41	7.88	4.58	2.67	100.00	17.56	
January	90	6	12.61	3.34	74.98	4.58	2.78	1.61	8.71	3.07	.	.	.	0.92	0.56	.	87.38	9.82	
March	90	4	8.52	2.47	86.02	4.30	4.20	2.69	1.26	0.79	91.47	7.77	
May	90	6	2.03	1.06	57.66	17.35	39.55	15.67	0.76	0.76	97.97	33.78	
Average			12.54		68.90		21.17		4.14		0.70			1.06			90.88		
Standard Error			4.16		4.83		5.30		0.89		0.14			0.06			3.90		
Low Tide	Year	n	Total PIM		Kelp		Pellets		Other algae		Animal		Wood		Diatoms		Total POM		SE
			SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	SE	
March	89	6	17.86	1.35	57.18	12.34	7.15	3.69	14.48	5.22	0.78	0.78	2.57	0.56	.	.	82.16	22.02	
April	89	6	1.77	1.16	73.75	3.29	21.53	3.62	1.94	1.18	1.00	1.00	98.23	9.09	
June	89	6	10.26	0.00	45.91	14.19	35.39	12.89	4.56	0.01	1.80	0.06	1.20	0.95	0.96	.	89.81	27.08	
July	89	6	10.58	2.63	88.16	2.94	.	.	1.26	0.74	89.42	3.67	
August	89	6	5.48	1.19	79.47	7.30	11.93	8.29	3.13	3.13	94.52	18.71	
October	89	6	11.37	4.14	88.00	4.56	.	.	0.63	0.63	88.62	5.18	
November	89	6	8.04	8.04	70.76	13.55	4.89	0.89	14.06	5.34	2.10	0.00	.	0.23	.	.	92.04	19.78	
January	90	6	12.46	4.26	87.55	4.26	87.55	4.26	
March	90	6	6.64	6.64	87.51	4.76	2.46	1.52	3.39	2.36	93.36	8.63	
May	90	6	3.73	2.17	87.06	5.05	7.11	4.67	1.56	1.20	0.54	0.54	96.27	11.46	
Average			8.82		76.53		12.92		5.00		1.24		1.88		0.60		91.20		
Standard Error			1.42		4.47		3.53		1.63		0.20		0.29		0.16		1.42		

Table 4. Monthly average percentage (± 1 SE) of the total PIM, total POM, and main particle types of POM on sheltered rocky shores at Groenrivier.

High Tide	Year	n	Total PIM	SE	Kelp	SE	Pellets	SE	Other algae	SE	Animals	SE	Wood	SE	Diatoms	SE	Total POM	SE
March	89	6	10.31	1.13	64.31	6.11	10.22	4.05	8.39	5.08	6.77	3.93	89.68	19.17
May	89	6	4.64	2.95	56.00	2.91	34.17	3.16	5.19	2.42	95.36	8.49
June	89	6	2.26	1.48	70.34	13.72	23.09	10.63	2.61	2.61	1.71	97.74	28.66
July	89	5	0.44	0.44	95.84	2.55	3.14	1.82	0.57	0.57	99.55	4.93
August	89	6	1.67	1.02	73.30	1.97	16.61	0.88	2.29	1.34	4.43	2.56	1.71	1.71	.	.	98.33	8.46
October	89	6	6.15	2.36	63.26	3.02	14.67	1.66	15.29	1.02	0.15	0.15	0.46	0.46	.	.	93.83	6.31
November	89	6	1.26	0.74	90.17	4.38	.	.	8.57	3.98	98.73	8.36
January	90	6	2.28	2.28	44.86	5.64	27.67	10.40	21.22	5.27	3.98	97.72	25.29
March	90	6	16.26	8.11	66.87	4.27	4.84	3.75	5.09	3.14	0.69	0.42	.	.	6.25	.	83.74	11.58
May	90	6	1.85	0.77	87.68	2.99	6.29	2.87	4.19	1.36	98.17	7.22
Average			4.71		71.26		15.63		7.34		2.19		1.08		6.51		95.28	
Standard Error			1.59		5.05		3.42		2.03		0.61		0.28		0.12		1.59	
Low Tide	Year	n	Total PIM	SE	Kelp	SE	Pellets	SE	Other algae	SE	Animals	SE	Wood	SE	Diatoms	SE	Total POM	SE
March	89	6	4.89	2.40	62.06	7.24	7.58	5.22	12.96	4.57	82.60	17.04
April	89	6	14.88	4.67	75.24	5.31	8.21	4.22	1.67	1.67	85.12	11.20
June	89	5	4.43	4.43	81.18	2.52	8.75	2.27	4.95	3.98	0.69	0.69	95.57	9.46
July	89	6	.	0.00	86.25	6.57	6.90	.	1.56	.	1.25	1.25	0.50	.	3.54	.	100.00	7.82
August	89	6	14.00	0.89	61.99	13.91	13.91	7.89	6.54	1.65	0.72	0.63	1.50	.	1.32	0.63	85.98	24.70
November	89	6	6.05	6.25	52.48	12.79	15.24	6.03	21.06	11.22	2.01	.	.	.	3.15	.	93.94	30.04
January	90	6	5.59	0.48	64.38	6.61	11.97	5.07	12.63	2.14	4.54	3.67	0.89	0.89	.	.	94.41	18.39
March	90	4	25.00	4.80	63.93	1.71	0.69	0.69	10.38	5.33	75.00	7.73
May	90	6	5.99	3.81	82.22	3.77	9.96	3.76	1.10	1.10	0.74	0.74	94.02	9.36
Average			10.10		69.97		9.25		8.09		1.66		0.96		2.67		89.63	
Standard Error			2.31		3.65		1.36		2.13		0.47		0.16		0.37		2.50	

Of all six organic particle categories, particulate kelp detritus was invariably the most abundant, accounting for more than 70% of all POM, regardless of exposure or tidal period (Tables 3 and 4). The second-most important particle type was faecal pellets, which at exposed shores accounted for more than 12-21% of the total POM (Table 3). At sheltered shores, pellets represented in excess 9-15% of the total POM (Table 4). Fragments of other (non-kelp) macroalgae however, never exceeded 5% of the total POM at exposed shores (Table 3), while at sheltered shores they averaged 7-8% of the total POM (Table 4).

Animal-derived particles, mostly shell fragments and pieces of crustacean exoskeleton, never averaged >2.2% of the total POM (Tables 3 and 4). Unexpectedly, diatoms were poorly represented in the samples of intertidal water, often being absent and never exceeding 7% of the total POM (Tables 3 and 4).

Water Turnover.

The rate of dilution of rhodamine in the water samples at exposed and sheltered shores is shown in Figure 5. During the first 8 minutes after released into the sea, the rhodamine solution was rapidly diluted by one order of magnitude (from 100 to ≈ 10 mg l⁻¹) at both exposed and sheltered rocky shores. At exposed shores, the rhodamine was diluted two orders of magnitude within 10 minutes, to about 0.07 mg l⁻¹ (Fig. 5), and after 15 minutes, there was no detectable rhodamine in the sea water samples - i.e., a rhodamine concentration had dropped below 0.001 mg l⁻¹ (Fig. 5). At the sheltered shores, the rhodamine concentrations remained almost constant from 15 to 45 minutes, dropping slowly from 5 to 2 mg l⁻¹ (Fig. 5). From 45 to 75 minutes, it decreased further to about 0.01 mg l⁻¹ and only after 80 minutes did it decline to undetectable levels (< 0.001 mg l⁻¹) (Fig. 5). The rates of water turnover derived from this exercise cannot be meaningfully extrapolated to annual rates, but they do provide measures of the differences that can be expected between exposed and sheltered shores. In this spirit they were employed in the filter-feeder model described below, which simulated the potential significance of the rate of water turnover on the filter-feeder standing stock.

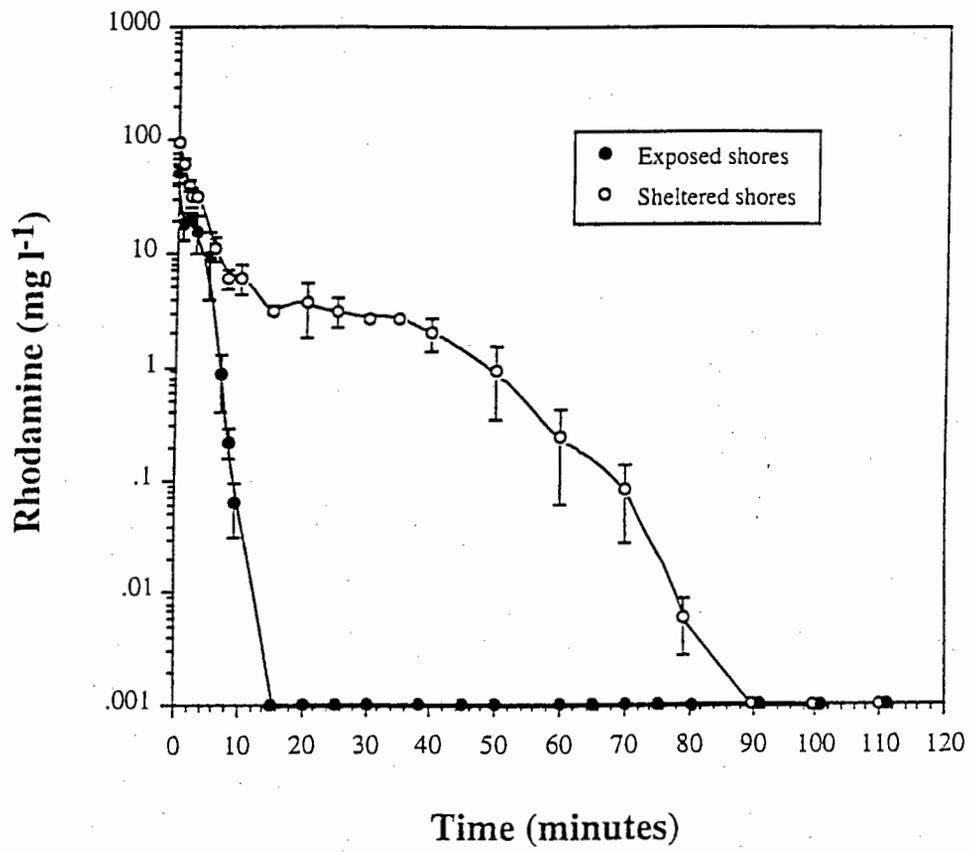


Figure 5. Dilution through time of 100 mg l⁻¹ rhodamine solutions released at exposed and sheltered sites at Groenrivier.

Filter-feeder model

I simulated the fate of a initial 'seed' population of 200 g m^{-2} of mussels, at both exposed and sheltered shores, under average conditions, assuming no seasonal variation in food supply, population growth or mortality. On exposed shores, the trajectory of the mussel standing stock was predicted to increase over a period of three years to a stable carrying capacity of about 478 g m^{-2} , a value that falls well within observed field values for exposed shores on the west coast (Fig. 6). In contrast, under average conditions of food supply and water turnover experienced on sheltered shores, the population decreased rapidly over a period of two years, reaching a stable level of the mussel standing stock of 23 g m^{-2} . This value similarly falls within the observed biomasses measured in the field on sheltered shores (Fig. 6).

Discussion

Measurement of the natural abundance of stable isotopes is a powerful way to study dietary organization of species assemblages or entire ecosystems, and it is sometimes the only mean of tracing the fate of different food sources (Peterson and Fry 1987; Owen 1987; Gearing 1991). However, like all methods, it has certain limitations, especially due to spatial and short- and long-term temporal variations of the dietary sources (Wiencke and Fisher 1990; Simenstad *et al.* 1993). These changes generate a significant variation in the natural isotopic fractionation and turnover between the sources and their consumers. To overcome the 'noise' of natural variation, long-term experimental studies have to be conducted to measure fractionation, in which consumers are maintained on a specific and unique food source with a constant isotopic composition, sometimes for several generations (e.g. DeNiro and Epstein 1978, 1981; Hayes 1982; Tieszen *et al.* 1983; Minagawa and Wada 1984). Rather than extrapolate from these experiments, I measure the natural fractionation between a grazer (*P. longicosta*) and its food source (*Ralfsia verrucosa*), relying on the unusual circumstance that this particular limpet is a territorial specialist with a monospecific diet, at least when adult (Branch 1975). The results yielded isotopic fractionation of 1.41‰ (for carbon) and 4.53‰ (for nitrogen) between *P. longicosta* and *Ralfsia verrucosa* (Fig. 1), that can be applicable to intertidal grazers. These fractionation values are comparable to earlier values derived from long-term experiments (see Minagawa and Wada 1984). I then applied the values obtained from *P. longicosta* to the other grazer investigated, assuming that they would have comparable fractionation rates because most of them were congeners.

The use of stable isotopes to establish trophic linkages between subtidal production of macrophytes and coastal ecosystems has been extensively reported for estuarine systems (e.g. Peterson *et al.* 1985; Simenstad and Wissmar 1985) and shallow-water benthic marine communities (e.g. Stephenson *et al.* 1986; Dunton and Schell 1987; Simenstad *et al.* 1993). Seagrasses detritus (together with its associated microbial communities) is known to contribute to planktonic ecosystems (e.g. Deegan *et al.* 1990; Thresher *et al.*

1992) and even to abyssal food chains (Suchanek *et al.* 1985). However, the trophic linkage between subtidal production and intertidal ecosystems has been explored only in the last few years. The evidence indicates that macrophyte-derived carbon, specifically that from kelps, can be distributed throughout the food web of intertidal rocky-shore ecosystems (Duggins *et al.* 1989). However, none of these benthic studies have used more than one stable isotope.

The results of the isotopic analyses applied in this Chapter to the intertidal rocky-shore communities of the west coast of South Africa, revealed that there is a strong trophic link between consumers in the intertidal community and subtidal primary producers. I use two lines of evidence. First, the analyses of the particle load of intertidal waters showed that the suspended particulate organic matter in the intertidal zone is dominated by small particles of kelp, originated from subtidal production (Figs. 3 and 4). Second, the results obtained using two stable isotopes (nitrogen and carbon) suggested strong trophic linkages between intertidal and subtidal producers and intertidal consumers (Fig. 1). The filter-feeders examined here appeared to use particulate kelp detritus as their major source of organic carbon and nitrogen (Fig. 2). Similarly, two herbivorous grazers, *P. argenvillei* and *P. granatina*, appear to depend on subtidal kelps as the major sources of carbon and nitrogen (Fig. 5).

Isotopic analyses of *Patella granularis* and *Haliotis midae* suggested that they are much less reliant on kelp. Both nitrogen and carbon signals differentiated *P. granularis* and *H. midae* from those species tightly linked to the kelp source (i.e., *P. granatina* and *P. argenvillei*, Figs. 1 and 2). *P. granularis* is known to be a high shore species with a generalized diet (Branch 1971) and has never been recorded trapping drift kelp. *H. midae* does trap kelp frond beneath its foot (Tarr 1989) and research on its gut contents has indicated that the kelp *Ecklonia maxima* represents 40-80% of the crop contents (Barkai and Griffiths 1986). Contrasting, the results of the mixing model presented here imply that only 35% of carbon and 20% of the nitrogen incorporated into the abalone tissue is likely to be derived from a kelp source (Fig. 2). However, it has been shown for the

Australian abalone *H. rubra* that the digestibility of non-phaeophyte (e.g. rhodophyte) seaweeds is faster than it is for phaeophytes (Foale and Day 1992). These authors suggested that the results of Barkai and Griffiths (1986) may be biased in favor of the kelps due to their higher rate of persistence in the gut compared to the more rapidly digested red algae (Foale and Day 1992). Furthermore, in food preference experiments involving *H. roei*, kelp is in general the least preferred food (Wells and Keesing 1989; Shepherd and Steinberg 1992). More recent evidence for the South African *H. midae* has shown that its growth in culture is faster on a diet of red seaweeds than when they feed on kelps (B. Simpson pers. comm.), indicating less efficient use of kelp as a source of food.

The inclusion of two carnivore species (*Jasus lalandii* and *Burnupena* spp.) showed that there was fractionation between these carnivores and primary consumer species (Fig. 1). However, only *J. lalandii* is trophically linked to filter-feeders, specifically *A. ater* and *G. capensis* (Barkai 1987), as was evidenced in their nitrogen signature (Fig. 1B). The whelk *Burnupena* spp. feeds mostly on the carrion of all sort of dead invertebrates (Branch and Branch 1981).

The analysis of intertidal waters samples from Groenrivier on the West coast, demonstrate that the majority of the organic particles in suspension are kelp-derived (>65%, Fig. 3-4 and Table 3-4). This result is in line with a large number of studies conducted on the Benguela subtidal kelp-bed ecosystem, which have consistently shown that much of the detrital material in suspension in shallow waters consists of fragmented kelp (e.g. Field *et al.* 1977; Stuart *et al.* 1981; Seiderer and Newell 1985; Mann 1988; Stenton-Dozey and Brown 1992). In a local-scale study at False Bay (see Fig. 1, Chapter 3 for the position of this localities), Cliff (1982) assessed the relative importance and influences of phytoplankton, detritus, and dissolved organic matter for an intertidal rocky reef. He concluded that detritus was the major component of the total particulate organic matter (POM) available in the intertidal zone and, consequently, that it plays a major role as a source of food for filter-feeders. Since then, many studies of kelp-bed ecosystems

have successfully established that fragmented macrophytes make a major contribution to the total POM in inshore waters (Newell 1984).

The utilization of such macrophyte-derived detritus by higher trophic levels is a urgent topic for further ecological studies (Mann 1988). It has been difficult, however, to provide quantitative evidence for the degree to which benthic consumers depend on fragmented and partially decomposed kelp-derived material (Dunton and Schell 1987). The results presented here demonstrate that the presence of kelp-derived detritus in the water column is constantly high throughout the year (Figs. 1 and 2), providing a potentially steady food supply for filter-feeders, which are known to filter, ingest and utilize kelp particles (Stuart 1982; Griffiths and Griffiths 1987).

Possible explanations for the existence of high biomasses of filter feeders on exposed shores include a higher concentration of particulate food, or a higher water turnover that will replenish food more rapidly than on sheltered shores. Both condition were met. The results showed that average POM levels were significantly higher on exposed shores (1.39 mg l^{-1}) than on sheltered shores (0.89 mg l^{-1}) (Figs. 3-4). Furthermore, the rate of turnover was approximately seven times greater on exposed shores than sheltered shores (Fig. 5).

Using the empirically observed average conditions, the results of the model developed for mussel standing stock, confirm that the differences in food concentration and water turnover between exposed and sheltered shores (Fig. 5) may be sufficient to explain the disparate biomasses of mussels that are observed in habitats with contrasting wave exposure.

These findings confirm the existence of significant bottom-up effects that may structure and regulate intertidal rocky shore communities of the west coast of southern Africa. The benthic intertidal consumers may rely heavily on inputs from subtidal kelp beds, in the form of particulate kelp for filter-feeders and fragments of fronds for herbivorous grazers. Indeed, their populations and the overall community structure may

be regulated by these inputs, as was suggested by the two trophic pathways diagram in Chapter 3 (see Fig. 12). Much of the carbon and nitrogen incorporated into the tissues of intertidal filter-feeders appears to come from kelp-derived detritus which is a constant source of food, instead of relying on highly seasonal phytoplankton blooms. Phytoplankton levels have consistently been shown to be low in the intertidal zone (Cliff 1982; Demers *et al.* 1989), and several energy flow models for the kelp-bed ecosystem (e.g. Wulff and Field 1983; Wickens and Field 1986; Field *et al.* 1986) have demonstrated that phytoplankton is of little use for nearshore consumers, since the major blooms following upwelling events are shifted offshore, sustaining pelagic production rather than nearshore benthic food chains.

The limpets *P. granatina* and *P. argenvillei* also rely to a large extent on subtidal kelps as the major source of carbon and nitrogen. The results of this Chapter thus clearly demonstrate that a significant fraction of kelp carbon and nitrogen is channeled through detritus and debris to the intertidal community, and strongly suggest that this influences the biomass of intertidal species. All the indications are that the adjacent kelp-bed ecosystem supports a large proportion of the primary and secondary production of intertidal rocky-shore communities on the west coast of South Africa.

References

- Azam, F, T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil, and F. Thingstad. 1983. The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* **10**: 257-263.
- Barkai, R., and C. L. Griffiths. 1986. Diet of the South African abalone *Haliotis midae*. *South African Journal of Marine Sciences* **4**: 37-44.
- Barkai, A. 1987. Biologically induced alternative states in two subtidal rocky subtidal benthic communities. Ph. D. Thesis, Zoology Department, University of Cape Town, Cape Town.
- Bayne, B. L. 1976. *Marine Mussels: their Ecology and Physiology*. Cambridge University Press, London.
- Branch, G. M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. *Zoologica Africana* **6**: 1-38.
- Branch, G. M. 1975. Mechanisms reducing intraspecific competition in *Patella* spp.; migration, differentiation and territorial behaviour. *Journal of Animal Ecology* **44**: 575-600.
- Branch G. M., and M. Branch 1981. *The living shores of southern Africa*. C. Struik, Cape Town, South Africa.
- Branch, G. M., and C. L. Griffiths. 1988. The Benguela ecosystem Part V. The Coastal zone. *Oceanography and Marine Biology Annual Review* **26**: 395-486.

- Branch, G. M., J. M. Harris, C. Parkins, R. H. Bustamante, and S. Eekhout. 1992. Algal 'gardening' by grazers: a comparison of the ecological effects of territorial fish and limpets. Pages 405-424 *in* D. John editor. Plant-animal interactions in the marine benthos. Systematic Association Special Edition **46**, Claredon press, Oxford.
- Boutton, T. W. 1991. Stable Carbon Isotope Ratios of Natural Materials: I. Sample Preparation and Mass Spectrometric Analysis. Pages 155-172 *in* D. C. Coleman, and B. Fry editors. Carbon Isotopes Techniques. Academic Press Ltd. London.
- Castilla, J. C. 1981. Perpectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II. Depredadores de alto nivel trófico. *Medio Ambiente* **5**: 190-215.
- Cliff, G. 1982. Dissolved and particulate matter in the surface waters of False Bay and its influence on a rocky shore. *Transactions of the Royal Society of South Africa* **44**: 539-549.
- Coleman, D. C., and B. Fry. 1991. Carbon isotope techniques. Academic Press, New York.
- DeNiro, M. J., and S. Epstein. 1978. The influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**: 495-506.
- DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* **45**: 341-351.
- Dayton, P. K. 1985. The structure and regulation of some South American kelp communities. *Ecological Monographs* **55**: 447-468.
- Deegan, L. A., B. J. Peterson, and R. Portier. 1990. Stable isotopes and cellulase activity as evidence for detritus as a food source for the juvenile Gulf Manhaden. *Estuaries* **13**: 14-19.

- Demers, S., J. C. Therriault, E. Bouget, and D. Desilets. 1989. Small-scale gradients of phytoplankton productivity in the littoral fringe. *Marine Biology* **100**: 393-399.
- DeNiro, M. J., and S. Epstein. 1978. Influences of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**: 495-506.
- Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* **245**: 170-173.
- Dunton, K. H., and D. M. Schell. 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an Arctic kelp community. *Marine Biology* **93**: 615-625.
- Ehleringer, J. R., P. W. Rundel, and K. A. Nagy. 1986. Stable Isotopes in physiological ecology and food web research. *Trends in Ecology and Evolution* **1**: 42-45.
- Fenchel, T., and T. H. Blackburn. 1979. *Bacteria and mineral cycling*. Academic Press, London.
- Field, J. G., C. L. Griffiths, E. A. Linley, R. A. Carter, and P. Zoutendyk. 1977. Upwelling in the nearshore marine ecosystem and its biological implications. *Estuarine and Coastal Marine Science* **11**: 133-150.
- Field, J. G., P. A. Wickens, and C. L. Moloney. 1986. Modelling studies of material flows in shallow ecosystem compared to the open ocean. Pages 75-97 *in*: P. Lasserre and J. M. Martin, editors. *Biogeochemical Processes and the Land-Sea Boundary*. Elsevier, Amsterdam.
- Fielding, P. J., and C. L. Davis. 1989. Carbon and nitrogen resources available to kelp bed filter feeders in an upwelling environment. *Marine Ecology Progress Series* **55**: 181-189.

- Foale, S., and R. Day. 1992. The recognizability of algae ingested by abalone. *Australian Journal of Marine and freshwater Research* **43**: 131-1358.
- Foster, M.S., A. P. De Vogelaere, C. Harrold, J. S. Pearse and A. B. Thum. 1988. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. *Memoirs of the California Academy of Sciences* Number 9, California Academy of Sciences, San Francisco.
- Fry, B., and E. B. Sherr. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* **27**: 13-47.
- Fry, B. 1991. Stable isotope diagrams of freshwater food webs. *Ecology* **72**: 2293-2297.
- Gearing, J. N. 1991. The study of diet and trophic relationships through natural abundances ^{13}C . Pages 201-218 in D. C. Coleman and B. Fry editors. *Carbon Isotopes Techniques*. Academic Press, New York.
- Harger, J. R. E. 1972. Competitive co-existence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. *Veliger* **14**: 387-410.
- Hayes, J. M. 1982. Fractionation, *et al.*: an introduction to isotopic measurement and technology. *Spectra* **8**: 3-8.
- Johnson, C. R., and K. H. Mann. 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecological Monographs* **58**: 129-154.
- Jørgensen, C. B. 1990. Bivalve Filter Feeding: Hydrodynamics, Bionergetics, Physiology and Ecology. Olsen and Olsen, Fredensborg.
- Kain, J. M. 1979. A view of the genus *Laminaria*. *Oceanography and Marine Biology Annual Review* **17**: 101-161.

- Koop, K. R., R. C. Newell, and M. I. Lucas. 1982. Biodegradation and carbon flow based on kelp (*Ecklonia maxima*) debris in a sandy beach microcosm. *Marine Ecology Progress Series* 7: 315-326.
- Koop, K. R., R. C. Newell, and M. I. Lucas. 1982. Microbial regeneration of nutrients from decomposition of macrophyte debris on the shore. *Marine Ecology Progress Series* 9: 91-96.
- Lewis, J. R. 1964. *The Ecology of the Rocky Shores*. The English University Press Ltd., London.
- Lewis, J. R. 1976. The role of physical and biological factors in the distribution and stability of rocky shore communities. Pages 417-423 *in*: B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden editors. *Biology of Benthic Organisms*. Pergamon Press, New York.
- Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* 48: 67-94.
- Mann, K. H. 1972. Macrophyte production and detritus food chains in coastal waters. *Memorias del Instituto Italiano de Idrobiologia* 29 (supp.): 353-383.
- Mann, K. H. 1982. *Ecology of coastal waters*. Blackwell.
- Mann, K. H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems *Limnology and Oceanography* 33: 910-930.
- Mann, K. H., and J. R. N. Lazier. 1991. *Dynamics of Marine Ecosystems*. Blackwell Scientific Publications, Oxford.
- McConnaughey, T, and C. P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology*. 53: 257-262.

- Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**: 730-757.
- Menge, B. A., and T. M. Farrell. 1989. Community structure and interactions webs in shallow marine hard-bottom communities: test of an environmental stress model. *Advances in Ecological Research* **19**: 189-262.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends in Ecology and Evolution* **5**: 52-67.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Cosmochimica Acta* **48**: 1135-1140.
- Moloney, C. L. 1992. Simulation studies of trophic flows and nutrient cycle in Benguela upwelling foodwebs. *South African Journal of Marine Sciences* **12**: 457-476.
- Monteiro, P. M. S., A. G. James, A. D. Sholto-Douglas, and J. G. Field. 1991. The $\delta^{13}\text{C}$ trophic position isotope spectrum as a tool to define and quantify carbon pathways in marine food webs. *Marine Ecology Progress Series* **78**: 33-40.
- Newell, R. C. 1984. The biological role of detritus in the marine environment. Pages 317-344 in *Flows of energy and materials in marine ecosystems: Theory and practice*. NATO Conference Series 4, Marine Sciences V. **13**. Plenum.
- Newell, R. C., and J. G. Field. 1983. The contribution of bacteria and detritus to carbon and nitrogen flow in a benthic community. *Marine Biology Letters* **4**: 23-36.
- Newell, R. C., M. I. Lucas, B. Velimirov, and L. J. Seiderer. 1980 The quantitative significance of dissolved organic losses following fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). *Marine Ecology Progress Series* **2**: 45-59.

- Newell, R. C., C. L. Moloney, J. G. Field, M. I. Lucas, T. A. Probyn. 1988. Nitrogen models at the community level: plant-animal-microbe interactions. Pages 379-414 in T. H. Blackburn and J. Sorensen, editors. Nitrogen cycling in coastal marine environments. John Wiley and Sons Ltd.
- Nielsen, N. F., P. S. Larsen, H. U. Riisgård, and C. B. Jørgensen. 1993. Fluid motion and particle retention in the gill of *Mytilus edulis*: video recordings and numerical modelling. *Marine Biology* **116**: 61-71.
- Owen, N. J. P. 1987. Natural variations in ^{15}N in the marine environment. *Advances in Marine Biology* **24**: 389-451.
- Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* **100**: 65-75.
- Paine, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* **52**: 1096-1106.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93-120.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscape: disturbance and the dynamics of pattern. *Ecological Monographs* **5**: 145-178.
- Paine, R. T., J. C. Castillo, and J. Cancino. 1985. Perturbation and recovery patterns of starfish dominated intertidal assemblages in Chile, New Zealand, and Washington state. *The American Naturalist* **125**: 679-691.
- Painting, S. J., C. L. Moloney, T. A. Probyn, and B. Tibbles. 1992. Microheterotrophic pathways in the southern Benguela upwelling system. *South African Journal of Marine Sciences* **12**: 527-543.

- Peterson, B. J., and B. Fry. Stable isotopes in ecosystem studies. *Annual Reviews in Ecology and Evolution* **18**: 293-320.
- Peterson, B. J., R. W. Howarth, and R. H. Garrit. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* **227**: 1361-1363.
- Rau, G. H., Mearns, A. J., Young, D. R., Olson, R. J., Schafer, H. A. and Kaplan, I. R. 1983. Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* **64**: 1314-1318.
- Rundel, P. W., J. R. Ehleringer, and K. A. Nagy. 1989. *Stable Isotopes in Ecological Research*. Ecological Studies 68. Springer-Verlag, New York.
- Santelices, B., J. Cancino, S. Montalva, R. Pinto, y E. González. 1977. Estudios ecológicos en la zona costera afectada por contaminación del "Northern Breeze" II. Comunidades de playas de rocas. *Medio Ambiente* **2**: 65-83.
- SAS. 1986. SAS[®] System for linear models, 1986 Edition. SAS Institute Inc., Cary, NC, USA.
- Schiel, D. R., and M. Foster. 1986. The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology Annual Review* **24**: 265-307.
- Sealy, J. C., and N. J. van der Merwe. 1986. Isotopes assessment and the seasonal-mobility hypothesis in the southwestern Cape of South Africa. *Current Anthropology* **27**: 135-150.
- Sealy, J. C., N. J. van der Merwe, J. L. Thorp, and J. L. Lanham. 1987. Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. *Geochimica et Cosmochimica Acta* **51**: 2707-2717.

- Seiderer, L. J., R. C. Newell, and P. A. Cook. 1982. Quantitative significance of style enzymes from two marine mussels (*Choromytilus meridionalis* Krauss and *Perna perna* L.) in relation to diet. *Marine Biology Letters* **3**: 257-271.
- Seiderer, L. J., and R. C. Newell. 1985. Relative significance of phytoplankton, bacteria and plant detritus as carbon and nitrogen resources for the kelp bed filter-feeder *Choromytilus meridionalis*. *Marine Ecology Progress Series* **22**: 127-139.
- Shepherd, S. A., and P. D. Steinberg. 1992. Food preferences of three Australian abalone species with a review of the algal food of abalone. Pages 169-181 in: S. A. Shepherd, M. J. Tegner, and S. Guzmán del Poó, editors. *Abalone of the World: Biology, Fisheries and Culture*. Blackwell Scientific, Oxford.
- Sholto-Douglas, A. D. 1992. The use of stable isotope ratios of carbon and nitrogen to elucidate pelagic marine food webs of the Benguela and Agulhas bank regions of South Africa. M. Sc. thesis, University of Cape Town, Cape Town, South Africa.
- Sholto-Douglas, A. D., Field, J. G., James, A. G., and N. J. van der Merwe. 1991. $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotope ratios in the Southern Benguela Ecosystem : indicators of food web relationships among different size classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. *Marine Ecology Progress Series* **78**: 23-31.
- Siemenstad, C. A., and R. C. Wissmar. 1985. $\delta^{13}\text{C}$ evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. *Marine Ecology Progress Series* **22**: 141-152.
- Siemenstad, C. A., D. O. Duggins, and P. D. Quay. 1993. High turnover of inorganic carbon in kelp habitats as a cause of $\delta^{13}\text{C}$ variability in marine food webs. *Marine Biology* **116**: 147-160.
- Steele, J. H. 1974. *The structure of marine ecosystems*. Blackwell, Oxford.

- Stephenson, R. L., F. C. Tan, and K. H. Mann. 1986. Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and kelp bed in Nova Scotia, Canada. *Marine Ecology Progress Series* **30**: 1-7.
- Stuart, V. 1982. Absorbed ratio, respiratory cost and resultant scope for growth in the mussel *Aulacomya ater* (Molina) fed on a diet of kelp detritus of different ages. *Marine Biology Letters* **3**: 289-306.
- Stuart, V., J. G. Field, and R. C. Newell. 1982. Evidence for absorption of kelp detritus by the ribbed mussel *Aulacomya ater* using a new ^{51}Cr -labelled microsphere technique. *Marine Ecology Progress Series* **9**: 263-271.
- Suchanek, H. T., S. L. Williams, J. C. Ogden, D. K. Hubbard, and I. P. Gill. 1985. Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauna: $\delta^{13}\text{C}$ evidence. *Deep Sea Research* **32**: 201-214.
- Tarr, R. J. Q. 1989. Abalone. Pages 62-69 in A. I. L. Payne and R. J. M. Crawford, editors. *Oceans of life*. Vlaeberg Publishers, Cape Town, South Africa.
- Thingstad, T. F., M. Heldal, G. Bratbak, and I. Dundas. 1993. Are viruses important in pelagic food webs? *Trends in Ecology and Evolution* **8**: 209-213.
- Thresher, R. E., P. D. Nichols, and J. S. Gunn. 1992. Seagrass detritus as the basis of a coastal planktonic food chain. *Limnology and Oceanography* **37**: 1154-1158.
- Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1984. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* **57**: 32-37.
- Velimirov, B., J. G. Field, C. L. Griffiths, and P. Zoutendyk. 1977. The ecology of kelp bed communities in the Benguela upwelling system. Analysis of biomass and spatial distribution. *Helgoländer Wissenschaftliche Meeresuntersuchungen* **30**: 495-518.

- Wallentinus, I. 1991. The Baltic sea gradient. 83-108 in A. C. Mathieson and P. H. Nienhuis editors. Ecosystems of the World 24. Intertidal and littoral Ecosystems. Elsevier, Amsterdam.
- Wells, F., and J. Keesing. 1989. Reproduction and feeding in *Haliotis roei* (Gray). Australian Journal of Marine and freshwater Research **40**: 187-197.
- Wickens, P. A., and J. G. Field. 1986. The effects of water transport on nitrogen flow through a kelp-bed community. South African Journal of Marine Sciences **4**: 79-92.
- Wiencke, C., and G. Fisher. 1990. Growth and stable carbon isotope composition of cold-water macroalgae in relation to light and temperature. Marine Ecology Progress Series **65**: 283-292.
- Witman, J. D. 1988. Stability of Atlantic kelp forests. Trends in Ecology and Evolution **3**: 285-286.
- Wulff, F. V., and J. G. Field. 1983. Importance of different trophic pathways in nearshore benthic community under upwelling and downwelling conditions. Marine Ecology Progress Series **12**: 217-228.

Chapter 5

*Maintenance of an Exceptional Grazer Biomass on South African Intertidal
Shores: Trophic Subsidy by Subtidal Kelps*

Summary: Dense populations of patellid limpets characterize the mid to low intertidal communities of the southwestern rocky shores of South Africa. The patellid limpets *Patella argenvillei* and *P. granatina* reach average densities up to $200 \cdot \text{m}^{-2}$, representing in some cases *ca.* $10\text{-}13 \text{ kg} \cdot \text{m}^{-2}$ whole wet biomass, and attain sizes up to 100 mm shell length. Traditionally these limpets have been regarded as generalized grazers, but they in fact have highly specialized feeding mechanisms. *P. granatina* is found primarily on the mid-to-low shore of sheltered boulder-bays, while *P. argenvillei* forms a conspicuous monospecific 'belt' low on semi-exposed shores in association with adjacent kelp beds. Both species are space dominants in their respective habitats. I have investigated the main pathways and supply of food necessary to maintain these high limpet biomasses. Intertidal epilithic micro- and macroalgae and the kelps *Ecklonia maxima* and *Laminaria pallida* are common sources of food for these two limpets. Gut contents show that kelp represents $>50\%$ of the total diet of both limpet species. An abundant source of food is provided to *P. granatina* by drifting kelp and seaweed debris, and to *P. argenvillei* by nearby attached kelp plants which they actively prune. Differences in the timing and method of feeding exist. *P. granatina* captures drifting kelp and seaweeds while underwater during incoming and outgoing tides, while *P. argenvillei* prunes the fronds of nearby attached kelp plants during the rising tide. *P. argenvillei* feeds collectively, several individuals sharing a piece of kelp trapped by a single limpet. This overcomes the intraspecific competition normally experienced in high density limpet populations. *P. granatina* does not feed collectively and its maximum size declines with density. When the limpets were experimentally deprived of kelp they suffered a significant increase mortality and a reduction in body mass. Subtidal production of kelp fronds subsidizes both limpet populations and is vital for the maintenance of the remarkably high limpet biomass. Supplied with a super-abundance of food, both species achieve such high 'packing' that primary space becomes their limiting factor. This Chapter explore the trophic linkage between subtidal and intertidal systems, as well as the impact of a subsidized food web on the structure and functioning of the rocky-shore intertidal community.

Introduction

Interactions between grazers and plants are of major importance in many marine benthic food webs (see reviews by Lubchenco and Gaines 1981; Branch 1981; Hawkins and Hartnoll 1983). Within trophic animal-plant interactions, a wide range of relationships exist: from generalized epilithic grazers, which control algal vegetation at the sporeling stage, to epiphytic grazers that have less influence on the composition and abundance of the plants (Creese 1980; Branch 1981; Hawkins and Hartnoll 1983; Beovich and Quinn 1992). Specific limpet-kelp interactions have been described in many parts of the world, with special reference to the regulation of the abundance and distribution of either the algal or limpet species (Graham and Fretter 1947; Vahl 1971; Bishop and Bishop 1973; Black 1976; Choat and Black 1979; Branch 1975a, 1985; Muñoz and Santelices 1989).

A high diversity of limpets occurs on the shores of South Africa, with up to 14 species of patellids coexisting (Branch 1971; 1975a). Many of these species are both large and occur in dense populations that achieve extraordinary biomass per unit area. How such high biomasses of grazers can be maintained in the face of an apparently limited source of food is poorly understood. Some of the species are territorial and act as "gardeners" in the sense that they promote the productivity of specific algae with which they are associated (Branch 1971; 1975a, 1981, 1984). Gardening is thus one possible mechanism that allows limpets to maintain high biomasses and reduce intraspecific competition. Branch *et al.* (1992) hypothesized that gardening is more likely to be found in regions where productivity is low relative to the grazers' demands. The west coast of South Africa is a clear example of a highly productive marine system (Shannon 1985; Bosman *et al.* 1987). In the intertidal communities of this system, grazers represent an important guild, which includes nine species of patellid limpets. Of these, only a single species exhibits gardening behavior, i.e. *Patella cochlear* Born, and it attains high

biomasses of up to 125 g m⁻² wet flesh weight (Branch 1975b). However, in terms of biomass, densities, and individual size, the most important grazers on the west coast of southern Africa are *P. granatina* Linn. and *P. argenvillei* Krauss (Eekhout *et al.* 1992), neither of which is territorial or acts as a gardener. Their populations reach biomasses greater than any intertidal invertebrate grazer elsewhere in the world. The question thus remains - how do these two species of limpets manage to maintain such high population densities and biomasses? Is the *in-situ* intertidal productivity enough to maintain these populations, or do they rely on other sources of food that might be regarded as unorthodox for a grazing limpet? As was qualitatively demonstrated in Chapter 4, kelp-derived organic carbon and nitrogen is found throughout the intertidal food web. The aim of this Chapter is to explore with empirical data an apparently strong trophic interactions between these limpets and subtidal kelp which, together with a study of their feeding behavior, may explain their extraordinary abundance.

My approach to this problem follows the basic hypothesis that an input of subtidal kelp into the intertidal zone provides a vital component of the limpets' diets, permitting the maintenance of high biomasses. Specifically, I examine (a) geographic distribution and local zonation for correlations between these two limpet species and kelp species, (b) the feeding behaviour of the limpets, (c) the effects of excluding kelp from the limpets' diets, and (d) the implications of the trophic linkage between subtidal kelp production and intertidal limpets.

The findings of this Chapter have broader significance than the specific interaction examined, for they relate to three issues of current general ecological interest. Firstly, the work casts light on food web theory (Fretwell 1987) and its recently deconstruction (Paine 1988), particularly on whether grazers are controlled by bottom-up factors (food supply) rather than top-down factors (enemies) (Paine 1988; Carpenter *et al.* 1985; Power 1992). Second, it addresses linkages between systems, specifically the degree to which the intertidal zone can be subsidized by input from the subtidal zone. In the present case, this raises a related issue of whether such subsidies can lead to a situation whether

the grazers are not restricted by food supply, but by space alone-- a limitation not normally associated with grazers (Branch 1984). Finally, the results allow exploration of the interesting possibility that high densities may sometimes be beneficial for the procurement of food by grazers, an outcome that is counterintuitive, given that intraspecific competition for food is frequently associated with increases in grazer densities (Underwood 1976; 1978, Ebert 1977; Branch 1975b; Branch and Branch 1981; Creese 1980; Branch 1984).

Materials and Methods

Study site and species

The study was carried out at several localities, particularly in the Namaqualand region of the west coast of southern Africa (Fig. 1). Extensive subtidal kelp forests are present along the coast, and extend up to the level of low water spring tides, where they end abruptly, often abutting on dense stands of the limpet *P. argenvillei* (see Fig. 6A). These forests are formed by the kelps *Ecklonia maxima* (Osbeck) and *Laminaria pallida* Grev (M. L. Branch 1974; Field *et al.* 1980).

Rocky shores on the west coast are subject to a wide range of wave exposures. As was described in Chapter 2, Palumbi's wave force device (Palumbi 1984) was used to measure maximum drag force, and three habitats were distinguished: a) *sheltered boulder-bays*, characterized by forces below 1000 N m^{-2} ; b) *semi-exposed rocky shores*, mostly in the lee of kelp beds, with drag forces from 1000 to *ca.* 8000 N m^{-2} ; and c) *exposed rocky shores*, on which forces between 8000 and 16000 N m^{-2} are common. The limpets *P. granatina* and *P. argenvillei* are the dominant grazers in mid to low regions of intertidal at sheltered and semi-exposed rocky shores respectively (see Table 1 in Chapter 2). The abundance of these two species is, however, low on exposed rocky shores where filter-feeders (mainly mussels, see Table 1 in Chapter 1) are the space dominants, so this habitat is not considered further.

Distribution, abundance and sizes of limpets:

The geographic range and a quantitative estimate of abundance for both limpets and kelp were obtained either from the literature (M. L. Branch 1974; Kensley and Penrith 1980) or from our own surveys. The main populations for both limpet species are concentrated in an area between Tweepad and the Olifants River (see Fig. 1), where an aerial survey was conducted by helicopter, during spring low tide on two consecutive

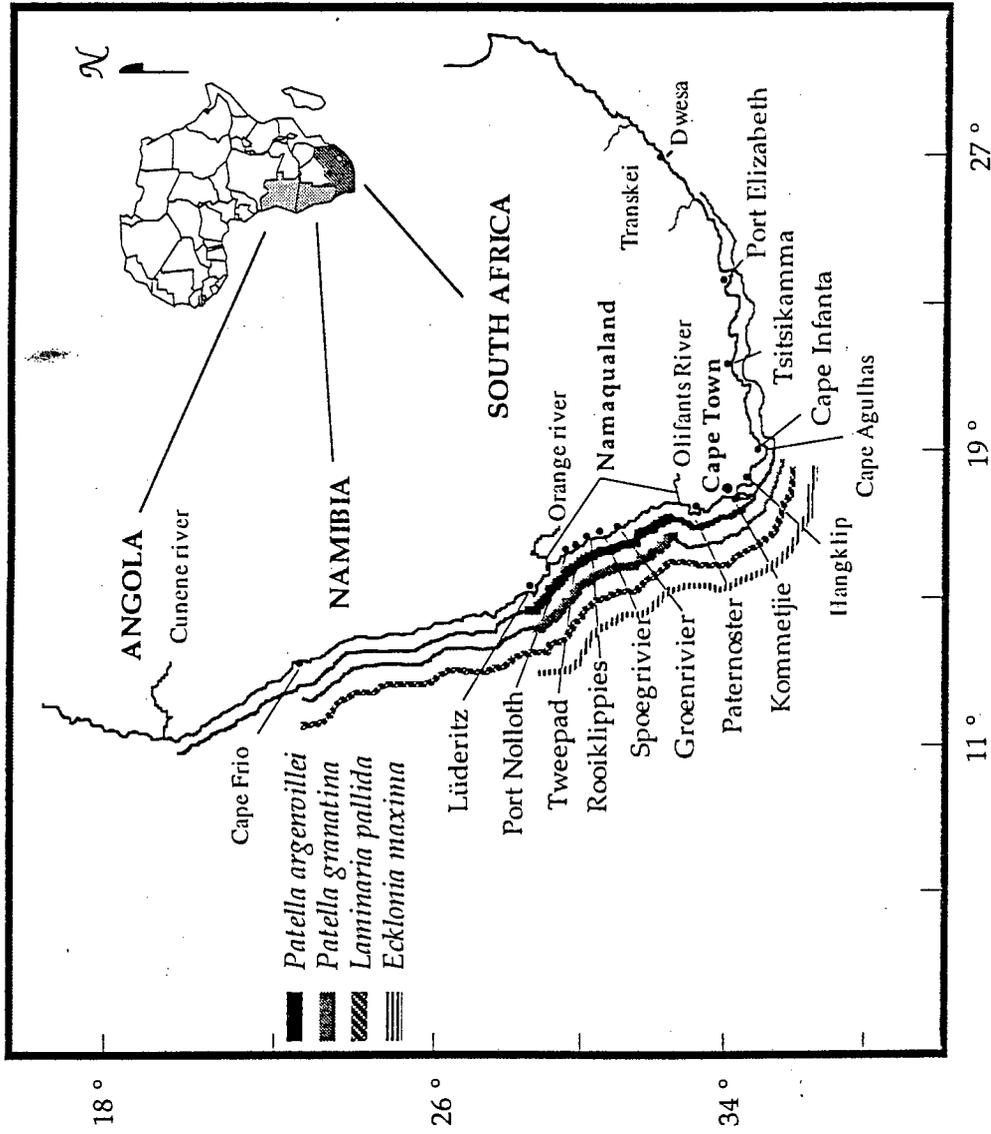


Figure 1. Map of southern Africa naming the study sites mentioned in the text. Shaded lines indicate the geographical distributions of the limpets *E. maxima* and *L. pallida* and the limpets *P. argenvillei* and *P. granatina*, and the width of these lines is an indication of their relative abundance

days in January 1987. A total of 1500 photographs was taken over about 300 km of coastline (from Tweepad to Olifant River, Fig. 1). Flying at a height of 3-10 m, it was possible to identify the limpet species accurately down to a size of 30 mm. Both limpet species form monospecific stands on the mid- to low-shore (see Figs 6A, C, E and F), which aided our aerial identification of species. I verified that the aerial identification of the two limpets was correct in all cases by undertaking intertidal ground-truth transects between Rooiklippies and the Olifant River (Fig. 1). The relative abundance of limpets in each of 100 randomly selected aerial photographs was quantified as the percentage cover of monospecific stands ('belts') of limpets within the zones that can potentially be occupied by the two species (i.e. mid to low shores only). For both limpets were defined as 'high density' between 30 and 250 · m⁻², and 'moderate density' between 10 and 30 · m⁻². For the same 100 aerial pictures, a 4-level kelp-abundance ranking was developed, according to the abundance and accessibility of attached plants to each of the limpets: 0=absent 1=present, 2=abundant but not all accessible ('accessible' being defined as attached plants which were within the reach of the limpets), and 3=abundant and accessible. Spearman rank correlation coefficient between the ranked scores of the kelp and the percentage cover of limpets was performed with the data obtained from the 100 randomly chosen aerial pictures.

The accumulation of drift kelp (both *E. maxima* and *L. pallida*) was measured monthly, over a 21 month period, at sheltered and semi-exposed shores at Rooiklippies and Groenrivier (Fig. 1). Three permanent transects, each 36 m long were set parallel to the shoreline in the low- and mid-intertidal zones. Along each transect, 0.5 m² quadrats were placed every 3 m apart (n=12), and the density of *P. granatina* and the wet mass of drift kelp accumulating each tidal cycle were recorded. The coast experiences a semi-diurnal tidal cycle, so that drift kelp can be deposited twice a day; during each high tide the drift is re-suspended and re-distributed.

The density, biomass and shell lengths of both limpet species were determined at 12 localities between Lüderitz and Port Elizabeth, thus covering most of their geographical

range (Fig. 1). At each site the distribution and abundance data were derived from eight transects running perpendicular to the coastline from MLWS (Mean Low Water Springs tide), to the upper end of the zonation of the limpets. The transects were placed at regular intervals (*ca.* 30 m apart) at sheltered and semi-exposed habitats and their lengths varied from 30 to 60 m, depending on the slope of the shore ($> 15^\circ$ and $< 45^\circ$). Between six and ten quadrats of 0.5 m^2 were placed along each transect, and shore height in relation to MLWS, and limpet densities (number per m^{-2}), wet mass, and shell lengths were recorded. Limpet biomass was obtained directly by removing all limpets from the sampled quadrats and measuring their wet whole mass and their wet flesh mass. For both limpet species, significant differences existed in biomass between transects at different grades of wave action (semi-exposed versus sheltered), and between different sites (Kruskall-Wallis $F_{(6,2)}=152.86$; $p<0.05$), but within sites and grades of wave exposure, no significant differences existed (Kruskall-Wallis $F_{(6,2)}=4.78$; $p>0.05$). As a result, the data for semi-exposed and sheltered transects were separately averaged for each site. I compare these data (densities, mass and sizes) with published figures and unpublished data gathered by GM Branch for other limpet species elsewhere in the world. I include all comparable data available to me.

Feeding behaviour and activity rhythms

Limpet feeding behaviour was observed at Groenrivier and Rooiklippies over a tidal cycle. Direct observations were made during low tide when the limpets were exposed, and by SCUBA diving during high tide. The activity of animals was quantified hourly within 0.25 m^2 quadrats placed at random in areas where there was a high density of each limpet species. Shell lengths, numbers of limpets elevating their shells off the substratum, numbers trapping kelp beneath their shells, numbers sharing a piece of kelp, and the wet mass of each piece of trapped kelp were recorded.

Limpet *activity* was considered as the proportion of individuals lifting their shell up or 'mushrooming'. *Success* was defined as the proportion of limpets holding down a piece of drift kelp or pinning down a frond of a nearby attached kelp plant. The feeding activity

of both limpet species was monitored during spring tidal cycles. In the semi-exposed and sheltered habitats respectively, 107 *P. argenvillei* (all > 40 mm shell length) and 70 *P. granatina* (all > 50 mm) were individually tagged using rapid setting epoxy glue, in four randomly located plots within the high density limpet belts, positioned at least 3 m apart. Every 0.5 h, starting 1.5 h before MLWS and ending at high tide (7.5 h later), I recorded the proportions of active, resting (shell down), and successful limpets.

Gut contents

In both sheltered and semi-exposed habitats approximately 50 individuals of each species with shell lengths greater than 40 mm were collected along their full intertidal range. Stomachs were dissected and the contents removed using forceps, identified under stereoscopic microscope, and dry weighed. Gut contents were classified into four food items, according to coloration and texture; viz. *kelp*, *ephemeral greens*, *fleshy reds*, and *calcareous* (this item includes mainly encrusting corallines and traces of sand and shell remains). These four categories included a variety of intertidal seaweed species, but for this work, I concentrated on the importance of the kelp species in the limpets' diets. The kelp category included both kelp species available to the limpets (*L. pallida* and *E. maxima*). Other brown seaweeds present in the intertidal are rarely found in the limpet beds. Diatoms were seldom detectable in the gut contents and were not quantified. The analysis of intertidal water described in Chapter 4 indicates that also planktonic diatoms are seldom common and often absent.

Exclusion experiments

The importance of kelp as a food item for both limpet species was experimentally tested as described below. However, differences in feeding behavior, food supply and the relative survival of the two species after transplantation forced us to use different experimental designs for the two species (Fig. 2).

The effects of an absence of drift kelp on the survival of *P. granatina* was tested in cages under constant natural density (averaging 35 ± 3 limpets per cage). Five cages (0.5 x

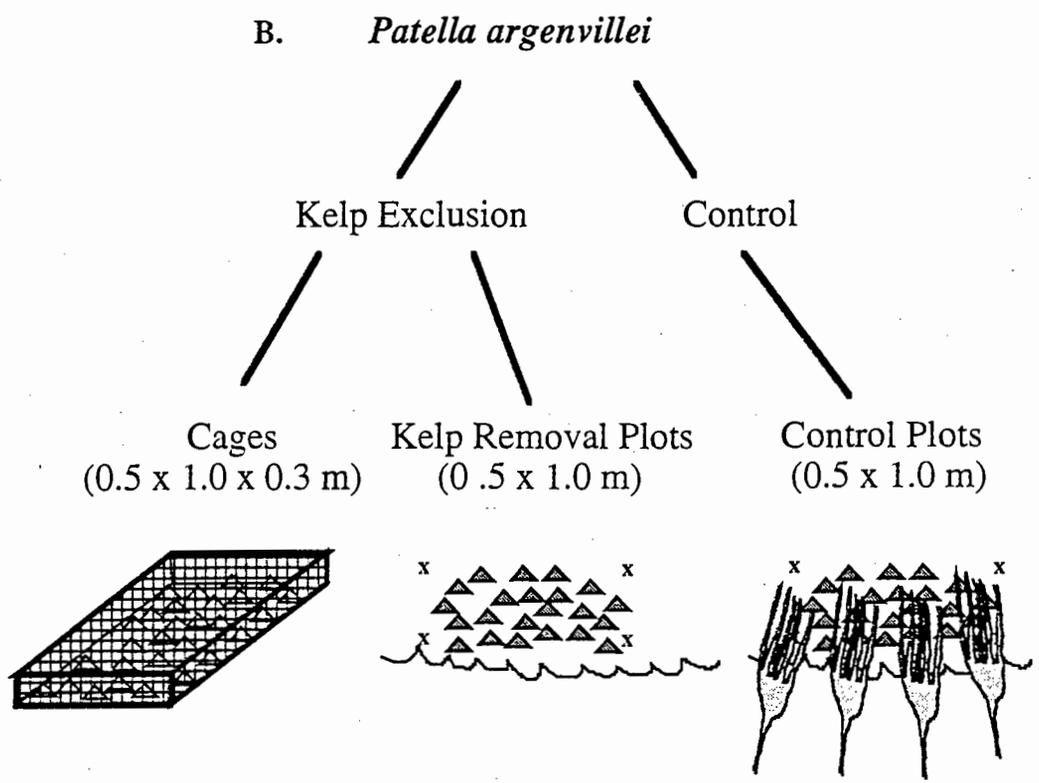
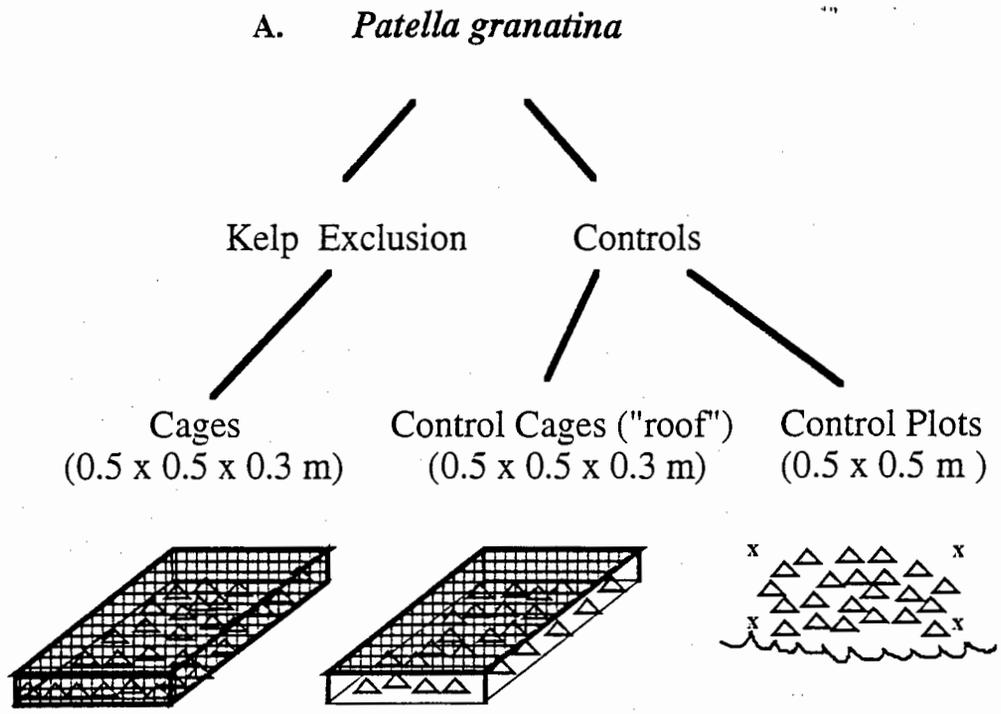


Figure 2. Diagrams showing the layout of the two kelp exclusion experiments. (A.) *Patella granatina*. (B.) *Patella argenvillei*.

0.5 x 0.3 m), with enclosed sides and a roof covered with metallic mesh (mesh size 2.0 cm), were used to enclose limpets and exclude drift kelp (Fig. 2A). All cages were placed at Rooiklippijs (Fig 1) in five randomly situated areas within the mid-low intertidal zone normally occupied by this limpet. Individuals of *P. granatina* were removed from adjacent rocks and translocated to the cages. Translocation had no deleterious effects on limpets, which survived for at least 2.5 years after the experiment was terminated.

Several potential confounding effects ('artifacts') induced by the use of cages/enclosures have been reported in the literature (e.g. Hayworth and Quinn 1990; Quinn and Keough 1993). By using cage controls, I controlled for the potential side-effects of caging on *in-situ* primary production, temperature, limpet movements and survival. For this purpose, five roofed cage controls (0.5 x 0.5 x 0.3 m), with open sides and a metallic mesh 'roof' were employed. These allowed potential limpet movements and permitted drift kelp to enter, but shaded the plots in a manner comparable to the exclusion cages (see Fig. 2A). Measurements of relative primary production were made by measuring the monthly growth of microalgae on six 25 cm² roughened acrylic plates per plot. No significant difference in the average chlorophyll-*a* level per plot existed between any of the treatments (ANOVA, $p > 0.05$). The mesh used for the exclusion and control cages only reduce 1-5% of photosynthetic active radiation (PAR). Similarly, no significant differences in substrate temperatures were detected between the treatments (ANOVA, $p > 0.05$). Thus, differences in primary production caused by shading or temperature are unlikely to have confounded the experimental results. *P. granatina* is relatively sedentary when it occurs at high densities: only 3% of the labeled experimental limpets moved out of the open cage controls and control plots in spite of the fact that their movements were not constrained.

Five plots (0.5 x 0.5 m) containing uncaged translocated *P. granatina* were used as controls. All limpets in exclusion cages, cage controls, and control plots were tagged with epoxy putty. Any limpets which died during the course of the experiment were replaced by distinctively tagged live ones of similar size taken from the areas immediately

adjacent to the experimental plots. Over the entire experimental period, tag loss was recorded for only four individuals from a total of 525 tagged limpets. Survival and dry body masses at the end of the experiment were recorded for each of the treatments, based only on the limpets originally included in the plots and cages at the start of the experiment. Initial body masses were measured for limpets in areas adjacent to controls and experimental plots.

High mortality of *P. argenvillei* (almost 100%) occurs when individuals are detached. This constrained transplantation and replacement of individuals. Experiments on this species were therefore done without replacement of dead individuals. The kelp exclusion experiment (Fig. 2B) was done using five cages (1.0 x 0.5 x 0.3 m) covered with metallic mesh (mesh size of 4.0 cm). Such cages were placed over naturally dense limpet stands (averaging 53 ± 13 per plot). Five plots (1.0 x 0.5 m) with uncaged limpets were used as controls. Cage controls (roof only) were attempted. However, the fronds of nearby attached kelp plants became massively entangled on the frame of the open cage control. This situation precluded the use of such cage controls. Instead, an additional method of excluding kelp was used, which did not make use of cages. In an area of ca. 10 m^2 around each of five plots (1.0 x 0.5 m) all live kelp plants were removed to deny the limpets access to attached kelp (Fig 2B). All individual limpets in the three treatments were tagged. The cages, kelp removal and control plots were randomly situated within the limpets' belt. The exclusion experiments were monitored four times during a six month period (at 0, 31, 96, and 160 days). On each occasion a census was taken and initial and final body masses were recorded for each treatment as outlined above for *P. granatina*. Using the protocol described above, measurements of the relative *in-situ* primary production and substratum temperatures were made for each plot, and failed to reveal any significant differences between the treatments (ANOVA, $p > 0.05$). None of the 507 tagged *P. argenvillei* moved out of the open control or kelp removal plots, being restricted by the presence of surrounding high-density conspecifics. No tag loss was experienced.

Results

Distribution and abundance

The limpet *P. argenvillei* has a wide geographical distribution, from the Cunene River in the west, to Transkei in the east, while *P. granatina* is constrained to a narrower range, from Cape Frio in the west to Cape Infanta in the south (Fig. 1). For both limpet species, the area of maximum abundance lies between Lüderitz and the Olifants River i.e. Namaqualand (GM Branch, unpubl. data). The geographical distribution of *P. granatina* is coupled with that of kelp, in particular *L. pallida*. *P. argenvillei* extends north and east of the range of the kelps, but dense populations only occur in areas where kelp occurs.

The relative abundance of limpets in Namaqualand (percentage of the substratum covered by dense monospecific stands of limpets) in relation to the ranked abundance of kelp (as estimated from 100 intertidal aerial pictures), is depicted in Figure 3. *P. granatina* shows a negative correlation (Spearman rank $r_s = -0.67$; $p < 0.0001$) with the abundance of attached kelp. In aerial pictures, sheltered boulder-bays supported the densest stands and greatest cover of *P. granatina* but appeared devoid of live kelp. *P. granatina* had no direct access to living kelp, but drift kelp frequently accumulated in these bays in large quantities (up to 12 kg wet mass m^{-2} ; see Fig. 4). In contrast, *P. argenvillei* density was strongly correlated with the presence of attached kelp (Spearman rank $r_s = 0.78$; $p < 0.0001$) in semi-exposed habitats (Fig. 3).

A positive asymptotic relationship was found between the density of *P. granatina* and the biomass of drift kelp (Fig. 4). This relationship was significant at sheltered shores, where the most of the drift kelp was deposited each tide, whereas at semi-exposed shores the relationship was non-existent and very little drift settled (Fig. 4).

The maximum values of size, density, and whole wet biomass achieved by the two limpet species between Port Elizabeth and Lüderitz are listed in Table 1. *P. granatina*

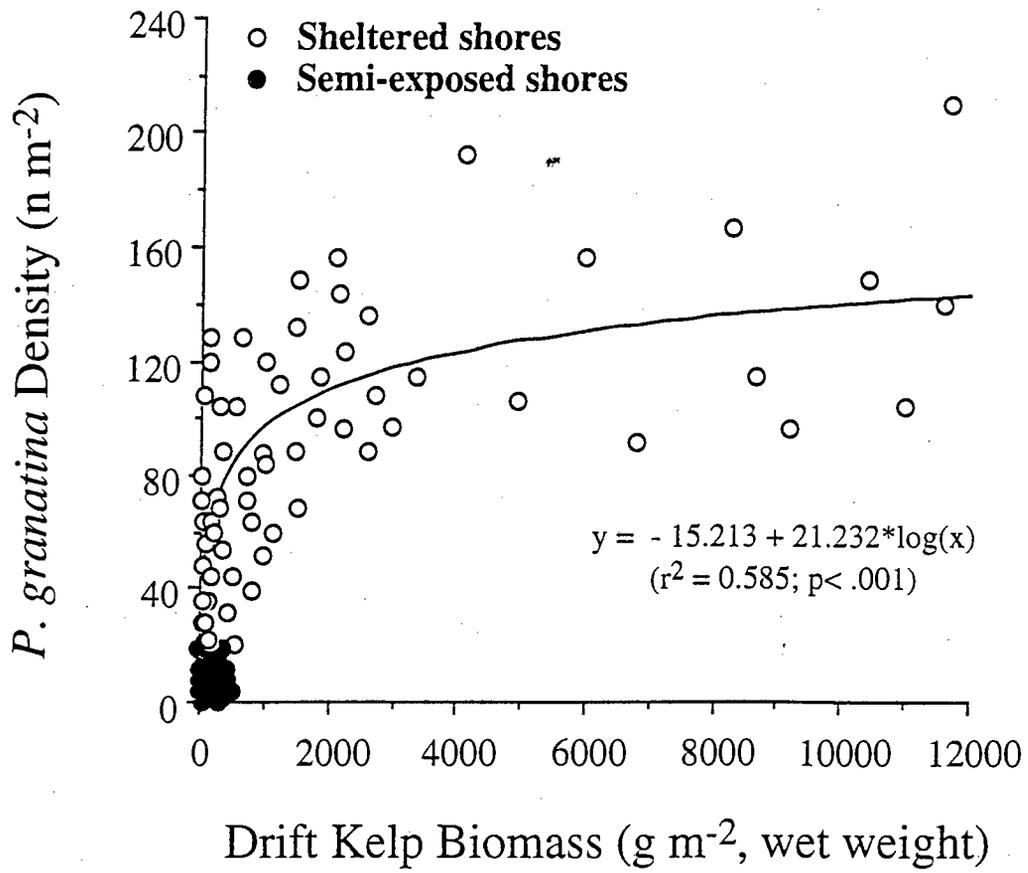


Figure 4. Relationship between the wet biomass of drift kelp and *P. granatina* density at both sheltered shores (open circles), and semi-exposed shores (solid circles).

populations were found at only 9 of the 12 sampled sites (i.e. from Cape Infanta to Lüderitz, see Fig. 1), and maximum sizes and biomass values were achieved in central Namaqualand (see Fig. 1), where up to 91 mm shell length and $7788 \text{ g} \cdot \text{m}^{-2}$ were recorded. Density increased progressively from south to north, from 10.0 up to $288 \cdot \text{m}^{-2}$ (Table 1).

The populations of *P. argenvillei* showed a clear unimodal distribution pattern along the coast, with maximum peak of density ($338 \cdot \text{m}^{-2}$) and biomass ($13110 \cdot \text{m}^{-2}$) in the Namaqualand region (see Fig. 1), whereas further south-east and north their abundance decreased (Table 1). At Port Elizabeth, Tsitsikamma and Cape Infanta (where kelps are absent) and at Lüderitz, where kelps begin to decline, *P. argenvillei* achieved only low maximum values of size, biomass and density.

A marked spatial segregation existed between the two limpet species. Figure 5 depicts their average (± 1 SD) density in relation to height above MLWS on sheltered and semi-exposed rocky shores in Namaqualand. Populations of *P. granatina* were primarily found between the low- and mid-shore of sheltered boulder-bays (Fig. 5), reaching a peak in average density of $180 \cdot \text{m}^{-2}$. Individuals were found up to 80 cm above MLWS (in the mid intertidal), but only at low densities of *ca.* $10 \cdot \text{m}^{-2}$. By contrast, very few individuals of *P. granatina* were found in semi-exposed habitats, even on the low shore (about 3 to $10 \cdot \text{m}^{-2}$). Higher on semi-exposed shores (>0.75 m above MLWS) *P. granatina* was confined to sheltered gullies and tidal pools, but still at relatively low densities ($< 10 \cdot \text{m}^{-2}$).

Semi-exposed habitats were dominated by *P. argenvillei* which reached at an average densities as high as $200 \cdot \text{m}^{-2}$ low on the shore (Fig. 6C). In sheltered habitats *P. argenvillei* was rare and confined to the very low shore.

In summary, the geographic range of *P. granatina* did not extend beyond that of kelp forests, and *P. argenvillei* achieved its maximum size, density and biomass in the region where dense kelp beds are present (Table 1). On a local scale, both limpets had similar

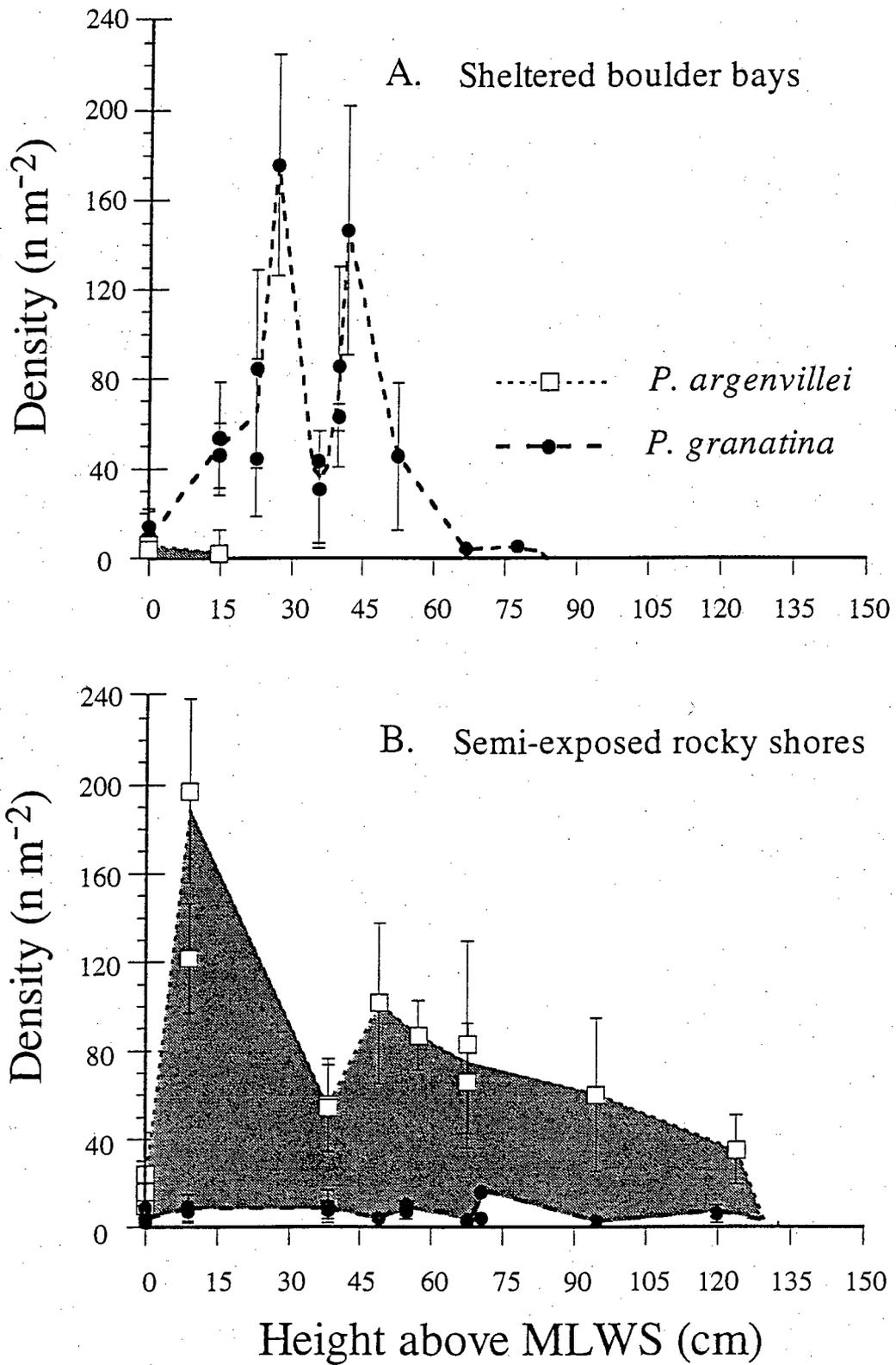


Figure 5. Average (± 1 SD) limpet density in relation to shore height at three west coast localities (Kommetjie, Groenrivier and Tweepad) in (A.) sheltered and (B.) semi-exposed habitats. The trend lines were fitted with a weighted least squares error and 50% smoothing through the data

zonation patterns. However, *P. argenvillei* was most common at semi-exposed sites where attached kelp was abundant and accessible to the limpet, whereas *P. granatina* predominated in sheltered boulder-bays where attached kelp was absent but drift kelp deposited.

Feeding behavior

Both *P. granatina* and *P. argenvillei* graze epilithically on sporelings and diatoms (Branch 1971) but also have the capacity to feed on kelp, although the two species employ different mechanisms to do so. *Patella argenvillei* reaches its greatest densities low on semi-exposed shores adjacent to the kelp beds, a habitat it often dominates, forming an almost monospecific belt (Fig. 6A). In these situations it traps fronds of attached kelp during the low-tide period. The shell is lifted up from the substratum (Fig. 6B) and once fronds of nearby kelp plants are washed under the shell, touching the foot of the limpet, the animal responds immediately with a quick downwards movement (about 1 to 2 sec.) and firmly pins down the kelp frond. The shell has a sharply serrated edge, forming numerous teeth which help maintain purchase on the blade (Fig. 6G). The combined effect of the serrated shell and wave movement may then break the trapped frond off, leaving the animal with a piece of kelp that normally varies from 5 to 150 g wet mass. Consumption starts immediately after kelp is trapped.

In the sheltered bays where *P. granatina* occurs at high density (Fig. 6C) it 'catches' drift kelp underwater during incoming tides, which bring large quantities of drift kelp into these bays. It lifts its shell and the front of the foot, splaying the anterior lobes of the foot, which secrete abundant mucus making them very 'sticky' (Fig. 6D), and waits until drifting kelp sticks to the foot. Limpets with trapped pieces hold their kelp fragments with their foot and consumption starts while the shell is still elevated. The edge of the shell is smooth and lacks any serration or structures resembling teeth (Fig. 6G). When downward shell movement does occur it happens slowly, over 15 - 20 sec.

P. granatina and *P. argenvillei* are large limpets, attaining shell lengths close to 100 mm. Both only begin to actively trap kelp when they reached 40 mm. Above this size, the proportion of animal trapping kelp increases with shell length and all individuals > 85 mm feed in this manner (Fig. 7). In the case of *P. granatina* 30% of the entire population or 52% of animals > 50 mm trap drift kelp during each tidal cycle. About 33% of all *P. argenvillei*, or 62% of those > 50 mm, trap fronds of attached kelp each low tide.

For *P. argenvillei*, a significant positive linear relationship ($r^2=0.81$; $p<0.0001$) was found between the wet mass of a kelp fragment trapped by a limpet, and the number of limpets feeding on each piece (Fig. 8). Once an individual limpet trapped a large piece of kelp frond, the surrounding limpets were then able to feed on the same piece. This relationship can be interpreted as 'sharing' or collective feeding. Contrary to this, *P. granatina* shows no significant relationship ($r^2=0.03$; $p>0.5$). It appears that the capture of drift kelp most often occurs individually in this species; the number of limpets feeding on a single piece of kelp was usually one or two and was independent of the mass of the kelp fragment (Fig. 8).

Activity rhythms

The proportions of limpets raising their shells or catching kelp during a 7.5 h diurnal period are shown in Figure 9. An hour before low tide no more than 5% of the monitored *P. argenvillei* were active, with a success rate of no more than 1%. Activity rose sharply with the incoming tide. Between 2.0 and 2.5 h after low tide, 33% of the limpets were active and success was about 12%. Once the *P. argenvillei* population was completely covered by the inflowing tide (4.5 h after low tide), activity and success decreased to 5% and 0% respectively.

In the case of *P. granatina*, no activity was recorded for the first 3.0 h of observation (until 1.5 h after low tide), but as soon as the limpets were covered by the incoming tide, activity rose steadily to 58%, with a maximum success of ca. 45%. Over a period of 1.5

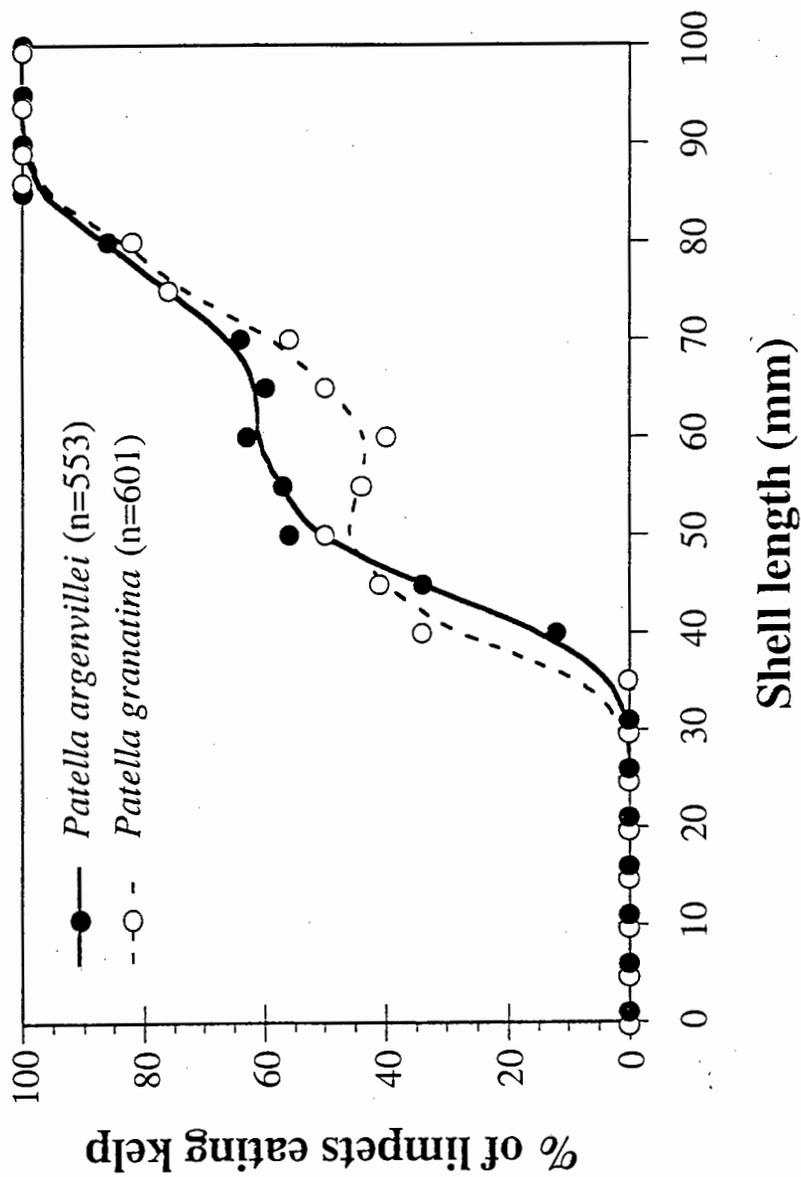


Figure 7. Relationship between limpet size and the percentage of limpets eating kelp. Data was obtained from 30 quadrats of 0.25 m² randomly chosen on the limpet beds. The trend lines were fitted with a weighted least squares error and 50% smoothing through the data.

to 2.0 h before high tide virtually every individual was active or had successfully trapped kelp. Thereafter, a drastic decrease in activity and success was observed.

Gut contents

The gut analyses for both *P. granatina* and *P. argenvillei* included only individuals greater than 40 mm (Fig. 10). These analyses show that kelp represented the largest component in the overall diet, contributing 50.1% and 54.3% of the total diet for *P. granatina* and *P. argenvillei* respectively. Ephemeral greens, red algae and calcareous items were also significant for *P. argenvillei*. The remainder of the diet of *P. granatina* was made up largely of ephemeral green algae (42.1%), while red algae and calcareous items together comprised <3% of the diet. Neither species ingested detectable amounts of epilithic diatoms. The amount of food material extracted from *P. argenvillei* stomachs was twice that from *P. granatina*, averaging 0.367 ± 0.06 g (dry mass per limpet) as compared to 0.175 ± 0.08 g for *P. granatina* (Fig. 10).

Kelp exclusion

The percentages of limpets surviving in controls or in treatments where they were denied access to kelp is shown in Figures 11A and 11B. Without access to kelp, both limpet species experienced significantly lower survival rates, whether their density was held constant (*P. granatina*) or allowed to decline as mortality occurred (*P. argenvillei*). In the latter case this result is conservative, because mortality would probably have been even higher if the density had been held constantly high.

In the *P. granatina* experiment, exclusion of drift kelp by cages resulted in significant decreases in limpet survival compared with control plots and cage controls ($F = 12.59$, $df_{(12, 92)}$; $p < 0.0001$). In the cages, only 40% of the initial population survived after 170 days. A significantly higher mortality relative to both limpet controls (Tukey's *t*-test, $p < 0.05$), was found from 45 days onwards after initiation of kelp exclusion (Fig. 11A). On the other hand, in both control treatments (plots and roofs), *P. granatina* showed a

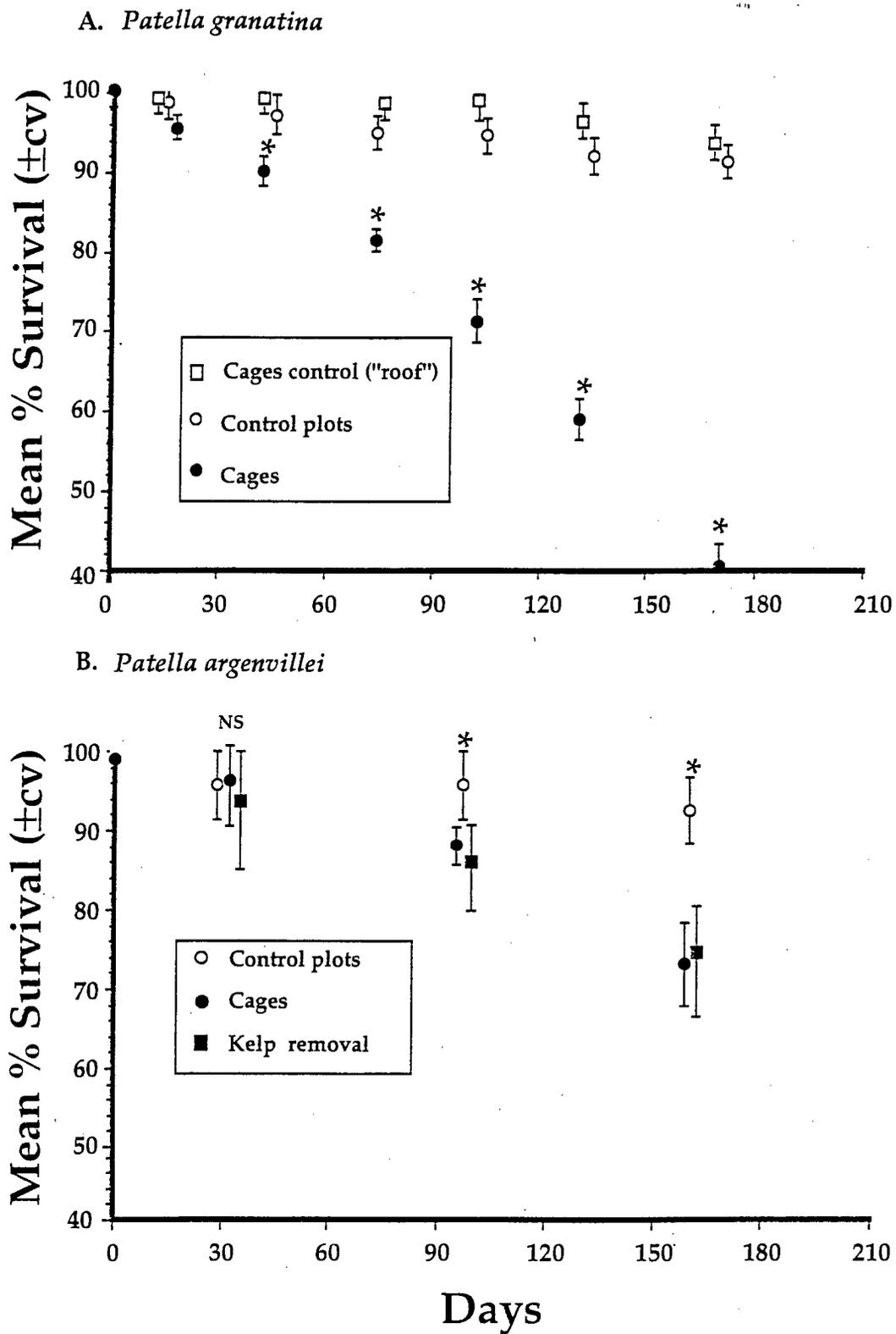


Figure 11. Mean (\pm 1 S.D) survivorship of limpets during the kelp exclusion experiments: (A) *P. granatina*, and (B) *P. argenvillei*. Asterisks indicates dates on which treatments differed significantly from controls (Tukey *t*-test, $p < 0.05$).

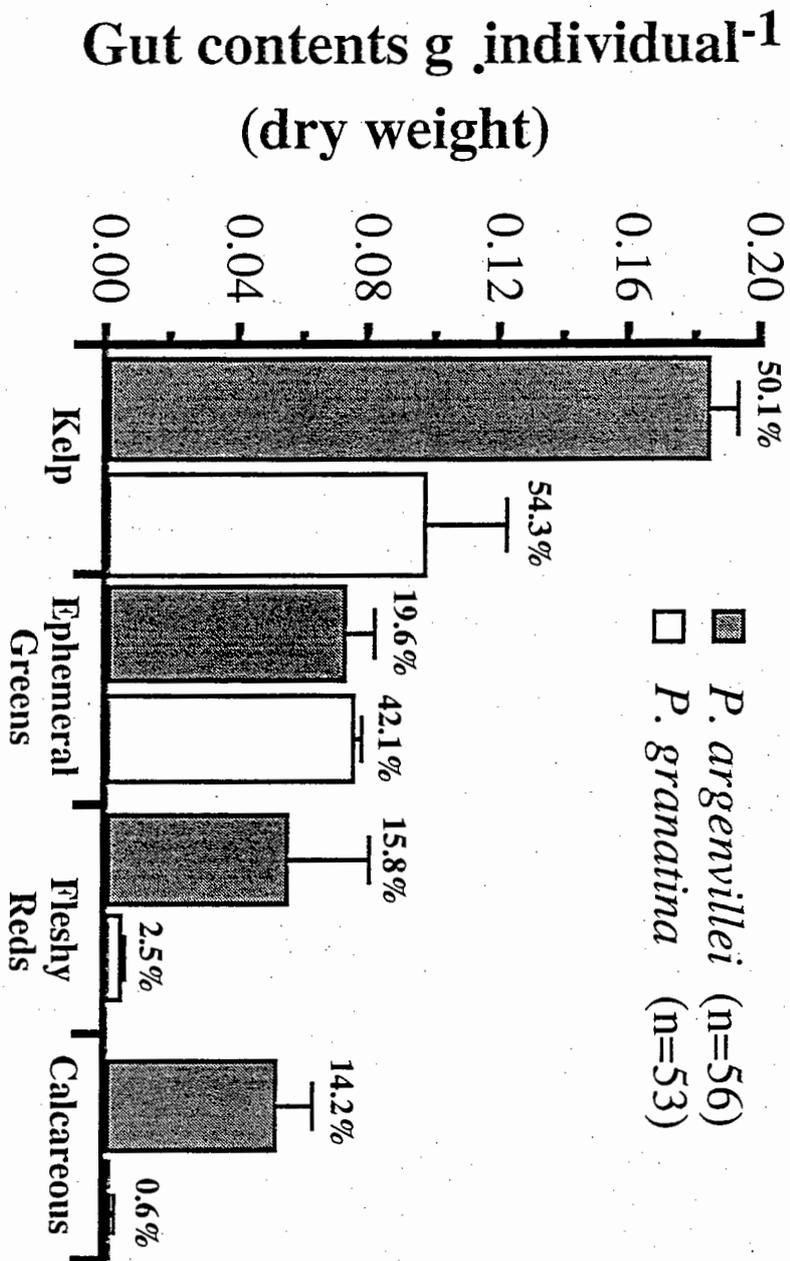


Figure 10. Average dry biomass (± 1 S.E.) of the four main food items found in stomach analyses of *P. granatina* and *P. argenvillei*. The % figures given in each bar are the mean contributions of each food category.

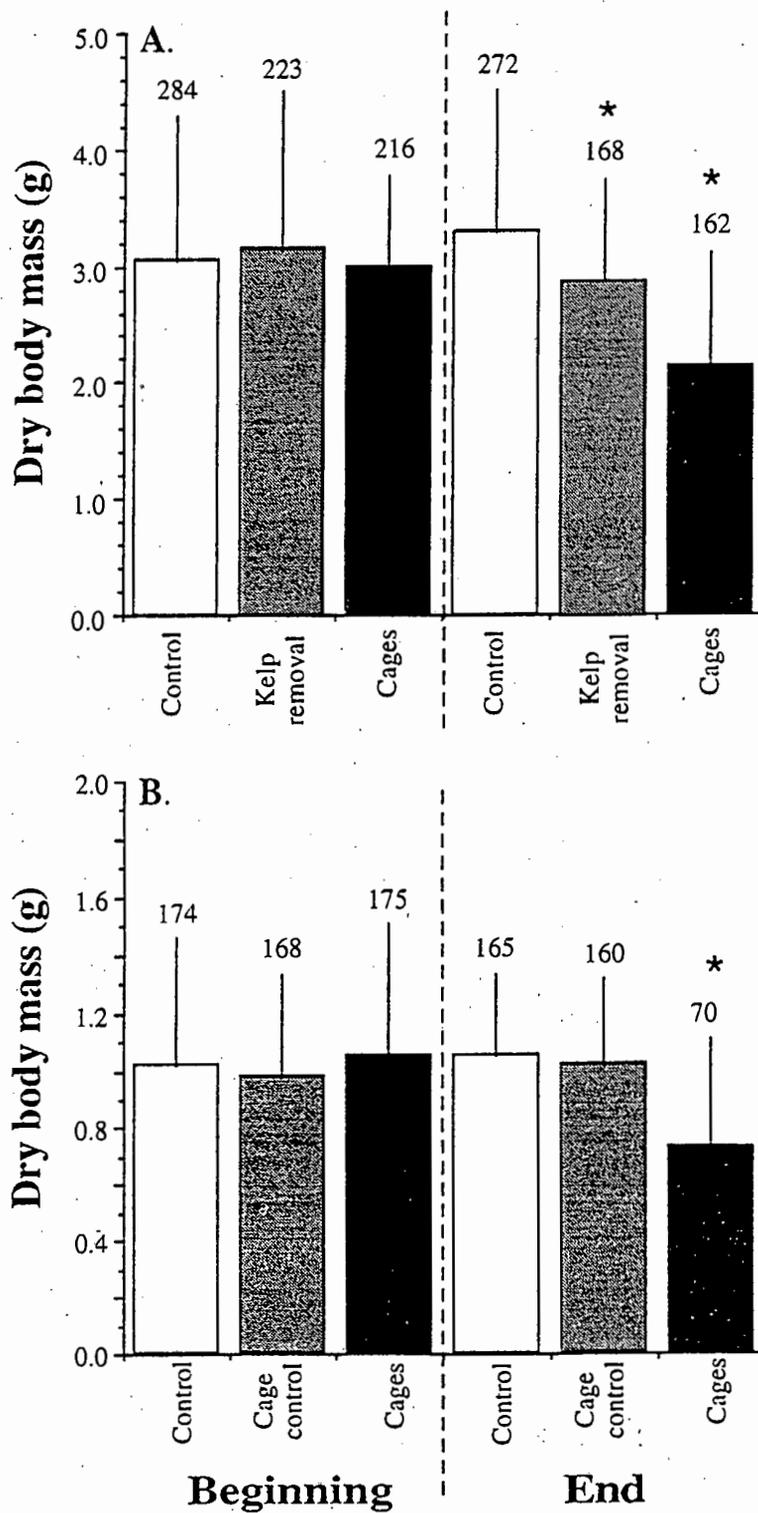


Figure 12. Mean (± 1 S.D.) dry flesh mass per individual (A.) *P. argenvillei* and (B.) *P. granatina* in each of the three treatments. Data on the left reflect masses of limpets at the initiation of the experiment (removed from the areas adjacent to each of the plots); those on the right show results for the experimental animals at the end of the experiment. Asterisks indicate which treatments differed significantly from controls (Tukey *t*-test $p < 0.05$). Numbers indicate the total number of limpets per treatment.

survival of *ca.* 95%. Survival of limpets under roofed conditions (cage controls) showed no significant differences from that of undisturbed control limpets (Tukey *t*-test, $p > 0.05$).

In the case of *P. argenvillei* (Fig. 11B), individuals subject to either form of kelp exclusion (by caging or physical removal of adjacent attached plants) showed a significant decrease in survival relative to controls ($F = 18.03$, $df_{(9, 46)}$; $p < 0.0001$). These differences were only detected after 95 d of kelp exclusion (Tukey *t*-test, $p < 0.05$), although they could have been manifested at any time between 30 and 95 d (Fig. 11B). At the end of the kelp removal and caging experiments, the survival of *P. argenvillei* was *ca.* 75%, while in the control plots their survival was *ca.* 95%. No significant differences in the survival of limpets existed between the kelp removal and cage treatments (Fig. 11B).

In the case of both *P. granatina* and *P. argenvillei*, the initial average body masses of limpets taken from areas adjacent to the experimental treatments (cages and control plots) were not statistically different ($F = 1.37$, $df_{(14)}$, $p > 0.26$ for *P. argenvillei* and $F = 1.27$, $df_{(12)}$, $p > 0.24$ for *P. granatina*: Fig. 12). However, exclusion of kelp - or denial of access to kelp - led to a significant decline in mean body mass relative to the control values. The animals in controls retained the same mean body mass as that recorded at the beginning of the experiment (Fig. 12). This provides evidence that exclusion of kelp led to starvation and that this was the most probable cause of mortality.

Discussion

Dense limpet populations have frequently been reported elsewhere in the world (e.g. Creese 1980; Parry 1982a, b; Hawkins and Hartnoll 1983; Workman 1983; Blankley and Branch 1985; Guerra and Gaudencio 1986), but although biomass, density and size should be simple well-documented population parameters, differences in methods and data presentation make comparisons of the data difficult. Table 2 shows reported and calculated average values of wet flesh biomass, density and size of 18 limpet species at several localities around the world. It is clear that South African limpets exist at densities comparable with other species, but because they combine high density with large size, *P. argenvillei* and *P. granatina* have biomass values approaching an order of magnitude higher than those recorded elsewhere (Table 2). It is this phenomenon that prompted the investigation reported here. Of the six highest values of biomass per unit area recorded for limpets, two are territorial and/or gardening species (*Lottia gigantea* and *P. cochlear*), while three of the other four species make use of drift kelp (*P. argenvillei*, *P. granatina* and *Nacella delesserti*, see Table 2).

Several associations between limpets and kelps are known (for review see Branch 1981), but biogeographic relations between them have not been well addressed. The geographical distributions of the kelps *E. maxima* and *L. pallida* and the limpets *P. granatina* and *P. argenvillei* overlap in a suggestive manner (Fig. 1). In particular there is a clear match in distribution between *P. granatina* and kelps and a notable decrease in maximum values of *P. argenvillei* size and abundance beyond the geographical distribution of the kelps (Table 1). The case of *P. argenvillei* is particularly interesting, for at a smaller geographical scale (about 500 km of Namaqualand coast), its abundance is strongly correlated with the abundance and accessibility of attached kelp plants (Fig. 3). The populations of *P. argenvillei* are narrowly constrained in the low shore (Figs. 5A) and the overlap between limpet beds and subtidal kelp forests is limited to the

Table 2. Summary of reported and/or calculated figures for the average biomass, density and size of 18 species of limpets in different parts of the world. The data are for the zone in which each species occurs, not the whole shore.

Locality	Species	Average wet flesh Biomass (g m^{-2})	Average Density (No m^{-2})	Average Size (mm)	Source
S. Africa (West coast)	<i>Patella granatina</i>	477.6	184.0	45.0	This study
S. Africa (West coast)	<i>Patella argenvillei</i>	771.3	197.8	55.0	This study
S. Africa (South west coast)	<i>Patella cochlear</i>	125.0	850.0	35.0	Branch (1975b)
S. Africa (West coast)	<i>Patella granularis</i>	38.6	50.0	30.0	Bosman (1988)
S. Africa (Marion Island)	<i>Nacella delleresi</i>	86.7	200.0	25.0	Blankley and Branch (1985)
England (Plymouth)	<i>Patella vulgata</i>	20.0	79.0	20.0	Hawkins et al. (1983)
Scotland (Orkney Islands)	<i>Patella vulgata</i>	35.0	110.0	30.0	Baxter (1982)
USA (San Nicolas Island)	<i>Lottia gigantea</i>	57.8 †	31.0	35.0	Wright (1989); Wright (1982)
USA (San Juan Island)	<i>Lottia pelta</i>	38.0	36.4	15.3	Branch unpubl. data
USA (San Juan Island)	<i>Lottia digitalis</i>	28.5	72.3	12.4	Branch unpubl. data
USA (San Juan Island)	<i>Lottia strigatella</i>	2.8	231.8	9.1	Branch unpubl. data
USA (San Juan Island)	<i>Tectura scutum</i>	38.0	33.3	20.5	Branch unpubl. data
USA (Maine)	<i>Tectura testudinialis</i>	2.4	195.3	9.0	Steneck and Watling (1982)
Australia (South east coast)	<i>Cellana tramoserica</i>	23.9	60.0	25.0	Fletcher (1984a,b); Parry (1982a,b)
Australia (South east coast)	<i>Patelloida alticostata</i>	73.9	302.0	18.0	Fletcher (1987); Parry (1982a,b)
Australia (South east coast)	<i>Notoacmea petterdi</i>	57.9	500.0	12.0	Creese (1980); Parry (1982a,b)
New Zealand (Leigh)	<i>Cellana radians</i>	49.2	27.6	27.4	Branch unpubl. data
New Zealand (Motu Bay)	<i>Cellana ornata</i>	18.2	29.3	18.9	Branch unpubl. data

† The average flesh biomass per unit area was estimated using a flesh mass/shell length relationship (Flesh mass= $4.287 \cdot \text{Lt}^{3.443}$, $r^2=0.957$; $p<0.005$), and the median density and size composition given by Wright (1989, Fig. 3).

infratidal margin (Fig. 6A). But even this marginal overlap is of vital importance for the limpet population. For example, at any one feeding time during low tide, *ca.* 35% of the population will be engaged in trapping fronds of nearby kelp plants (Fig. 9).

Several species of marine invertebrates feed principally on kelp. For example, the kelp *Ecklonia maxima* represents more than 52% of the overall diet of the South African abalone *Haliotis midae* (Barkai and Griffiths 1986; Tarr 1989). On the shores of southern Chile (Beagle Channel), Castilla and Moreno (1981) found that the sea urchin *Loxoechinus albus* feeds almost exclusively on drifting fragments of kelp *Macrocystis pyrifera*. Gut contents of *P. argenvillei* and *P. granatina* show that kelp is the main item (> 50%, Fig. 10), although the analyses include only limpets greater than 40 mm shell length (and preliminary results of gut contents show smaller limpets do not contain kelp in their guts). These results are consistent with the kelp trapping behaviour exhibited by both species of limpets. Only large animals (> 40 mm shell length) are found feeding on kelp, whether drift or live attached plants (Fig. 7).

Capture of drift seaweed, especially drifting kelp, is a well known feeding behaviour for sea urchins (Castilla and Moreno 1981; Buxton and Field 1982; Dayton 1984; Harrold and Reed 1985), the sub-Antarctic limpet *Nacella delesserti* (Blankley and Branch 1985) and abalone species (Poore 1972; Shepherd 1973; Dayton 1984). Tutschulte and Connell (1988) describe the capture of loose drift algae, or sometimes the fronds of nearby kelp plants, by three North American abalone species. Elevation of the shell ('mushrooming') and capture of drifting seaweeds are also known for the Australian and South African abalone species, *Haliotis laevigata* and *Haliotis midae* respectively (Shepherd 1973; Tarr 1989). In some respects the intertidal abalone from the coast of California, *H. cracherodii*, is an ecological equivalent to the limpets considered here, being capable of microalgal grazing as well as trapping kelp. It is thus of interest that it too achieves high biomass values in areas where it is unexploited, e.g. a whole wet mass of up to 8662 g · m⁻² (B. Tissot, pers. comm.). This value rivals the highest recorded for *P. argenvillei* and exceeds that for *P. granatina* (Table 1).

The feeding behaviour of *P. granatina* and *P. argenvillei* appears to be similar in terms of their main food item (kelp) and the postural behaviour employed, but significant differences exist if they are compared in detail. The main features of feeding behaviour and activity rhythms, shell morphology, and habitat segregation of the two limpet species are summarized in Table 3. It is clear that spatial segregation is a major difference between the two limpet species, with *P. argenvillei* associated almost exclusively with semi-exposed rocky shores and *P. granatina* with sheltered boulder-bays. Branch and Marsh (1978) have suggested that wave action constrains their local distribution, and demonstrated that the force required to dislodge *P. argenvillei* is 1.72 times that required to dislodge *P. granatina*. Arising from this, spatial differentiation between the two intertidal limpets is more likely to be related to their ability to survive in environments with different degrees of wave action than to any notions of inter-specific competition.

The trapping the fronds of attached kelp by *P. argenvillei* can be considered as a more specialized feeding behaviour than that of *P. granatina*. The presence of 'teeth' in the shell of *P. argenvillei* (Fig. 6G) is a morphological characteristic which aids kelp trapping and cutting in a high energy environment. Furthermore, *P. argenvillei* has a rapid tactile response to trap kelp, and in dense limpet stands collective feeding may take place (Fig. 8). This specialized feeding behaviour of *P. argenvillei* demands low mobility and a 'sedentary' way of life. Tagging experiments show that *P. argenvillei* is indeed extremely sedentary when it occurs at high densities (S. Eekhout unpubl. data). A similar situation occurs when *P. granatina* occurs at high densities ($> 80 \text{ m}^{-2}$). Only 3% of the tagged *P. granatina* moved out of my control plots, and moved no more than 2 or 3 m; the rest remained at exactly the same site for *ca.* 3 years.

The results of this Chapter shown that the collective mode of feeding exhibited by *P. argenvillei* (Fig. 8) may result in a reversal of the negative relationship between density and body size normally exhibited by intertidal invertebrate grazers (e.g. Branch 1975b; Creese 1980; Branch and Branch 1981; Ebert 1982; Leviatan 1988). Indeed, analysis of the data in Table 1 reveals a significantly positive correlation ($r=0.645$, $n=12$, $p<.02$)

between maximum density and maximum body size. This leads to the interesting prediction that there will be more energy flow *per-capita* as density rises, assuming all other factors are equal. Conversely, *P. granatina*, which does not feed collectively, exhibits the more usual negative relationship between density and size (see Table 1; $r=-0.599$, $n=12$, $p<.05$), implying that intraspecific competition increases with density.

Sheltered bays act as natural collectors of drift seaweed (principally kelp fragments). Some estimations in California show that the rate of accumulation of drift kelp in sheltered bays exceeds the net production of *Macrocystis* kelp forests (1.6 times higher), because bays concentrate fragments that were produced over a large area of subtidal kelp forests (Tutshulte and Connell 1988). For *P. granatina*, a square meter of sheltered boulder-bay on the Namaqualand coast receives a daily input of drift kelp (mainly fronds) that can range from 0 to 12,000 g wet wt $m^{-2} day^{-1}$, with an average (\pm SD) of 960.0 ± 991 g $m^{-2} day^{-1}$ (Fig. 4). This mean figure greatly exceeds the average productivity of the local subtidal kelp forests, which has a mean frond production of 76.0 g wet wt $m^{-2} day^{-1}$ (estimated from Dieckmann 1978 and Mann *et al.* 1979).

The asymptotic relationship between drift kelp and *P. granatina* (Fig. 4) indicates that a plateau is reached, above which further increases in food supply do not yield increases in this limpet's density. This raises the intriguing probability that primary space becomes the ultimate limiting constraint. I know of no other grazer for which this has been suggested. Nevertheless, I am convinced that space is the major limiting factor for high density populations of both species. Supporting evidence comes from the extraordinary packing of *P. argenvillei* and *P. granatina* (Figs. 6A, C, and F); their almost completely sedentary life-style (as evidenced by the virtual lack of movements out of control areas), and the fact that juveniles are largely confined to refugia on the shells of adults (Eekhout *et al.* 1992).

When intertidal grazers coexist at high densities (or biomass) the potential for strong competition always exists, provided there are limited resources (Underwood 1978; Creese and Underwood 1982; Branch 1985; Fletcher and Creese 1985). In the case of

these two South African intertidal limpets, food resources appear super-abundant and include a high micro- and macroalgal *in-situ* intertidal production, fueled by the rich upwelled Benguela system (Shannon 1985), and an abundant supply of subtidal kelp. At one of our sites (Groenrivier) I recorded values for intertidal primary production of 53.3 ± 17.6 g dry wt m^{-2} day^{-1} during peak season (converted from Branch *et al.* 1992), an average daily input of drifting kelp fragments of 240.0 ± 247.8 g dry wt m^{-2} day^{-1} in sheltered rocky bays (wet to dry conversion 0.25), and on semi-exposed shores a production by attached fronds of nearby kelp plants of 141.6 ± 34.5 g dry wt m^{-2} day^{-1} (R. H. Bustamante unpubl. data). The sum of these figures gives a total intertidal production on sheltered shores of 293.3 g dry wt m^{-2} day^{-1} available to *P. granatina*, and on semi-exposed shores a total 194.9 g dry wt m^{-2} day^{-1} available to *P. argenvillei*. Results of feeding experiments in the field, under unlimited supply of food, have shown average *per-capita* consumption rate of 0.73 ± 0.12 and 0.62 ± 0.07 g dry wt day^{-1} for *P. argenvillei* and *P. granatina* respectively (Chapter 6). A simple calculation shows that to maintain an average limpet density of 180 m^{-2} of *P. granatina* (Fig. 5A), at least 120 g dry wt day^{-1} of food is needed (using a *per-capita* consumption of 0.67 g m^{-2} day^{-1}), 2.3 times more than the observed intertidal epilithic algal production on sheltered shores. Similarly, in semi-exposed habitats, a total production of 134 g dry wt m^{-2} day^{-1} is required in order to maintain a *P. argenvillei* density of 200 m^{-2} (Fig. 5B), about 2.5 times the *in-situ* algal production. However, when the kelp input is added to the intertidal production, the potential availability of food exceeds the limpets requirement by a factor of 2.4 in sheltered shores and by a factor of 1.5 in semi-exposed shores. The experimental kelp exclusions demonstrate that the availability and input of kelp play a critical role in the survival of both *P. argenvillei* and *P. granatina* at high natural densities. Kelp exclusion led to high mortality in both species relative to controls (Fig. 11), indicating that *in-situ* micro- and macroalgal production is inadequate to meet the needs of the limpets when they occur at high densities. My belief is that in the absence of kelp, the increase in mortality is caused by starvation, rather than any other side-effects, such as increased desiccation or predation that might inadvertently be associated with the

experimental kelp exclusions. This contention is supported by the fact that the surviving limpets had significantly lower body masses in the treatments that deprived them of kelp, compared with the control animals (Fig. 12).

Several important roles have been described in the recent literature for subtidal macrophytes and kelp forests in marine systems. For instance the abundance of drift kelp in open water has an important influence on the distribution, and potentially the movements, of some fish species (Kingsford 1992). Similarly, the availability of drift kelp as food determines the size of the onuphid polychaet worm *Diopatra ornata* (Kim 1992). Kelp-derived carbon is found throughout the nearshore food web and this has a wide-ranging and long-lasting influence on the productivity of coastal systems. For example, seaweed detritus appears to be utilized very effectively in coastal food chains leading to shellfish production (Stuart *et al.* 1982; Mann 1988; Duggins *et al.* 1989; Menge 1992). The composition of biota of sandy beaches on the west coast of South Africa is powerfully influenced by the deposition of drift kelp high on the shore (Koop *et al.* 1982; Griffiths *et al.* 1983).

My data also provide quantitative evidence of a strong trophic link between the subtidal production of kelp and intertidal standing stocks of grazers. It is quite clear that the bottom-up effects of kelp are vital for the maintenance of high-density stands of *P. granatina* and *P. argenvillei*. They, in turn, exert powerful top-down effects on *in-situ* algal growth, totally preventing the development of foliose macroalgae by continuously grazing on propagules. Experimental or natural catastrophic elimination of these limpets results in profuse macroalgal beds (Branch *et al.* 1990; Eekhout *et al.* 1992). Most experimental removals of other intertidal limpets have led to a similar proliferation of algae (e.g. Jones 1948; Creese 1978; Underwood 1980; Branch 1981; Hawkins and Hartnoll 1983; Moreno *et al.* 1984; Underwood and Jernakoff 1984), and in systems where limpets are held at low densities by predators, comparable development of algal beds takes place (e.g. Bosman and Hockey 1988b; Hockey and Branch 1984). Both phenomena imply that limpets have the potential to exert a powerful top-down effect on

algae. At least in the case of *P. argenvillei*, grazing indirectly enhances crustose corallines, which are practically the only algae to frequent rocks in the 'argenvillei zone' and are smothered by foliose algae and decline if *P. argenvillei* is removed (Branch *et al.* 1990; Eekhout *et al.* 1992). High density populations of *P. argenvillei* also retard or prevent invasion of primary rock space by the alien mussel *Mytilus galloprovincialis* (Eekhout *et al.* 1992) and those of *P. granatina* check the reef-building polychaete *Gunnarea capensis* (Branch *et al.* unpubl. data). No visible macroscopic organisms grow within dense patches of *P. granatina* (Fig. 6F).

The trophic subsidy that maintains high densities of *P. granatina* and *P. argenvillei* thus has profound implications for the structure and functioning of the intertidal communities, influencing macroalgal abundance and diversity, encrusting coralline cover, and space occupancy by filter-feeders. These indirect interactions correspond to 'interaction chains' (sensu Wootton 1993) in which, for example, kelp has an indirect negative effect on macroalgae by way of its direct positive effect on limpets. In the case of *P. argenvillei*, the interaction chain extends one step further, with kelp indirectly promoting crustose corallines via this indirect suppression of macroalgae (Eekhout *et al.* 1992).

The above points emphasize the importance of trophic subsidy: The results presented here show clearly that the extraordinary biomasses attained by limpets on the west coast of South Africa would never be maintained if it were not for the subsidy gained from the subtidal zone in the form of kelp. This effect corresponds to the magnification of secondary production by the input of kelp detritus, described by Duggins, Simonstad and Estes (1989).

Much ecological theory predicts that as productivity rises, grazers biomass will not necessarily rise in response, because predators may increase and control the herbivore trophic level (e.g. Oksanen *et al.* 1981; Oksanen 1991). Wootton and Power (1993) have tested this hypothesis in manipulated channels of a river and upheld these predictions when the system consists of three trophic levels. In the interaction I have explored,

primary 'production' occurs at extremely high levels, due to the subsidy provided by kelp, and in this case the biomass of secondary consumers (mainly limpets) is correspondingly high. Limpet predators do exist in this system, the most notable being the Oystercatcher *Haematopus moquini* (Hockey and Branch 1984) and the giant clingfish *Chorisochismus dentex* (Stobbs 1980; Lechanteur and Prochazka in prep.) but both are incapable of attacking large limpets (> 50 mm). In the narrow context of the examples I explored, the zones dominated by limpets are thus converted into ones that functionally consist of only two trophic levels (producers and grazers), since predators have no known controlling influence on the density of large *P. argenvillei* and *P. granatina*. For such even-numbered trophic chains, high production is predicted to yield high herbivore biomass (Menge and Olson 1990; Power 1992; Hairston and Hairston 1993).

This discussion highlights the difficulties of determining the numbers of trophic levels in a system; one of the reasons why some authors (e.g. Peters 1977; Polis 1991) regard trophic levels as "non-operational concepts with no useful correspondence to reality" (Power 1992, p. 733). Species that change their diet (and even trophic level) during ontogenetic development are a contributing problem (Werner and Gilliam 1984). The present case raises an analogous but different issue: species that change their vulnerability to predators during ontogeny. Such species may shift the local system from three trophic levels (when small and controlled by predators) to two trophic levels (when large and functionally immune to predation). Large size may thus be a contributing factor explaining the high density of *P. argenvillei* and *P. granatina*, allowing them to surpass sizes within the 'window of vulnerability' to predators.

Many of the issues discussed above arise because of local species-specific characteristics, endorsing the pleas of Paine (1988), Hunter and Price (1992) and others for food web and trophic analyses to be based on species, rather than lumping them, thus allowing considerations of the rich heterogeneity that arises from differences between organisms. The limpet-kelp interaction described in this Chapter illustrates specializations

References

- Barkai, R., and C. L. Griffiths. 1986. Diet of the South African abalone *Haliotis midae*. South African Journal of Marine Sciences **4**: 37-44.
- Baxter, J. M. 1982. Population dynamics of *Patella vulgata* in Orkney. Netherlands Journal of Sea Research **16**: 96-104.
- Beovich, E. K., and G. P. Quinn. 1992. The grazing effects of limpets on macroalgal community of a rocky intertidal shore. Australian Journal of Ecology **17**: 75-82.
- Bishop, M. L., and S. J. Bishop. 1973. Associations of mollusks and marine plants at San Diego, California. Journal of Conchology **28**: 43-54.
- Black, R. 1976. The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. Ecology **57**: 265-277.
- Blankley, W. O., and G. M. Branch. 1985. Ecology of the limpet *Nacella delesserti* (Phillipi) at Marion Island in the Sub-Antarctic Southern Ocean. Journal of Experimental Marine Biology and Ecology **92**: 259-281.
- Bosman, A. L. 1988. The influence of primary production rate on the dynamics of *Patella granularis*, an intertidal limpet. P.S.Z.N.I. Marine Ecology **9**: 181-198.
- Bosman, A. L., P. A. R. Hockey, and W. R. Siegfried. 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. Oecologia (Berlin) **72**: 226-232.
- Bosman, A. L., and P. A. R. Hockey. 1988a. Life-history patterns of populations of the limpet *Patella granularis*: The dominant roles of food supply and mortality rate. Oecologia (Berlin) **75**: 412-419.

- Bosman, A. L., and P. A. R. Hockey. 1988b. The influence of primary production rate on the population dynamics of *Patella granularis* an intertidal limpet. *Marine Biology* **9**: 181-198.
- Branch, G. M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. *Zoologica Africana* **6**: 1-38.
- Branch, G. M. 1975a. Mechanisms reducing intraspecific competition in *Patella* spp: migration, differentiation and territorial behaviour. *Journal of Animal Ecology* **44**: 575-600.
- Branch, G. M. 1975b. Intraspecific competition in *Patella cochlear* Born. *Journal of Animal Ecology* **44**: 263-281.
- Branch, G. M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography Marine Biology Annual Review* **19**: 235-380.
- Branch, G. M. 1984. Competition: its role in ecology and evolution in intertidal communities. Pages 97-104 in E. S. Vrba editor. *Species and speciation*. Transvaal Museum Monograph **4**, Transvaal Museum, Pretoria.
- Branch, G. M. 1985. Limpets: their role in littoral and sublittoral community dynamics. Pages 97-116 in P. G. Moore, D. Seed editors. *The Ecology of Rocky Coasts*. Hodder and Stoughton Educational, England.
- Branch, G. M., and A. C. Marsh. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. *Journal of Experimental Marine Biology and Ecology* **34**: 111- 130.
- Branch, G. M., and M. L Branch. 1981. Experimental analyses of intraspecific competition in an intertidal gastropod, *Littorina unifasciata*. *Australian Journal of Marine and Freshwater Research* **32**: 573-589.

- Branch, G. M., S. Eekhout, and A. L. Bosman. 1990. Short-term effects of the 1988 Orange River floods on the intertidal rocky-shore communities of the open coast. *Transactions of the Royal Society of South Africa* **47**: 331-354.
- Branch, G. M., J. M. Harris, C. Parkins, R. H. Bustamante, and S. Eekhout. 1992. Algal 'gardening' by grazers: a comparison of the ecological effects of territorial fish and limpets. Pages 405-424 in D. John editor. *Plant-animal interactions in the marine benthos*. Systematic Association Special Edition **46**, Clarendon press, Oxford.
- Branch, M. L. 1974. Limiting factors for the gametes of three South African Laminariales. Investigation Report Sea Fisheries Branch of South Africa **104**: 1- 38.
- Buxton, C. D., and J. G. Field. 1982. Feeding, defecation and absorption efficiency in the sea-urchin, *Parechinus angulosus* Leske. *South African Journal of Zoology* **18**: 12-14.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**: 634-639.
- Castilla, J. C., and C. A. Moreno. 1981. Sea urchins and macroalgae: an experimental test of their ecological relations in southern Chile. Pages 257-263 in J. M. Lawrence editor. *Echinoderms: Proceedings of the International Conference*. Balkema, Rotterdam, Tampa Bay.
- Choat, J. H., and R. Black. 1979. Life histories of limpets and the limpet-Laminarian relationship. *Journal of Experimental Marine Biology and Ecology* **41**: 25-50.
- Creese, R. G. 1978. The ecology and reproductive biology of intertidal limpets. Ph. D. Thesis, University of Sydney, N. S. W., Australia, 375 pp.
- Creese, R. G. 1980. An analysis of distribution and abundance of populations of high-shore limpets, *Notoacmea petterdi* (Tenison-Woods). *Oecologia (Berlin.)* **45**: 252-260.

- Creese, R. G., and A. J. Underwood. 1982. Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* (Berlin) **53**: 337-346.
- Dayton, P. K. 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs* **54**: 253-289.
- Dieckmann, G. 1978. Aspects of growth and production of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula. M. Sc. Thesis. Department of Botany, University of Cape Town, South Africa.
- Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* **245**: 170-173.
- Ebert, T. A. 1977. An experimental analysis of sea urchin dynamics and community interactions on a rocky jetty. *Journal of Experimental Marine Biology and Ecology* **27**: 1-22.
- Ebert, T. A. 1982. Longevity, life history, and relative body wall size in sea urchins. *Ecological Monographs* **52**: 353-394.
- Eekhout, S., C. M. Raubenheimer, G. M. Branch, A. L. Bosman, and M. O. Bergh. 1992. A holistic approach to the exploitation of intertidal stocks. *South African Journal of Marine Sciences* **12**: 1017-1030.
- Field, J. G., C. L. Griffiths, R. J. Griffiths, N. Jarman, P. Zoutendyk, B. Velimirov, and A. Bowes. 1980. Variation in structure and biomass of kelp communities along the south-west Cape Peninsula. *Transactions of the Royal Society of South Africa* **44**: 145-203.
- Fletcher, W. J. 1984a. Variability in the reproductive effort of the limpet, *Cellana tramoserica*. *Oecologia* (Berlin) **61**: 259-264.

- Fletcher, W. J. 1984b. Intraspecific variation in the population dynamics and growth of the limpet *Cellana tramoserica*. *Oecologia* (Berlin) **63**: 110-121.
- Fletcher, W. J. 1987. Intraspecific competition among subtidal limpets: effects of substratum heterogeneity. *Ecology* **68**: 387-400.
- Fletcher, W. J., and R. G. Creese. 1985. Competitive interaction between co-occurring gastropods. *Marine Biology* **86**: 183-192.
- Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? *Oikos* **50**: 291-301.
- Graham, A., and V. Fretter. 1947. The life history of *Patina pellucida* (L.). *Journal of the Marine Biological Association United Kingdom* **26**: 590-601.
- Guerra, M. T., and M. J. Gaudencio. 1986. Aspects of the ecology of *Patella* spp. on the Portuguese coast. *Hydrobiologia* **142**: 57-69.
- Griffiths, C. L., J. M. E. Stenton-Dozey, and K. Koop. 1983. Kelp wrack and the flow of energy of a sandy beach ecosystem. Pages 547-556 in A. McLachlan and T. Erasmus editors. *Sandy Beaches as Ecosystems*. W Junk Publishers, The Hague.
- Hairston, G. H. . and G. N. Hairston. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *The American Naturalist* **142**: 379-411.
- Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* **66**: 1160-1169.
- Hawkins, S. J., and R. G Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography Marine Biology Annual Review* **21**: 195-282.
- Hayworth, A. M., and J. F. Quinn. 1990. Temperature of limpets in the rocky intertidal zone: effects of caging and substratum. *Limnology and Oceanography* **35**: 967-970.

- Hockey, P. A. R., and G. M. Branch. 1984. Oystercatchers and limpets: impact and implications. A preliminary assessment. *Ardea* **72**: 199-206.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**: 724-734.
- Jones, N. S. 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. Proceedings and Transactions of the Liverpool Biological Society **56**: 60-77.
- Kensley, B., and M. L. Penrith. 1980. The constitution of the fauna of rocky intertidal shores of South West Africa. Part III. The north coast from Cape Frio to the Kunene River. *Cimbebasia (A)* **5**:201-214.
- Kim, S. L. 1992. The role of drift kelp in the population ecology of a *Diopatra ornata* Moore (Polychaeta: Onuphidae) ecotone. *Journal of Experimental Marine Biology and Ecology* **156**: 253-272.
- Kingsford, M. J. 1992. Drift algae and small fish in coastal waters of northeastern New Zealand. *Marine Ecology Progress Series* **80**: 41-55.
- Koop, K., R. C. Newell, and M. I. Lucas. 1982. Biodegradation and carbon flow based on kelp (*Ecklonia maxima*) debris in a sandy beach microcosm. *Marine Ecology Progress Series* **7**: 315-326.
- Leviatan, D. R. 1988. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Phillipi. *Oecologia* **76**: 672-629.
- Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* **12**: 405-437.

- Mann, K. H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnology and Oceanography* **33**: 910-930.
- Mann, K. H., N. G. Jarman, and G. Dieckmann. 1979. Development of a method for measuring the production of the kelp *Ecklonia maxima* (Osbeck) Papenf. *Transactions of the Royal Society of South Africa* **44**: 27-41.
- Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* **73**: 755-765.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* **5**: 52-57.
- Moreno, C. A., J. P. Sutherland, and H. F. Jara. 1984. Man as predator in the intertidal zone of southern Chile. *Oikos* **42**: 155-160.
- Muñoz, M., and B. Santelices. 1989. Determination of the distribution and abundance of the limpet *Scurria scurra* on the stipes of the kelp *Lessonia nigrescens* in central Chile. *Marine Ecology Progress Series* **54**: 277-285.
- Oksanen, L. 1991. Trophic levels and trophic dynamics: a consensus emerging? *Trends in Ecology and Evolution* **6**: 58-60.
- Oksanen, L., S. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**: 240-261.
- Paine, R. T. 1988. Food webs: roads maps of interactions or grist for theoretical development? *Ecology* **69**: 1648-1654.
- Palumbi, S. R. 1984. Measuring intertidal wave forces. *Journal of Experimental Marine Biology and Ecology* **81**: 171-179
- Parry, G. D. 1982a. The evolution of the life history of four species of intertidal limpets. *Ecological Monographs* **52**: 65-91.

- Parry, G. D. 1982b. Reproductive effort in four species of intertidal limpets. *Marine Biology* **67**: 267-282.
- Peters, R. H. 1977. Unpredictable problems with trophodynamics. *Environmental Biology of Fishes* **2**: 97-102.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *The American Naturalist* **138**: 123-155.
- Poore, G. C. B. 1972. Ecology of New Zealand abalones, *Haliotis* species (Mollusca, Gastropoda) I. Feeding. *New Zealand Journal of Marine and Freshwater Research* **6**: 11-22.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* **73**: 733-746.
- Quinn, J. P., and M. J. Keough. 1993. Potential effects of enclosure size on field experiments with herbivorous intertidal gastropods. *Marine Ecology Progress Series* **98**: 199-201.
- Shannon, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. *Oceanography Marine Biology Annual Review* **23**: 105-182.
- Shepherd, S. A. 1973. Studies on southern Australian abalone (Genus *Haliotis*) I. Ecology of five sympatric species. *Australian Journal of Marine and Freshwater Research* **24**: 217-257.
- Stuart, V., J. G. Field, and R. C. Newell. 1982. Evidence for the absorption of kelp detritus by the ribbed mussel *Aulacomya* after using a new ¹⁵C-labelled microsphere technique. *Marine Ecology Progress Series* **9**: 263-271.
- Stobbs, R. E. 1980. Feeding habits of the giant clingfish *Chorisochismus dentex* (Pisces: Gobiesocidae). *South African Journal of Zoology* **15**: 146-149.

- Tarr, R. J. Q. 1989. Abalone. Pages 62-69 in A. I. L. Payne and R. J. M. Crawford, editors. Oceans of life. Vlaeberg Publishers, Cape Town, South Africa.
- Tutschulte, T. C., and J. H. Connell. 1988. Feeding behavior and algal food of three species of abalone (*Haliotis*) in southern California. Marine Ecology Progress Series **49**: 57-64.
- Underwood, A. J. 1976. Food competition between age-classes in the intertidal neriticean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). Journal of Experimental Marine Biology and Ecology **23**: 145-154.
- Underwood, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. Oecologia (Berlin) **33**: 185-202.
- Underwood, A. J. 1980. The effects of grazing by gastropods and physical factors on the upper limits and distribution of intertidal macroalgae. Oecologia (Berlin) **46**: 201-213.
- Underwood, A. J., and P. J. Jernakoff. 1984. The effects of tidal height, wave exposure, seasonally and rock pools on grazing and the distribution of intertidal macroalgae in New South Wales. Journal of Experimental Marine Biology and Ecology **75**: 71-96.
- Vahl, O. 1971. Growth of *Patina pellucida* (L.) (Gastropoda: Prosobranchia) on *Laminaria hyperborea* (Gunnerus) from western Norway. Ophelia **9**: 31-50.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**: 393-425.
- Wootton, T. J., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. Proceedings at the National Academy of Sciences **90**: 1384-1387.

Workman, C. 1983. Comparisons of energy partitioning in contrasting age-structured populations of the limpet *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology* **68**: 81-103.

Wright, W. G. 1989. Intraspecific mediated density sex-change in the territorial patellacean limpet *Lottia gigantea*. *Marine Biology* **100**: 353-364.

Wright, W. G. 1985. The behavioral ecology of the limpet *Lottia gigantea*: interaction between territoriality, demography, and protandric hermaphroditism. Ph. D. Dissertation, University of California, San Diego.

Chapter 6

*The Dynamics of an Algal-Kelp-Limpet Interaction: an Ecological and
Resource Management Simulation*

Summary: Two key ecological and physiological processes underlie the dynamics of biological populations: resource extraction and resource conversion. Extraction, also known as predation or consumption, is the process of biomass flow from one species to another, and biomass conversion from one species to another is the process that accounts for the biomass growth of populations. Because these processes involve the whole population, they are regarded as 'metaphysiological' in scope. This simplified view of the interaction of biological populations is highly relevant in the case of marine benthic invertebrate species subjected to exploitation, because enough ecological manipulations can be done in order to obtain the empirical data needed for the construction of reliable management models. I have used this metaphysiological modeling approach to simulate the dynamics of an algal-kelp-limpet system, using empirical data gathered specifically for the model and also data presented in the previous Chapter. I also determined the production curve of epilithic algae in relation to their biomass, the input of drift kelp into the system, and the field consumption rates of individuals of the limpet *P. granatina* feeding on both algae and kelp. I test whether the model is able to predict the population growth of *P. granatina* reasonably well in two ecological situations, (a) in the presence and (b) in the absence of kelp, and over a range of observed limpet and algal population densities. I then discuss the development of a potential limpet fishery, using the model to predict limpet stand growth under various harvesting regimes, and I develop a maximum sustainable yield policy for the harvesting of limpets. Finally I suggest how this ecological modeling approach can be combined with other 'standard' approaches to obtain a more reliable and applicable model than either method on its own.

Introduction

In the Chapter 2 it was shown how important the biomass contributions of the patellid limpets *Patella argenvillei* and *P. granatina* are to the general composition of west coast intertidal communities on semi-exposed and sheltered shores, respectively. Pristine limpet populations of these two limpet species currently exist along the sparsely populated northern west coast of South Africa (Fig. 1). These species are both large (up to 100 mm shell length) and occur in dense populations that achieve extraordinary biomasses. These limpets are primarily found between the low and mid-shore of sheltered boulder bays (*P. granatina*) and semi-exposed shores (*P. argenvillei*). *P. granatina*, the focus of this Chapter, forms monospecific stands that can reach densities up to 200 m⁻², representing a biomass up to ca. 8 kg m⁻² of whole wet body weight (Chapter 5). This high limpet biomass, among the highest in the world, can be explained partially by the fact that the west coast intertidal habitat is highly productive (see Chapter 3), being fueled by the nutrient-rich Benguela upwelling system (e.g. Shannon 1985; Brown and Cochrane 1991; Brown 1982) which supports a rapid growth of the epilithic micro-and macro-algae (hereafter referred to as algae) on which limpets graze intensively (Branch 1981; Bosman *et al.* 1987; Branch *et al.* 1992). Notwithstanding this high *in-situ* intertidal primary productivity, limpets do utilize other sources of food. As was shown in Chapter 5, during each tidal cycle the sheltered bays of the west coast act as natural collectors of significant amounts of drifting fronds of the kelps *Ecklonia maxima* and *Laminaria pallida*. Field observations on the feeding ecology of *P. granatina*, show that it has developed behavioral and morphological adaptations for capturing drifting kelp as source of food (Chapter 5, Fig. 6D). Thus, although the intertidal habitat is highly productive (see Chapter 3), *P. granatina* relies on the unorthodox source of food provided by the subtidal production and subsequent daily deposition of drifting kelp.

What are controlling factor(s) for the limpet populations? There is evidence that predation does take place on small-sized limpets (< 50 mm shell length). Two main predatory species have been identified: the African Black Oystercatcher *Hamatopus moquini* (Hockey and Branch 1984) and the Giant Clingfish *Chorisochismus dentex* (Stobbs 1980; Lechanteur and Prochazka in prep.). Nevertheless, these predators do not appear to affect large *P. granatina*, which are free of predation, and which represent more than 70-95% of the population biomass. However, prehistoric human predation was substantial. Archeological evidence indicates that this intertidal limpet species was an important part of the diet and a significant component of the protein budget of early coastal inhabitants of south western Africa (Parkington 1976; Buchanan 1988; Noli 1988; Webley 1992). Modern human utilization of *P. granatina* is minimal, although they have been recent applications for permits to commercially exploit the species (Bosman *et al.* 1990).

Given that there are no natural predators known to be capable of influencing the populations of adult *P. granatina*, the factors limiting them remains an open question.

Intertidal limpets are regarded as generalized grazers, *in-situ* epilithic micro- and macroalgal production providing their conventional source of food (e.g. Underwood 1980 1984; MacLulich 1986a, b ; Bosman 1988; Hill and Hawkins 1990). In Chapter 3 it was demonstrated that a high primary production does exist on the west coast of South Africa (see Figs. 2-4, Chapter 3), but it has been empirically demonstrated in Chapter 5 that this high intertidal production is not sufficient to sustain dense populations of *P. granatina*. In this Chapter a different approach is taken to the same problem -that of developing a metapopulation model to explore the relative importance of *in-situ* algae and kelp as energy sources sustaining dense populations of *P. granatina*.

Recent advances in ecological modeling have stressed the need for individual-based models, in recognition of the importance of local interactions between individuals (between and within species) in ecological systems (e.g. Getz 1980, 1991, 1993, in press; Lomnicki 1988; DeAngelis and Gross 1992; Judson 1993). These models have

sometimes proved to give more realistic results than the traditional models (i.e. demographic models). The local interaction between epilithic algal production, subtidal kelp, and intertidal limpets is one such system that can be successfully modeled using an individual-based approach.

The biomass dynamics of a population (e.g. a consumer) can be modeled by treating the population as a single meta-organism. That is, their dynamics can be determined by the rate that the population consumes resources and by the efficiency with which these resources are incorporated into the population's biomass: this is a metaphysiological approach (Getz 1993).

In contrast to many fisheries, the algal-kelp-limpet system is one that can be manipulated and used to test harvesting strategies, using both theoretical analyses and experimental manipulations. This is because limpets are relatively sessile, and individuals can be measured and counted with virtually no impact on their well-being. Similarly, the dynamics of the limpet's main sources of food, i.e. kelps and algae, can be experimentally determined. Thus, the accessibility, and relatively simple trophic characteristics of this system, make of it very attractive and suitable for modeling studies.

During the last five years, private fishing companies have begun to show an interest in starting a commercial fishery based on this limpet's populations, especially because of the existence of an expanding Asian market (Blankley 1988). This situation has created an imperative need for a better understanding of the ecological role of these limpets and the potential impact of future commercial exploitation of their populations. A preliminary harvesting analysis of *P. granatina*, based on experimental manipulations of limpets along this coast, has already been undertaken using a demographic approach, in which a size-structured model was developed, with growth, survival, and recruitment process parameters selected to fit output from the model to empirical limpet size distribution data (Raubenheimer 1991; Eekhout *et al.* 1992). The difficulty with this approach is that these parameters reflect population processes at high pre-exploitation population densities, while they are likely to be very different at lower, post-exploitation densities.

Consequently, although it is desirable to incorporate size-structure in models of resources where size-structured harvesting policies are easy to implement, a more accurate assessment of the productivity of the resource might be obtained from an ecologically-oriented model that is able to incorporate changes in the rate of population processes as a function of population density.

Sufficient ecological data are available for *P. granatina* and *P. argenvillei* to allow the development of an individually-based, stand-growth model simulating the algal-kelp-limpet system. This modeling approach can also be used to analyze the potential effects of exploitation if the limpets are treated as a commercial resource. This modeling approach is used here in three different ways. Firstly, it is used to simulate the algal-kelp-limpet interaction to explain the relative roles of algae and kelp in maintaining the limpet populations. Second, the performance of the model is tested by manipulating the input of kelp to validate the model's prediction output against the empirical results described in Chapter 5. Finally, having tested the model, it is employed to obtain a maximum sustainable yield policy based on the exploitation of limpets of specific size on a rotational basis. I also use this model to discuss alternative strategies derived from the size-structured model mentioned above, and conclude that these strategies may well lead to overexploitation of the resource. Since both non-ecological size-structured models and lumped ecological models have serious shortcomings, I discuss the type of data needed to construct a model that has both the size-structured and ecological elements required for a more reliable and comprehensive sustainable management of limpet populations that can be achieved by either approach on its own.

Materials and Methods

Metaphysiological model

The metaphysiological approach was proposed by Getz (1991, 1993, in press), as an alternative to modified Lotka-Volterra or Tilman-MacArthur equations, to model the biomass density of consumer-resource populations interacting in simple food webs. This approach is based on the idea that each population is subject to two metaphysiological processes: (i) a biomass conversion process that determines net growth rate (which can be negative) in terms of a per-unit-consumer consumption rate of other populations regarded as resources, and (ii) an extraction rate for the cases where the consumer acts as a resource for other populations.

As can be justified from empirical biological data presented in the previous Chapters, I model a limpet population consuming both a logistically growing algal resource and a constant flux of kelp resource. A logistic growth pattern emerges in a population that is exploiting a constant flux of food and has a hyperbolically shaped biomass conversion rate response (the simplest response satisfying the necessary properties of increasing rates of decline as resources go to zero, as well as saturating growth rates as resources become unlimiting) (Getz 1991, 1993, in press). In this case the biomass densities x_a and x_l of the algal and limpet populations respectively satisfy the dynamic equations

$$\begin{aligned} \text{algae: } \frac{dx_a}{dt} &= rx_a \left(1 - \frac{x_a}{K}\right) - x_l g_a \\ \text{limpets: } \frac{dx_l}{dt} &= x_l f(qg_a + g_k), \end{aligned} \tag{1}$$

where the limpet biomass conversion rate, f , and the per-unit-limpet consumption rate of algae g_a , and kelp, g_k have appropriate forms, and the parameter q reflects the relative

nutritional value of the algae as against that of the kelp, and where K and r are the carrying capacity and intrinsic rate of growth of the algae.

Here I will assume a hyperbolic form (logistic) for limpet consumption rate $f(g)$, with the total consumption of both algae and kelp $g = g_a + qg_k$, is represented by the function

$$f(g) = \rho \left(1 - \frac{K}{g}\right), \quad (2)$$

where the parameter ρ bounds the per-unit-limpet growth rate and the parameter κ represents per-unit-limpet resource extraction rate required for maintenance alone (Getz 1991; 1993; in press). I will also assume that the consumption functions g_a and g_k are Holling type II response functions generalized to incorporate a self-interference term. The importance of this self-interference term is fully discussed by Getz (1991; 1993), and can be interpreted as an intraspecific competition parameter, i.e. the limpet biomass that reduce the *per-capita* consumption to a third ($\delta_{\alpha+\kappa}/3$). This self-interference parameter is particularly appropriate for species such as limpets, with limited movement and where space plays an important role in determining their abundance, where at low resource densities, the amount of resources per-unit individual is more important than absolute resource density in determining resource extraction rates (Akçakaya 1992; Arditi *et al.* 1991; Arditi and Saïah 1992). Specifically, letting k represent a constant level of kelp available to the population, I assume that

$$g_a = \frac{\delta_a(1-p)x_a}{\beta_a + \gamma_k x_l + pk + (1-p)x_a}, \quad (3)$$

and

$$g_k = \frac{\delta_k pk}{\beta_k + \gamma_k x_l + (1-p)x_a}, \quad (4)$$

where δ_α and δ_κ are the maximum or satiation consumption rate of limpets eating respectively algae or kelp, β is a half-saturation parameter (the level at which algae or kelp consumption is $\delta/2$ when consumer densities are very low), γ is an interference

parameter that can be estimated from data that evaluate consumer density dependent effects on resource extraction, and p is a preference parameter that allows us to account in a simple way for any propensity that the limpets have for feeding on one type of food more intensely than another (a preference model that accounts for dietary switching would be much more complicated - see, for example, Houston and McNamara 1985; Mangel and Clark 1988; Real 1990).

I have not incorporated a seasonal component into the model, although there is some justification for so doing (Branch *et al.* 1992). Since a potential limpet harvesting is considered on a seasonal basis and is incorporated as an impulse function that is imposed on the system at an appropriate time of the year, to a first approximation the seasonal component can be replaced by average rates over the season. I do not simulate complete removal of the biomass at harvesting time, but only removal of a certain percent of the biomass, with the remaining stock playing the role of a "seed" population from which the stand is then naturally regenerated.

Limpet population parameters

The data used to estimate the theoretical *per-capita* population parameters ρ and κ of function (2) were obtained empirically from individual limpets growing in three experimental plots (*ca.* 6.0 m² each) placed in areas where limpets occurred naturally at high biomass density (i.e. at around their environmental carrying capacity, see Fig. 6F, Chapter 5). Growth was then determined using individually labeled limpets, all greater than 20 mm, and of different initial sizes (data reanalyzed from Bosman *et al.* 1990; and Raubenheimer 1991). The parameter ρ was initially estimated by informally fitting a hyperbolic growth curve by eye to growth rate data as a function of *per-capita* food intake (see Getz 1991, Fig. 2). The data were obtained after experimentally "thinning" unexploited limpet stands (Bosman *et al.* 1990). Specifically, the densities of stands were reduced to 50, 33, and less than 1% of their original biomass density, and individual growth increments were recorded in each treatment over a period of three years.

An annual growth increment in length of individual limpets was determined for each of the thinning treatments and subsequently converted to a daily base and expressed in terms of dry body (flesh) weight using the allometric equation

$$W = 2.731 \times 10^{-5} L^{3.201}, \quad (5)$$

where the dry flesh mass W is in grams and the length L is in mm. This procedure assumes that a reduction in limpet density represents an increase in the amount of resources that can be extracted per individual, which is the functional argument of expression (2). The parameter κ was then estimated using the expression

$$\kappa = \frac{\delta \bar{x}_l}{\beta + \gamma \bar{x}_a + \bar{x}_l}, \quad (6)$$

where \bar{x}_l and \bar{x}_a are a pair of limpet and algal densities at which limpet stand growth appears to be zero under the experimental exclusion of kelp (i.e., at this pair of kelp and algal densities, $k = \bar{g}$ in function (2) and \bar{g} is expression (3) evaluated at the densities \bar{x}_l and \bar{x}_a in question, assuming the parameters $\kappa = \rho = 0$), and β and γ have the values discussed below. These initial estimates of ρ and κ were then modified (through a sensitivity analysis) until the model was able to reproduce simultaneously observed biomass levels of unexploited limpet and algal stands, also as discussed below.

The pristine populations of *P. granatina* were assumed to be at their carrying capacity (K), so the initial population values entered in the model were those of observed natural densities. These density values were expressed in dry flesh biomass per square meter using an average modal size of the adult population of 55 mm shell length, with adults being defined as limpets > 35 mm shell length.

Epilithic algal production

The dynamic growth of the epilithic algae, measured as grams of dry matter per meter-squared per day ($\text{g m}^{-2} \text{d}^{-1}$), was experimentally measured for a mid-low intertidal shore at Groenrivier on the west coast of South Africa (Fig. 1). Production *in-situ* was



A.



B.

Figure 2. (A.) General view of limpet exclusion "corral" for measurement of the primary production placed on the mid-low shore in the middle of a limpet bed. Each column of rock strips represent one month of production. (B.) Close-up of the rock strips showing some rock strips with two (first from left) and with one (second from left) month of production.

determined by using four 0.5 m² plots, which were cleared of all biological growth, and fenced in order to stop invasion by vagrant grazers. Every month, for a period of seven months, a row of 24 rock strips (each about 50 cm² each) were removed from surrounding substrata, sterilized, and 6 of these were glued down in each of the four cleared plots (Fig. 2). Thus, after seven months, I had rock strips on which algal growth was anywhere from one to seven months old. This allowed calculation of the rate of production per unit area per month, which in turn was converted to daily production rates as a function of the accumulated algal biomass measured in g m⁻² of dry matter.

In order to verify the daily production of algae, a short-term experiment was conducted at the locality of Oudekraal (Fig. 1). In each of four 0.25 m² cleared plots, 30 sterile rock chips were glued down; each plot was fenced to stop invasions of invertebrate grazers. The rock chips were lifted at 1, 4, 6, 12, 16, 19, 22, 33, and 37 days after commencement of the experiment. On each rock strip, the total content of Chlorophyll-*a* was determined (see Materials and Methods of Chapter 3). Subsequently, the total chlorophyll-*a* was converted to dry biomass using the relationship presented in Chapter 3, where the intercept was forced through zero ($a=0$), and described by the linear equation

$$DM = 0.00491 * Chl - a, \quad (7)$$

where *DM* is the dry algal mass per cm⁻² and *Chl-a* is the amount of chlorophyll *a* in µg per cm⁻².

Drift kelp input

The average daily amount of drift kelp biomass (g m⁻² d⁻¹) available for limpet consumption, as represented by the parameter *k* in expressions (3) and (4), was determined over a 21-month period at the localities of Groenrivier and Rooiklippien on the west coast (Fig. 1). Kelp accumulation at different intertidal levels (i.e. low, mid, and high shore) was recorded each month over a three to four days during a tidal period. At each of the intertidal levels, a fixed transect about 30 m long was placed parallel to the

A.



B.

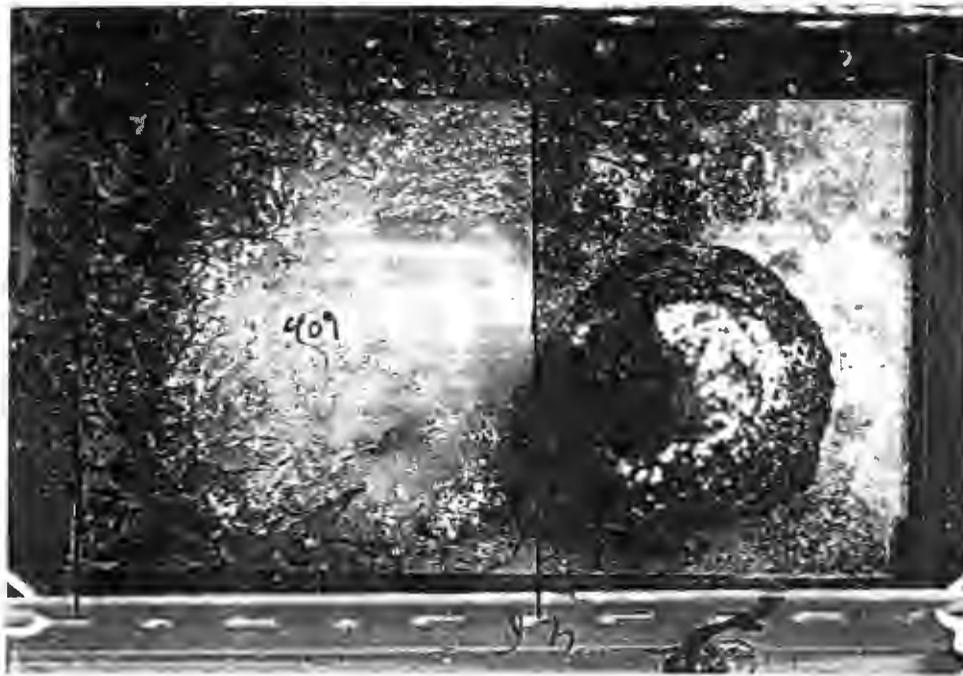


Figure 3. General view of a plot for the measurement of consumption of epilithic algae (A.), and (B.) close-up of a individual cage.

sea, and 15 quadrats of 0.5 m^2 each were chosen randomly along each of the transects. In each quadrat the wet biomass of accumulated drift kelp was recorded, and this value was subsequently converted to dry biomass. The west coast of South Africa has a semi-diurnal tidal regime that allows kelp to be deposited in large quantities during low tides occurring roughly twelve-and-a-half hours apart. The daily variation in kelp biomass available to limpets is greater than any seasonal or interannual fluctuations (Kruskall-Wallis $F_{(df=20,2,3)}=23.8$, $p<0.0001$). For the 21 months series, I recorded a running mean of at least $100 \text{ g m}^{-2} \text{ d}^{-1}$ of drift kelp is deposited daily, and this value was used as the constant kelp flux in expressions (3) and (4). This figure might be conservative as wet biomasses up to $12000 \text{ g m}^{-2} \text{ d}^{-1}$ are commonly found during low tides (see Fig. 4, Chapter 5). However, when the input of kelp is large, most of it is surplus to the limpets' needs, so the assumption of constant k seems reasonable. However, all deposited kelp is re-suspended at high tide and redistributed over the same and/or different areas, so the exact amount available to limpets for grazing is hard to estimate. Although this approximation has been employed, the parameter k can be "tuned" until the values of limpet and algae biomass predicted by the model under a variety of appropriate conditions match those observed.

Limpet consumption

Epilithic algae

The maximum (saturation) consumption of epilithic algae by individual limpets in the field was determined by using a series of 15 ground-glass settlement plates, on which algae were grown for one to two months in the absence of limpets. After this period, average-sized adult limpets (50-60 mm shell length) were starved for a 5 days, and single starved limpets were introduced onto the plates for a 6-day period (Fig. 3). Daily consumption was calculated by measuring the area of algae cleared by the limpet per day, and subsequently converting area to dry biomass. For that purpose, a photograph was taken each day of each glass plate with a feeding limpet on it, digitized, and the area cleared by the feeding limpet was measured. Each plate was divided into two halves, one

half with the limpet and one ungrazed. The ungrazed area was scrapped to provide an estimate of the algal mass per-unit-area available to the limpet. The other (grazed) half allowed estimation of how much alga the limpet removed. At the end of the feeding experiment, the maximum *per-capita* consumption rate δ_a of epilithic algae in equation (3) was obtained from these data by plotting consumption as a function of feeding time (i.e. per day) and expressed as grams of algae per day (g d^{-1}).

Drift kelp

Similarly, the *per-capita* consumption of kelp by individual limpets was determined in the field, by offering kelp fragments of pre-determined area and biomass to a series of individually labeled limpets. The premeasured kelp pieces were removed hourly over an 8-hour period from beneath the limpets, and their area and mass measured. The same procedure was repeated on three different days in two different localities (Groenrivier and Rooiklippias, see Fig. 1) and used to derive an average rate of consumption of kelp per limpet.

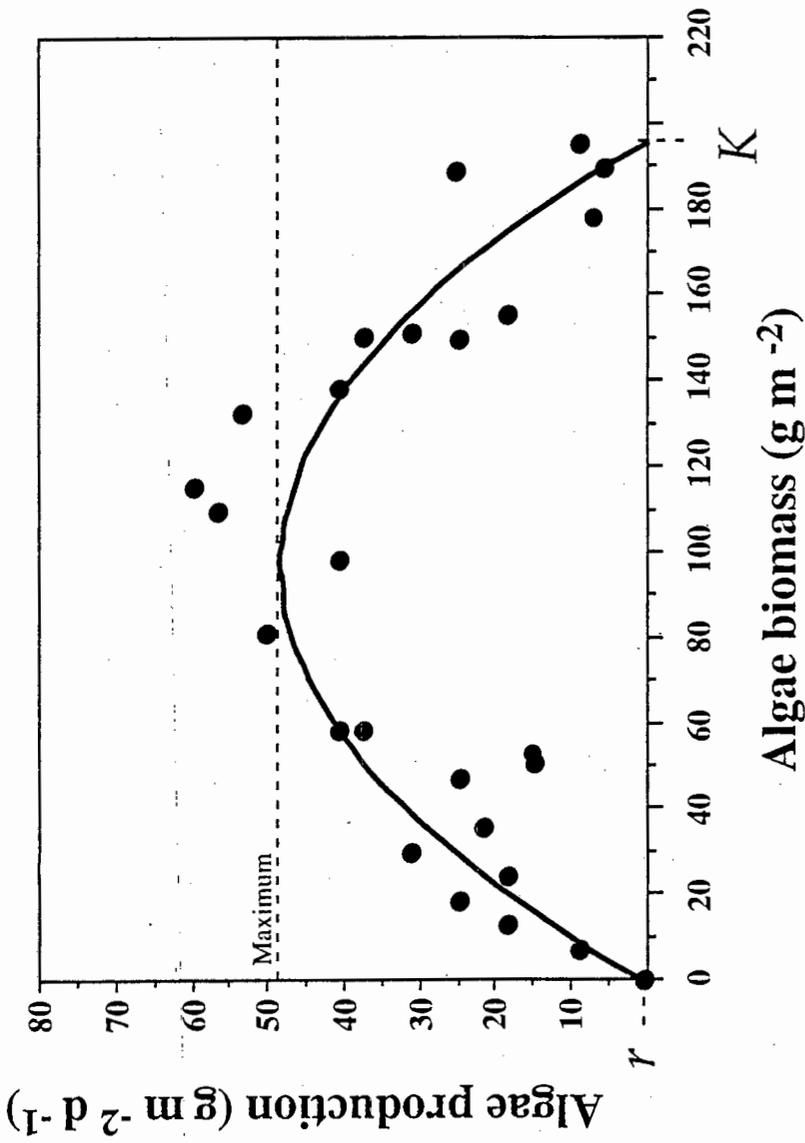


Figure 4. Epilithic algae production data. Each dot represents an empirically measured algal production rate as a function of the algal biomass density indicated on the abscissa using protocols outlined in the text. The parabolic (quadratic) growth curve was fitted by non-linear regression and maximum likelihood estimate of the parameters; $r = 0.5$ ($\text{g m}^{-2}\text{d}^{-1}$) and $K = 195$ (g m^{-2}).

Results

Algal production

A parabolically shaped (logistic) curve was obtained for the rate of algal production as a function of the biomass accumulated (Fig. 4). The rate of algal production rose sharply until it reached a plateau or maximum production rate of $Kr/4 \approx 49 \text{ g m}^{-2} \text{ d}^{-1}$. After that, the available space for algal settling becomes limiting (saturation), leading to a decline of the rate of production as the system approaches the carrying capacity (Fig. 4). Thus, the production curve was described by the logistic parameters of the algal equation in system (1), where the values estimated from the field data are $r \approx 0.55 \text{ g m}^{-2} \text{ d}^{-1}$ and $K \approx 195 \text{ g m}^{-2}$ (intercept on algal biomass axis) which corresponds to the algal carrying capacity.

Kelp input

Large quantities of drift algal material were found in the sheltered bays along the west coast. Kelp fronds were by far the largest component of the total algal drift (Fig. 5), achieving up to 2000 g m^{-2} of dry matter (Fig. 5). The dry biomasses of drifting fronds of kelp were on average an order of magnitude greater than those of the other groups of algae (i.e. other phaeophytes, rhodophytes, and chlorophytes), whose biomass never exceeded 150 g m^{-2} . During the 3 years of monitoring, there was a clear seasonal trend in the drift accumulation, the summer-autumn seasons having significantly (Bonferroni *t*-test, $p < 0.05$) larger amounts of the kelp ($700\text{--}1200 \text{ g m}^{-2}$), than winter-spring (about 200 g m^{-2}) (Fig. 5). The variations of drift kelp were significantly explained by monthly (ANOVA, $p < 0.0004$) and seasonal variations (ANOVA, $p < 0.0015$), but no significant differences were found between years (ANOVA, $p > 0.4787$) (Table 1). The average deposition of the other drift algae was highly variable (Fig. 5), being significantly explained by variations between years (ANOVA, $p < 0.0001$), between seasons (ANOVA, $p < 0.0004$) and between months (ANOVA, $p < 0.0028$) (Table 1). There was an inverse

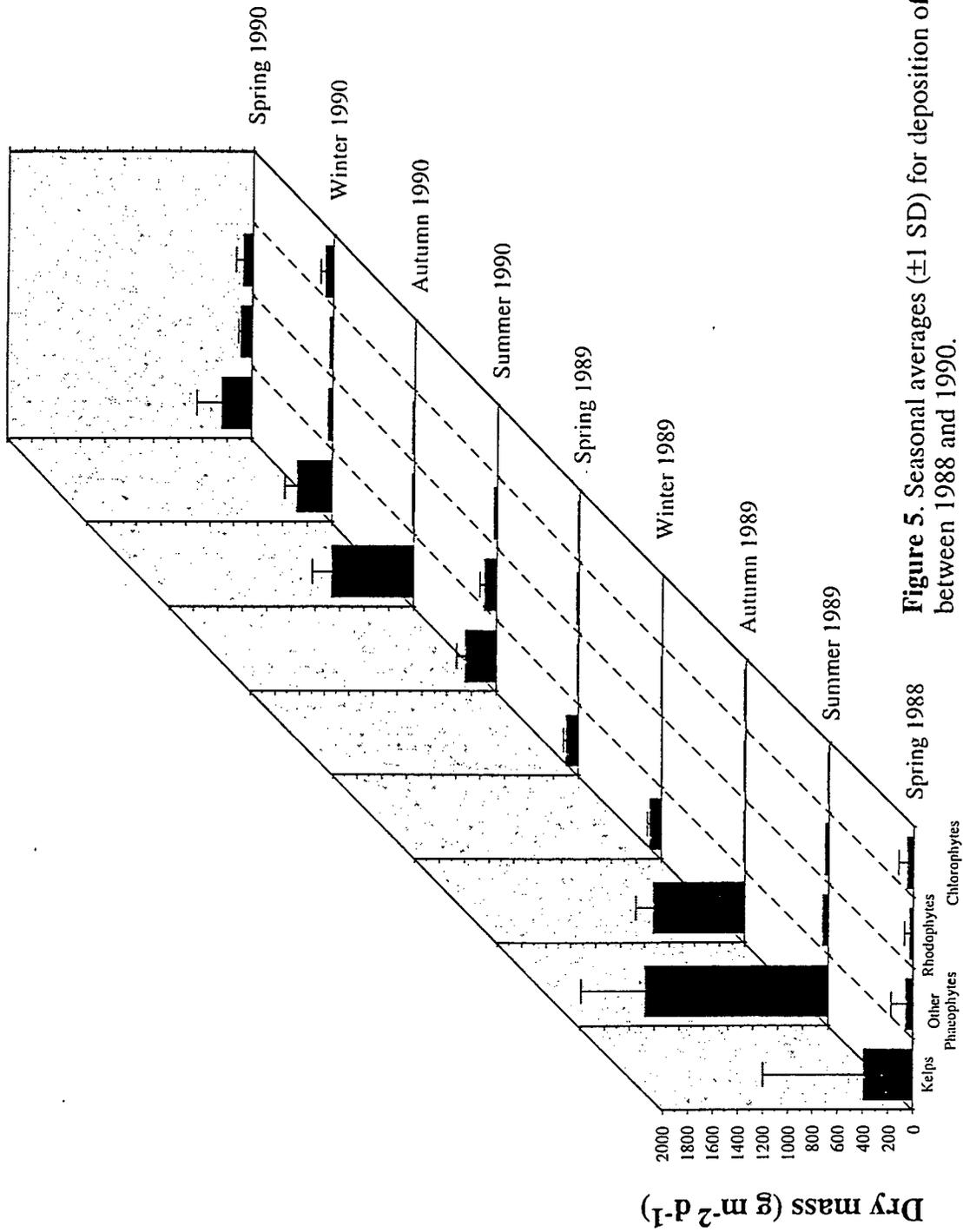


Figure 5. Seasonal averages (± 1 SD) for deposition of drift algae between 1988 and 1990.

Table 1. ANOVA for the main effects explaining variation in the dry biomass of drift algae over a 21 month period at the locality of Groenrivier.

Source of variation	Response variables							
	Kelp fronds			Other algae				
	df	Mean square	F	p	df	Mean squares	F	p
Seasons	3	20069186.7	5.22	0.0015	3	16558.2901	6.18	0.0004
Years	2	2837731.8	0.74	0.4787	2	24632.9314	9.20	0.0001
Months	20	16229569.8	4.22	0.0004	20	9005.1178	3.36	0.0028
Error	416	3845197			713	2678.221		

Table 2. Spearman rank correlation coefficients between drift kelp and other drift algae at Groenrivier.

Seasons	r	n	p	Years	r	n	p
Winter	-0.855	210	<0.0001	1988	-0.822	333	<0.0001
Spring	-0.800	364	<0.0001	1989	-0.839	545	<0.0001
Summer	-0.776	328	<0.0001	1990	-0.819	275	<0.0001
Autum	-0.858	251	<0.0001				

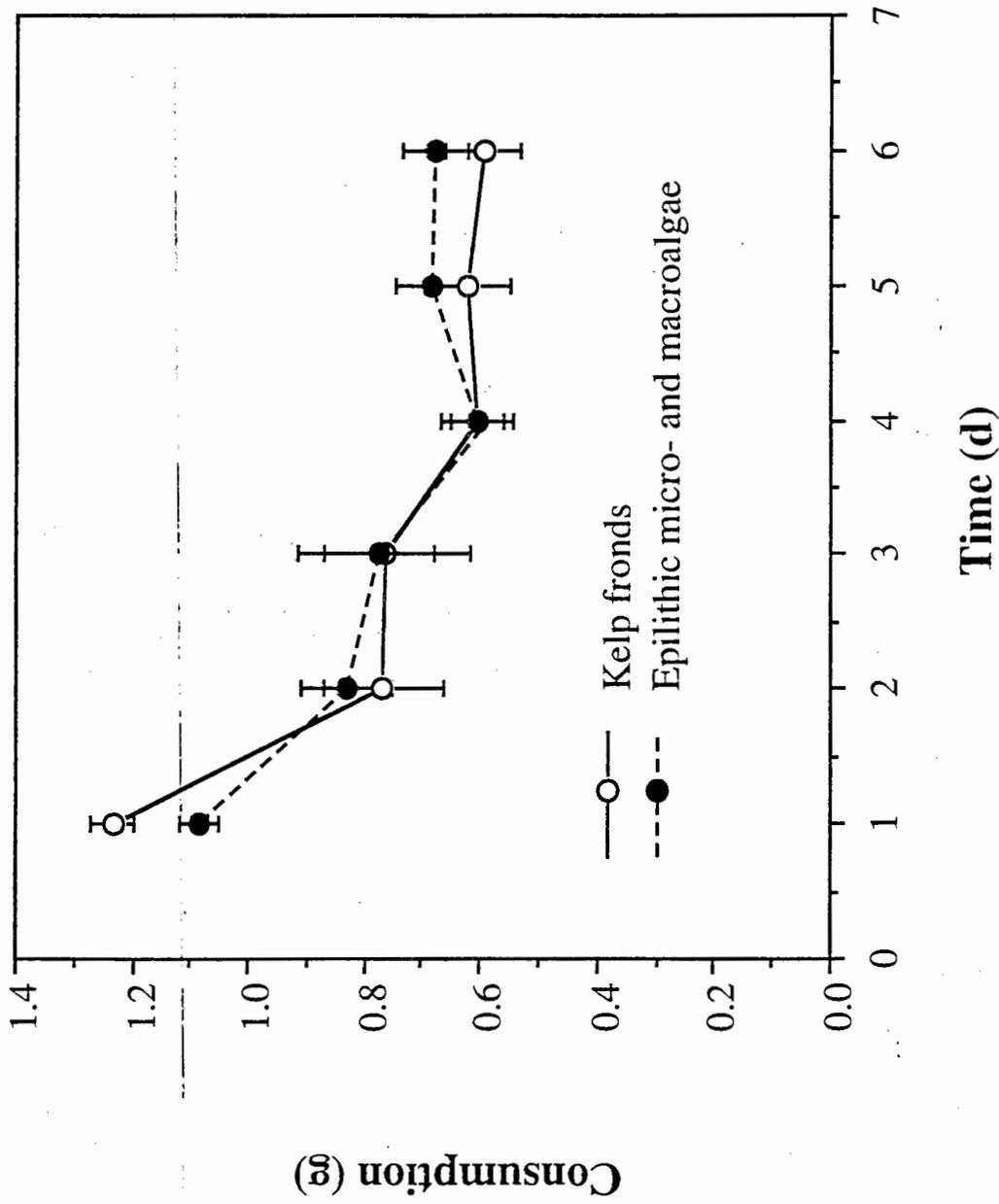


Figure 6. Individual *P. granatina* average (± 1 S.D.) consumption rates when feeding on kelp fronds and epilithic algae as a function of feeding time.

correlation between the biomass of drift kelp and the biomass of other algae, being consistently negative throughout the different seasons and years (Table 2).

Limpet consumption

Given an unlimited supply of kelp, *P. granatina* initially fed at a maximum intake ($\pm 1.37 \text{ g d}^{-1}$) but decreased the rate of intake thereafter, until it reached a level in which individual limpets grazed at a stable rate ($\pm 0.68 \text{ g d}^{-1}$, see Fig 6). A similar pattern was found when the limpets fed on epilithic micro- and macroalgae, i.e. a maximum intake at the beginning (about 1.52 g d^{-1}) and followed by a stable intake (Fig. 6). The high ingestion at the beginning of the experiment appears to be a reflection of the 5 days of starvation time. During the feeding experiment, individuals of *P. granatina* fed slightly more on kelp fronds, than on epilithic algae.

In (3) and (4) the parameters δ_a and δ_k , which represent the saturation consumption rates, in the field, of algae and kelp respectively. The running average of individual consumption were calculated, being $0.73 \pm 0.10 \text{ g d}^{-1}$ and $0.81 \pm 0.05 \text{ g d}^{-1}$ for algae and kelp respectively. Because both consumption rates were similar in magnitude and variability I used the same average value $\delta_a = \delta_k = 0.78 \text{ g d}^{-1}$ for both in resource extraction rate expressions (3) and (4).

Parameters tuning

The feeding rate experiments were not specifically designed to help estimate the searching efficiency parameters β_a and β_k and the self-interference parameters γ_a and γ_k . Feeding rate experiments performed with lone individuals, as was done with the limpets, cannot be used to estimate interference which is a group feeding effect. Given the limitations of the experimental data, for the sake of simplicity I assumed $\beta_a = \beta_k = \beta$, and $\gamma_a = \gamma_k = \gamma$.

A sensitivity analysis was done in order to evaluate the performance of the model under different values of parameters β and γ , and by consequence, suitable values of

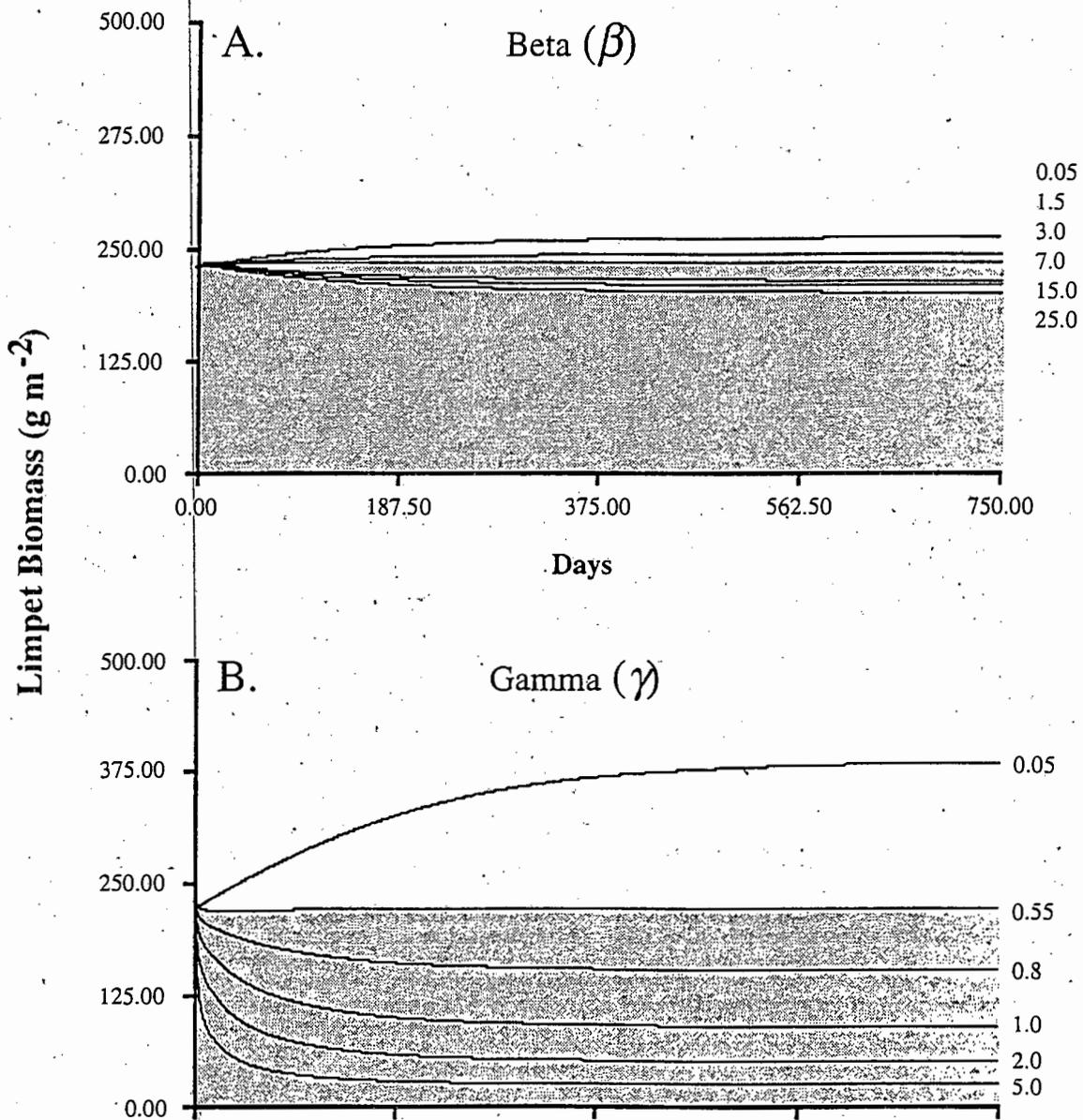


Figure 7. Predicted limpet biomass levels from the kelp-algal-limpet model (equations (1) - (4)) under a sensitivity analysis of (A.) half saturation parameter β and (B.) the self-interference parameter γ . Values of the sensitivity scenarios are indicated on the right hand-side.

these parameters. The searching efficiency parameter β (or the concentration of food that reduces the grazing rate δ to half) was tested over a range of four order of magnitudes (from 0.01 to 25 g m⁻²), while the self-interference parameter γ (or the limpet density that diminish the *per-capita* consumption δ to a third) was tested over variations of three order of magnitudes (from 0.01 to 5 g m⁻²).

The model turned out to be relatively insensitive to the value of β , but over the tested range the best fit to observed data was obtained at $\beta = 3$ g m⁻² (top of the shaded area in Fig. 7A). When the parameter β was increased from 0.05 to 25 g m⁻² the limpet biomass was reduced only 13% relative to the original carrying capacity (226 g m⁻²), and stable populations were always obtained at the end of simulation (Fig 7A).

Changes in the value of self-interference parameter γ , yielded substantial variations on the predicted limpet biomass. That is, increasing limpet biomass has deleterious effects on individual consumption efficiency, resulting on drastic decrease in the population biomass (Fig. 7B). However, the parameter value that seemed to fit the time course of the observed data the best was $\gamma = 0.55$ g m⁻² (top of the shaded area in Fig. 7B).

The preference parameter p in models (3) and (4) was set at 0.6, which represent the observed proportion of kelp in the limpet's diet, whereas algae occur in a proportion of 0.4 (see detailed in Fig. 10, Chapter 5). To account for nutritional differences between algae and kelp, a food quality factor q was included (see equation (1)), based on the average C:N ratio (Carbon to Nitrogen) of both algae and kelp. The average C:N ratios for several species of algae and for the fronds of two kelp species respectively have been estimated at 10:1 and 22:1 (Levitt 1991; S. Tugwell pers. comm.). Therefore, I considered that one unit of epilithic algae corresponds nutritionally to two units of kelp and so set $q = 2$, giving more nutritional value to the epilithic algae.

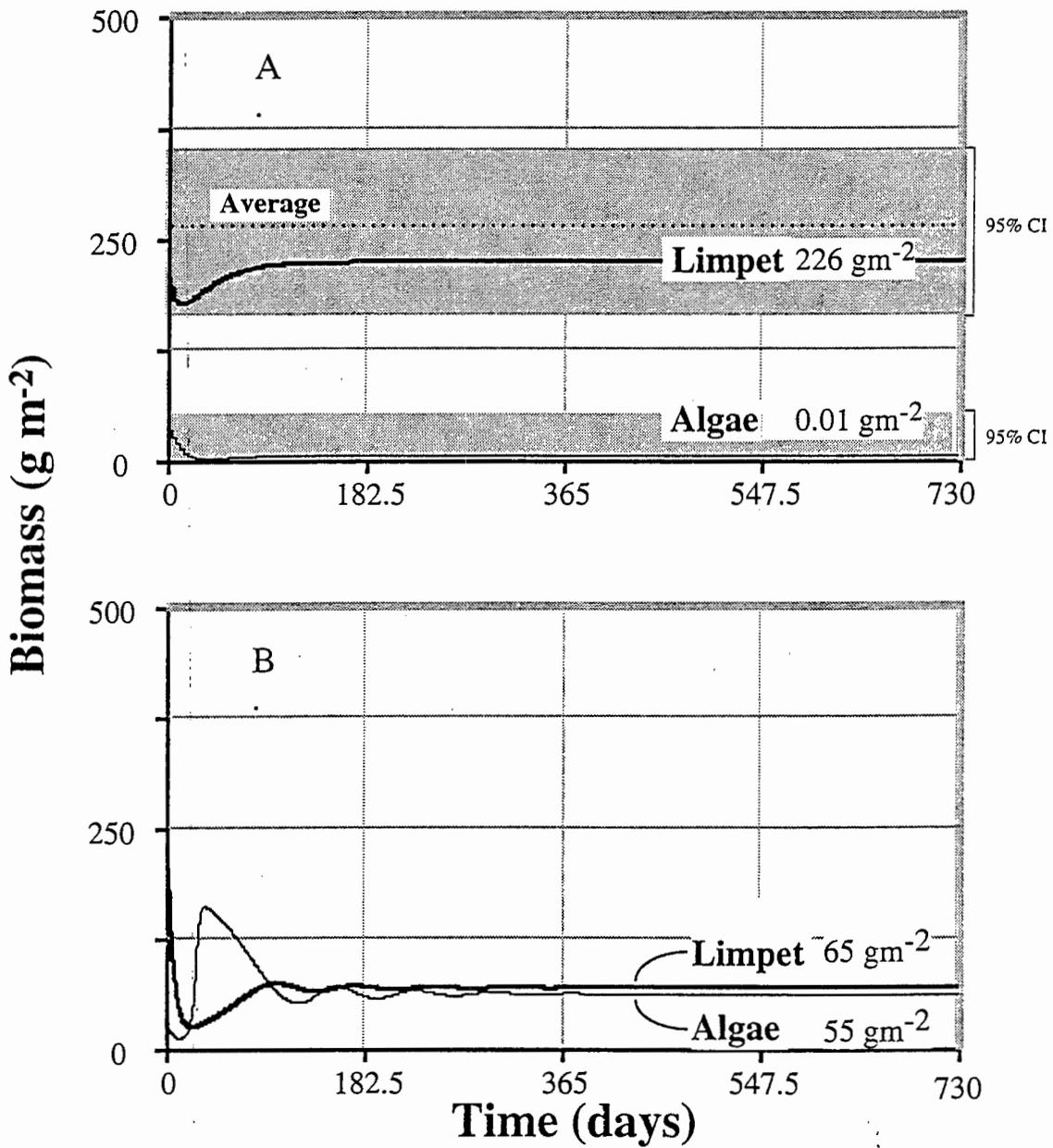


Figure 8. Simulated limpet-algae scenarios. The thick and thin solid lines represent the output from the algal-kelp-limpet model (equations (1)-(4)) for background kelp levels of (A.) $100.0 \text{ g m}^{-2} \text{ d}^{-1}$ and (B.) $0.0 \text{ g m}^{-2} \text{ d}^{-1}$. The shaded areas represent the 95% confidence intervals estimated from observed limpet and algal levels in the field.

Model verification

Once I had obtained initial estimates for all parameters associated with equations (1) - (4), I then evaluated the performance of the model of the algal-kelp-limpet system under consideration by comparing model output with empirically obtained data on limpet and algae biomass levels presented in the Chapters 2 and 3 (which were obtained independently of the data used to obtain the parameter estimates). This also provided an opportunity to tune certain parameters of the model (see previous section) to improve its fit to the data, so that the model could be more reliably applied to the analysis of various ecological and management questions. Confidence in a model is increased if it can be shown to simulate the behavior of a real system under a variety of conditions. I was able to verify that the model performed reasonably well in two situations: a) in the presence of drift kelp input, set at a conservative average observed level ($k = 100 \text{ g m}^{-2} \text{ d}^{-1}$), and b) in the complete absence drift kelp input into the system, i.e. the limpets relying only on the *in-situ* micro- and macroalgal production ($k = 0.0 \text{ g m d}^{-1}$). The latter condition was set to verify whether the model is able to reproduce the empirically-determined effect of kelp exclusion (see Figs. 11 and 12, Chapter 5).

First, I compared limpet and algal population levels predicted by the model with data obtained from an unexploited system (Fig. 8A). The model predicts that limpet and algal populations should reach stable equilibrium densities of 226 g m^{-2} and 0.01 g m^{-2} respectively, both being within the range of values observed in the field (shaded areas of the 95% of confidence intervals in Fig. 8A). The predicted limpet biomass is equivalent to average recorded values at a density of about 200 m^{-2} (see Fig. 5, Chapter 5), while the prediction of algae biomass corresponds to the background level of primary standing stock that remains after limpet grazing (endolithic algal standing stock, see Hill and Hawkins 1990).

Second, I compared model simulations of another scenario, in which input of kelp into the system is zero, with data obtained from manipulations done in the field where drift kelp was experimentally excluded from the system (see data presented in Chapter 5). In

this case, the model predicted a rapid initial reduction of the limpet biomass to a minimum level of *ca.* 30 g m⁻² (about 34 limpets per m⁻²), followed by an increase to a stable equilibrium at 65 g m⁻² (Fig. 8B). This represents a 71.3% decrease in the limpet population relative to the equilibrium level predicted under natural conditions (shaded area in Fig. 8A). The reduction of the limpet biomass in turn results in diminishing grazing pressure on the epilithic algal growth. This produces an initial "bloom" of algal growth during the first 45 days that is subsequently reduced to an equilibrium level of 55 g m⁻², as the limpet population approaches its equilibrium, consequently increasing grazing pressure. Note again, that the predicted algal levels are also within (but at the high end of) the 95.5% confidence interval of observed algal levels (as indicated by lower shaded area in Fig. 8A). Thus, under two sets of contrasting conditions the model simulates values of limpet and algal standing stocks within the range of values empirically measured in the field.

Management analysis

An exploitation regime for intertidal limpet stands can be compared with that of a plantation management regime for a forest stand of same-aged trees (even-aged stand management - see, Clark 1976, or Getz and Haight 1989). This consists of harvesting all trees in the stand at the end of each rotation cycle and then planting the stand with seedlings. The optimal rotation period can be calculated, if the trajectory of the value of the stand from time of planting onwards is known, and if every rotation cycle is assumed to have the same biological and environmental parameters (e.g., no depletion of nutrients, no change in climate averaged across the seasons). A stand of limpets can be regarded in the same way, except harvesting consists of removing all limpets over a certain size and letting the smaller (and immigrant) limpets form a "seed" population for the subsequent growth of the limpet stand.

First, the model was used to simulate the growth of a bare stand, assuming average empirically observed recruitment conditions of 200 individuals with an average shell lengths of less than 20 mm (Bosman *et al.* 1990), which in turn represents a flesh dry

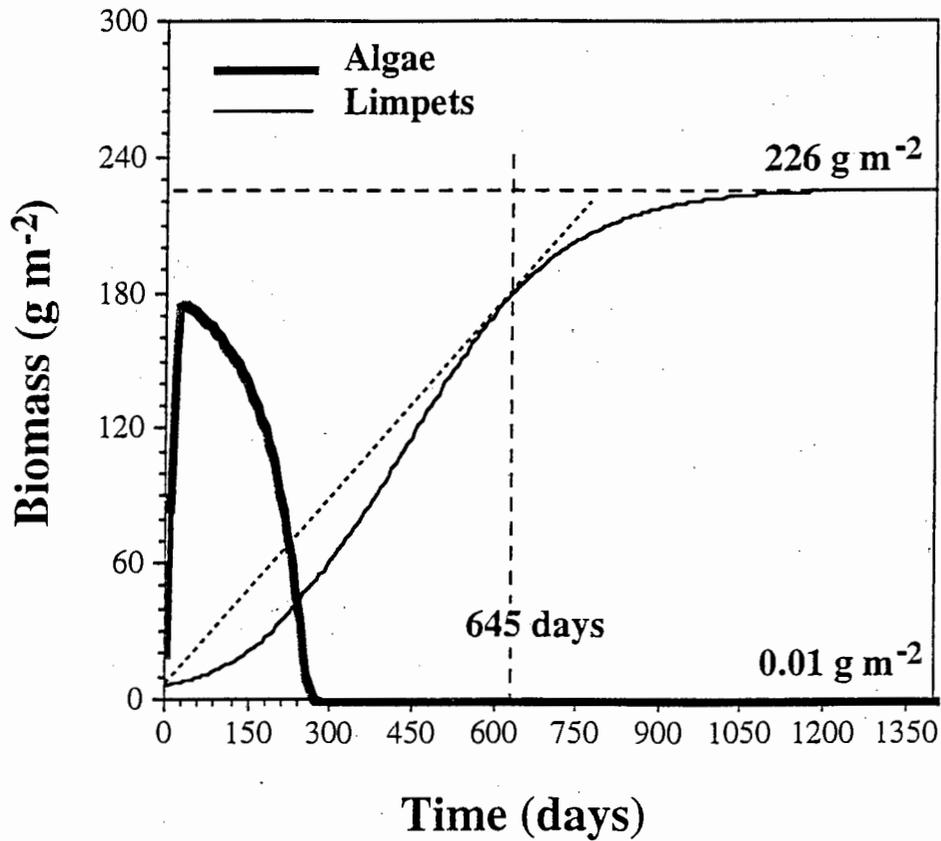


Figure 9. Stocking-up of a *P. granatina* population. The thin and thick curves respectively represent the simulated growth of limpets on a stand (appropriate intertidal rock substrate) and associated algal density levels over a 1400 day period. The maximum production of biomass per unit time is achieved around 645 days and the stand density saturates at 226 g m² a little after 3 years.

mass of 8 g m^{-2} . Allowing the limpet biomass to grow freely ('stocking-up'), after a hypothetical removal of the adult biomass (in the absence of density dependent effects), the initial limpet biomass of 8 g m^{-2} rises to a saturation level of around $220\text{-}230 \text{ g m}^{-2}$ after about 3 years (Fig 9). Over the 3.7 year simulation period, the model predicts that the initial low limpet biomass permits a rapid algae growth during the first 45 days (as in Fig. 8B). Once the limpet population has built-up its biomass, thereby increasing its grazing pressure, the algae biomass is rapidly reduced to a minimum equilibrium level of 0.01 g m^{-2} (or background levels) over a period of around 9 months. After the first two years the biomass growth rate of the stand declines rapidly as the system approaches its limpet carrying capacity. The maximum biomass produced per unit time occurs at around 180 g m^{-2} , which is reached around 645 days (Fig. 9).

The results of this simulation imply a two-year optimal rotation period for total-stand harvest policy (i.e., when all limpets are removed regardless of size).

Second, I used the model to analyze predicted sustainable yield levels under annual and biennial (two-year) pulsed harvesting policies that remove a fixed proportion of the population (all limpets over 40 mm) at the beginning of each cycle (Fig. 10). In unexploited or virgin limpet stands 60 to 90 % of the total biomass density is represented by adult limpets (Bosman *et al.* 1990). The first year's yield from a virgin stand (Fig. 10, curve a) is always more than can be obtained in subsequent years, even under equilibrium conditions (Fig. 10, curve c). Note that the "equilibrium" value, plotted in Fig. 10, was obtained from the model after 15 years of annual pulsed harvesting of a fixed proportion of the available stand biomass starting with a virgin stock of 226 g m^{-2} (Fig. 10, horizontal dotted line--and see Fig. 8A). This value is an upper estimate of the equilibrium in the sense that it represents less than a 0.01% decrease from the values obtained after 14 years.

Third, I compared pulsed harvesting on an annual (Fig. 10, curve c) and a biennial basis (Fig. 10, curve b) with the annual average of the latter (Fig. 10, curve d). The biennial yield (curve b) is close to first-year levels for all levels of proportional harvesting

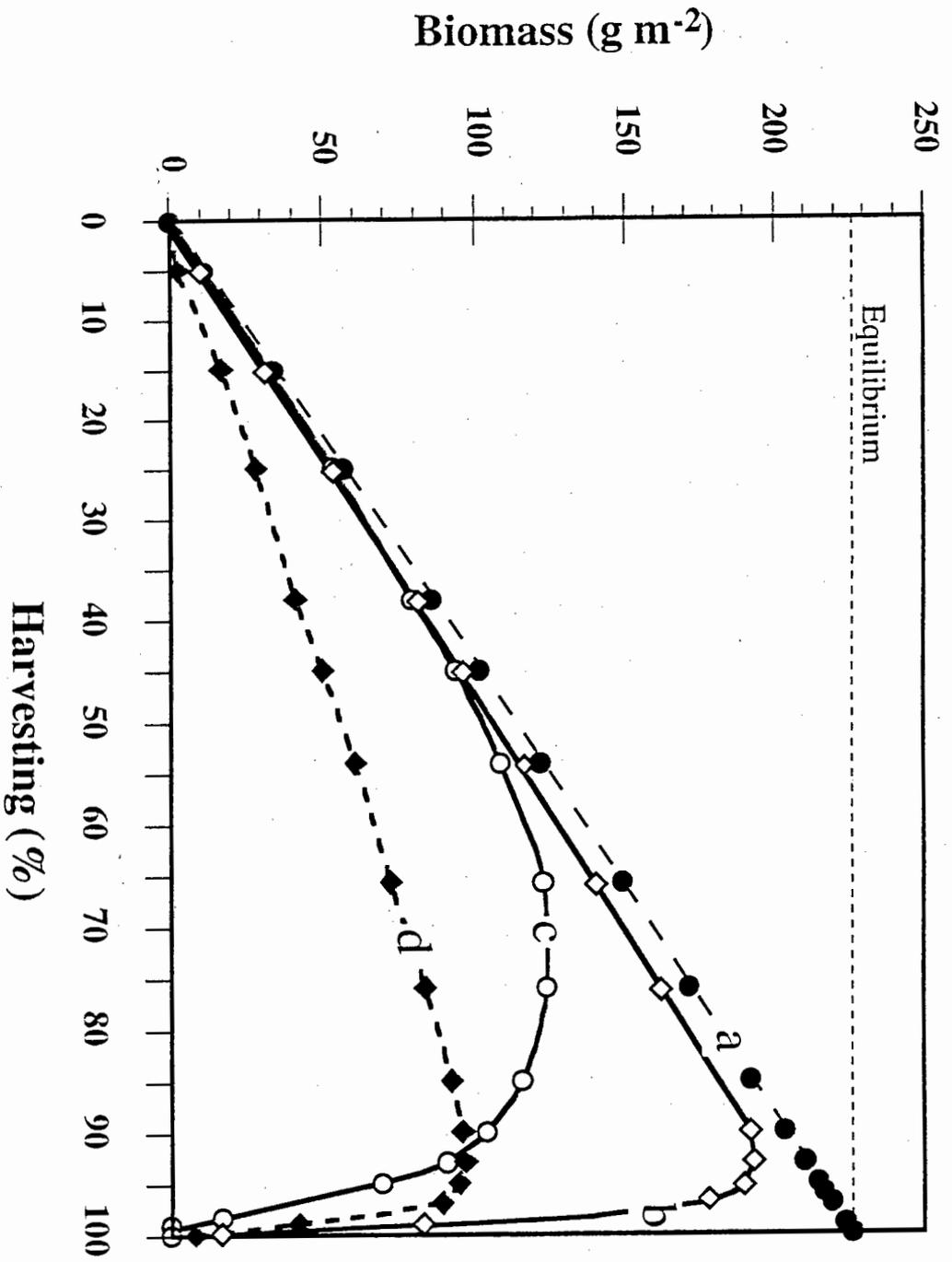


Figure 10. Sustainable yields. Line a (dotted, solid circles) represents the amount of biomass that would be removed from a fully stocked (mature or pristine) limpet stand under a proportional (percent) pulsed-harvesting regime. Curve b (solid, open diamonds) represents the equilibrium yield as a function of the indicated level of pulsed-harvesting every second year, while curve d (dotted, solid diamonds) is the annualized equilibrium value of this biennial yield (i.e., half of the value of b). Curve c (solid, open circle) represents the equilibrium yield as a function of the indicated level of pulsed-harvesting every year.

below 90%, and then drops off dramatically between 90 and 100%. At this high levels of harvesting, insufficient seed population is left behind to initiate stand growth. Immigration should contribute to a slow recolonization, but this is not taken into account in the model. Annualized biennial yields (curve d) result in harvests that are considerable smaller than the annual rate except for proportional harvesting levels above 85%. The sustainable pulsed annual yield is maximized at around 70% proportional harvesting, representing a biomass of around 130 g m^{-2} , and corresponding to about two thirds of the limpet first-year harvesting under this policy (compare curves a and c at 70% proportional harvesting). On the other hand, the biennial maximum sustainable yield (MSY) is as much as 93% of the total limpet biomass, but on an annualized basis this only yields a little less than 100 g m^{-2} (maximum value for curve d in Fig. 10). Although the model predicts that the annualized MSY from the biennial policy is 30% less than the MSY of the annual policy, the costs of harvesting are not included. Since I might expect the harvesting costs associated with the annual policy to be almost double those of the biennial policy, the biennial policy may compare favorably with the annual policy from a net profit point of view. Further, biennial exploitation of different areas in alternate years would smooth out the market on an annual basis. Finally, although stand growth simulation from a seed population (Fig. 9) predicts an optimal rotation period of almost two years, greater yields are obtained on a one-year rather than two-year basis if the harvesters are free to remove any fixed proportion of the population that they may choose (Fig. 10).

Discussion

The predictions arisen from the metaphysiological model developed in this Chapter re-emphasize that the input of drift kelp into the intertidal system (Fig. 5) is the limiting factor that sets the carrying capacity of *P. granatina* populations (Fig. 8). Despite the fact that intertidal epilithic algae production is high (Fig. 4), it is clearly insufficient to maintain dense stands of limpets (Fig. 8B), a finding that agrees with the empirical evidence that resulted from experiments in which kelp is excluded (see Chapter 5).

The dynamics of intertidal primary production (epilithic micro- and macroalgal production) has been one of the most consistently neglected components in studies of marine benthic communities, mainly due to technical difficulties (e.g. Underwood 1979; Hawkins and Hartnoll 1983; Hill and Hawkins 1990; 1991). However, the results presented in this Chapter (in addition to those presented in Chapter 3), show that the dynamics of intertidal primary productivity (per-unit-area) can be assessed in a simple way, and more important, its trophic relationship with herbivore consumers can be established and modeled using a predator-prey, or better, a consumer-resource approach (i.e. Lotka-Volterra-Gause systems).

A hyperbolic curve has been predicted for autotrophic productivity as a function of accumulated biomass (Oksanen 1981). The production data show that the per-unit-area dynamics of the intertidal algal production do have a logistic growth (Fig. 4). This is in line with the findings of terrestrial pastures where logistic-shaped curves have been also reported (Brooke 1989; Dyer *et al.* 1993) and rivers (Hart *et al.* 1991). The significance of these results is that intertidal systems can be successfully compared on similar basis, according to their intrinsic productivity dynamics. Furthermore, large-scale comparison can be made across systems (e.g. subtidal/intertidal) and the impact of herbivore consumers can effectively evaluated.

The input of subtidal kelp (drift) into the intertidal system constitute a super-abundant food supply for *P. granatina*, whose populations can be successfully maintained by an input of $100 \text{ g m}^{-1} \text{ d}^{-1}$ drift into sheltered bays; the total input generally greatly exceeds this figure (see Fig. 5). This and the findings of the previous Chapters demonstrate the importance of two processes in the maintenance of high grazer biomass on the west coast of South Africa. First, this is another clear example of secondary magnification of an intertidal system by kelp subsidy (e.g. Dunton and Schell 1986; Duggins *et al.* 1989; Simenstad *et al.* 1993), in which the *in-situ* intertidal productivity is insufficient to sustain a dense herbivore population. The second is that, given a consistently high food supply (in the form of both *in-situ* productivity and kelp subsidy) the carrying capacity for *P. granatina* is set by limitation of the space available to them (see also Fig. 4, Chapter 5).

The 'bloom' of epilithic algae growth following reduction of limpet grazing pressure is a well known ecological phenomenon that has been extensively documented by field experiments (e.g. Jones 1948; Underwood and Jernakoff 1984; Bosman 1988). The model that I have applied to the algal-kelp-limpet system clearly shows this phenomenon, with a reduction of the *P. granatina* population leading to a rapid growth of epilithic algae (Fig. 8B).

Similarly, the model was able to reproduce another ecological phenomenon that has been empirically demonstrated, i.e. the reduction of limpet biomass that occurs if the input of drift kelp is set at zero (Fig. 8B). The empirical results arising from the kelp exclusion experiment (see Chapter 5) revealed that limpet mortality increase significantly when limpets were denied access to drift kelp, and limpets that survived to the end of the experiment, lower body mass than control animals that could feed on drift kelp (Figs. 11 and 12, Chapter 5). Theoretical supporting evidence for the importance of food supply comes from the results of the sensitivity analysis performed to the model, which show that slight increases (0.55 to 1.0) in the self-interference parameter γ (i.e. intraspecific competition) result in a *ca.* 65% decrease in the limpet biomass (see Fig. 7B).

The validation of the model under two contrasting scenarios gave some confidence that the simulations of the ecological processes at work were reasonable. In future experiments, however, it would be desirable to obtain direct estimates of the limpet growth parameters ρ , κ and the consumption parameters β and γ so that the ecological assumptions in the model can be tested in a formal statistical evaluation of the fit of output from the model to observed data.

The advantage of functionally modeling populations, especially using the metaphysiological approach, is that with a knowledge of simple processes (e.g. production and consumption) it is possible to set a theoretical scenario based on sound ecological principles (e.g. predation and competition). Another advantage is that once the general dynamics of the undisturbed natural system have been described and modeled, they can be subjected to hypothetical harvesting regime in which a proportion of the limpet population is removed from the system and the recovery time is evaluated.

From a processing and marketing point of view, it is only worth harvesting larger limpets (typically the adults which are usually 40+ mm in shell length). Further, a reproductive adult core must always be left in place to spawn and generate a new cohort of recruits. The latter can be achieved by harvesting only after the spawning season (set a 'fishing season') or, alternatively, harvesting a fixed proportion rather than all of the adult limpets (all those > 40 mm shell length) in a fixed rotation period (years).

The difference between the first year and equilibrium yields, however, only begins to diverge strongly for proportional harvesting above 50% (Fig. 10). This difference represents the nonsustainable portion of the resource and, when large, often leads to initial overcapitalization of the equipment used to exploit the resource (e.g., boats and gear in most marine fisheries). However, in the case of limpet exploitation boats are not needed and capitalization is relatively small.

An alternative strategy to harvesting a fixed proportion of individuals in a population is to remove all individuals above a certain size. Further, it has been shown (Getz 1980,

1988; Reed 1980; Getz and Haight 1989) that the optimal harvesting strategy for a population in which recruitment and size- or age-class transition is influenced by stock biomass is one based on two size classes i and j ($j \geq i$): harvest all individuals as large or larger (as old or older) than class j and a given fraction of all individuals of class i . A more general MSY result pertaining to populations where immigration of individuals of various sizes occurs, as it does to some extent in limpet stand dynamics (Eekhout *et al.* 1992), is to remove proportions from several different size classes (Getz 1988; Getz and Haight 1989). However, this harvesting strategy impose logistics limitations because it requires a knowledge of the total amount taken from each size class (which is labor intensive); furthermore, for an intertidal resource, such as limpets, accessibility to the resource is limited to relatively short periods of time constrained by tides.

As pointed out in the introduction, any purely demographic approach such as the size-based model applied by Eekhout *et al.* (1992) to *P. granatina*, fails to take potentially critical ecological factors into account. Such size-structured models can be embedded in an ecological framework by making the values of the transition parameters p_{ij} and the survival parameters s_i dependent on the amount of food resources (g_i) removed per-unit-limpet in the i th size class. In this case, the interference term in the i th size class exploitation function g_i will depend not only on the value of x_i , but on the other size classes $x_j, j \neq i = 1, \dots, n$ (e.g. the effects of adult interference may differ from those of juveniles and 'recruits'). Furthermore, if x_i measures numbers rather than biomass, then the values x_i will have to be weighted in the interference term to bring them to comparable units, such as biomass. The dynamics of the algal population can be incorporated by using an equation, such as that in system (1); and replacing the term $x_i g_a$ with the term $\sum_{i=1}^n x_i g_i$, which represent the sum of the different rates of consumption of epilithic algae by the i th size classes. Size-related variations in kelp consumption need not be considered because individual smaller than 40 mm do not consume kelp (see Fig. 7, Chapter 5).

An evaluation of harvesting strategies related to size classes, of course, requires the construction of a size class model. Eekhout *et al.* (1992) used this type of model to estimate that MSY is obtained by harvesting all individuals larger than 55 mm every year. Their MSY of 13 metric tons is not directly comparable to results derived from the present analysis, since my work is calculated on a per-unit-area basis, while the size-based analysis had a fixed population in mind. As Eekhout *et al.* (1992) point out, their analysis is contingent on very crude assumptions about size dependent rates of mortality, and they also use growth rates that did not depend on density. I obviated these two difficulties by using a metaphysiological approach that does not explicitly require mortality and size-at-age relationships. However, this approach has a disadvantage in that it does not relate the harvesting strategies to size. Obviously, it would be much better if size structure could be incorporated into the approach, but the data are at present inadequate to pursue this level of analysis. To do so it would need, at least, empirical assessments of the size-distributions (assuming approximate constancy of these distributions over the long run) that would arise under contrasting harvesting regimes, so that the distributions under intermediate regimes can be appropriately extrapolated from data. The more stage-classes present in the model, the more survival parameters and, especially, transition parameters that will need to be estimated from field data (Eekhout *et al.* 1992). The situation becomes even more complicated if these parameters are themselves, as I might expect, functions of the type of ecological consumption and physiological growth processes implicit in model (1).

Apart from a limited number of multispecies interaction studies, such as the analyses of May *et al.* (1979) and Flaaten (1988), surprisingly little effort has been devoted to incorporating ecological information into marine fisheries management analyses. Hilborn (1992), for example, in an extensive review of current trends in fisheries stock assessment and management, concluded that fisheries management in the future will focus on the behavior of fishermen and on Bayesian decision analysis. Although those approaches are highly relevant, they are no more critical than ecological approaches to the issue of the sustainable management of marine resources and the preservation of

commercially valuable species. I agree with Ludwig *et al.* (1993) that improved techniques for decision-making under uncertainty are essential if we are to manage the resources in a more rational fashion. Ecological considerations, however, are neglected with a consequent lack of reality. Here I propose a "strategic" model that has little biological detail and hence does not rely on extremely hard-to-get parameters (Holling 1966; Yodzis 1991). Yet I believe that this kind of modeling still embodies sound ecological principles pertaining to population growth and consumptive processes, and could be used to provide an ecological complement to more conventional single-species studies of population exploitation

Ideally, the present study should be interconnected with the size-based, single-species approach used by Eekhout *et al.* (1992) in developing management recommendations for the commercial harvesting of *P. granatina*. The two approaches are complementary, require different kind of inputs, and are constrained by different sort of problems.

References

- Akçakaya, H. R. 1992. The population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecological Monographs* **62**: 119-142.
- Arditi, R., and H. Saïah. 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* **73**: 1544-1551.
- Arditi, R., N. Perrin, H. and Saïah. 1991. Functional responses and heterogeneities: an experimental test with cladocerans. *Oikos* **60**:69-75.
- Blankley, W. O. 1988. Commercial potential and appropriate management strategies for limpets on the coast of Namaqualand, South Africa. MBA Thesis, Graduate School of Business, University of Cape Town.
- Bosman, A. L. 1988. The influence of primary production rate on the dynamics of *Patella granularis*, an intertidal limpet. *P.S.Z.N.I. Marine Ecology* **9**: 181-198.
- Bosman, A. L., P. A. R. Hockey and W. R. Siegfried. 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. *Oecologia (Berlin)* **72**: 226-232.
- Bosman, A. L., S. Eekhout and G. M. Branch. 1990. The exploitation potential of limpets on the coast of Namaqualand. Final report to the Chief Director, Marine Development, Sea Fisheries Research Institute. Marine Biology Research Institute, Zoology Department, University of Cape Town, April 1990, p. 69.
- Branch, G. M. 1975. Mechanisms reducing intraspecific competition in *Patella* spp.; migration, differentiation and territorial behaviour. *Journal of Animal Ecology* **44**: 575-600.

- Branch, G. M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography Marine Biology Annual Review* **19**: 235-380.
- Branch, G. M, J. M. Harris, C. Parkins, R. H. Bustamante and S. Eeekhout. 1992. Algal 'gardening' by grazers: a comparison of the ecological effects of territorial fish and limpets. Pages 405-424 *in* D. John editor. *Plant-animal interactions in the marine benthos*. Systematic Association Special volume **46**, Claredon press, Oxford.
- Brown, P. C. 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. *South African Journal of Marine Sciences* **12**: 515-525.
- Brown, P. C., and K. L. Cochrane. 1991. Chlorophyll-*a* distribution in the southern Benguela, possible effects of global warming on phytoplankton and its implication for pelagic fish. *South African Journal of Marine Sciences* **87**: 233-242.
- Buchanan, W. F. 1988. Shellfish in prehistoric diet. Elands Bay, S. W. Cape coast, South Africa. *Cambridge Monographs in African Archeology* **31** BAR International series 455.
- Brooke, A. 1989. Evaluation of optimum stocking rate for steer on dry-land pastures. B. Sc. (Hons.) Project, Department of Applied Mathematics, University of Cape Town
- Clark, C. W. 1976. *Mathematical Bioeconomics: the Optimal Management of Renewable Resources*, Wiley-Interscience, New York.
- DeAngelis, D. L., and L. J. Gross. 1992. *Individual-based models and approaches in ecology: Populations, communities and ecosystems*. Chapman and Hall.
- Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1993. Herbivory and its consequences. *Ecological Applications* **3**: 10-16.

- Eekhout, S., C. M. Raubenheimer, G. M. Branch, A. L. Bosman and M. O. Bergh. 1992. A holistic approach to the exploitation of intertidal stocks. *South African Journal of Marine Sciences* **12**: 1017-1030.
- Flaaten, O. 1988. *The Economics of Multispecies Harvesting*. Springer-Verlag, Berlin.
- Getz, W. M. 1980. The ultimate sustainable yield problem in non-linear age-structured populations. *Mathematical Bioscience* **48**:279-292.
- Getz, W. M. 1988. Harvesting discrete nonlinear age and stage structured populations. *Journal of Optimization and Theoretical Application* **57**:69-83.
- Getz, W. M. 1991. A unified approach to multispecies modeling. *Natural Resources Modeling* **5**: 393-421.
- Getz, W. M. 1993. Metaphysiological and evolutionary dynamics of populations exploiting constant and interactive resources: r-K selection revisited. *Evolutionary Ecology* **7**:1-19.
- Getz, W. M., in press. A metaphysiological approach to modeling ecological populations and communities. Pages *in* S. A. Levin editor. *Lecture Notes in Biomathematics*, Vol. **100**, Springer-Verlag, New York.
- Getz, W. M. and R. G. Haight. 1989. *Population Harvesting. Demographic Models of Fish, Forest and Animal Resources*. Monographs in Population Biology **27**, Princeton University Press, New Jersey.
- Hart, D. D., S. L. Kohler, and R. G. Carlton. 1991. Harvesting of benthic algae by territorial grazers: the potential for prudent predation. *Oikos* **60**: 329-335.
- Hawkins, S. J., and R. G Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography Marine Biology Annual Review* **21**: 195-282.

- Hilborn, R. 1992. Current and future trends in fisheries stock assessment and management. *South African Journal of Marine Sciences* **12**: 975-988.
- Hill, A. S., and S. J. Hawkins. 1990. An investigation of methods for sampling microbial films on rocky shores. *Journal of Marine Biology Association of the United Kingdom* **70**: 77-88.
- Hill, A. S., and S. J. Hawkins. 1991. Seasonal and spatial variation of epilithic microalgal distribution and abundance and its ingestion by *Patella vulgata* on a moderately exposed rocky shore. *Journal of Marine Biology Association of the United Kingdom* **71**: 403-423.
- Hockey, P. A. R., and G. M. Branch. 1984. Oystercatchers and limpets: impact and implications. A preliminary assessment. *Ardea* **72**: 199-206.
- Hockey, P. A. R., A. L. Bosman. 1986. Man as intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* **46**: 3-14.
- Holling, C. S. 1966. The strategy of building models of complex ecological systems. Pages 195-214 *in*: K. E. F. Watt editor. *Systems Analysis in Ecology*, Academic Press, New York.
- Houston, A. I. and J. M. MacNamara. 1985. The choice of two prey types that minimizes the probability of starvation. *Behavioral Ecology and Sociobiology* **17**: 135-141.
- Jones, J. G. 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society* **56**: 60-77.
- Judson, O. P. 1993. The rise of the individual-based model in ecology. *Trends in Ecology and Evolution* **9**: 9-14.

- Levitt, G. J. and J. J. Bolton. 1991. Seasonal patterns of photosynthesis and physiological parameters and the effects of emersion of littoral seaweeds. *Botanica Marina* **34**: 403-410.
- Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press.
- Ludwig, D., R. Hilborn and C. Walters. 1993. Uncertainty, resource exploitation and conservation: lessons from history. *Science* **260** : 36.
- MacLulich, J. H. 1986a. Colonization of bare rock by microflora in a rocky intertidal epilithic microalgae. *Marine Ecology Progress Series* **32**: 91-96.
- MacLulich, J. H. 1986b. Experimental evaluation of methods for sampling and assaying intertidal epilithic microalgae. *Marine Ecology Progress Series* **34**: 275-280.
- Mangel, M. and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey, USA.
- May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt and R. M. Laws. 1979. Management of multispecies fisheries. *Science* **205**: 267-277.
- Noli, D. 1988. Results of the 1986 excavation at Hailstone midden (HSM), Eland's Bay, western Cape province. *South African Archaeological Bulletin* **43**: 43-48.
- Oksanen, L., S. Fretwell, J. Arruda and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**: 240-261.
- Oliva, D. and J. C. Castilla. 1986. The effect of human exclusion on the population structure of key-hole limpet *Fissurella crassa* and *F. Iimbata* on the coast of central Chile. *P.S.Z.N.I.: Marine Ecology* **7**: 201-207.
- Parkington, J. E. 1976. Coastal settlement between the mouths of the Bergh and Olifants rivers, Cape province. *The South African Archeological Bulletin* **31**: 127-140.

- Real, L. A. 1990. Predator switching and the interpretation of animal choice behavior: the case for constrained optimization. Pages 1-20 *in*: R. N Hughes editor. Behavioural mechanisms of food selection. NATO ASI series **20**, Springer-Verlag.
- Reed, W. J. 1980. Optimum age-specific harvesting in a nonlinear population model. *Biometrics* **36**:579--593 .
- Raubenheimer, C. M. 1991. Length-based simulation model for assessing the exploitation potential of the limpet *Patella granatina*. M. Sc. Thesis, University of Cape Town, South Africa.
- Siegfried, W. R, P. A. R. Hockey and A. A. Crowe. 1985. Exploitation and conservation of brown mussels stocks by coastal people of Transkei. *Environmental Conservation* **12**: 303-307.
- Shannon, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, Physical features and processes. *Oceanography Marine Biology Annual Review* **23**: 105-182.
- Stobbs, R. E. 1980. Feeding habits of the giant clingfish *Chorisochismus dentex* (Pisces: Gobiesocidae). *South African Journal of Zoology* **15**: 146-149.
- Underwood, A. J. 1979. The ecology of intertidal gastropods. *Advances in Marine Biology* **16**: 111-210.
- Underwood, A. J. 1980. The effects of grazing by gastropods and physical factors on the upper limits and distribution of intertidal macroalgae. *Oecologia (Berlin)* **46**: 201-213.
- Underwood, A. J. 1984. The vertical distribution and seasonal abundance of intertidal microalgae on a rocky shore in New South Wales. *Journal of Experimental Marine Biology and Ecology* **78**: 199-220.

Underwood, A. J., and P. J. Jernakoff. 1984. The effects of tidal height, wave exposure, seasonally and rock pools on grazing and the distribution of intertidal macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology* **75**: 71-96.

Webley, L. 1992. Early evidence for sheep from Spoeg River cave, Namaqualand. *Southern African Field Archeology* **1**: 3-13.

Yodzis, P. 1991. Predatory-prey theory and management of multispecific fisheries. Greenpeace Internal Report, 28 pages.

Chapter 7

Synthesis

Introduction

One of the goals of ecology is to derive general principles based on the observation of repetitive patterns of variation, which may contribute to the understanding of whole ecosystems (Steele 1974). In this spirit, a satisfactory line of research on community structure and regulation may rely heavily on quantitative descriptions of natural patterns. In this thesis I have uncovered and evidenced many of the large (Chapter 1, 2 and 3) and small scale geographical patterns and processes (Chapter 4, 5 and 6) involved in the structuring of southern African intertidal rocky-shore communities.

Although the results of this project involve a multitude of ecological phenomena, I have concentrated on particular patterns that appear to be relevant for understanding the processes (mainly trophic) involved in the structure of southern African rocky-shore communities. The time involved in the work prevented equal attention being given to both the west and east coasts of southern Africa. This 'imbalance' does not affect the overall contributions arising from this work, mostly concentrated on the west coast. Nevertheless, the results of this thesis, have led to the creation of new working hypotheses which contribute to the general theory of community ecology (e.g. linkages between adjacent system, trophic subsidy, magnification of biotic production) and, in particular, to knowledge of the scarcely studied west coast of southern Africa. The occurrence of equivalent systems elsewhere in the world (e.g. eastern Pacific, southern Australia) also suggests that the results reported here may not be specific to the west coast of southern Africa.

Biogeography

There are several main objectives in this thesis, among them the re-examination of a biogeographic delimitation for South African intertidal rocky shores. The results presented in Chapter 1 revealed that on the basis of binary and biomass data for 231 species identified at 15 localities around the coast, it is possible to justify the division of the region into three main biogeographic provinces; the West, South and East. The results of that Chapter are the first quantitative confirmation of the earlier biogeographic divisions proposed by Stephenson and Stephenson (1972). They also agree with the recent zoogeographic division proposed by Emanuel *et al.* (1992), who found the same 3 biogeographic divisions, covering most of the Namibian coast (which is not considered here). Emanuel *et al.* employed an extensive binary data set which included all well known shallow-water marine invertebrate groups.

Another large-scale biogeographic pattern revealed in Chapter 1 is the existence of a gradient of species richness around the southern African rocky coast, with low values in the west, increasing towards the south and east coast. In general, the west coast intertidal communities support about half the number of species that occur in equivalent communities on the south and east coasts.

One of the immediate implications of these biogeographic patterns impinges on the necessity of establishing priority areas for conservation of the marine coastal biodiversity. Unfortunately, conservation biology has focused mainly on terrestrial species and ecosystems, particularly those of moist tropical forests, and scant attention has been given to marine species and ecosystems. Present marine scientific literature and the press report that many marine systems, particularly coastal ones, are severely depleted, drastically altered, overfished, and polluted. The above evidence has led scientists to define discrete marine biological units for protection. On a global scale, several marine ecosystems have been identified (i.e., tropical coral reefs, temperate reefs, kelp forests, oceanic vents, etc.), but their geographical variation at regional scales has been poorly

studied. The lack of a broadly accepted marine biogeographic scheme is a serious gap in marine conservation and management (Ray 1991; Ray and Grassle 1991; Orians 1993). However, even the identification of distribution patterns and the definition of marine biogeographic provinces, although essential, are but one step towards conservation. The results of Chapter 1 provide a useful starting point in the understanding of regional coastal marine biodiversity, emphasizing that the identification of large-scale biotic distribution patterns is necessary. Thus, this thesis is a reminder of how biogeographic and large-scale community distribution patterns can be directly related to coastal biotic diversity and its future conservation.

Community Structure

One of the major goals of community ecology is to determine the causes of spatial and temporal variation in community structure. The potential causes can only be identified once repeated patterns of variation and composition emerge from a given community. The results presented in Chapter 1 revealed that the trophic structure of the intertidal rocky-shores communities of southern Africa consistently varies over a large scale due to differences among biogeographic provinces, while small-scale variation (within localities) was explained mainly by local wave action. Higher biomass levels are achieved by west-coast communities relative to those present on the south and east coasts. This pattern was consistent across the small-scale variation imposed by a range of wave action. Similarly, at a local scale, the levels of community biomass achieved in habitats with contrasting wave action were different in a manner that was consistent at all 15 localities investigated. At each locality, the main pattern was that community biomass decreased from exposed to sheltered shores. The results presented in Chapter 1 also show that filter-feeders dominate the community biomass (and space) of wave beaten habitats, while grazers prevail on sheltered habitats. The extraordinary degree to which grazers dominate west-coast semi-exposed and sheltered shores appears to be unique to the west coast of southern Africa. The restrictions imposed by the action of waves are not only reflected in the levels of community biomass, but also in the species richness. Exposed shores were

always dominated by fewer species (mostly filter-feeders), while a greater number of species was found in semi-exposed and sheltered habitats. At this level of analysis, generalizations about the structuring of natural communities are still in the earliest stages of development, and there are insufficient comparable studies available to test existing models of community structure and regulation (Menge and Farrell 1989). As a result, descriptions of large-scale patterns of community structure provide an important data base to test the applicability of existing models.

Zonation

Chapter 2 revealed local vertical and horizontal distribution patterns of intertidal community biomass and species richness which were consistent over the full geographical range examined. Again, it was obvious that the influence of wave action determined the horizontal distribution of both biomass and species richness, while the interaction between rock temperature and shore elevation strongly influenced vertical distribution. Except for the work of Menge and Farrell (1989), there is no study that compares vertical distribution patterns in a comparable manner. The vertical 'spread' of the community biomass on exposed shores increased exponentially from the high shore, reaching a maximum just below the mid shore, while the lowest zone supported intermediate biomass levels. Semi-exposed shores at the west coast showed similar vertical distribution patterns. By contrast, sheltered habitats protected from direct wave action concentrated the community biomass in the lowest intertidal zone, decreasing exponentially towards the high zones. Independent of geographical variation, these patterns were evident at all localities investigated. For both horizontal and vertical patterns of distribution, species richness paralleled the patterns evidenced for community biomass.

The results of the direct gradient analyses presented in Chapter 2 again emphasized the relative importance, at a local scale, of gradients of wave action and desiccation as the main determinants of observed vertical and horizontal zonation. The multivariate nature of these environmental factors also revealed that in the upper shore community structure

converges in species composition and abundance, driven mainly by the effects of the desiccation gradient. On the other hand, communities of the lower intertidal zone diverge conspicuously depending on the intensity of wave action.

Gradients of Intertidal Productivity

Menge and Olson (1990) have developed models for the role of nutrients/productivity in the regulation of rocky-shore communities, predicting a strong influence at both large and meso geographical scales. The results presented here support their predictions. In Chapter 1, I proposed several working hypotheses to explain the observed patterns of abundance of different intertidal trophic groups (Table 3); one of these implied the existence of differential levels of primary production around the southern African coast. This gradient was clearly evidenced in Chapter 3. The intertidal *in-situ* primary production decreases substantially around the southern African coast, being high on the west and decreasing progressively towards the east coast. A clear seasonality in the productivity was evident in different biogeographic provinces, peak production for the west coast being achieved on the spring-summer, and that for the south coast in autumn-winter. Productivity was low year-round on the east coast. Productivity was significantly and positively correlated with the nutrient concentrations in intertidal waters, with a parallel gradient of micronutrients in intertidal waters around the southern African coast: high concentrations on the west coast, decreasing progressively towards the east. The tight correlation between productivity and nutrient concentration led to the conclusion that the levels of micronutrients are likely to be the responsible for the corresponding levels of intertidal primary productivity around the southern African coast.

Because the intertidal is an open system, I used the Redfield ratio between concentrations of nitrogen and phosphorus in intertidal waters (Redfield 1958) to explore the nutrients most likely to control primary productivity. The results suggested that the availability of nitrogen is likely to be the potential controller on west and south coasts, but phosphorus appears to determine intertidal primary production on the east coast.

Intertidal production was closely related to the levels of biomass achieved by intertidal primary consumers - i.e. species of invertebrate grazers and filter-feeders. These relationships were significant for grazers but not for the maximum values recorded for filter-feeders. These simple relationships suggest that the level of biomass achieved by grazers is likely to be set by the levels of *in-situ* production because grazers consume this source of food directly. Another important consequence arising from the existence of a gradient of intertidal primary production around the southern African coast is the potential effect that productivity has on the sizes and growth rates of grazers. *Patella granularis* was selected as an indicator of these effects because it is distributed right around the coast. Its maximal body sizes increased linearly with levels of primary production, coinciding with the findings of (Bosman 1988), who demonstrated that maximum size and growth rates of *P. granularis* were detected on islands where primary production was enhanced as a result of the input of bird guano. The effect of increased productivity in regulating the abundance of primary consumers has been well studied on other systems with similar results (e.g. Wootton and Power 1993; Abrams 1993; Hairston and Hairston 1993; Tilman 1993). However, its potential effects have not been considered in the construction of models of evolution of individual body size (Brown *et al.* 1993). I consider this an aspect that needs to be urgently addressed.

Filter-feeders do not directly consume *in-situ* intertidal production, but rely on the input of 'production' in the water column and, principally, on inputs of subtidal macrophyte production (Chapter 3 and 4). The maximum biomass achieved by filter-feeders did not change with geography or with the gradient of intertidal primary production around the coast, suggesting that a biomass 'ceiling' is set by the availability of space.

From the results of Chapter 3, it is also clear that mere macroalgal standing stock is a poor predictor of the productivity potential of a given intertidal system. Standing stocks were highest on the west and east coasts, the two regions spanning the extremes of productivity. However, the use of functional-form groups of macroalgae and the

variation of their standing stock, revealed patterns of algal composition that are likely to be caused by different structuring processes. Foliose forms of algae were prevalent in west coast while corallines and turfs dominated on the south and east coasts. The existence of such patterns of predominance of different functional-form groups of algae is a challenge to identify potential underlying causes that generate these patterns. There is substantial knowledge of seaweed taxonomy and biology, but the understanding of ecological roles of algal assemblages still lags behind that available for rocky-shore fauna. Thus, elucidation of descriptive patterns must be combined with future mechanistic approaches (including experiments) to accelerate an understanding of algal assemblages in intertidal ecosystems (Littler and Littler 1988).

This thesis also provides a methodological and theoretical basis for the measurement and evaluation of the dynamics of intertidal primary production (Chapter 6). For a very long time scientists have consistently neglected the effects of primary production on the structure and function of intertidal communities. In Chapters 3 and 6, I provide a common methodological basis for the establishment of comparative studies at different spatial scales, that could contribute to the formal insertion of productivity into causative models of community organization.

The Subtidal-Intertidal Link, and Maintenance of Intertidal Primary Consumers

There are few studies that have demonstrated a significant trophic link between the subtidal and intertidal rocky ecosystems. In Chapter 4 I explore potential linkages using double stable-isotope analyses for the investigation of the main sources of carbon and nitrogen for intertidal primary consumers. The results of the isotopic analyses (Chapter 4) of particular species of intertidal filter-feeders on the west coast revealed that more than 70% of the carbon and nitrogen incorporated into the body tissues of filter-feeders is likely to be derived from particulate kelp detritus (which is abundant year round), whereas phytoplankton plays a minor role in the maintenance of filter-feeders. Another

important trophic linkage evidenced by the isotopic analyses, was between the two most abundant limpet species, *Patella argenvillei* and *P. granatina*, and the subtidal kelps. On the west coast, these two limpet species dominate the primary space on semi-exposed and sheltered shores, achieving the highest biomasses ever recorded for limpets anywhere in the world. Both of these limpets obtain more than 65% of their carbon and nitrogen from consumption of subtidal kelp - either by capture of drift kelp or by pruning the fronds of attached plants.

The two hypotheses I proposed to explain biomass patterns of filter-feeders around the coast and across local gradients of wave action, included large- and local-scale processes (Table 3, Chapter 1). At the large scales, average biomass of filter-feeders (as distinct from maximal biomass) is highest on the west coast, declining eastwards (Chapter 4). I hypothesize that this is due to the large-scale effect of the gradient of primary production around the coast, coupled with the potential inputs of particulate kelp detritus, which together enhance the availability of food for filter-feeders on the west coast.

Isotopic analyses established that west-coast intertidal filter-feeders depend on the 'importation' of food from the adjacent pelagic and benthic subtidal ecosystems. Although these results are not causative, they agree with recent field and experimental evidence that suggested that water column processes (e.g. food concentration, flow speed, temperature) can powerfully affect rocky-shore organisms, and that oceanographic conditions may often leave a strong signature on the distribution, abundance and dynamics of assemblages of sessile filter-feeders (Eckman and Duggins 1993; Sanford *et al.* 1994).

At a local-scale, I hypothesized that the role of water turnover will powerfully influence the supply of food sources and thus have a direct effect on filter-feeder biomass. The monitoring of west coast intertidal waters exposed that particulate kelp detritus accounted for more than 70% of the total monthly particulate organic matter. Furthermore, a short-term experiment revealed that water turnover in exposed habitats is an order of magnitude higher than of sheltered habitats, with consequent enhancement of

food replacement. The results of dynamic a steady-state model based on empirical observations of food availability and water turnover unveiled (at least theoretically) that differences in food replacement could sufficiently explain the differences of filter-feeder standing stock observed between exposed and sheltered habitats (Chapter 4).

The congeneric limpets *Patella granatina* and *P. argenvillei* were closely related to subtidal kelp. These species are a classical example of niche segregation. Both use the same food resources, which at first sight appear limited if we makes the assumption that the limpets depend on intertidal production (as do most limpets). However, *Patella granatina* and *P. argenvillei* are spatially segregated and exhibit differences in the timing and the behaviour of food procurement. These differences virtually preclude interspecific competition. Nevertheless, their populations still occur at a remarkably high densities and high biomasses. Thus two question are still relevant: do they compete intraspecifically, and how are these dense populations maintained? Although *in-situ* algal production is high, it cannot be assumed to meet the requirements of the limpets. Conversely, the daily inputs of subtidal kelp into the intertidal appear to exceed by far the limpets' requirements. Hence, the strength of these trophic links were tested in Chapter 5. A large proportion of the adults of both species capture kelp and feed on it. One of the species, *Patella argenvillei*, feeds collectively. Once a single individual captures a blade of kelp, others can share it. This leads to an unusual situation in which procurement of food may be enhanced at high densities. Indeed, the maximum sizes attained by *P. argenvillei* are positively correlated with density. High density may thus be beneficial rather than leading to intraspecific competition. This situation does not apply to *P. granatina*, which generally feeds in a solitary manner on drift kelp.

Experimental kelp exclusion resulted in significant mortality of both limpet species, reducing their original density up to 60%. In addition, the surviving individuals experienced a significant decrease of their body mass, providing evidence that starvation is the cause of limpet mortality if they are deprived of kelp. Thus, although the intertidal primary production is high on the west coast, it is insufficient to maintain the natural high

densities and biomasses of these unusual limpets. So, again, what sets their carrying capacity? At least at the adult stage, they do not have any significant top-down control by predators, they do not compete for food, and they have an abundant supply of food in the form of kelp. The results presented on Chapter 5 led me to conclude that the mere availability of primary space is the factor that ultimately limits the density of both limpets. I know of no other case in which space is the limiting factor for a grazer.

The above results, in addition to the strong linkage between filter-feeders and kelp-derived detritus, provide substantial evidence for a bottom-up effect that regulates the abundance of some key functional groups of intertidal rocky-shore communities. However, the bottom-up controlling effects do not work in isolation. The main consumers of the *in-situ* primary production on the west coast communities are the highly abundant grazing limpets, and they exert top-down effects controlling the algal communities. A similar rationale can be applied to intertidal filter-feeders. The availability and turnover of food influence their relative abundance on particular habitats and, by consequence, the amount of free primary space. Thus, the subtidal production and dynamics of kelp detritus modify filter-feeder dynamics and abundance, and are likely to trigger cascading effects on the structure of intertidal assemblages. Filter-feeder densities are so high on wave beaten habitats that they monopolize most of the primary substratum, but on semi-exposed and sheltered habitats the cover of mussels declines allowing the establishment of different communities.

It is clear that the trophic maintenance of many west coast intertidal primary consumers is highly dependent on the inputs of an external food supply, or trophic subsidy. Both filter-feeders and grazers depend on the subtidal production of kelp. Moreover, the magnification of primary consumer production by an input of subtidal macrophytes has been reported elsewhere (e.g. Tutschulte and Connell 1988; Duggins *et al.* 1989), so this phenomenon is probably more frequent than previously supposed. Thus, these results not only impinge on the trophic functioning and structure of intertidal communities, but

on the way that food webs are structured at different productivity levels (e.g. Oksanen 1981; Abrams 1993).

Implications for Resource Management

Good field observations, experimental evaluations and theoretical framework are the best combination of approaches for understanding a given ecological phenomenon. The work presented in Chapter 6 has this combination. Populations of *Patella granatina* were successfully simulated, based on sound ecological principles (e.g. predator-prey theory, intraspecific competition, logistic dynamics) using empirical data. Employing a novel metaphysiological approach (Getz 1991), I was able to reproduce theoretically the population levels of *P. granatina* observed under natural and experimental conditions. The model also predicted that *in-situ* intertidal production does not match the trophic needs of limpets when they occur at high densities (Chapter 6). This modelling exercise involved a multispecific system, i.e., the simultaneous forecasting of both an exploitable resource (limpet) and its main source of food (algae). This approach is seldom used during traditional marine fisheries analyses. Using this modeling approach, I developed a hypothetical limpet fishery, concluding that it is possible to use ecological and individual-based data to set management policies (i.e. maximum sustainable yields) for a natural resource. I am not proposing the replacement of traditional stock assessment management strategies by ecological ones, but rather that both approaches can be combined to improve management of a given natural resource.

References

- Abrams, P. A. 1993. Effects of increased productivity on the abundance of trophic levels. *The American Naturalist* **141**: 351-371.
- Bosman, A. L. 1987. Avian determinants of rocky intertidal community structure in South Africa. Ph. D. Dissertation University of Cape Town, Cape Town.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *The American Naturalist* **142**: 573-584.
- Eckman, J. E., and D. O. Duggins. 1993. Effects of flow speed on growth of benthic suspension feeders. *Biological Bulletin* **185**: 28-41.
- Emanuel, B. P., R. H. Bustamante, G. M. Branch, S. Eekhout, F. J. Odendaal. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of Africa. *South African Journal of Marine Science* **12**: 341-368.
- Getz, W. M. 1991. A unified approach to multispecies modeling. *Natural Resources Modeling* **5**: 393-421.
- Hairston, G. H. . and G. N. Hairston. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *The American Naturalist* **142**: 379-411.
- Littler, M. M., and D. S. Littler. 1988. Structure and role of algae in tropical reefs. Pages 29-56 *in* C. A. Lembi and J. R. Waaland editors. *Algae and Human Affairs*. Cambridge University Press, Cambridge.
- Menge, B. A., and T. M. Farrell. 1989. Community structure and interactions webs in shallow marine hard-bottom communities: test of an environmental stress model. *Advances in Ecological Research* **19**: 189-262.

- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends in Ecology and Evolution* **5**: 52-67.
- Oksanen, L., S. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**: 240-261.
- Orians, G. H. 1993. Endangered at what level? *Ecological Applications* **3**: 206-208.
- Ray, G. C. 1991. Coastal-zone biodiversity patterns. *BioScience* **41**: 490-498.
- Ray, G. C., and J. F. Grassle. 1991. Marine biological diversity. *BioScience* **41**: 490-498.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. *The American Scientist* **46**: 205-222.
- Sanford, E., D. Bermudez, M. D. Berteness, and S. D. Gaines. 1994. Flow, food supply and acorn barnacle population dynamics. *Marine Ecology Progress Series* **104**: 49-62.
- Steele, J. H. 1974. *The Structure of Marine Ecosystems*. Blackwell, Oxford.
- Stephenson T. A., and A. Stephenson. 1972. *Life between tidemarks on rocky shores*. Freeman, San Francisco, USA.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitations? *Ecology* **74**: 2179-2191.