AVIAN DETERMINANTS OF ROCKY INTERTIDAL COMMUNITY STRUCTURE IN SOUTH AFRICA

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ABSTRACT

Rocky islands in Saldanha Bay, southwestern Cape, South Africa, support aggregations of seabirds. Guano produced by the seabirds is washed off the islands into intertidal and nearshore waters, where it provides a source of inorganic and organic nutrients. The concentrations of nutrients in intertidal rockpools at island and mainland sites in the Saldanha Bay area were measured, and the biological structures of intertidal communities at these sites were compared in the light of differences in intertidal nutrient status. Monthly measurements were made of algal production and of the growth, density, reproductive condition and mortality of the dominant intertidal herbivore, *Patella granularis*.

The rate of intertidal algal production was enhanced on shores washed by nutrient-rich waters, and the growth rates and life-history patterns of populations of *P. granularis* were, in turn, modified by the increased availability of algal food. On unenriched shores rates of algal production and limpet growth and reproduction were slow. Seabirds thus influence trophic relationships between intertidal organisms, without themselves being components of the community.

Islands in Saldanha Bay also support dense populations of African Black Oystercatchers *Haematopus moquini*, which forage intertidally. Predation by oystercatchers on *P. granularis* resulted in a modification of limpet densities

and population size structures, and a reduction in the intensity of grazing. The impact of predation was, however, modified by the presence, in intertidal waters, of nutrients from seabird guano, and the consequences thereof. It is proposed that differences in the structures of communities on rocky shores, and in the roles of processes influencing structure, might be due, in part, to differences in the nutrient status of intertidal waters.

INTRODUCTION

Rocky shores support assemblages of plants and animals which often are mutually sustaining and interdependent. These assemblages of interacting species form communities (sensu Whittaker 1975) and display characteristic patterns of organization based on the spatial distributions and abundances of the component species. Ecologists have long been fascinated by the patterns of organization of intertidal organisms, and have consistently sought the mechanisms which produce these patterns. Both physical and biological processes have been identified as influencing patterns of organization (Menge 1976; Paine 1980; Underwood 1985), but the relative importance of each process varies between communities (Glynn 1976; Underwood and Denley 1984; Underwood and Fairweather 1985). Communities in various parts of the world have been compared in terms of their biological structure, i.e. their species composition and the abundances, size distributions and demographies of component species (Paine 1966, 1980; Menge and Sutherland 1976; Bertness et al. 1981; Menge and Lubchenco 1981; Sousa et al. 1981; Ben-Eliahu and Safriel 1982; Choat 1982; Paine and Suchanek 1983), but no generally applicable theory predicting the relative importance of processes influencing community structure has been developed (Underwood and Fairweather 1985).

Recent research on temperate rocky shores has indicated that physical factors (such as wave action and tidal range) limit the vertical occurrence (or zonation) of intertidal organisms (Menge 1976, Connell 1975). Within these limits, however, observed patterns of organization often are a product of biological processes such as predation and competition for food and space (Luckens 1970; Dayton 1971; Connell 1972, 1975; Paine 1974; Newell 1979; Underwood 1979; Lubchenco 1980; Creese and Underwood 1982). Examples of the ways in which invertebrate components of rocky intertidal communities may influence community structure abound in the literature (Branch 1984; Lubchenco and Gaines 1981; Paine 1969, 1974, 1976; Menge 1974; Paine et al. 1985; Moreno et al. 1986). Vertebrate components, particularly birds, have received much less attention however (Edwards et al. 1982), despite their common occurrence in the rocky intertidal habitat. Birds are unpredictable visitors to intertidal sites, and are difficult to observe and study quantitatively, although their high metabolic rates and energy requirements make them potentially important in modifying the abundances and size structures of intertidal prey populations (Feare and Summers 1985).

In this study I examine the biological structure of rocky intertidal communities on 3 islands off the west coast of southern Africa. These islands (Malgas, Marcus and Jutten Islands - Fig. 1) support dense populations of predatory shorebirds, including resident African Black Oystercatchers *Haematopus moquini* and migratory waders (Hockey 1983; Ryan 1983). Oystercatchers are common on many of the world's shores and have been shown to modify prey population densities and size structures, and prey morphology, as a

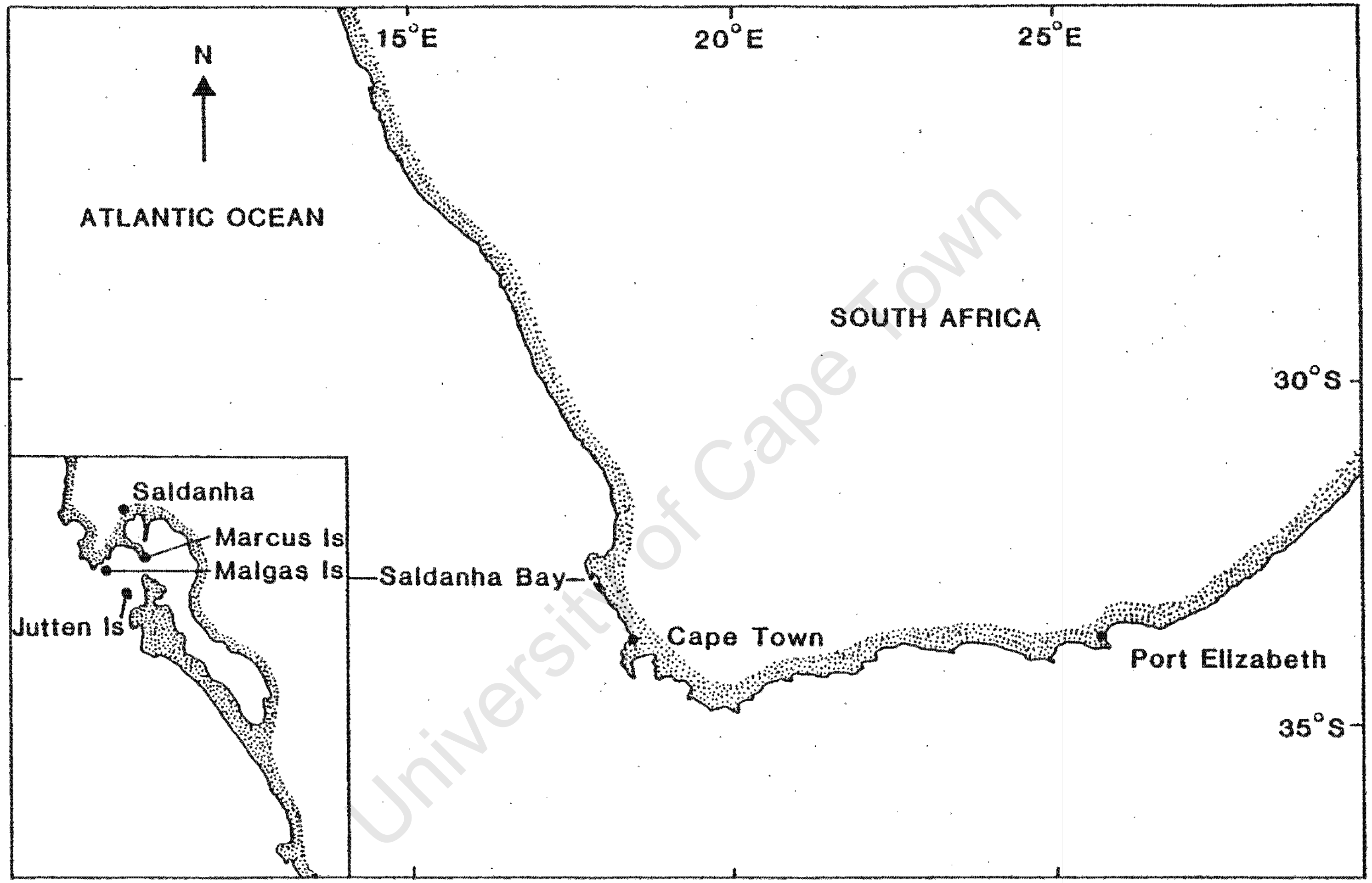

Fig. 1. Map of the southwestern coast of South Africa, showing Saldanha Bay, the major study area

result of their predatory activity (Hockey and Branch 1983; review by Feare and Summers 1985). Migratory waders commonly forage in flocks in soft-bottomed intertidal habitats, where they may influence the densities and spatial distributions of prey (Evans et al. 1979; Schneider and Harrington 1981; Quammen 1984). Their impact on rocky shore communities has seldom been investigated (Feare and Summers op. cit., Marsh 1986). In this study I assess the impact of predation by shorebirds on the densities and size structures of intertidal prey populations on Malgas, Marcus and Jutten Islands, and discuss the role of predation by shorebirds in modifying intertidal community structure on these islands.

In addition to populations of shorebirds, islands off the west coast of southern Africa support colonies of breeding seabirds, including Cape Cormorants *Phalacrocorax capensis*, Cape Gannets *Sula capensis* and Jackass Penguins *Spheniscus demersus*. The guano produced by seabirds is commonly used as an agricultural fertilizer and, historically, southern African islands have been an important source of guano for commercial export (Speight 1940; Hutchinson 1950). Guano washed from the shores of the seabird-breeding islands may provide an enhanced supply of nutrients to intertidal algae and may thereby modify the rate of primary production. In all communities trophic relationships are influenced by the rate of primary production (Tilman 1982), and in this way seabirds may influence the interactions between intertidal organisms without themselves being components of the intertidal community. In this study I measure the concentrations of intertidal nutrients and the rates of primary production at sites both with and without colonies of seabirds. I compare intertidal community structure at these sites in the light of differences in nutrient availability and primary production.

The availability of nutrients in the intertidal waters has seldom been considered an important environmental variable in the study of rocky shore communities. Since this variable may be the major factor influencing the rate of primary production which may, in turn, affect trophic relationships within the community, it is possible that the impact of processes such as predation and competition for food may be mediated by the availability of intertidal nutrients. In this study I assess the extent to which differences in intertidal community structure are explicable in terms of differences in intertidal nutrient levels, at sites on the west coast of southern Africa, and also in disparate geographical regions.

Methods involving both observation and experimental manipulation are used in this study, with a view to testing the following specific hypotheses:

- that nutrients from the dissolved guano of seabirds enrich the intertidal waters around seabird-breeding islands in Saldanha Bay;

- that the rate of algal production on nutrient-rich shores is enhanced as a direct consequence of the presence of dissolved guano in the intertidal region;
- that enhanced rates of algal production on nutrient-rich shores affect the growth rates, population size structures and population reproductive outputs of the intertidal herbivore *Patella granularis*;
- and that predation by shorebirds modifies the species composition, abundances and population size structures of intertidal prey on islands.

In all instances deductions are made based on comparisons of island intertidal communities with the communities of nearby mainland shores that do not support aggregations of seabirds.

The research presented in this thesis attempts to identify processes operational in communities of organisms on rocky shores in southern Africa. With the aim of integrating the primary and secondary effects of these processes, a large amount of data from different rocky shores has been collected. The sites chosen represent the minimum range of variation required before any comparison between sites, and any predictions about the importance of different processes in influencing community functioning, can be made. A consequence of the attempt to investigate a number of intertidal communities simultaneously is that the limitation of time has prevented true replication of the data obtained.

Many of the data are pseudoreplicated - replicates are not necessarily independent of oneanother.

The concept of pseudoreplication has made an appearance in the biological literature only recently, and is cogently discussed by Hurlbert (1984), who states that pseudoreplication is probably the single most common fault in the design and analysis of ecological field experiments. In an earlier review of the application of statistical techniques (particularly analysis of variance) in recent marine ecological research, Underwood (1981) does not mention pseudoreplication, nor does he identify it as a common error in experimental design. At the time that the experiments described in this thesis were set up (1982), it was considered that sufficient replication had been incorporated in the design of the experiments, although it is now clear that many of these replicates are, in fact, pseudoreplicates.

The application of inferential statistics to pseudoreplicated data is unacceptable, and, where possible in this thesis, this has been avoided. In many instances the trends in the data are clear without the application of statistical analyses, which would be invalid anyway. Hurbert (op. cit.) makes an appeal to critics to be liberal in accepting papers that refrain from using inferential statistics where these cannot be applied validly. Despite the flaws in design in several of the experiments discussed in this thesis, I feel that the results are nevertheless informative and interesting.

The results of this study are presented as a series of discrete papers, written in the format of an international journal. This approach allows the rapid communication of results, but also entails a certain amount of repetition, particularly in the documentation of the methods used. The concluding section is synthetic and aims to summarize the results of this study and to highlight their contribution to the quest for a general theory explaining variation in observed patterns of organization in rocky intertidal communities.

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PART 1

SEABIRDS AND NUTRIENT ENRICHMENT

The role of seabirds in modifying the nutrient status of intertidal and nearshore waters

Summary. Levels of soluble inorganic nutrients present in fresh, and in older, accumulated seabird guano on seabird-breeding islands were measured. In addition, levels of these nutrients and of the organic nitrogenous compound, urea, were measured monthly in intertidal rockpools at sites both with and without permanent aggregations of seabirds.

It was found that seabird guano contains large quantities of nutrients which have been shown to be important for the growth and reproduction of intertidal algae. Intertidal rockpools on the shores of seabird-breeding islands had higher mean levels of nutrients than did rockpools on shores from which seabirds were absent. A narrow zone of nutrient enrichment was apparent in nearshore waters around seabird-breeding islands, although the extent and shape of the zone were influenced by swell, wind and tidal conditions. Guano deposited on islands entered the intertidal region by means of wave action, wind and, to a lesser extent, rain.

Seabird guano enriches the intertidal waters with nutrients that may stimulate primary production, and thereby seabirds may modify the rate of algal growth, without themselves being components of the intertidal community.

Introduction

The growth of almost all plants is limited by the availability of inorganic nutrients. Rates of plant growth and reproduction increase with the addition of certain nutrients (Ellis 1971; Powers et al. 1972; Silvertown 1980), and competition for nutrients is considered to be a major factor determining the species composition and organization of natural plant assemblages (see review by Tilman 1982). Within any community the rate of primary production influences all trophic relationships, and therefore changes in the rate of primary production may lead to changes in the organization and functioning of the entire community.

The excrement of colonially-nesting seabirds has long been recognized as a valuable fertilizer (Voelcker 1877; Watson 1930; Speigt 1940) and has been shown to enhance the nutrient status of marine, estuarine and inland-fresh waters (Golovkin 1967; Ganning and Wulff 1969; Golovkin and Garkavaya 1975; Grobbelaar 1978; Bedard et al. 1980; Tatur and Myrcha 1983). Terrestrial plants which are manured by seabird guano exhibit enhanced vitality, cover and production (Gillham 1977; Smith 1978), and research in the Barents Sea (74°00'N, 36°00'E) indicates that enrichment of nearshore waters by seabird guano deposited in the sea is associated with enhanced phytoplankton production (Golovkin

1967; Zelickman and Golovkin 1972; Golovkin and Garkavaya 1975).

Historically the seabird-breeding islands in Saldanha Bay (33°03'S, 17°58'E), southwestern Cape, South Africa, were important sources of seabird guano for commercial export. In the early years of exploitation Malgas Island (Fig. 1) regularly yielded in the region of 1000 tonnes of guano per year (Hutchinson 1950). Numerous seabirds, including Jackass Penguins *Spheniscus demersus* (L.), Cape Gannets *Sula capensis* (Licht.) and Cape Cormorants *Phalacrocorax capensis* (Sparrman), breed on the islands in Saldanha Bay (Cooper et al. 1982; Crawford et al. 1983; Shelton et al. 1984) and the guano accumulation rate on Malgas Island continued to warrant annual commercial collection until 1986, when the islands were incorporated into a national park.

This study aims to assess the extent to which seabird guano enhances the nutrient status of nearshore and intertidal waters around seabird-breeding islands, and the significance of this enrichment for intertidal primary production. Intertidal and nearshore nutrient levels were measured monthly at sites where seabirds aggregate, and the results are compared with those from sites where seabirds are absent. The mechanisms of transport of guano into the intertidal region are discussed.

Materials and methods

Study sites

Seven intertidal study sites in the Saldanha Bay area (Fig. 1.1) were visited monthly between December 1982 and April 1984. Two sites were on the shores of seabird-breeding islands (Malgas and Jutten Islands) and a third was on the shore of Marcus Island, a seabird-breeding island which is joined to the mainland by means of a causeway, completed in 1976 (Fig. 1.1). A further 2 sites were on mainland shores outside the Bay, where no aggregations of seabirds occurred (Mauritz Bay and Cape Columbine), and 2 more were on mainland shores within the Bay (North Bay and Bomgat). These last 2 sites, although having no regular aggregations of seabirds, were considered to be within the possible zone of influence of guano run-off from the seabird-breeding islands. Such sites were expected to show features intermediate between the 'nutrient-rich' island sites and the unenriched mainland sites. All sites were in the Benguela Current region (Shannon and Stander 1977), and the direction of the prevailing wind was SSW (Hockey 1982).

At all sites the shore was of gently sloping granite, and was exposed frequently to strong wave action. The intertidal zone was considered to extend from the upper limit of the low-shore mussel bed (Stephenson and Stephenson 1972), and at each site the zone was divided into a low-, mid- and high-shore region of equal horizontal width.

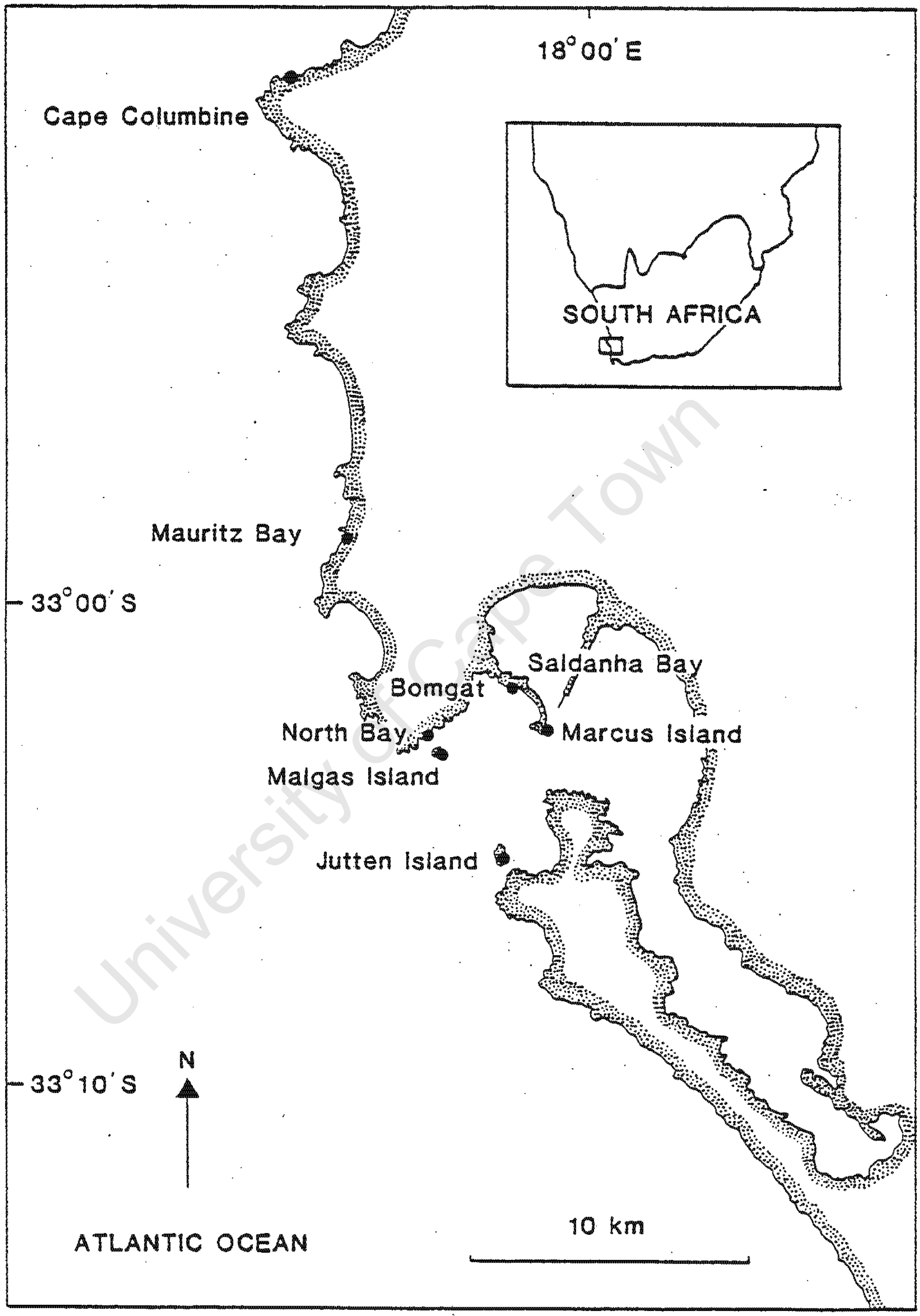

Fig. 1.1. Map of the Saldanha Bay area showing the positions of intertidal study sites

Intertidal nutrients

A low-, mid- and high-shore rockpool was chosen at each site and these were sampled monthly, 2 water samples being taken from each pool during a spring low-tide. The high-shore pools were chosen at the upper limit of the occurrence of the limpet *Patella granularis* L., the dominant invertebrate herbivore (Stephenson and Stephenson op. cit.). Although the pools were not of a uniform size, they were flushed during each tidal cycle, thus keeping contamination by organisms growing in the pools to a minimum. There were macro-algae growing in many of the rockpools, particularly on the island shores. The uptake of nutrients by algae could have affected nutrient levels in these pools, although regular flushing of the pools would keep this effect to a minimum. Water samples were filtered using Whatman glass-microfibre filters, and then wrapped in aluminium foil and stored frozen.

Concentrations of nitrite- and nitrate-bound nitrogen (NO_2^--N, NO_3^--N), ammonium-bound nitrogen (NH_4^+-N) and phosphate-bound phosphorus (PO_4^{3-}-P) were determined using a Technicon autoanalyser. Levels of urea-bound nitrogen ($CO(NH_2)_2$-N) were determined using the method of Grasshof (1976). Only those samples collected after July 1983 were analysed for NH_4-N and $CO(NH_2)_2$-N levels. The data were discarded in instances where the nutrient levels from the 2 replicate samples differed by more than 20% (6% of instances).

Extent of enriched zone

During 1983 surface water samples were collected at three-monthly intervals from a series of sample stations across the mouth of Saldanha Bay and around Malgas Island (Fig. 1.2). Duplicate water samples collected at each site were filtered using glass-microfibre filters, and were stored frozen before being analysed for NO_2-N, NO_3-N, NH_4-N and PO_4-P using an autoanalyser. The stations were divided into mainstream and island stations on the basis of detailed current flow patterns in the Bay (Huizinga 1982). The mainstream stations are those to which guano run-off from the islands is unlikely to be transported under the influence of normal currents. The island stations lie in the path of currents deflected past islands under normal weather and wind conditions. Nutrient levels at mainstream and island stations were compared using Kruskal-Wallis statistical tests (Sokal and Rohlf 1981).

Nutrients in seabird guano

The quantities of nutrients potentially available in fresh cormorant guano from intertidal rocks on Marcus Island, and in older, accumulated ('cap') gannet guano from Malgas Island, were determined. Solutions of cap guano in double-distilled water and in seawater were incubated at 10°C for 24 h. Thereafter 10 replicate 2 ml subsamples were removed and prepared for nutrient analysis in an autoanalyser. The effect of rain on the leaching of nutrients from fresh and cap guano was simulated in the laboratory using a spray-gun with an adjustable nozzle. The spray-gun was connected to a

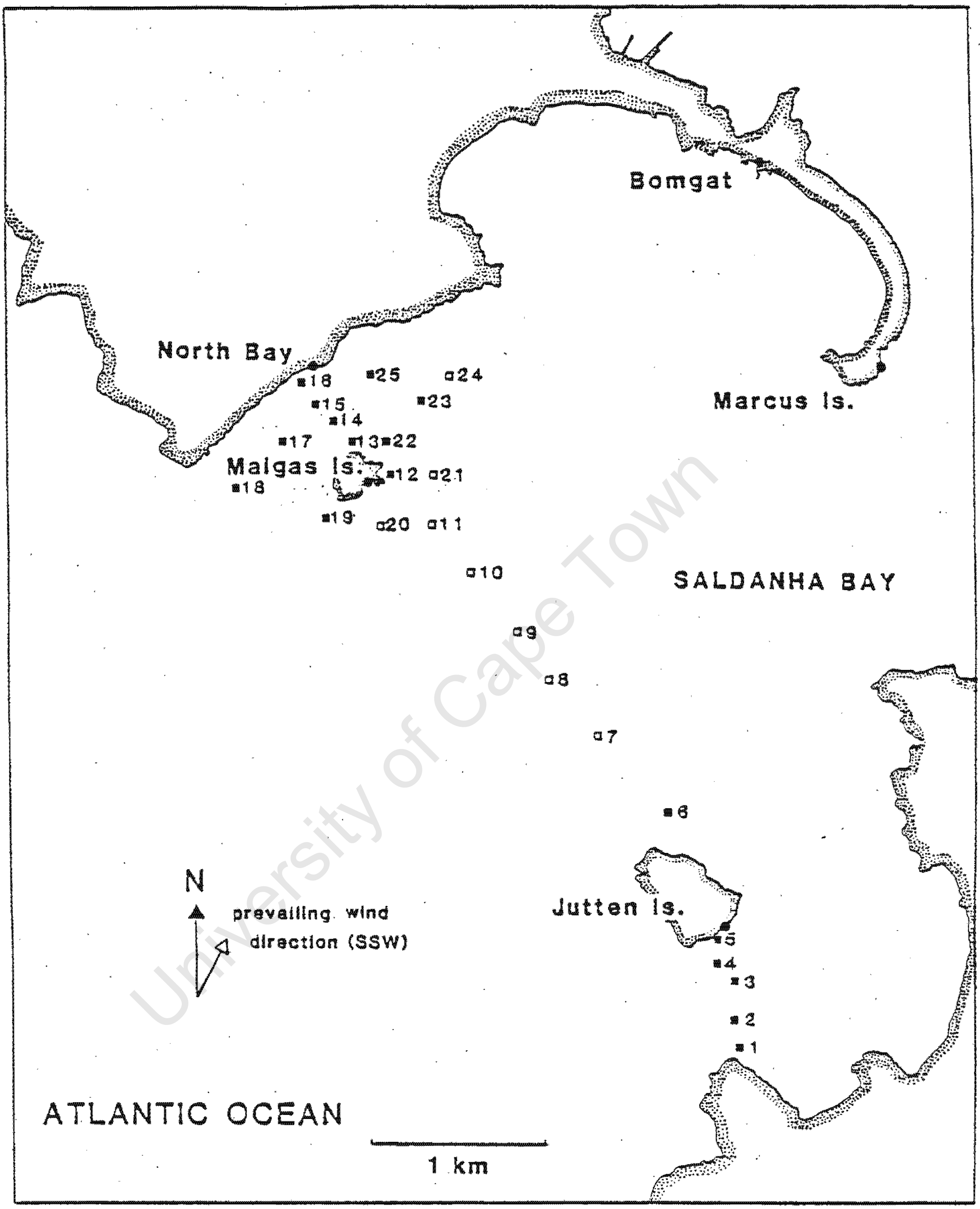

Fig. 1.2. Map of the mouth of Saldanha Bay showing the positions of island (■) and mainstream (□) water sampling stations

tap-water supply with regulated water pressure, and artificial rain was sprayed onto an angled stage on which was positioned a sample of cap or fresh guano. Over a period of 30 min, 12 mm of 'rain' fell on the sample, and guano run-off was collected in a plastic beaker. Subsamples were prepared for nutrient analysis as described above.

The relationship between monthly nutrient levels in rockpools at the study sites in Saldanha Bay and the amount of rain that fell at each site during the 5 days prior to sampling was investigated using regression analysis. Rainfall measurements cited are those recorded at the nearby Cape Columbine weather station (32°49'S, 17°51'E) (monthly weather reports of the Weather Bureau, South African Transport Services).

Results

Intertidal nutrients

On island shores, where seabird guano is deposited above the high-tide level, there is a tendency for nutrient levels (mean of 2 samples per month) to be higher in high-shore rockpools than in low-shore pools (Wilcoxon test), but none of the differences is statistically significant. At Mauritz Bay and Cape Columbine there is a similar lack of significant difference between high- and low-shore nutrient levels except for the levels of NO_2-N and NO_3-N which are significantly higher in low-shore pools than in high-shore pools (Wilcoxon tests; NO_2-N: $n = 29$, $T = 112.5$, $P < 0.05$; NO_3-N: $n = 19$, $T = 19.0$, $P < 0.01$). In view of the comparability of nutrient levels in the 3 shore regions, monthly mean nutrient levels for the whole intertidal zone at each site were calculated using the mean of nutrient levels measured in the low-, mid- and high-shore rockpools at each site (6 samples per site per month). These monthly mean intertidal nutrient values are used in subsequent analyses and are shown for selected sites in Fig. 1.3 with the values for NO_2-N, NO_3-N, NH_4-N and $CO(NH_2)_2$-N combined and expressed as total nitrogen.

Monthly mean levels of NO_2-N, NO_3-N, NH_4-N, $CO(NH_2)_2$-N and PO_4-P at study sites in the Saldanha Bay area vary significantly between months (Friedman tests; NO_2-N: $X^2_{15} = 45.29$, $P < 0.001$; NO_3-N: $X^2_{15} = 38.39$, $P < 0.001$; NH_4-N: $X^2_{9} = 47.82$, $P < 0.001$; $CO(NH_2)_2$-N: $X^2_{8} = 35.70$, $P < 0.001$; PO_4-P: $X^2_{15} = 26.77$, $P < 0.05$). However, there is no consistent pattern of variation, suggesting that stochastic rather than seasonal factors are the cause. The dissimilarity of months makes the statistical testing of monthly mean nutrient levels invalid (Hurlbert 1984), and consequently Wilcoxon tests have been used to identify the differences in nutrient status between sites (Zar 1984).

Intertidal nutrient levels at Malgas, Jutten and Marcus Islands do not differ significantly for any of the 5 nutrients considered (Wilcoxon tests) and mean nutrient levels are always higher at these sites than at any others

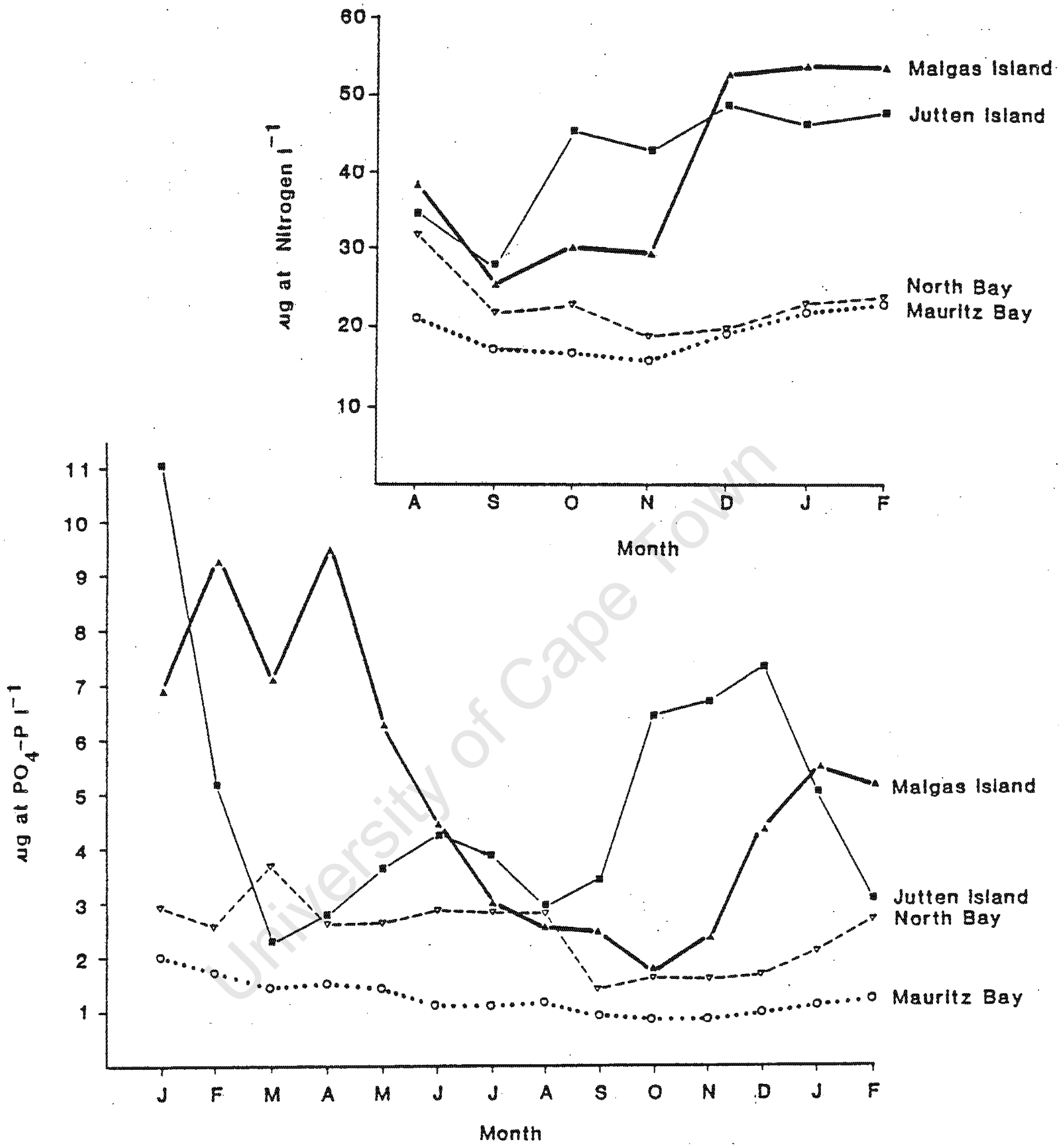

Fig. 1.3. Three-month running means of concentrations of nitrogen (in the form of NO_2-N, NO_3-N, NH_4-N and $CO(NH_2)_2$-N) and phosphorus (in the form of PO_4-P) recorded in intertidal rockpools at selected sites in the Saldanha Bay area

(Table 1.1). Levels of NO_2-N, NO_3-N and PO_4-P are consistently higher at North Bay than at Bomgat (Wilcoxon tests; NO_2-N: $n = 16$, $T = 7.00$, $P < 0.005$; NO_3-N: $n = 16$, $T = 14.00$, $P < 0.01$, PO_4-P: $n = 16$, $T = 28.00$, $P < 0.05$), and levels of NO_2-N and NO_3-N are consistently higher at Mauritz Bay than at Cape Columbine (NO_2-N: $n = 15$, $T = 24.00$, $P < 0.05$; NO_3-N: $n = 15$, $T = 23.00$, $P < 0.05$). Although levels of urea do show the expected trend of increased mean concentrations at island sites (Table 1.1), this is the only nutrient considered which did not show significant differences in concentration between study sites (Friedman test; $X^2_6 = 5.62$, $P > 0.25$). Intertidal nutrient status at North Bay and Bomgat generally is intermediate between that at islands and that at mainland sites outside the Bay (Table 1.1).

Nutrients in seabird guano

Ammonium is the dominant inorganic nitrogen compound released from guano in solution and occurs, in solution, at 100 times the concentration of NO_2-N (Table 1.2). Rain delivered by artificial apparatus to samples of cap guano and fresh guano causes the leaching of nutrients from the guano. However, less than 1% of the nutrients released from cap guano after solution in double-distilled water for 24 h are released by 12 mm of continuous artificial rain (Table 1.2). Up to 8% of nutrients potentially available in fresh guano are released by 12 mm of artificial rain (Table 1.2). In 90% of instances the cumulative rainfall at each study site in the Saldanha Bay area during the 5 days prior to

Table 1.1. Mean monthly nutrient concentrations (ug at l^{-1}) (± S.D.) at intertidal study sites in the Saldanha Bay area. Asterisks indicate significant differences between sites (Wilcoxon tests)

STUDY SITES	NO_2-N (n = 16)		NO_3-N (n = 15,16)		NH_4-N (n = 10)		$CO(NH_2)_2$-N (n = 9)		PO_4-P (n = 15,16)	
Malgas Island	1.34	(1.49)	11.81	(7.15)	20.51	(12.94)	9.83	(8.78)	5.15	(3.85)
Jutten Island	1.23	(0.63)	12.59	(6.81)	22.00	(11.47)	7.97	(4.79)	10.03	(18.13)
Marcus Island	1.97	(4.57)	10.50	(9.04)	18.18	(21.83)	7.48	(6.70)	16.94	(50.75)
North Bay	0.75	(0.38) *	9.70	(9.34) *	12.24	(5.55)	4.43	(2.13)	2.48	(1.50) *
Bomgat	0.55	(0.35)	4.89	(4.27)	10.34	(3.84)	5.92	(4.39)	1.58	(1.03)
Mauritz Bay	0.54	(0.22) *	7.42	(3.20) *	8.70	(4.24)	3.96	(2.13)	1.40	(0.65)
Cape Columbine	0.49	(0.21)	5.40	(2.68)	12.59	(13.85)	5.57	(3.23)	1.55	(0.50)

Table 1.2. Mean (± S.D.) quantities of nutrients (ug at g^{-1} dry guano) released from cap guano and from fresh guano after solution in double-distilled (DD) water and in seawater (SW) for 24 h, and after treatment with 12 mm of artificial rain. The nutrients released after rain are also expressed as a percentage of the nutrients released after solution in double-distilled water for 24 h. In all instances n = 10

		NO_2-N	NO_3-N	NH_4-N	PO_4-P
CAP GUANO	24 h (SW)	12.2 ±3.7	113.2 ±55.0	2490.8 ±740.6	160.7 ±46.0
	24 h (DD)	10.0 ±3.9	98.7 ±62.3	2636.5 ±666.5	304.5 ±38.5
	12 mm rain	0.1 ±0.0	0.2 ±0.0	8.5 ±0.7	0.5 ±0.1
	%	1.0%	0.2%	0.3%	0.2%
FRESH GUANO	24 h (SW)	15.9 ±5.2	337.9 ±25.3	2126.4 ±356.9	137.1 ±51.2
	24 h (DD)	12.0 ±1.6	83.9 ±15.6	1988.0 ±433.3	207.6 ±92.7
	12 mm rain	0.1 ±0.0	1.2 ±0.1	154.4 ±15.0	15.6 ±0.4
	%	0.8%	1.4%	7.8%	7.5%

sampling was less than 12 mm (weather reports of the South African Weather Bureau). However, in only 19% of cases was the concentration of a nutrient in a low-, mid- or high-shore island rockpool significantly ($P < 0.05$) related to the amount of rain that had fallen during the 5 days prior to sampling. There was no consistent pattern to these relationships and although one might expect dependence between rainfall and the nutrient levels in high-shore pools to be more likely, since nutrients washed from terrestrial guano deposits would reach the high-shore region first, this was not the case. Significant regressions between rainfall and nutrient levels were equally likely in low-shore and in high-shore pools. In no instance was the level of a nutrient in a rockpool at a mainland site related to rainfall.

Extent of enriched zone

Nutrient levels at island stations across the mouth of Saldanha Bay generally are higher than those at mainstream stations (77% of instances - Table 1.3), but this relationship is seldom statistically significant (Table 1.3). It is noteworthy that the July samples, which do not show the expected trend, were collected during a period when the forces of wind and swell were operating in different directions, which would lead to extensive mixing of the water column (Table 1.3).

Table 1.3. Results of Kruskal-Wallis statistical tests on the mean nutrient levels recorded at island and mainstream stations across the mouth of Saldanha Bay during 1983, and the weather conditions prevailing at the time of sampling. 'x' indicates whether island (I) or mainstream (M) stations have the higher mean

MONTH	NUTRIENT	N_I	N_M	STATISTIC	*P*	I	M	WIND SPEED (Knots)	WIND DIRECTION	WAVE HEIGHT (m)	WAVE DIRECTION
JAN	PO_4-P	11	5	0.03			x	6.0	201° (SSW)	2.0	201° (SSW)
APR	NO_2-N	17	8	4.50	<0.05	x		1.2	246° (SW)	0.3	200° (SSW)
	NO_3-N	17	8	9.53	<0.005	x					
	NH_4-N	17	8	0.82		x					
	PO_4-P	17	8	1.30		x					
JUL	NO_2-N	16	7	0.07		x		13.4	350° (NNW)	2.5	252° (WSW)
	NO_3-N	16	7	1.70			x				
	NH_4-N	16	7	0.07		x					
	PO_4-P	16	7	0.71			x				
OCT	NO_2-N	15	6	0.12		x		17.5	194° (SSW)	3.0	232° (SW)
	NO_3-N	15	6	8.30	<0.005	x					
	NH_4-N	15	6	0.01		x					
	PO_4-P	15	6	4.83	<0.05	x					

Discussion

Intertidal nutrients

Seabird guano has long been recognized as a powerful fertilizer, comprizing some 14% (dry weight) soluble organic compounds, and 3% soluble mineral salts such as salts of Mg, K, Ca and Na (Galkina 1974). The composition of seabird guano is comparable between species (Burger et al. 1978; Bedard et al. 1980; Fugler 1985), the dominant soluble organic compound being uric acid which is converted, invariably totally, to ammonia by the action of aerobic and anaerobic microbes (Lindeboom 1984). Certain bacteria form urea as a product of uric acid metabolism (Barker 1961; Kaltwasser 1971; Stanier et al. 1976), and this may be hydrolysed to form ammonia (Metzler 1977). Although some of the ammonia subsequently volatilizes from the deposit, much is converted into nitrite and nitrate by nitrifying bacteria. Solutions of cap and fresh seabird guano from the islands in Saldanha Bay contain large amounts of inorganic nutrients in forms available to algae.

The availability of nitrogen and phosphorus are particularly important for marine primary production (de Boer 1982). Marine algae absorb nitrogen in inorganic form (as nitrite, nitrate and ammonium) as well as in organic form (as amino acids and proteins, such as urea - Mohsen et al. 1974). Ammonium and nitrate are most readily absorbed (de Boer 1982) and the experimental enrichment of growth media with nitrogen in these two forms, as well as with phosphorus in the form of phosphate, enhances the growth rates of benthic and intertidal algae in the laboratory (Waite and Mitchell 1972; Prince 1974; Steffensen 1976; Topinka and Robbins 1976; Chapman and Craigie 1977).

In Saldanha Bay the intertidal and nearshore waters around seabird-breeding islands are enriched with nutrients from seabird guano. Mean intertidal levels of NO_2-N, NO_3-N, NH_4-N, $CO(NH_2)_2$-N and PO_4-P are always higher on the shores of seabird-breeding islands than on adjacent mainland shores. Levels of $CO(NH_2)_2$-N, although showing the same trend, are not significantly different between sites, due possibly to the derivation of intertidal urea from sources other than uric acid metabolism, such as from the excretory products of rockpool organisms. Although such excretory products might contaminate nutrient samples, this was hopefully kept to a minimum by choosing rockpools which are flushed out regularly during each tidal cycle. Shannon and Stander (1977), in their assessment of the chemical characteristics of the waters of Saldanha Bay, report mean NO_3-N and PO_4-P levels, taken over a period of 18 months at 18 sample stations, of 5.6 ± 5.1 ug at l^{-1} ($n = 190$) and 1.4 ± 1.0 ug at l^{-1} ($n = 191$) respectively. The low-shore rockpools on Malgas, Jutten and Marcus Islands contain mean concentrations of these nutrients which are almost double the mean background levels; viz 10.3 ± 5.5 ug at NO_3-N l^{-1} ($n = 39$) and 2.2 ± 0.8 ug at PO_4-P l^{-1} ($n = 37$). Although a sampling frequency of once a month is not sufficient to characterize the nutrient field at each study site, the elevated levels of selected nutrients in the waters around the seabird-breeding islands are indicative of generally elevated levels of nutrients which are potentially available to enhance the growth of intertidal algae.

The means of entry of guano into the intertidal and nearshore waters probably are multiple. Some guano is deposited directly into the sea by birds which fly over the nearshore, or bathe close to the islands, but this is probably negligible in comparison with the amount deposited by birds which roost on the islands (the seabird species considered spend at least 50% of their time on the islands, and substantially more when they are tending chicks). It is likely that rain is not the overriding mechanism by which guano is transported from the land to the sea, particularly in the case of cap guano which is highly porous. Guano is probably transported mainly by waves, particularly during stormy conditions, and dry guano may also be transported by wind.

Extent of enriched zone

Golovin et al. (1976), working near seabird colonies in the Barents Sea, report a zone of nutrient enrichment, the radius of which is more than 6 km. In Saldanha Bay the movement of guano run-off from the shores of seabird-breeding islands is dependent on the directions of the major tidal currents in the Bay. Analysis of surface current flow patterns in Saldanha Bay (Huizinga 1982) shows there to be transport of surface waters between Malgas Island and North

Bay under the influence of normal ebbing and flowing tidal movement, and under the influence of the prevailing SSW wind. Consequently North Bay falls within the zone of nutrient enrichment from Malgas Island and has nutrient-rich intertidal waters (Table 1.1). Bomgat lies in a sheltered region on the western side of the harbour breakwater, and the transport of surface waters to and from the site probably is negligible except under abnormal, stormy conditions. Nutrient-rich waters from the shores of Marcus Island would be unlikely ever to reach Bomgat.

Seabird guano is a rich source of certain nutrients essential for plant growth and reproduction. Its entry into waters around seabird-breeding islands leads to nutrient enrichment, and provides the potential for enhanced intertidal primary production. In this way seabirds, which are not components of intertidal communities, may modify the rate of intertidal algal production.

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PART 2

NUTRIENT ENRICHMENT AND INTERTIDAL PRIMARY PRODUCTION

The influence of nutrient enrichment from seabird guano on the production rate of intertidal algae

Summary. Nutrient status is an important factor influencing the production rate and structure of many plant assemblages. Production in terrestrial plants and marine phytoplankton is stimulated by the addition of nutrients in the form of dissolved seabird guano, and it was hypothesized that seabirds may be determinants of the rate of algal production in the intertidal zone, where guano transported from terrestrial deposits into the sea enriches the waters with nutrients.

Rates of algal production on artificial settlement strips were measured at sites on rocky shores, using extracted chlorophyll as an index. Measurements were made on shores known to be washed by waters enriched with nutrients from the dissolved guano of seabirds, and the results were compared with measurements made on nearby, unenriched shores. Algal production generally was higher on nutrient-rich shores. The hypothesis that seabird guano provides nutrients which stimulate the production of intertidal algae was tested experimentally when dissolved guano was dripped down an unenriched rocky shore. Algal production was enhanced in response to the presence of additional nutrients from guano.

The combination of enhanced algal production rate and heavy predatory pressure by shorebirds on the dominant intertidal herbivore, *Patella granularis*, leads to the development of extensive mats of foliose algae on nutrient-rich shores. These mats are absent on unenriched shores. Thus seabirds, as producers of guano, can modify profoundly the production rate, abundance and distribution of intertidal algal assemblages.

Introduction

Extensive, permanent mats of foliose macro-algae grow on the rocky shores of seabird-breeding islands off the southwestern Cape, South Africa. In marked contrast, such mats are absent from the shores of nearby mainland sites where no large aggregations of seabirds occur. Hockey and Branch (1984) suggest that on 3 islands in Saldanha Bay (33°03'S, 17°58'E) heavy predation by African Black Oystercatchers *Haematopus moquini* Bonaparte on the dominant intertidal limpet *Patella granularis* L. results in a decrease in limpet numbers and consequently in a reduction in herbivory on algal sporelings. More algae thus reach the foliose stage and form intertidal mats. On nearby mainland shores, where oystercatchers are much less common (Hockey 1983) and limpets numerous, such algal mats are entirely absent (Hockey and Branch op. cit.).

However, in addition to the large numbers of oystercatchers present on these 3 islands, there are permanent colonies of seabirds which number in total approximately 200 000 individuals (Cooper et al. 1982; Crawford et al. 1983; Shelton et al. 1984). Guano deposition from these seabirds is considerable, both terrestrially, where breeding birds have their nests, and intertidally, where birds roost. The value of seabird guano as an agricultural fertilizer has long been recognized (Speigt 1940; Hutchinson 1950) and its entry into the sea around seabird-breeding islands in Saldanha Bay leads to the enrichment of intertidal and nearshore waters with inorganic and organic nutrients capable of enhancing rates of primary production (Part 1).

Nutrients from seabird guano have been shown to enhance phytoplankton production in the Barents Sea (74°00'N, 36°00'E) (Golovkin 1967, Zelickman and Golovkin 1972) and terrestrial plant production on islands where seabirds breed and roost (Gillham 1961, 1977; Smith 1976a, b, 1978; Allaway and Ashford 1984). The influence of seabird guano on intertidal algal production has not been investigated, although Hansen (1981) has shown that peak intertidal algal standing crop on Ano Nuevo Island (37°07'N, 122°19'W) is associated with unusually high levels of NH_4-N in the waters surrounding the island. Numerous seals haul out on the island shores and their excreta are washed from the island by waves. Peak NH_4-N levels in nearshore waters correspond with peak numbers of seals utilizing the island.

Should it be found that enhanced intertidal production in the field is associated with guano-derived nutrient enrichment of intertidal and nearshore waters, then the presence of seabirds at those sites could be considered a factor influencing intertidal community structure. They may also modify intertidal invertebrate and avian population dynamics, since enhanced primary production and increased food availability for herbivores would lead to changes in herbivore production that could affect their avian predators.

In this study, algal production on rocky shores enriched and not enriched with nutrients from seabird guano was measured using 2 techniques. The hypothesis that nutrients from seabird guano can enhance intertidal algal production was tested experimentally by measuring production on a rocky shore which was artificially enriched with dissolved guano.

Methods and materials

Study sites

Two study areas were used: algal production was measured monthly at 7 intertidal sites in the Saldanha Bay area (Fig. 2.1) between December 1982 and April 1984, and a field experiment to determine the effects of artificial nutrient enrichment of a rocky shore was conducted at Menskoppunt, a rocky promontory on the west coast of the Cape of Good Hope peninsula (Fig. 2.1). In Saldanha Bay 3 sites were on rocky

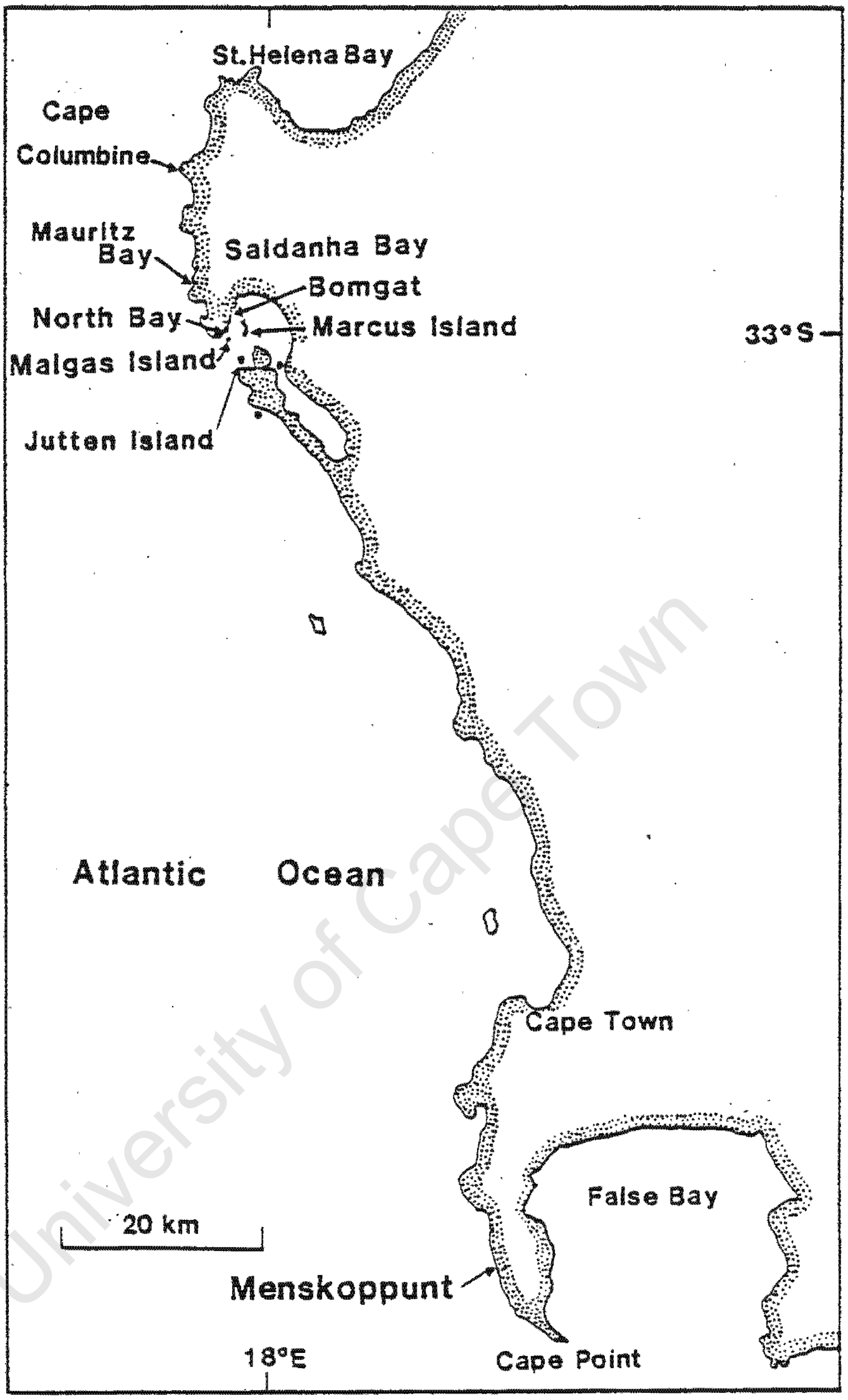

Fig. 2.1. Map of the southwestern Cape coast, South Africa, showing the 2 study areas and the intertidal study sites in each area

shores enriched by seabird guano: 2 were on the shores of seabird-breeding islands (Malgas and Jutten Islands), and the third was on Marcus Island, a seabird-breeding island that is connected to the mainland by a causeway (Fig. 2.1). Sites were also established at Mauritz Bay and Cape Columbine which are on the mainland north of Saldanha Bay and which do not have seabird aggregations or nutrient-rich intertidal waters (Part 1). Lastly, 2 sites (North Bay and Bomgat) were established on mainland shores within the Bay. Although neither of these sites had aggregations of seabirds, both were within the possible zone of influence of guano run-off from the seabird-breeding islands (Fig. 2.1), and the North Bay site has been shown to have nutrient-rich intertidal waters as a result of current movement which transports dissolved guano from Malgas Island to North Bay (Part 1).

At all sites the rocky shore was gently sloping and exposed to strong wave action. The substratum was granite at all Saldanha Bay sites, and hard Table Mountain sandstone at Menskoppunt. The zone between the upper limit of the low-shore mussel beds and the upper limit of occurrence of the limpet *Patella granularis* was studied. At each site the zone was divided into a low-, mid- and high-shore region of equal area. On the shores in and around Saldanha Bay *P. granularis* was the dominant intertidal herbivore in terms of number and biomass; the limpets *P. granatina* (L.) and *P. oculus* Born occurred in the low-shore zone, and *Siphonaria capensis* Quoy and Gaimard inhabited shallow pools, but no species was as numerous or as widely distributed as *P. granularis*. Low-shore mussel beds, dominated by *Choromytilus meridionalis* (Krauss), *Mytilus galloprovincialis* Lamarck and *Aulacomya ater* (Molina), were present at all sites except Cape Columbine. Extensive mats of foliose *Enteromorpha* sp. and *Porphyra capensis* Kutz. occurred in the high- and mid-shore regions at the island sites and at North Bay, covering up to approximately 50% of the rocky surface. Algal mats were absent from all mainland sites except North Bay.

At Menskoppunt the small whelk *Littorina africana* Phillipi was abundant on the exposed high-shore, and the dominant mid-shore grazers were the limpet *P. granularis* and the winkle *Oxystele variegata* (Anton). The low-shore region was dominated by *P. granatina*, *P. granularis* and *Oxystele tigrina* (Chemnitz), and the infratidal fringe supported a sparse population of *Patella argenvillei* (Krauss). There were few intertidal macro-algae at Menskoppunt: small patches of *Porphyra capensis*, *Ulva* sp., *Chaetangium erinaceum* (Turn.) Papenf., *C. ovale* (Suhr) Papenf. and *Gigartina radula* (Esp.) J. Ag. were present in the low-shore region. *Enteromorpha* sp. was present in rockpools and gullies together with the moss-like rhodophyte *Caulacanthus ustulatus* (Suhr) Papenf. The rocky surface of almost the entire study site at Menskoppunt was colonized by *Hildenbrandia* sp., a red encrusting alga (see Stephenson and Stephenson (1972) for detailed shore descriptions).

Algal production

At each study site in the Saldanha Bay area monthly algal production was measured in the low-, mid- and high-shore regions. A herbivore exclusion plot was established in each region by enclosing a 0.1 m^2 rectangular area with a strip of copper-based marine anti-fouling paint. Intertidal grazers such as *Patella* spp. are repelled by the chemical components in this paint. Initially, after the rocky surface had been scraped and burned (with a blow-torch) to remove settled algae, 8 high-intensity polystyrene settlement strips measuring 30 x 50 x 2 mm were glued to the rock inside each exclusion plot. A rapidly setting epoxy (Araldite) was found to be most durable.

After a month 4 strips were removed from each plot, and 8 fresh ones were glued down. The remaining initial strips were only lifted after 2 months in position. Subsequently, 8 strips were lifted each month, 4 of which had been in position for 1 month, and 4 for 2 months. The 8 lifted strips were replaced with fresh ones, after the rock within the herbivore exclusion plot had been burned and scraped to remove settled algae. All lifted strips were wrapped in aluminium foil to exclude light, and stored frozen. Chlorophyll-a extracted from the algae growing on each strip (Strickland and Parsons 1972) was used as an index of algal production, both on a monthly and a bi-monthly basis. The chlorophyll-a estimations were obtained using the colorimetric techniques of Jeffrey and Humphrey (1975). Resultant values were corrected for the exact area of the strip and for the number of days that the strip had been in position, such that the final index of algal growth was expressed in ug chlorophyll-a cm^{-2} $month^{-1}$. Each month, and at each shore level only the chlorophyll-a values from the 2 strips with the maximum algal growth (1 from the sample of 4 one-month strips and 1 from the 4 two-month strips) were used in analysis, as this was considered the best indication of potential algal production at that shore level.

Monthly maximum algal production rates at different shore levels within sites were compared using Wilcoxon matched-pairs signed-ranks tests (Sokal and Rohlf 1981). Since it was possible that there might be a seasonal influence on monthly algal production, multiple linear regression analyses were used to regress the dependent variables (rate of algal production in 1 and in 2 months) on a series of independent variables, and to determine the linear equations which best predict the dependent variables (Sokal and Rohlf 1981). It is not possible, using this technique, to perform significance tests between the algal growth rates recorded at different sites.

Monthly algal production at each site was also measured in terms of the biomass of algae that developed in a set 7 x 7 cm area within each exclusion plot. Each month this area was scraped clean using a stiff brush with plastic bristles, and the algae removed were stored frozen until they could be oven dried and weighed. Regression analysis was used to determine the relationship between algal dry biomass and monthly total chlorophyll (*a*, *b*, c_1 and c_2 - Strickland and Parsons 1972; Jeffrey and Humphrey 1975), using the mean value for total chlorophyll extracted from algae growing on each of 4 replicate settlement strips. The differences in algal production between island and mainland sites were not investigated using algal biomass data as there were many instances when wave action did not permit the meticulous scraping and collection of settled algae, and consequently data are missing.

Field experiment

Concurrently with the collection of data in the Saldanha Bay area, a field experiment was conducted at Menskoppunt to establish whether a direct relationship exists between nutrient enrichment from dissolved seabird guano, and the rate of algal production. A section of rocky shore from the upper limit of macro-algal occurrence to the low-shore mussel bed was enriched using a solution of dried, sifted seabird guano (from Malgas Island in Saldanha Bay) and seawater. Two kg of dried, sifted guano were dissolved in 1350 l of seawater, thus increasing the nutrient status of the seawater that was to enter the intertidal zone such that, even after dilution by waves, excess nutrients would be available to intertidal algae. After the first week, weekly samples of the guano solution were analysed for concentrations of NO_2-N, NO_3-N and PO_4-P using an autoanalyser.

The guano solution was stored in a 1350 l capacity asbestos-cement tank which was installed above the high-tide level. From this reservoir, the guano solution passed through a constant-pressure tank, which regulated the flow, and down a short length of plastic irrigation piping. At the high-shore level the piping was joined, using a T-piece, to the two arms of the drip-bar which measured approximately 4 m in length (Fig. 2.2). Nozzles inserted in the drip-bar provided a flow of 2 l h^{-1} of guano solution. Similar apparatus was used to drip unenriched seawater down an adjacent section of shore approximately 5 m to one side of the guano-drip area. The tanks were filled every week. A third section of adjacent shore, approximately 5 m to the opposite side of the guano-drip area, was a 'dry-control' which had neither seawater nor guano solution running over it from the high-shore region (Fig. 2.2).

Algal growth rates were measured using settlement strips glued to the rock inside herbivore exclusion plots as described previously. In the guano-drip and dry-control areas there were exclusion plots at the low-, mid- and high-shore levels, but the topography of the shore prevented the establishment of a high-shore plot in the seawater-drip area. In this instance algal growth was measured at 2 levels only (Fig. 2.2). Four strips were glued down inside each plot and after a month in position 2 were removed from each set of 4 and were replaced with new strips. After a further month all remaining strips were lifted. Relationships between algal production in each experimental

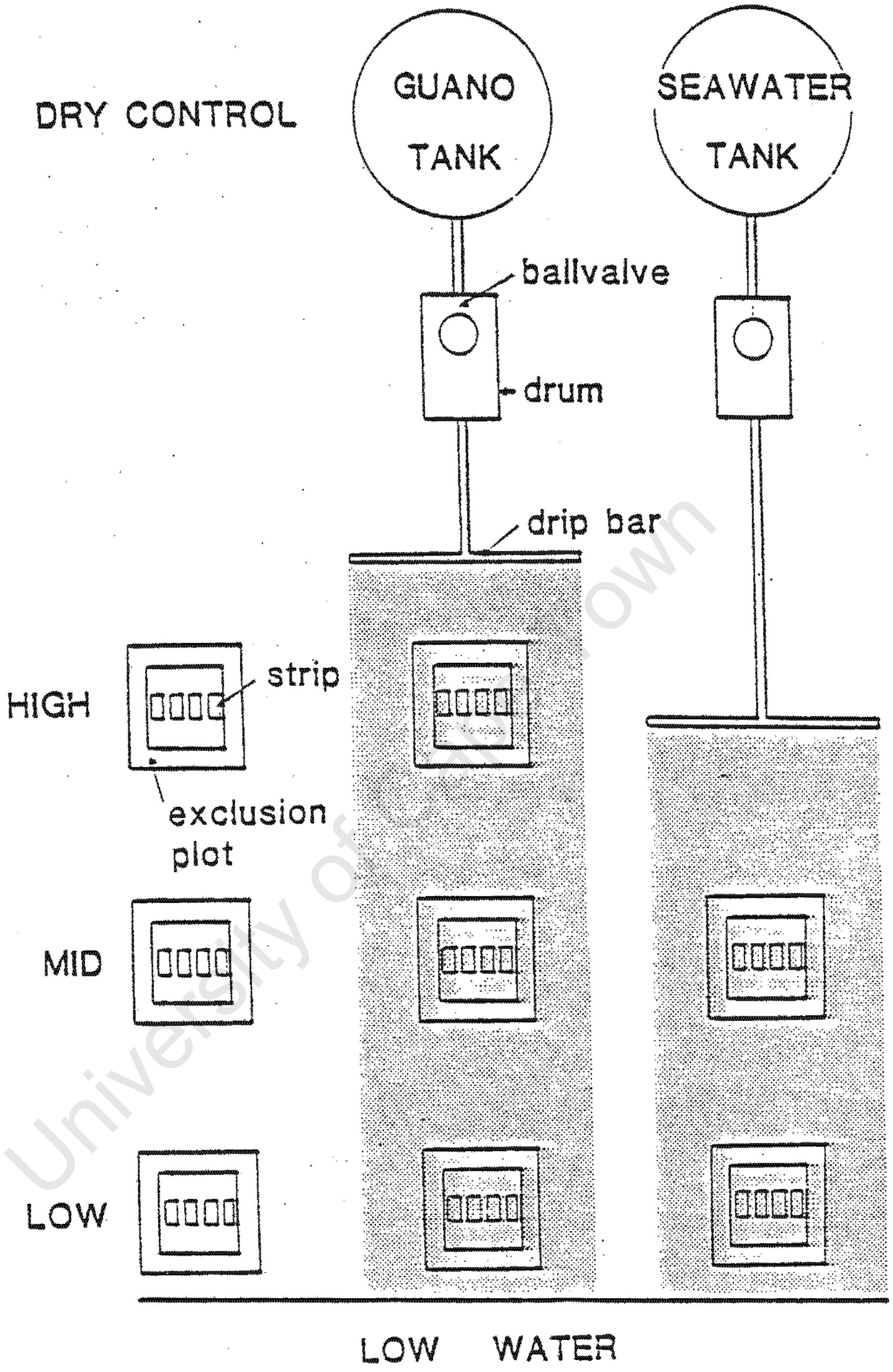

Fig. 2.2. Plan diagram of the apparatus layout and sampling stations at the study site at Menskoppunt (not drawn to scale)

area, and at different shore levels in the same area were investigated statistically using Wilcoxon tests.

Results

Algal production

Various algal species settle on the experimental strips; *Enteromorpha* sp. is the dominant foliose algae, although *Porphyra capensis*, micro-algae and diatoms also are present. On rocky shores in the Saldanha Bay area monthly maximum algal production is consistently greater in the low-shore region than in the mid-shore region at the same site (Wilcoxon test; $n = 102$, $T = 305.0$, $P < 0.001$) and similarly, mid-shore algal production is greater than high-shore production at the same site ($n = 99$, $T = 319.0$, $P < 0.001$ - Fig. 2.3). The relationship (as determined using multiple linear regression) between algal production in 1 month and the independent variable shore level confirms these results, with growth in the low-shore region having a co-efficient of 0.00 whereas growth in the high-shore region has the most negative estimated co-efficient (Table 2.1).

The independent variables site and month also influence the rate of algal production. Production in 1 month is greatest on Jutten and Marcus Islands and least at Cape Columbine (Fig. 2.3, Table 2.1). Production on Malgas Island, with an estimated co-efficient of 0.00, is significantly lower than that on either Jutten (d.f. = 311, $t = 7.28$, $P < 0.001$) or

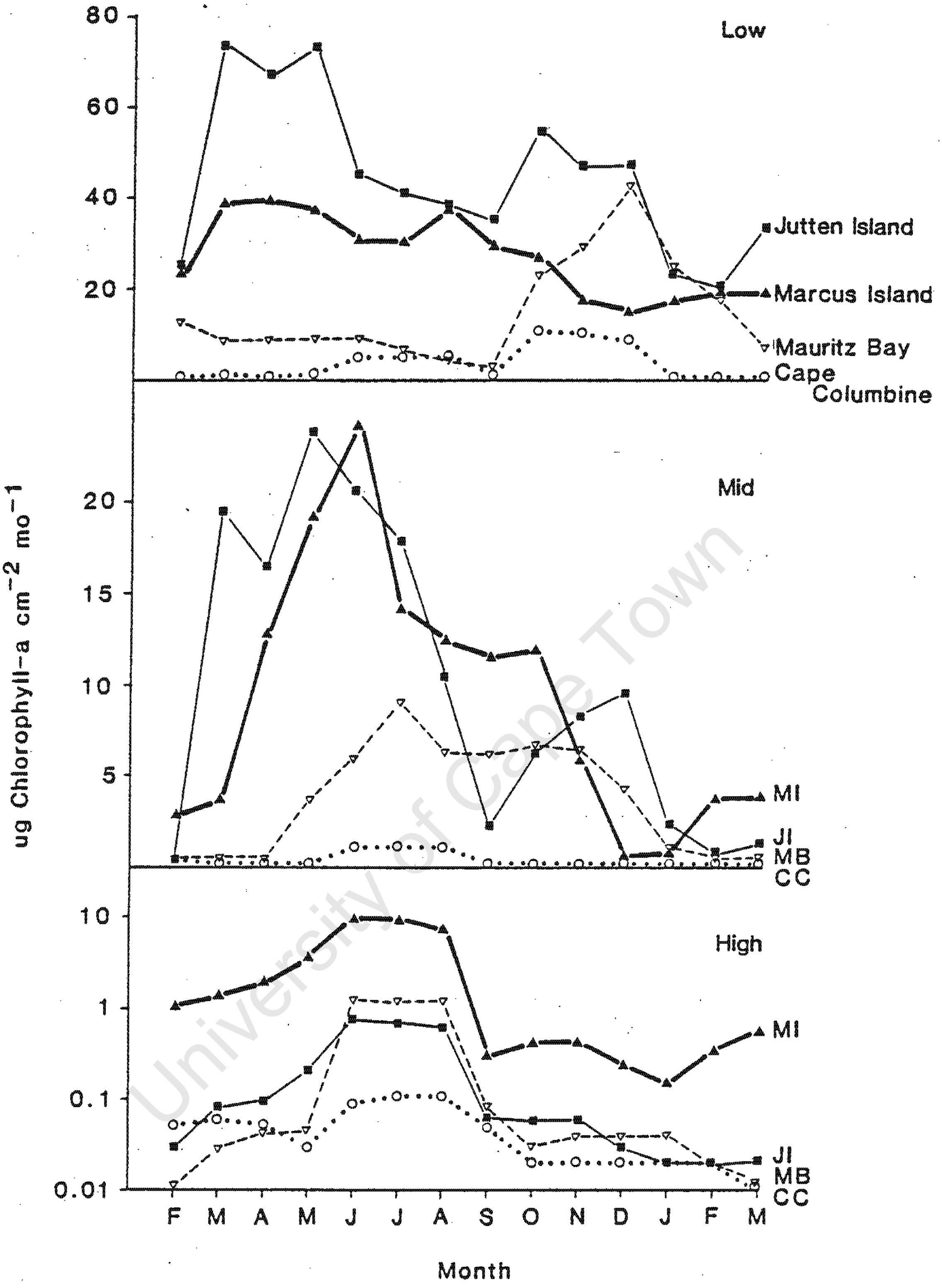

Fig. 2.3. Monthly maximum algal production (ug chlorophyll-a cm^{-2} mo^{-1}) recorded in 3 shore regions at selected study sites in the Saldanha Bay area. Closed symbols and solid lines indicate island sites whereas open symbols and broken lines indicate mainland sites outside the Bay

Table 2.1. Estimated co-efficients, standard errors and significance levels resulting from the multiple linear regression analysis of algal production in 1 month at 7 sites in Saldanha Bay (d.f. = 311)

INDEPENDENT FACTOR	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	1.86	4.40	0.42	
Jutten Island	35.09	4.82	7.28	<0.001
Marcus Island	18.29	4.82	3.79	<0.001
Bomgat	11.50	4.82	2.38	<0.02
North Bay	9.90	4.82	2.05	<0.05
Mauritz Bay	7.19	4.82	1.49	
Cape Columbine	-3.75	4.82	-0.78	
March 1983	2.10	4.08	0.52	
April	10.16	4.08	2.49	<0.02
May	9.19	4.08	2.25	<0.05
June	7.31	4.08	1.79	
July	7.62	4.08	1.87	
August	3.81	4.13	0.92	
September	3.87	4.08	0.95	
October	2.68	4.08	0.66	
November	11.38	4.08	2.79	<0.01
December	14.79	4.08	3.63	<0.001
January 1984	2.16	4.08	0.53	
February	2.42	4.13	0.59	
March	2.41	4.08	0.59	
April	2.29	4.08	0.56	
Mid-shore	-6.43	4.82	-1.33	
High-shore	-7.51	4.91	-1.53	
Jutten Island mid-shore	-27.15	6.82	-3.98	<0.001
Jutten Island high-shore	-34.73	6.88	-5.05	<0.001
Marcus Island mid-shore	-10.56	6.82	-1.55	
Marcus Island high-shore	-15.76	6.88	-2.29	<0.05
Bomgat mid-shore	-12.29	6.82	-1.80	
Bomgat high-shore	-11.30	6.88	-1.64	
North Bay mid-shore	-9.55	6.88	-1.39	
North Bay high-shore	-9.25	6.88	-1.34	
Mauritz Bay mid-shore	-4.64	6.82	-0.68	
Mauritz Bay high-shore	-6.76	6.88	-0.98	
Columbine mid-shore	3.09	6.82	0.45	
Columbine high-shore	3.97	6.88	0.58	

Marcus Islands (d.f. = 311, $t = 3.79$, $P < 0.001$) and is not significantly different from that at Bomgat or Cape Columbine. In addition, algal production is significantly enhanced in the months of November, December, April and May (Table 2.1). Although neither of the 2 mainland sites within Saldanha Bay has permanent aggregations of seabirds, algal production is consistently greater on the shores at North Bay than at Bomgat (Wilcoxon test; $n = 40$, $T = 89.50$, $P < 0.0001$ - Fig. 2.4).

Although variations in site, shore level and month explain only 39.4% of the variation in algal production in 1 month, the results are supported by multiple linear regression analysis of algal production in 2 months (Table 2.2). Algal production is again greatest in the low-shore region and lowest in the high-shore region. Comparing all months, strips collected in November (i.e. in position during October and November) support the most algae. Sites on Jutten and Marcus Islands again have the most prolific algal growth, and Cape Columbine has the least. (The rate of algal growth at Malgas Island is used as a 'yardstick' and has a co-efficient of 0.00. In this analysis algal growth at the other sites estimated relative to algal growth on Malgas Island). However, in this analysis algal production at Cape Columbine, Bomgat and Mauritz Bay is not significantly different from production on Malgas Island, while production is significantly enhanced on Jutten and Marcus Islands, and at North Bay (Table 2.2). In this

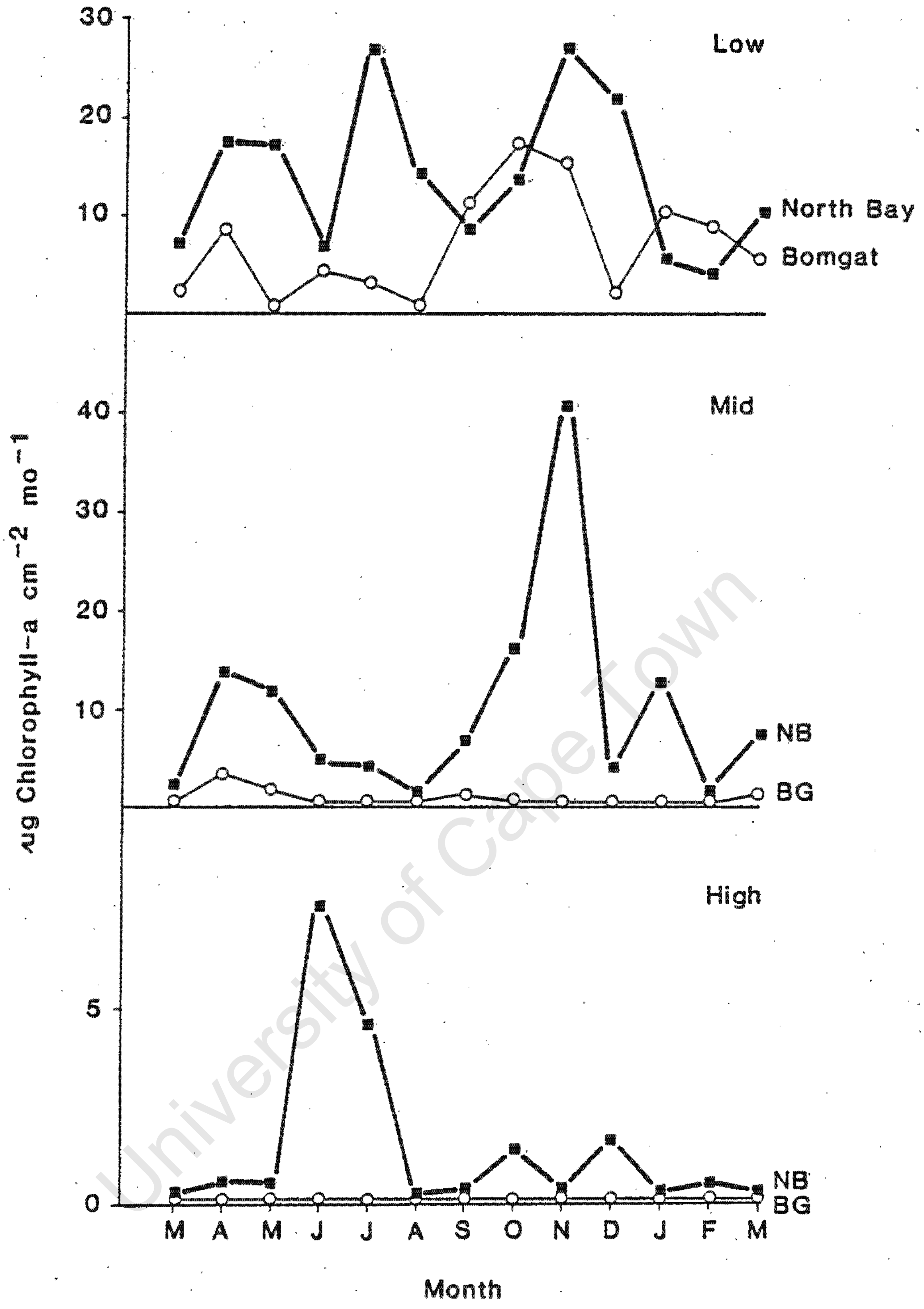

Fig. 2.4. Monthly maximum algal production (ug chlorophyll-a cm^{-2} mo^{-1}) in 3 shore regions at the nutrient-rich North Bay site and the unenriched Bomgat site

Table 2.2. Estimated co-efficients, standard errors and significance levels resulting from the multiple linear regression analysis of algal production in 2 months at 7 sites in Saldanha Bay (d.f. = 269)

INDEPENDENT FACTOR	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	7.53	2.21	3.40	<0.001
Jutten Island	16.78	2.61	6.42	<0.001
Marcus Island	11.35	2.50	4.54	<0.001
North Bay	5.08	2.50	2.03	<0.05
Mauritz Bay	-0.64	2.50	-0.26	
Bomgat	-1.87	2.50	-0.75	
Cape Columbine	-4.66	2.50	-1.87	
April 1983	2.84	1.97	1.45	
May	2.68	1.97	1.35	
June	3.46	1.97	1.76	
July	1.84	1.99	0.92	
August	1.46	1.97	0.74	
September	1.53	1.97	0.78	
October	3.86	1.99	1.94	
November	4.00	1.97	2.04	<0.05
December	-0.57	1.97	-0.29	
January 1984	-1.96	1.97	-1.00	
February	-1.22	1.97	-0.62	
March	-1.10	1.97	-0.56	
Mid-shore	-3.47	2.50	-1.39	
High-shore	-8.66	2.50	-3.47	<0.001
Jutten Island mid-shore	-13.97	3.62	-3.86	<0.001
Jutten Island high-shore	-15.43	3.62	-4.27	<0.001
Marcus Island mid-shore	-5.67	3.53	-1.61	
Marcus Island high-shore	-7.06	3.53	-2.00	
North Bay mid-shore	-0.53	3.53	-0.15	
North Bay high-shore	-3.87	3.53	-1.10	
Mauritz Bay mid-shore	2.50	3.53	0.71	
Mauritz Bay high-shore	0.61	3.53	0.17	
Bomgat mid-shore	-2.81	3.53	-0.80	
Bomgat high-shore	1.73	3.53	0.49	
Columbine mid-shore	-0.44	3.53	-0.12	
Columbine high-shore	4.55	3.53	1.29	

analysis 50.7% of the variation in algal production is explained by variation in the 3 independent variables.

Algal production in 2 months is not necessarily twice the production obtained after 1 month. In instances of very fast rates of production (e.g. in the low-shore region on Jutten and Marcus Islands) the rate of algal growth decreases during the second month (Fig. 2.5). At sites showing extremely low rates of algal production (e.g. in the high-shore region at Mauritz Bay and Cape Columbine) algal growth does not necessarily increase during the extra month available.

The mean total chlorophyll (a, b, c_1 and c_2) extracted from 4 replicate settlement strips after a month in position is significantly related to the biomass of algae present on 49 cm^2 of rock in the same herbivore exclusion plot (d.f. = 280, $r^2 = 0.14$, $P < 0.0001$). The relationship is linear and is given by the equation:

$$\text{tot. chlorophyll (ug cm}^{-2}\text{ mo}^{-1}) = \frac{30.79\text{ (g dry algae)} + 0.92}{49}$$

Field experiment

Levels of NO_2-N and PO_4-P (but not of NO_3-N) are very much higher in the guano solution at Menskoppunt than in intertidal rockpools on seabird-breeding islands in Saldanha Bay (Table 2.3, Part 1). As was the case at the Saldanha Bay sites, Menskoppunt shows a trend of increasing algal production from high- to low-shore (Table 2.4). All

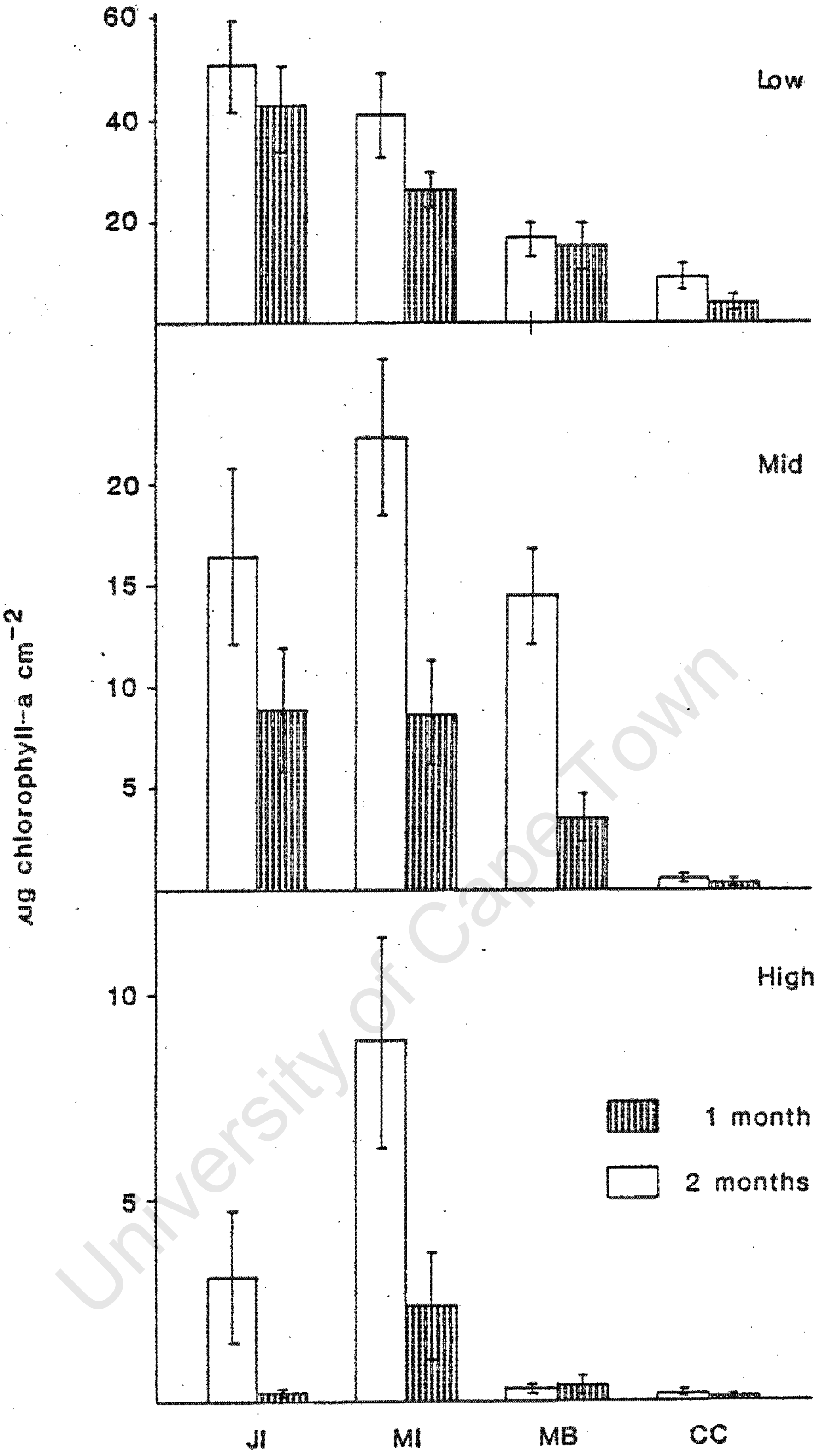

Fig. 2.5. Comparison of mean monthly (± S.D.) and bi-monthly maximum algal production (ug chlorophyll-a cm^{-2}) in 3 shore regions at selected island and mainland study sites in the Saldanha Bay area (JI = Jutten Island, MI = Marcus Island, MB = Mauritz Bay, CC = Cape Columbine)

Table 2.3. Concentration of nutrients (ug at l^{-1}) in the guano solution tank at Menskoppunt each week. Values are the means of 2 replicate samples

Week	NO_2-N	NO_3-N*	PO_4-P
2	151	>15	576
3	171	>15	987
4	165	>15	991
5	164	>15	800
6	157	>15	986
7	156	>15	422
8	150	>15	734

* Due to an error in analytical procedure the NO_3-N levels could not be determined accurately. In all instances they were greater than mean levels in intertidal rockpools on seabird-breeding islands in Saldanha Bay (Table 1.1, Part 1)

Table 2.4. Algal production rates (ug chlorophyll-a cm^{-2} month^{-1}) on settlement strips from exclusion plots at low-, mid- and high-shore levels in the guano-drip (G), seawater-drip (S) and dry-control (C) areas at Menskoppunt. Each value is the mean of chlorophyll-a concentrations from algae on 2 replicate settlement strips

Duration	Area	LEVELS		
		Low	Mid	High
1 month (first sample)	G	0.34	0.14	0.06
	S	0.09	0.10	No strips
	C	0.14	0.10	0.00
1 month (second sample)	G	0.49	0.29	0.01
	S	0.14	0.08	No strips
	C	0.23	0.13	0.02
2 months	G	0.41	0.48	0.00
	S	0.11	0.11	No strips
	C	0.10	0.08	0.01

settlement strips removed from herbivore exclusion plots in the guano-drip area show more algal settlement and growth than do strips from comparable positions in the seawater drip area. Similarly, strips in the guano-drip area show more algal growth than strips in comparable positions in the dry-control area. Algal growth on strips in the seawater-drip and dry-control areas is similar, indicating that nutrient content, rather than moisture, is the stimulus leading to enhanced algal production.

Discussion

Algal production rates

The availability of nutrients is likely to be a major factor regulating the growth rates of intertidal algae (de Boer 1982; Tilman 1982) and any process which increases the availability of important nutrients is likely to stimulate algal production, as experimental nutrient enrichment of growth media both in the laboratory and in the field has shown (Waite and Mitchell 1972; Topinka and Robbins 1976; Chapman and Craigie 1977). Intertidal algal production rates in Saldanha Bay are enhanced on the shores of Jutten and Marcus Islands and at North Bay, where the intertidal and nearshore waters are enriched with nutrients from seabird guano (Part 1). Algal growth on the shores of Malgas Island does not show the expected trend, although intertidal nutrient levels at this site and at the other island sites are not different statistically (Part 1). In particular, algal production in the mid- and low-shore regions on Malgas Island is unusually low, and it is possible that the herbivore exclusion plots selected at this site and at others are not comparable in terms of height and exposure to wave action. Although the data were insufficient to indicate a causal relationship between enhanced algal production and elevated levels of any one particular nutrient, it is known that the dissolved guano of seabirds is rich in inorganic nitrogen and phosphorus compounds that are important for marine primary production (Hutchinson 1950; Galkina 1974; de Boer 1982; Part 1).

Nutrient enrichment of intertidal waters by the artificial introduction of dissolved guano produced similar results. The nutrient composition of commercially-available, dried guano is different from that of fresh guano, particularly in the nitrogen content, as uric acid-bound nitrogen in fresh seabird guano is quickly converted to ammonium-bound nitrogen as the guano dries, and ammonia soon volatilizes from the deposit (Lindeboom 1984). In addition, the guano solution at Menskoppunt was rich in organic matter, and bacterial activity would have made the solution anaerobic. Under such conditions nitrification is inhibited (Leentvaar 1967; Knowles 1982) and assimilatory and dissimilatory reductions of NO_2-N and NO_3-N occur readily (Atlas and Bartha 1981). Nitrate is more commonly reduced than nitrite due to the more general occurrence of nitrate reductase in denitrifying bacteria (Knowles 1982).

Despite differences in the exact nature of nutrient enrichment from commercially-available, dried guano and from guano run-off on seabird island shores, in both instances the guano provided sufficient additional nutrients to enhance intertidal algal production. The correlations between nutrient levels and rate of primary production on shores in the Saldanha Bay area, as well as the experimental evidence from Menskoppunt indicate that the availability of inorganic nutrients does limit the rate of intertidal algal growth. The lack of true replication in the experimental design does not allow this limitation to be demonstrated conclusively, although the response of algae to increased availability of nutrients is clear. Both on nutrient-rich shores in the Saldanha Bay area and in the guano-drip area at Menskoppunt, nutrient enrichment occurred at all shore levels. However, the response of algae was most noticeable in the low-shore region where, in general, settling algae are subject to the least stress from desiccation and heat (Jernakoff 1983). Although the seawater-drip area at Menskoppunt received a continuous flow of water, algal growth on the strips was not significantly different from growth on strips in the dry-control area. This result is contrary to expectations. However, the amounts of chlorophyll-a involved in this analysis are very small (cf Figs 2.3 and 2.4) and an experimental design involving proper replication of results would have allowed more reliable interpretation. After 2 months in position strips in the seawater-drip area do appear to show more algal growth than comparable strips in the dry-control area (Table 2.4).

Several previous workers have found a vertical gradient of increasing micro- and macro-algal abundance towards the lower shore regions (Castenholz 1963; Nicotri 1977; Underwood 1984) and have attributed this to the shorter periods of emersion, desiccation and exposure to high temperatures and light intensities experienced by low-shore algae. This trend also is apparent in the production rates of macro-algae on the shores of sites in the Saldanha Bay area (Figs 2.3 and 2.4). In addition, there is a seasonal influence on algal production at all sites, highest rates of production occurring in mid-summer (Tables 2.1 and 2.2).

Influence of shorebirds and seabirds

It is likely that the removal of large numbers of *P. granularis* by African Black Oystercatchers on the shores of seabird-breeding islands enhances the survival of algal sporelings to the foliose stage (Hockey and Branch 1984). Even on shores not enriched by seabird guano, where settling algae are rapidly grazed by the large numbers of limpets (Hockey and Branch op. cit.), foliose algae do develop when herbivores are excluded (Dayton 1971). The anti-fouling paint used in the present study was an effective deterrent to limpets - on only 2 occasions was a limpet found inside on of the exclusion plots. Limpets are able to alter the distribution and abundance of intertidal algae by their grazing and 'bulldozing' activity (Jara and Moreno 1984), and the experimental removal of limpets from rocky shores has led to increased abundance and ground-cover of certain species of intertidal algae (Cubit 1984; Jara and Moreno op. cit.).

However, in addition to the effects of oystercatcher predation on *P. granularis* on islands in Saldanha Bay, algal growth rates are faster on most island shores than on mainland shores outside the Bay, due to the enrichment of intertidal waters around island shores by nutrients from seabird guano. Consequently, algae on nutrient-rich shores may reach the foliose stage more rapidly, after which they are largely immune to herbivory by *P. granularis* (Branch 1981, Underwood and Jernakoff 1981; Hawkins and Hartnoll 1983). Foliose algae are abundant at the North Bay site which, although having only approximately 20% the density of oystercatchers recorded on island shores (Hockey 1983), has intertidal waters enriched with nutrients from Malgas Island guano run-off (Part 1). At the Bomgat site, where oystercatcher densities are comparable with those at North Bay, but where intertidal waters are not nutrient-rich (Part 1), algal production is low (Fig. 2.4) and foliose algae seldom develop.

Algal mats

Both predation by shorebirds and nutrient enrichment by seabird guano are likely to contribute to the formation of mats of foliose algae. These develop, on undisturbed rocky shores (including the shores of Malgas Island) and on artificial settlement strips, in a predictable, successional manner, as described by Brokenham and Stephenson (1938). The first phase of this development comprises the formation of a film layer of bacteria and diatoms, after which the rapidly growing green alga *Enteromorpha* sp. proliferates. *Enteromorpha* may die back completely within 3-4 weeks, or it may persist while *Porphyra capensis* and other, less transient species become established. This succession is evident when comparing algal production on settlement strips after 1 month and 2 months (Fig 2.5). At sites where algal growth is very rapid in the first month, growth in the second month, by which time the slower-growing, more permanent *Porphyra capensis* has become established, is much slower. At sites with less rapid algal production rates the settlement and proliferation of *Enteromorpha* continues into the second month, and growth after 2 months may surpass twice the growth of 1 month.

Algal biomass and chlorophyll concentrations

Although a significant positive relationship exists between the amount of chlorophyll extracted from algae growing on strips in the Saldanha Bay area, and the biomass of algae produced on the shore, the relationship between these 2 parameters is notoriously variable, and is dependent on the physiological state of algal cells and the prevailing environmental conditions (Humphrey 1961; Strickland and Parsons 1972). Underwood (1984) found that chlorophyll assays provided reliable, repeatable estimates of the number of micro-algal cells present on and in the surface of intertidal rocks. However, it was clear in the present study that the same technique did not give complete extraction of chlorophyll from foliose macro-algae. Extraction was particularly inefficient in the larger samples, and it is likely that the differences between algal production rates on nutrient-rich and on unenriched shores have been underestimated. It is proposed that, for the purpose of comparison between sites, the method is standardized and suffices, although no comparison in terms of absolute chlorophyll concentrations or algal biomass is warranted.

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PART 3

SEABIRDS, SHOREBIRDS AND LIMPETS

Section (1): Primary production - a neglected factor in the consideration of rocky intertidal communities

Summary. The rate of primary production in a rocky intertidal system may regulate the outcome of interactions between organisms in that system. The importance of predation on, and competition between, intertidal herbivores in determining intertidal community structure (in particular the species composition, density and distribution of organisms present) may be altered where algal food supplies are not limiting to herbivore growth. On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, the intertidal region is enriched with nutrients from the dissolved guano of seabirds. The rate of algal production on nutrient-rich shores in the Bay is enhanced when compared with rates of production on unenriched mainland shores, where seabird colonies are absent. Nutrient-rich shores are characterized by the presence of foliose algae which have grown rapidly enough to escape herbivory as sporelings and which form extensive, permanent algal mats.

The growth rate of the dominant intertidal herbivore, the limpet *Patella granularis*, is positively correlated with algal production rate and consequently limpet populations on nutrient-rich and on unenriched shores differ in their size distributions, densities, reproductive outputs and maximum

sizes. Limpets translocated from an unenriched mainland to an island shore (and vice versa) soon show life-history patterns similar to those of the limpets at the new locality, indicating that these differences are, in part, a response to local environmental factors.

Furthermore, the species composition and density of intertidal avian assemblages is affected indirectly by an enhanced algal production rate. Nutrient-rich island shores support dense populations of African Black Oystercatchers *Haematopus moquini*, large shorebirds which prey on intertidal invertebrates, on *P. granularis* in particular. Oystercatchers are uncommon on adjacent mainland shores where algal and limpet production rates are low. Thus the biological structure of rocky intertidal communities may be affected profoundly by differences in the nutrient status of intertidal waters and the primary and secondary consequences thereof.

Introduction

The maximum adult size attainable by individuals of most intertidal herbivorous gastropod species is a function of the rate of growth (Branch 1974b; Lewis and Bowman 1975; Balaparameswara Rao 1976). Since gamete production in these species increases exponentially with increment in size (Branch 1974a), individuals which grow faster will be fitter in terms of their contribution of gametes to ensuing generations. Consequently, factors which influence the growth rate of intertidal invertebrates will be important in the consideration of the life-history patterns and population dynamics of the species involved. Several studies have attempted to identify the extent to which the expression of life-history parameters (such as growth rate and reproductive output) in intertidal invertebrates is an outcome of genotypic or environmental influences (Lewis and Bowman op. cit.; Spight and Emlen 1976; McKillup and Butler 1979; Creese 1980; Parry 1982a, b; Fletcher 1984a, b), and it has been found that local environmental factors can be important in determining the life-history patterns observed (Stearns 1976). Indeed, variability in life-history patterns between populations of the same species may be at least as large as variability between species, when considered over a similar environmental gradient (Fletcher 1984a, b). In particular, differences in growth rate often have been ascribed to differences in the availability of micro- and macro-algal food (Paine 1969; Stearns 1976; Creese and Underwood 1982; Creese op. cit.; Underwood 1984 a, c).

It is notoriously difficult to measure the settlement and availability of intertidal micro- and macro-algae, and many studies have neglected direct measurement, relying instead on experimental manipulations of herbivore densities, and the consequent increases or decreases in the growth rates of individuals, from which to infer the importance of variations in food availability (Sutherland 1970; Underwood

1976, 1978; Choat 1977; Creese and Underwood 1982; Fletcher 1984a). In a few instances direct measurements of food availability have been made using chlorophyll analysis of micro-algae in rock-surface scrapings (Nicotri 1977; Creese 1980; Underwood 1984a). Underwood (op. cit.) demonstrated that growth of the intertidal snail *Nerita atramentosa* Reeve was correlated with the amount of food in the substratum, and was not influenced by the time available for feeding (during submersion), whereas growth of another species of snail *Bembicium nanum* Lamarck, at the same site, was not correlated with food availability or duration of submersion.

The factors affecting growth rate are complex, and it is possible that monthly or 'one-off' measurements of the number of algal cells present in the substratum do not provide a realistic index of food availability. After all, this approach has involved an assessment of the number of spores and algal cells remaining after herbivores have been foraging (perhaps selectively - see Nicotri 1977) in the area for a given time. Underwood (1978) noted that, in addition to the direct measurement of food availability, it is important to quantify the rate at which stocks of micro-algae and sporelings are renewed in areas grazed by herbivores. The rate of food renewal and production can be expected to modify the effects of biological interactions (such as predation and competition) on intertidal herbivores. This approach involves an assessment of the rate of primary production on rocky shores.

In this study I investigate the importance of variation in algal production rate in modifying the growth rates, densities and size distributions of populations of the dominant limpet *Patella granularis* L. which is a generalist intertidal grazer (Branch 1971). The rates of algal production at sites chosen are influenced by the nutrient status of intertidal waters (Part 2). Measurements of limpet growth rate are made on a monthly basis, and differences are discussed in terms of variations in algal production, season, time available for foraging, and the biomass of limpets supported on the shore.

Materials and methods

Study sites

Seven intertidal study sites in the Saldanha Bay area, southwestern Cape, South Africa (Fig. 1.1), were visited monthly between December 1982 and April 1984. Two sites were on the shores of seabird-breeding islands (Malgas and Jutten Islands) and a third was on the shore of Marcus Island, a seabird-breeding island which is joined to the mainland by means of a causeway. These 3 sites had statistically comparable mean monthly intertidal nutrient levels for the duration of the study (Part 1). A further 2 sites (Mauritz Bay and Cape Columbine) were on mainland shores outside the Bay (Fig. 1.1), where no aggregations of seabirds occur. Intertidal waters on island shores are nutrient-rich when compared with the waters washing these 2 mainland sites (Part 1). Two more sites were on mainland shores within the Bay (North Bay and Bomgat) and, although neither site had regular aggregations of seabirds, both were within the possible zone of influence of guano run-off from the seabird-breeding islands. The North Bay site has nutrient-rich intertidal waters as a result of current movement which transports guano run-off from Malgas Island to North Bay (Part 1).

At all sites the granitic shore was gently sloping and exposed to strong wave action. The zone between the upper limit of the low-shore mussel beds and the upper limit of occurrence of the limpet *Patella granularis* was studied. At each site the zone was divided into a low-, mid- and high-shore region of equal area. The limpet *P. granularis* was the dominant intertidal herbivore (in terms of number and biomass) at all sites (see Stephenson and Stephenson 1972 for detailed shore description). Two species of algae, *Enteromorpha* sp. and *Porphyra capensis* Kutz., dominated the algal assemblage and formed extensive mats on nutrient-rich shores. Algal production rate is more rapid on the shores of Jutten and Marcus Islands and North Bay than on the mainland shores outside the Bay, enhanced algal growth rate at these sites being a consequence of nutrient enrichment of the intertidal waters by the dissolved guano of seabirds (Part 2).

Algal production and cover

A herbivore exclusion plot was established in the low-, mid- and high-shore region at each site, by enclosing a 0.1 m^2 rectanglar area with a strip of copper-based marine anti-fouling paint. The paint was renewed whenever it became worn. Each month, after the rock had been scraped clean and burned with a blow-torch to kill existing algal spores, 4 replicate high-intensity polystyrene settlement strips (each of 30 x 50 x 2 mm) were glued to the rock in the centre of the exclusion plot. After a month in position the strips were lifted, wrapped in aluminium foil to exclude light, and frozen for subsequent analysis.

Chlorophylls *a*, *b* and *c* were extracted from the algae that had grown on each strip, using the method of Strickland and Parsons (1972), and were quantified using a Beckman model 25 spectrophotometer and the equations of Jeffrey and Humphrey (1975) (see also Underwood 1984b and Part 2 for details of the method). The values obtained were corrected for the exact area of the settlement strip, and for the number of days in position, and were used as an index of algal production. The mean monthly production (of 4 replicate samples) was used in analysis.

At each study site the percentage cover by foliose algae in a fixed transect area was assessed monthly. A vertical transect at each site was divided into 0.5 m^2 quadrats and the percentage algal cover was assessed visually, using a 0.05 m^2 grid affixed to the quadrat. Transects varied in width between sites, but all extended from the low-shore mussel bed to the upper limit of the occurrence of *P. granularis*, thus including all 3 shore levels.

Limpet size structure, density, biomass and gonad production

To determine the relationship between shell length and gonad production in *P. granularis*, a sample of 30 limpets was collected bi-monthly from the low-shore region adjacent to the Marcus Island study site. Gonadial wet mass was determined for each individual and was regressed against shell length: males and females were considered separately. In addition, differences in the density, biomass and size distribution of limpets were measured at each site in June 1984. Limpets in 10 replicate 0.5 m^2 quadrats, placed randomly in each of the 3 shore regions, were counted and measured. Length measurements were converted to biomass using an equation derived from a dry gonadial and somatic mass/length regression which was calculated from 100 *P. granularis* collected from Marcus Island in June 1984 (viz dry mass = 1.9×10^{-6} length$^{3.5}$; $r^2 = 0.98$, $P < 0.001$). The biomass (and density) of limpets supported per 0.5 m^2 of shore was adjusted wherever the sample included sections covered by algae or mussels (i.e. uninhabitable by *P. granularis*). Thus the values presented represent biomass (and density) of limpets per 0.5 m^2 of vacant rock surface.

Limpet growth

Adjacent to each limpet exclusion plot, 50 *P. granularis* were labelled individually with punched plastic labels and rapidly setting glue (Araldite epoxy). Each month, for 15 months, the maximum shell length of recovered individuals was recorded. Predation and other factors caused mortality of limpets, and supplementary limpets were labelled when numbers at any site fell below 10. At each locality (a single shore level at a site), in each month, limpet growth rate was determined using a linear regression of limpet length in the current month (L_{t+1}) on limpet length in the previous month (L_t) (Ford-Walford plot). In all instances these two parameters were significantly related ($P < 0.05$). The regression line was described by the equation:

$$L_{t+1} = mL_t + I$$

where m = rate of increase in shell length and I = increase during the first month (Balaparameswara Rao 1976; Branch 1981).

The predicted monthly increment of a 'standard' 30 mm limpet was calculated from each regression. Limpets of ca. 30 mm in length were common at all sites, and the monthly increment in shell length of a limpet this size was deemed a useful index of overall rate of limpet growth, given that absolute growth rate is dependent on limpet size (Branch 1981). Results of this analysis are presented as the cumulative predicted increment in shell length of a limpet that was 30 mm at the start of the study, and that grew according to the predictions of the monthly Ford-Walford plots.

Translocation experiment

In November 1984, 100 individually labelled *P. granularis* were removed from the low-shore region at Cape Columbine, and were transported to, and resettled on, rocks adjacent to the Marcus Island low-shore site. Only 46 individuals survived the first tidal cycle at the new locality. The shell lengths of surviving limpets were recorded monthly for 5 months. Similarly, 100 *P. granularis* from the low-shore region at Marcus Island were labelled and translocated to low-shore rocks adjacent to the Cape Columbine site, and the shell lengths of surviving individuals were measured monthly for the subsequent 5 months. The predicted monthly shell increment of a 30 mm individual from the translocated populations was calculated for each month and each site, using the methods described above.

Statistical analysis

Multiple linear regression analysis was used to regress the dependent variable (limpet growth rate) on a series of independent variables, and to determine the linear equation which best predicts the dependent variable (Sokal and Rohlf 1981). It is not possible, using this technique, to perform significance tests between the limpet growth rates recorded at different sites.

Results

Limpet growth rates

The predicted growth of limpets on the shores of seabird-breeding islands in Saldanha Bay is consistently rapid, (Fig. 3.1), although in all 3 shore levels predicted limpet growth is fastest on the nutrient-rich shores at North Bay. At this site a limpet of 30 mm might more than double its initial length in 15 months. Limpets on the shore at Cape Columbine have the slowest predicted growth rate, barely increasing in length by more than 10 mm during the study.

It is not possible to identify, statistically, significant differences between limpet growth rates at the different study sites. However, when the predicted monthly increments in limpet shell length are ranked from 1 (lowest) to 7 (highest) the mean ranks (Table 3.1) support the observation that limpet growth rates are consistently higher at the nutrient-rich island sites than at the mainland sites outside the Bay (Mauritz Bay and Cape Columbine). It is noteworthy that when mean monthly algal production is ranked from 1 (lowest) to 7 (Table 3.2), the mean ranks of the island sites are again higher than those of Mauritz Bay and Cape Columbine. Malgas Island is an exception to this. Although the algal production rate generally is lower at the Malgas Island site than at the other two island sites (Table 3.3), the limpet growth rate is not lower. Several factors may influence the relationship between limpet growth and algal production, and multiple linear regression analysis

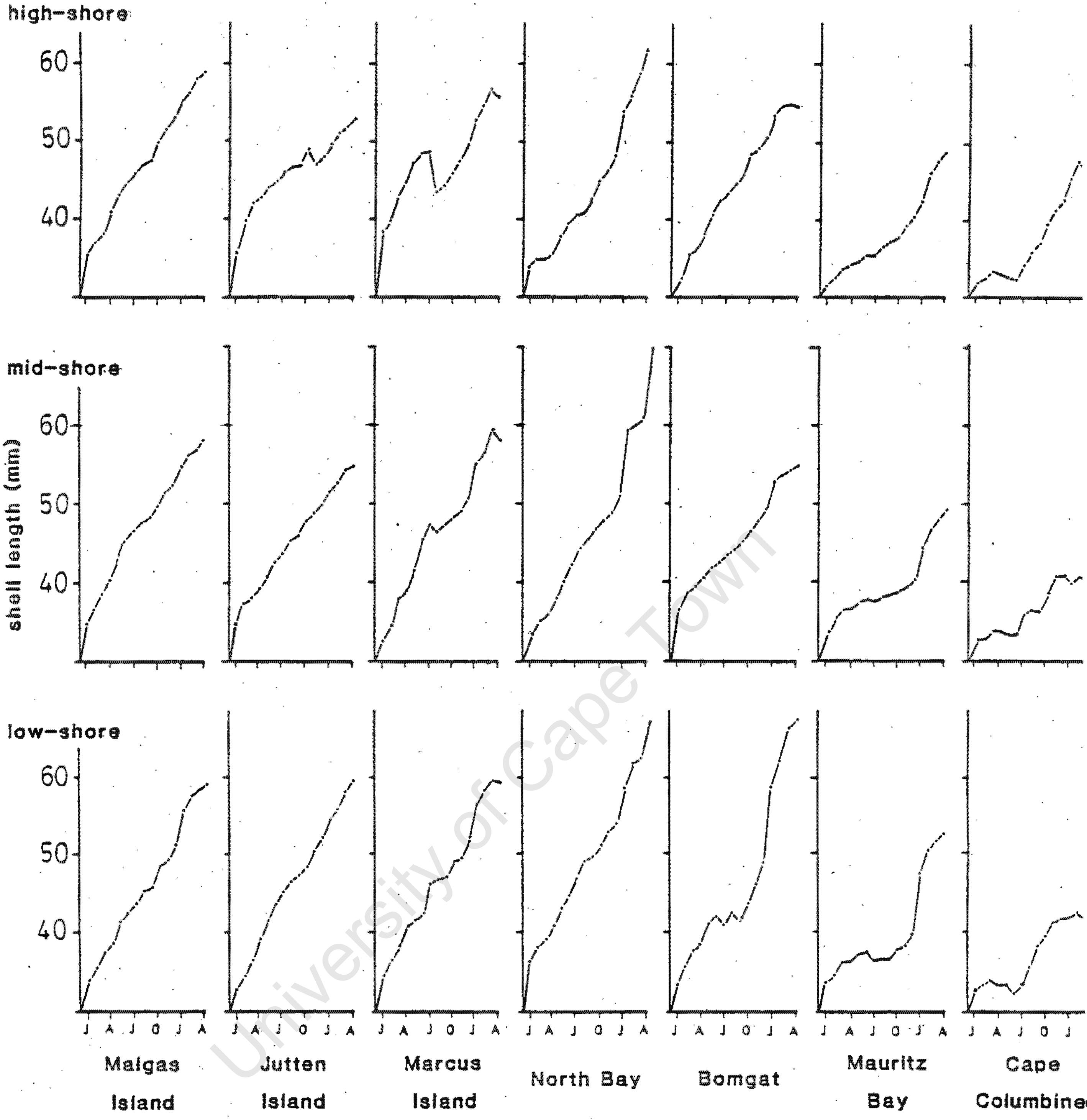


Fig. 3.1. Predicted monthly increment in shell length of limpets in the low-, mid- and high-shore regions at study sites in the Saldanha Bay area. In each case limpet initial length is 30 mm and growth is monitored monthly for 15 months. Divisions on the abscissa mark three-monthly intervals commencing in January 1983

Table 3.1. Mean ranks (±S.D.) obtained when the monthly predicted growth of a 30 mm limpet at study sites in the Saldanha Bay area is ranked from 1 (lowest) to 7 (highest)

	Malgas Island	Jutten Island	Marcus Island	North Bay	Bomgat	Mauritz Bay	Cape Columbine
High	5.3	3.4	5.1	3.0	5.3	3.0	2.8
	±1.2	±1.7	±2.1	±1.3	±1.4	±2.0	±1.9
Mid	5.9	4.2	3.7	3.6	4.3	3.3	2.9
	±1.1	±1.8	±2.1	±1.2	±2.0	±2.2	±2.0
Low	5.0	3.9	5.0	4.8	4.3	2.9	1.8
	±1.3	±1.5	±1.7	±1.8	±2.1	±1.4	±1.8

Table 3.2. Mean ranks (±S.D.) obtained when mean monthly chlorophyllproduction values in 3 shore regions at each study site are ranked from 1 (lowest) to 7 (highest)

	Malgas Island	Jutten Island	Marcus Island	North Bay	Bomgat	Mauritz Bay	Cape Columbine
High	3.8 ±1.5	3.7 ±1.8	6.5 ±0.9	4.5 ±1.9	2.7 ±1.7	3.4 ±1.5	3.1 ±1.6
Mid	3.4 ±0.9	5.7 ±1.3	6.0 ±1.0	4.8 ±1.4	1.8 ±0.6	5.0 ±1.3	1.4 ±0.4
Low	2.1 ±1.2	6.1 ±1.0	5.7 ±1.3	4.0 ±1.6	3.6 ±1.9	4.4 ±1.2	1.6 ±1.1

Table 3.3. Mean (± S.D.) monthly intertidal algal production (ug chlorophyll cm^{-2} $month^{-1}$) at study sites in the Saldanha Bay area

	LOW	MID	HIGH
Malgas Island	4.50 (5.09)	0.66 (1.22)	0.04 (0.03)
Jutten Island	41.81 (31.48)	7.51 (11.44)	0.14 (0.31)
Marcus Island	26.44 (14.52)	6.75 (7.91)	1.85 (4.13)
North Bay	18.01 (34.87)	1.27 (1.56)	0.26 (0.71)
Bomgat	19.43 (43.49)	0.05 (0.04)	0.03 (0.02)
Mauritz Bay	14.41 (17.52)	3.37 (4.24)	0.06 (0.10)
Cape Columbine	2.45 (5.28)	0.16 (0.47)	0.05 (0.06)

Table 3.4. Estimated co-efficients, standard errors and significance levels resulting from the multiple linear regression analysis of limpet growth rate in 3 shore regions at 7 intertidal study sites in the Saldanha Bay area

VARIABLE/FACTOR	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	2.17	0.49	4.44	<0.001
Algal Production	0.03	0.00	5.81	<0.001
Limpet Biomass	0.01	0.01	0.98	
Mid-shore	0.19	0.23	0.85	
High-shore	0.64	0.36	1.77	
Bomgat	-0.10	0.30	-0.33	
Marcus Island	-0.98	0.38	-2.61	<0.001
Mauritz Bay	-1.07	0.32	-3.38	<0.001
North Bay	-1.11	0.45	-2.46	<0.001
Jutten Island	-1.35	0.33	-4.13	<0.001
Cape Columbine	-1.81	0.29	-6.23	<0.001
March 1983	-0.45	0.42	-1.08	
April	-0.15	0.42	-0.35	
May	-0.94	0.42	-2.24	<0.001
June	-0.55	0.42	-1.31	
July	-0.38	0.43	-0.90	
August	-0.56	0.42	-1.34	
September	0.54	0.42	1.28	
October	-0.01	0.42	-0.02	
November	0.09	0.42	0.21	
December	2.98	0.43	6.98	<0.001
January 1984	0.90	0.42	2.14	<0.001
February	-0.14	0.42	-0.32	
March	-0.31	0.42	-0.74	

(mid-shore: $t = 0.85$, $P > 0.05$, high-shore: $t = 1.77$, $P > 0.05$).

None of the study sites has a positive estimated co-efficient, indicating that the contribution of variations in attributes uniquely associated with individual sites (such as shore slope, exposure and aspect) to the explanation of variation in limpet growth rate is highest on the shores of Malgas Island (co-efficient = 0.00) and lowest at Cape Columbine (Table 3.4). Limpet growth is lower in the winter months (March-August) than in the summer months (September-February), with the highest growth rates occurring in December and January (Table 3.4).

Althouth the analysis explains only 46.2% of the variation in limpet growth rates, the results are supported by changes in the growth rates of translocated limpets. Multiple linear regression indicates that limpet growth rate during the 5 months between November 1983 and April 1984 is significantly lower at the Cape Columbine site than at the Marcus Island site (d.f. = 18, $t = -3.98$, $P < 0.001$, Table 3.5). However, limpets translocated from Cape Columbine to Marcus Island show a growth rate that is not significantly different from that of the local Marcus Island limpets (Table 3.5). Similarly, limpets translocated from Marcus Island to Cape Columbine are characterized by a growth rate that is significantly lower than that of limpets of the original stock, viz those on the Marcus Island shores (d.f. = 18, $t = -2.88$, $P < 0.01$, Fig. 3.2).

Table 3.5. Estimated co-efficients, standard errors and significance levels resulting from the multiple linear regression analysis of the growth rates of translocated and local limpets

FACTOR	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	3.88	1.00	3.88	<0.01
Limpets translocated to Marcus Is	0.22	1.00	0.22	
Limpets at Cape Columbine	-3.98	1.00	-3.98	<0.001
Limpets translocated to C. Columbine	-2.88	1.00	-2.88	<0.01
December 1983	2.42	1.12	2.17	<0.05
January 1984	1.65	1.12	1.47	
February	0.35	1.12	0.31	
March	-0.75	1.12	-0.67	

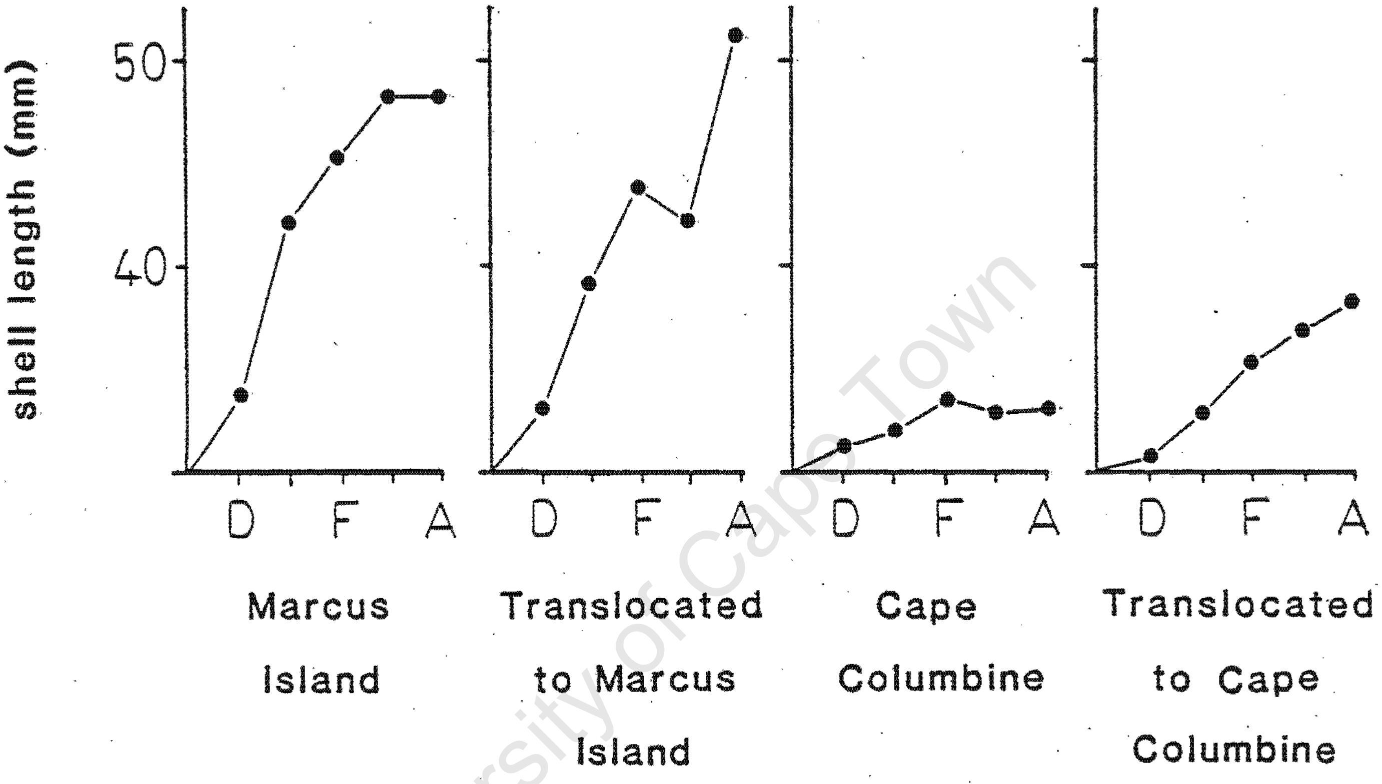


Fig. 3.2. Predicted monthly increment in shell length of limpets which occur on the shores of Marcus Island and Cape Columbine, and of those translocated to these sites. In each case the growth a limpet which measured 30 mm at the start of the experiment is considered

The growth rates of limpets in this analysis are also affected by season, although the experiment ran for 5 months only. Limpet growth is again fastest in the months of December and January (Table 3.5). Variation in the factors study site and month accounts for 61.1% of the variation in the monthly increment in the shell lengths of ~~translocated~~ limpets.

Limpet biomass, density and size distribution

At all sites the biomass of limpets supported per 0.5 m^2 of vacant rock surface is highest in the mid-shore region and lowest in the high-shore region (Fig. 3.3a). The North Bay shores support the highest biomass of limpets per unit area in both the mid- and low-shore regions, while the lowest biomass per unit area is present in the mid-shore region at Malgas Island and in the high- and low-shore regions at Cape Columbine. Limpet density per unit area generally is lowest in the high-shore region at each site (Fig. 3.3b), while the mid- and low-shore regions at Cape Columbine support the most densely-packed populations of limpets. The relationship between limpet length and gonad production in any 1 month is best described by an exponential curve (Table 3.6).

At all mainland study sites limpet sizes are normally distributed about a single modal size class (Fig. 3.4). Median limpet size is consistently small on the shores at Cape Columbine and limpets measuring over 50 mm are

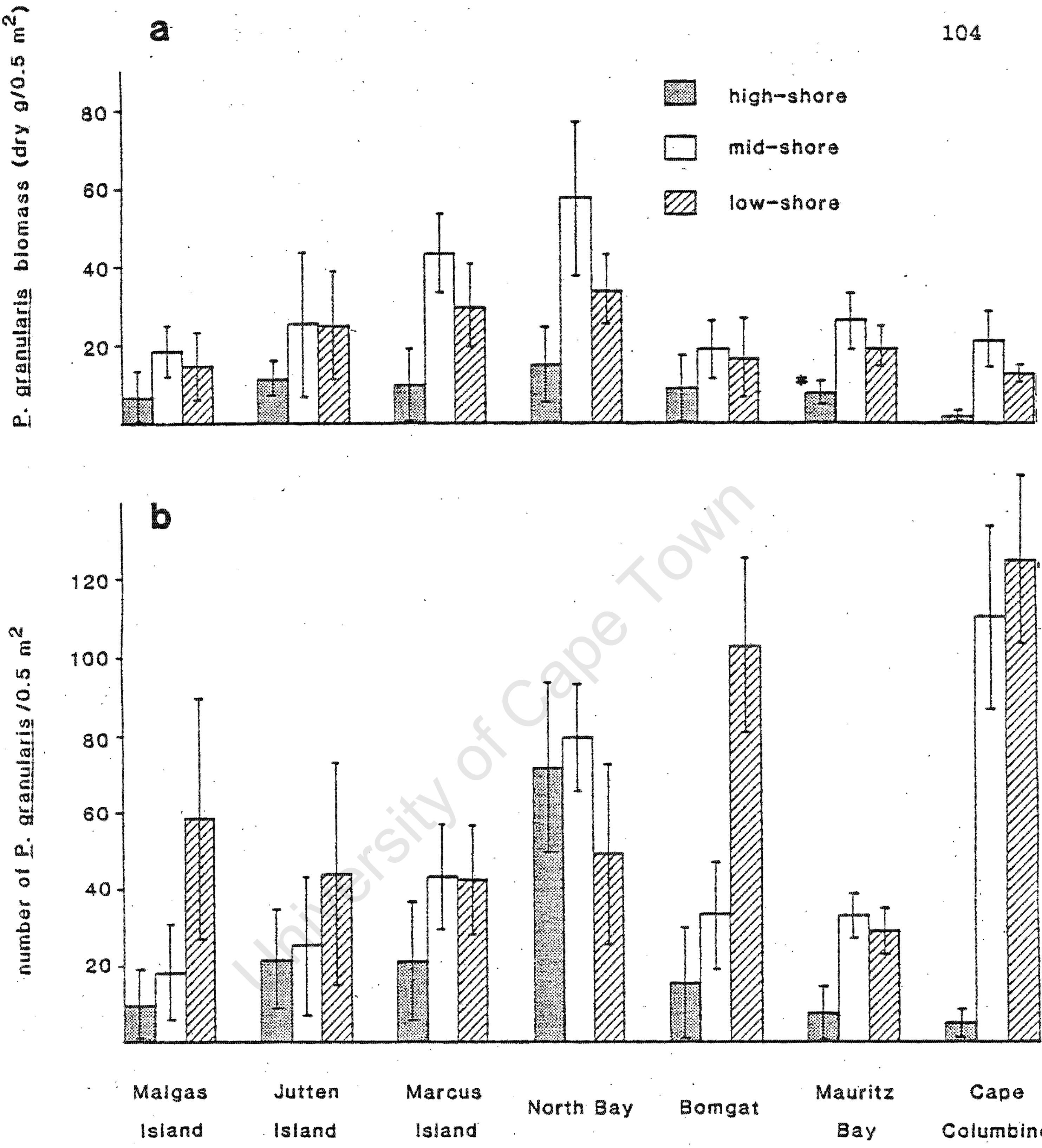
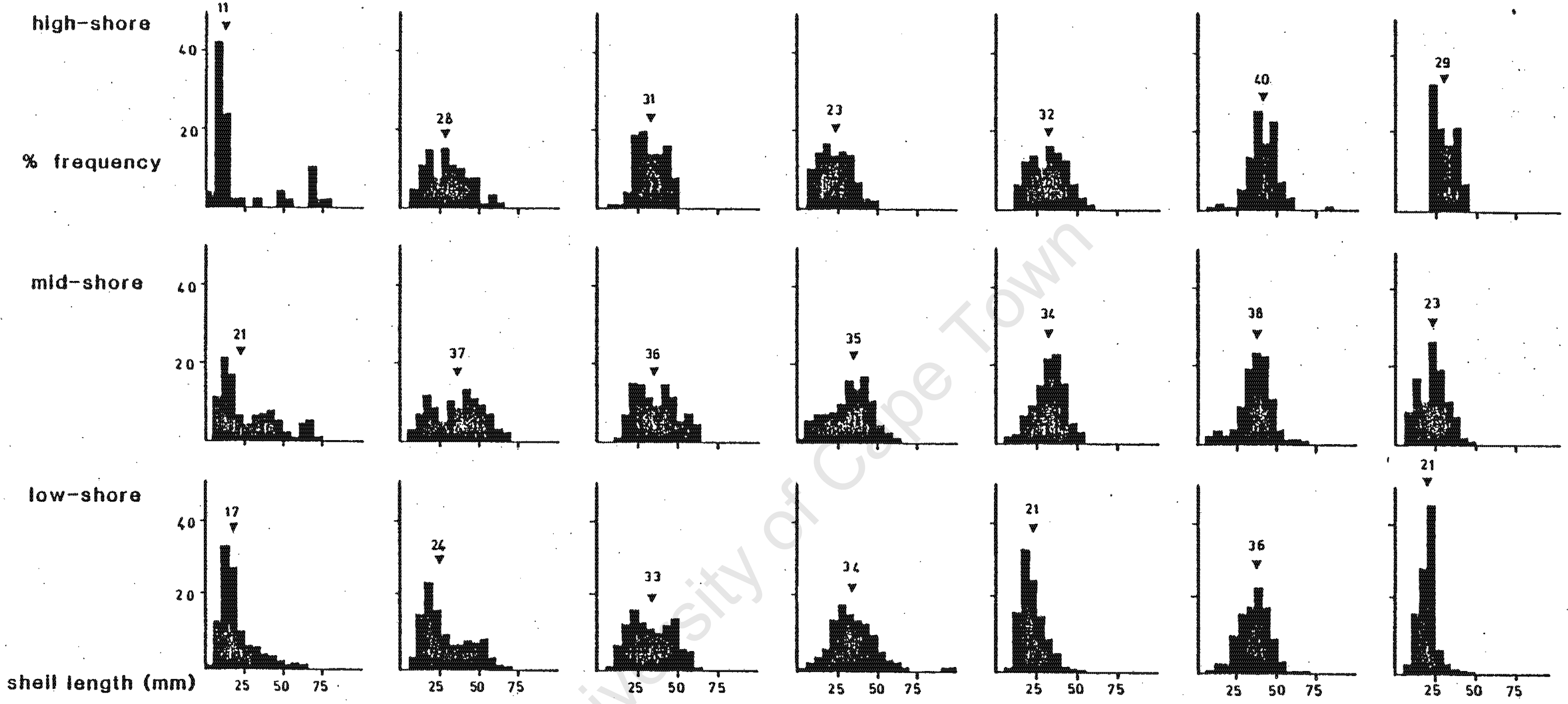


Fig. 3.3 a: Mean (± S.D.) *P. granularis* biomass per 0.5 m^2 in the low-, mid- and high-shore regions at study sites in the Saldanha Bay area. S.E. is presented in the high-shore region at Mauritz Bay (*). b: Mean (± S.D.) *P. granularis* density in the low-, mid- and high-shore regions at study sites in the Saldanha Bay area

Table 3.6. Equations describing the relationship between shell length and gonadial dry mass in *P. granularis* males and females

Month	Sex	Equation	*n*	*r*	*P*
June	M	$\text{mass} = 4.01 \times 10^{-7} (\text{length})^{3.4}$	17	0.70	<0.01
	F	$\text{mass} = 5.02 \times 10^{-5} (\text{length})^{2.0}$	13	0.70	<0.01
August	M	$\text{mass} = 2.01 \times 10^{-10} (\text{length})^{5.5}$	12	0.96	<0.001
	F	$\text{mass} = 1.09 \times 10^{-6} (\text{length})^{3.4}$	18	0.81	<0.001
October	M	$\text{mass} = 1.07 \times 10^{-8} (\text{length})^{4.5}$	13	0.88	<0.001
	F	$\text{mass} = 2.49 \times 10^{-13} (\text{length})^{7.2}$	16	0.91	<0.001
December	M	$\text{mass} = 8.72 \times 10^{-11} (\text{length})^{5.7}$	14	0.79	<0.001
	F	$\text{mass} = 1.12 \times 10^{-13} (\text{length})^{6.2}$	13	0.92	<0.001
February	M	$\text{mass} = 2.40 \times 10^{-9} (\text{length})^{4.9}$	8	0.89	<0.01
	F	$\text{mass} = 4.58 \times 10^{-10} (\text{length})^{5.2}$	17	0.77	<0.001
April	M	$\text{mass} = 8.44 \times 10^{-8} (\text{length})^{4.2}$	12	0.66	<0.02
	F	$\text{mass} = 3.66 \times 10^{-9} (\text{length})^{4.8}$	13	0.69	<0.01



	Malgas Island	Jutten Island	Marcus Island	North Bay	Bomgat	Mauritz Bay	Cape Columbine
% > 50 mm	7.5	14.9	11.6	5.6	1.3	5.5	0.0
% > 60 mm	5.8	2.5	1.8	1.0	0.1	0.7	0.0

Fig 3.4. *Patella granularis* population size distributions and median sizes (▼) in the low-, mid- and high-shore regions at sites in the Saldanha Bay area

unrecorded at this site. Similarly, very few (1.3%) limpets of greater than 50 mm are present at Bomgat, whereas 5.5% and 5.6% of the population at Mauritz Bay and North Bay respectively are greater than 50 mm in length (Fig. 3.4). Limpet size distributions on island shores typically are skewed and/or multi-modal (Fig. 3.4). The shores on Malgas Island support a preponderance of small limpets although 7.5% of limpets are greater than 50 mm in length. Limpets of over 50 mm in length make up 14.9% of the population on Jutten Island and 11.6% on the Marcus Island shores.

Algal cover

Rocky shore communities on seabird-breeding islands and at the North Bay site are characterized by the presence of extensive permanent mats of foliose algae (Fig. 3.5). Mean annual percentage cover by algae on the shores of Jutten Island is 54%. Algal cover is far less extensive on the mainland shores at Bomgat, Mauritz Bay and Cape Columbine.

Discussion

It has been shown repeatedly that limpets may influence the structure of rocky intertidal communities (Lodge 1948; Hay 1979; Branch 1981; Lubchenco and Gains 1981; Hawkins and Hartnoll 1983; Jernakoff 1983; Cubit 1984; Jara and Moreno 1984). In particular, the method of feeding of patellid limpets, which involves rasping the rock surface with strong radular teeth (Branch 1985) results in the removal of algal

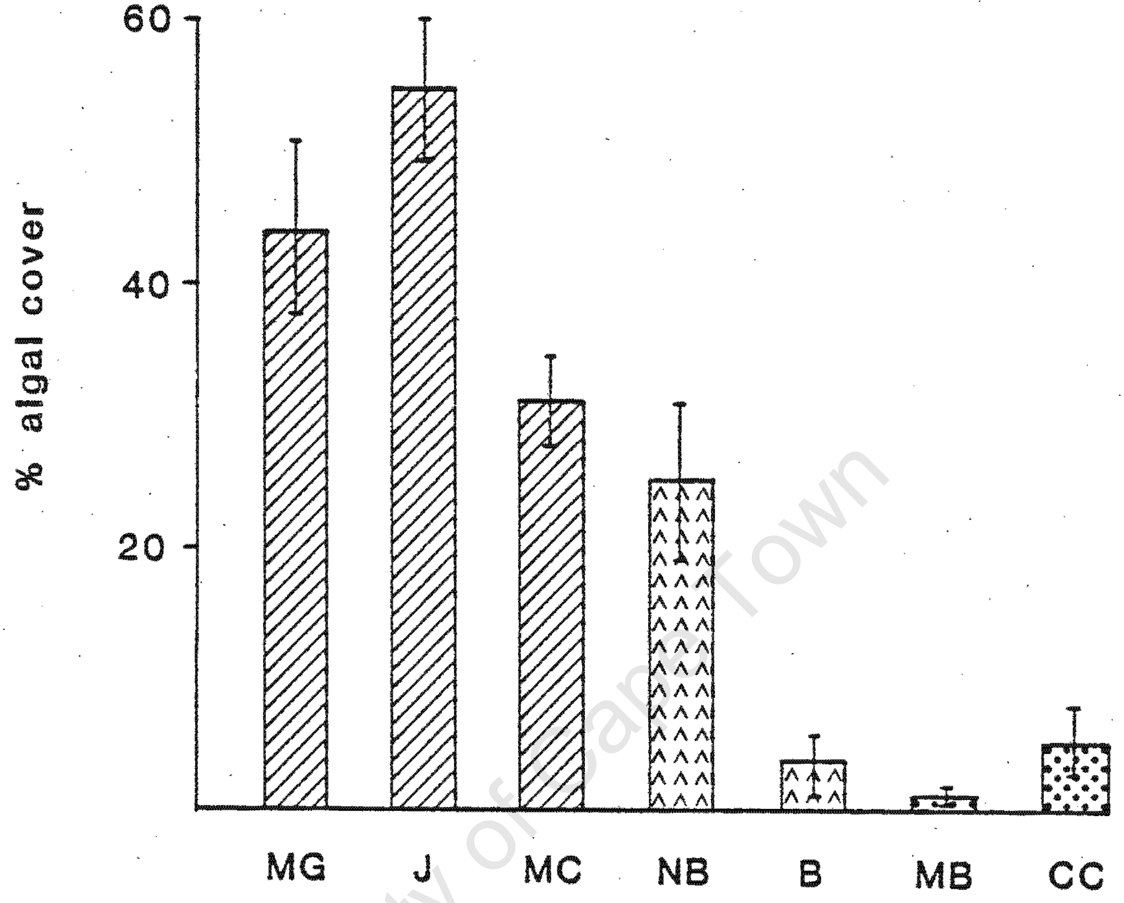


Fig. 3.5. Mean (± S.D.) monthly percentage algal cover in fixed transects at study sites in the Saldanha Bay area

sporelings. Limpets may thereby affect the abundance and distribution of intertidal algae, and in some cases may prevent their development totally (Underwood 1980, 1984b; Branch 1985). In addition, the 'bulldozing' activity of limpets moving about on the rocky substratum may crush and destroy the newly-settled spat of organisms such as barnacles and mussels (Connell 1961; Dayton 1971; Underwood et al. 1983), and may prevent the settlement of conspecifics. However, the interactions between limpets, algae and other intertidal organisms are affected by a suite of physical environmental factors such as temperature, insolation, desiccation and exposure to waves, all of which may influence the rate of algal production (Underwood 1985).

Systems characterized by slow algal production rates may be more susceptible to the effects of physical disturbance and predation (see review by Underwood 1985) whereas competition between herbivores is heightened (Creese and Underwood 1982; Underwood 1984b, c). Underwood and Jernakoff (1984) show that during summer, when the rate of algal production in the high-shore region at Cape Banks (N.S.W., Australia) is held in check by physical factors such as temperature, insolation and desiccation, intertidal grazers remove all accessible algae (see also Cubit 1984). In contrast, enhanced rates of primary production may lead to the rapid development of foliose algae which are immune to herbivory by limpets (Lubchenco 1983; Norton 1985) and which may form permanent mats on the shore (Hockey and Branch 1984; Underwood and Jernakoff 1984). In these instances herbivory has little influence on the abundance and distribution of intertidal algal assemblages, and limpets may even starve to death in the midst of a bed of foliose algae (Underwood and Jernakoff 1981).

Algal mats

The shores of Jutten and Marcus Islands in Saldanha Bay, and of the North Bay site on the mainland opposite Malgas Island, are characterized by rapid rates of algal production (Tables 3.2 and 3.3), associated with enhanced levels of intertidal nutrients from the dissolved guano of seabirds (Part 2). Permanent mats of rapidly colonizing algal species (*Enteromorpha* sp and *Porphyra capensis*) are present on these shores and on the shores of Malgas Island, the algae having escaped herbivory as sporelings and developed rapidly to the foliose stage (Fig. 3.5). In contrast, at Bomgat and the 2 mainland sites outside the Bay (which do not receive nutrients from seabird guano) algal production rates are relatively slow, and mats of foliose algae are absent. This difference emphasises the role of environmental factors in modifying outcomes of biological interactions, although nutrient levels have seldom been considered an important environmental variable on rocky shores.

Limpet growth rate

Multiple linear regression analysis explains only 46.2% of the variation in limpet growth rate between sites. This is due possibly to the choice of independent variables and factors, which often represent several variables themselves. For example the factor 'site' represents the shore slope, exposure and aspect at a particular study site, without any of these attributes being measured directly. Consequently the equation which defines the relationship between limpet growth and the independent variables is of little predictive value, although the important influence of algal production rate is clear.

Enhanced algal production rates directly affect population parameters of the intertidal herbivore *Patella granularis* on nutrient-rich shores in Saldanha Bay. Algal production rate is the most significant correlate of *P. granularis* growth rate (Table 3.4). Limpet shell increment is most significantly correlated with algal growth in the month prior to (rather than during) the month of limpet measurement, possibly indicating a lag between food consumption and incorporation of material into the shell. Underwood (1984a) recorded a significant correlation between the growth rate of the intertidal snail *Nerita atramentosa* and the concentration of chlorophyll in the rock surface at Cape Banks (N.S.W., Australia). However, in his study the monthly measurements of chlorophyll content (during 3 consecutive months) were pooled and a mean used in analysis, thus obscuring the time taken for snails to respond to changes in algal production rate, as well as the effects of different months on algal and snail growth rates (see Hurlbert 1984).

Limpets translocated from Cape Columbine, where the rate of intertidal algal production is relatively low, to Marcus Island (and vice versa) rapidly respond to environmental conditions at the new site. Although this indicates the effect of primary production rate on limpet growth, the experimental design does not demonstrate the absence of a genetic influence. Marcus Island limpets translocated to Cape Columbine did grow more rapidly than the local Cape Columbine limpets (Fig. 3.2). In addition, the effects of handling and transport were not controlled for, and the more rapid growth rate of both sets of translocated limpets (Fig. 3.2), albeit slight, may indicate that handling has a positive influence on limpet growth. Despite these shortcomings in experimental design, the plasticity of limpet growth rate, in response to local differences in primary production, is readily apparent.

Since the rate of algal production is the most significant correlate of limpet growth rate (Table 3.4), it is perhaps paradoxical that limpet growth is fastest in the high-shore region where the rate of algal production is least rapid (Table 3.3). *Patella granularis* forages while emersed and consequently high-shore limpets have more time in which to forage than either mid- or low-shore limpets. In addition, limpet biomass and density are lowest in the high-shore region at all sites (Fig. 3.3a and b). Limpet growth rate also varies significantly with season, the period of fastest growth being in summer. This is contrary to the findings of Branch (1974b) who did not detect seasonal changes in the growth rate of *P. granularis* on the South African west coast. In the present study fastest limpet growth is associated with the months in which algal production rates are highest (Part 2). Seasonal factors, in addition to algal growth rate, which might cause a decrease in limpet growth rate in winter include increased wave action and lower temperature.

Limpet growth rates are unaffected by the biomass of limpets present on the shore at each site. This is contrary to what was expected as it is known that the experimental decrease of limpet density results in a more rapid rate of growth in remaining individuals, implying intraspecific competition for food (Frank 1965; Sutherland 1970; Haven 1973; Underwood 1976; Choat 1977). However, at sites where mats of foliose algae do not develop (Bomgat, Mauritz Bay and Cape Columbine), it can be assumed that limpets graze all available algae and the biomass supported represents the carrying capacity of the system. In these cases the biomass supported would be a function of algal production rate and would not influence limpet growth rate.

On the island shores the extensive algal cover (Fig. 3.5) and the non-normal limpet size distributions (Fig. 3.4) suggest the removal of certain size classes of limpets by predators. The shores of these islands support very high densities of African Black Oystercatchers *Haematopus moquini* Bonaparte (as many as 78 birds per km of coast - Hockey 1983). These large shorebirds prey on intertidal limpets, particularly those between 20 mm and 40 mm in length (Hockey and Underhill 1984). Hockey and Branch (1984) estimate that oystercatchers remove approximately 2.8 million *P. granularis* annually from the shores of Jutten Island (with a coastline of 2.5 km), and show that this intense predation has a marked impact on the size structures of limpet populations. Thus the biomass of limpets occurring on island shores probably represents less than the potential carrying capacity of these shores. Consequently, on island shores, limpet growth rate is influenced, not only by the enhanced algal production, but also by reduced intraspecific competition. The shores of Malgas Island, for example, show the lowest algal production rate of any of the islands (Table 3.2) and the very high limpet growth rates (Table 3.1) are doubtless attributable in part to the low density and biomass of limpets at this site (Fig. 3.3a).

Limpet size distributions and gonad production

High percentages of large limpets (>50 mm in length) occur on the island shores (Fig. 3.4) where limpet growth rates are rapid and oystercatchers remove all but the smallest and largest size classes of limpets. At Cape Columbine, where limpet growth is slow and oystercatchers seldom number more than 5 birds per km coast (Hockey 1983), no limpet of greater than 50 mm was recorded. Since the production of gonadial material by *P. granularis* increases exponentially with increasing limpet length (Table 3.6), it is apparent that, although certain sites support similar biomasses of limpets (e.g. Malgas Island and Bomgat - Fig. 3.3a), the production of gonadial material per unit area potentially is higher at the nutrient-rich island site by virtue of the limpet size distribution. Hockey and Branch (1984) estimate that, on average, 66% (± 18 S.D.) of *P. granularis* female gametic output on the shores of Jutten Island is accounted for by limpets of over 60 mm in length (between 3 and 23% of the population). They calculate that total female gamete release ranges between 48 and 96 g (wet) per m^2 on the shores of Jutten Island and between 4 and 9 g per m^2 at Cape Columbine.

Limpet life-history patterns

Populations of *P. granularis* in the Saldanha Bay area have different growth rates in response mainly to local differences in the rate of primary production. Since size and gamete production are correlated, it can reasonably be assumed that these populations also differ in their ages at first reproduction and in their reproductive outputs. By certain criteria these populations may be judged to have different strategies for survival and reproduction. However, these differences can be explained, to a large extent, on the basis of the influence of environmental factors, in particular by variations in the rate of algal production. Limpets translocated to more productive shores soon (in less than 5 months) show life-history patterns similar to those of local limpets. Fletcher (1984a, b) notes that intraspecific variations in life-history patterns of *Cellana tramoserica* (Sowerby) in different habitats can be greater than those found between different intertidal species living in the same habitat.

The factors influencing interactions between limpets and algae on the shores of seabird-breeding islands in Saldanha Bay are complex and often interrelated. Predation by oystercatchers modifies limpet population size structures and may influence limpet biomass and density, as well as the extent of algal cover on the shore. However, the impact of predation is mediated by the enhanced rate of primary production on these shores. Fast rates of algal production and food renewal enable limpets to grow fast and to attain a large adult size. Adults of over 50 mm are not uncommon on island shores, and because of their refuge in size from oystercatcher predation, they produce a quantity of gametes which is many times more than that of similarly-aged individuals on mainland shores where oystercatchers are uncommon.

The rate of primary production mediates the effects of biological interactions on rocky shores, but the ultimate mediating factor, almost entirely neglected by intertidal ecologists in general, is the availability of organic and inorganic nutrients in the waters that wash the intertidal region.

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Section (2): Oystercatcher predation and limpet mortality: the importance of refuges in enhancing the reproductive output of prey populations

Summary. On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, limpets *Patella granularis* are preyed upon by African Black Oystercatchers *Haematopus moquini*. Limpets escape predation as a consequence both of the development of foliose algae on their shells, and of their rapid growth rate which results in their growing too large for oystercatchers to handle efficiently. Both these phenomena significantly enhance the probability of limpet survival. Although these means of escaping predation are co-incidental and not evolved adaptations, they probably contribute to the persistence of the limpet population through the reproductive output of large and fecund individuals. Fundamental to this relationship is the role of nutrient enrichment of intertidal and nearshore waters by the dissolved guano of seabirds which breed and roost on the islands. Intertidal algae respond to nutrient enrichment with rapid rates of production, and the consequent abundance of food for intertidal herbivores leads to enhanced limpet growth rates. On adjacent mainland shores, where intertidal waters are not enriched, algal and limpet production rates are slow and oystercatchers are all but absent from the intertidal system.

Introduction

Birds are important predators in many intertidal communities and their removal of large numbers of prey items (Gibb 1956; Feare 1966; Baird et al. 1985) may result in severe depletion of the food resource (Feare 1969; O'Connor and Brown 1977; Goss-Custard 1980; Goss-Custard et al. 1980; Frank 1982). In addition, the preference of avian predators for certain prey size classes and morphotypes may modify prey population demography and reproductive output (Giesel 1970; Hartwick 1981; Hockey and Branch 1983, 1984; Branch 1985).

In some instances intense avian predation on populations of rocky intertidal invertebrates has contributed to the evolution of adaptations which enable prey to escape detection and capture. For example, intertidal limpets *Collisella digitalis* Rathke actively seek vertical and overhanging rock faces, inaccessible to avian predators, on which to attach in the presence of American Black Oystercatchers *Haematopus bachmani* Audubon (Haven 1971; Hahn 1985). The activity patterns of *Collisella limulata* Carpenter and *C. scabra* Gould, and the homing behaviour of many species of gastropods, have been shown to enhance survival (Wells 1980; Garrity and Levings 1983). In addition, many intertidal prey organisms are cryptic and avoid detection by virtue of homochromy with the substratum

(Mercurio et al. 1985), or mimicry of a common but inedible species (Hockey et al. 1987).

Prey organisms may also escape predation by having refuges in space, time and size. Although not evolved adaptations, these means of escape may have a significant impact on prey population dynamics (Taylor 1984). On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, African Black Oystercatchers *Haematopus moquini* Bonaparte occur at some of the highest densities recorded (Hockey 1983). At the 3 major islands in the Bay (Malgas, Jutten and Marcus Islands) the densities range from 25 to 78 birds per km of coast. Intertidal limpets are important prey of these predators (Hockey and Underhill 1984), and their estimated annual removal of *Patella granularis* L. from the shores of Jutten Island is 1.1 million individuals per km of coast (Hockey and Branch 1984).

However, because oystercatchers prefer limpets of between 20 and 40 mm in length (Hockey and Underhill 1984), larger limpets have a refuge from predation. In addition, some limpets inevitably settle in, or move to, positions that render them inaccessible to oystercatchers (e.g. on vertical rock faces or the sides of crevices), thus attaining a refuge in space. The shores of seabird-breeding islands in Saldanha Bay support numerous foliose algae, which have a rapid rate of production in response to nutrient enrichment of intertidal waters by the dissolved guano of seabirds (Part 2). Foliose algae also develop on the shells of *P.*

granularis which may, as a consequence, be totally hidden from view. This crypticity, although transient and not genotypic in origin, may be expected to enhance limpet survival in the presence of visually-hunting predators.

In this study I assess the roles played by crypticity and refuges in size and space in enhancing the survival of limpets at sites with different levels of predatory pressure. None of these means of escaping predation represents an evolved adaptation and any influence on limpet survival rates is merely co-incidental. However, the escape from predation of certain segments of the prey population has potential long-term implications for prey population dynamics.

Methods and materials

Study sites

Seven intertidal study sites in the Saldanha Bay area (Fig. 1.1) were visited monthly between December 1982 and April 1984. Three sites were on the shores of seabird-breeding islands (Malgas, Jutten and Marcus Islands). These sites are washed by nutrient-rich water - a consequence of the run-off of quantities of dissolved seabird guano (Part 1). The rate of intertidal algal production on Jutten and Marcus Islands is enhanced in response to this nutrient enrichment (Part 2).

Survival rates

Each study site was divided into a low-, mid- and high-shore region of equal area. In each region 50 *P. granularis* were individually marked using punched plastic labels and rapidly setting epoxy glue. In subsequent months surviving individuals were relocated. If a limpet was absent in 1 month, but was relocated in a subsequent month, it was considered to have been present all the time. If a missing limpet was not relocated it was considered dead. Marked limpets suffered mortality from predation and other factors, and when numbers in any shore region fell below 10, supplementary limpets were labelled. The number of marked limpets present each month was used to estimate the finite rate of mortality per month and per year, using equations given by Caughley (1978). To test the durability of labels, 50 empty *P. granularis* shells were glued to the rock adjacent to the Marcus Island study site and were labelled in situ. The loss of labels was monitored in subsequent months.

Influence of limpet size and accessibility on survival

Each month the shell lengths of relocated limpets were measured, and subsequently the survival rates of individuals smaller than 50 mm in length were considered separately from those of larger individuals. In addition, from April 1983 onwards, the position of each relocated limpet was recorded, and the mortality rates of those accessible to avian predators were considered separately from those of inaccessible individuals.

The influence of size and accessibility on the probability of a limpet's surviving for 1 month were determined using a generalized linear model (McCullagh and Nelder 1984) with a binomial error distribution. The number of individuals present at the start of the month was equated with the number of trials, while the number surviving the month represented the number of successes. The roles of the independent variables in explaining variation in the probability of survival were expressed as a linear sum of the effects of each variable. The form of the model is thus

$$P = \frac{e^a}{1 + e^a}$$

where P is the probability of surviving 1 month and $a = c + \sum_{i=1}^{n} b_i x_i$, where c is a constant, b_i are regression co-efficients calculated by the model, and x_i are the explanatory variables, in this case study site, shore region, limpet size and limpet accessibility.

Influence of limpet crypticity

Each month, between April 1983 and March 1984, the amount of foliose algal growth on the back of each relocated limpet was assessed in terms of the percentage of shell that was obscured from view. Percentages were grouped into categories 0, 1 and 2, being 0%, 1-50% and >50% covered respectively. Seasonal trends in the proportions of limpets in each category at each site were analysed (with low-, mid- and high-shore limpets considered together).

The influence of algal cover on the survival of small (<50 mm in length), accessible limpets also was determined using a generalized linear model with a binomial error distribution (see above). In this case the prediction of variation in the dependent variable (probability of surviving 1 month) is attempted using variations in the independent variables study site, shore region and percentage algal cover.

Results

Limpet survival rates

The plastic labels used to mark limpets were very durable: no labels were lost from the sample of 50 empty shells glued to the rocky shore, although entire shells were occasionally washed away. In some instances live limpets still bore their individual labels 2 years after being marked. Limpet survival rates measured at the study sites range from 94% month^{-1} (47% year^{-1}) in the mid-shore regions at Mauritz Bay and Malgas Island, to 77% month^{-1} (4% year^{-1}) in the low-shore region at the Marcus Island site (Fig. 3.6). Limpets at the Jutten and Marcus Island sites have the lowest probability of survival (in all 3 shore regions), while survival generally is highest at the mainland sites outside

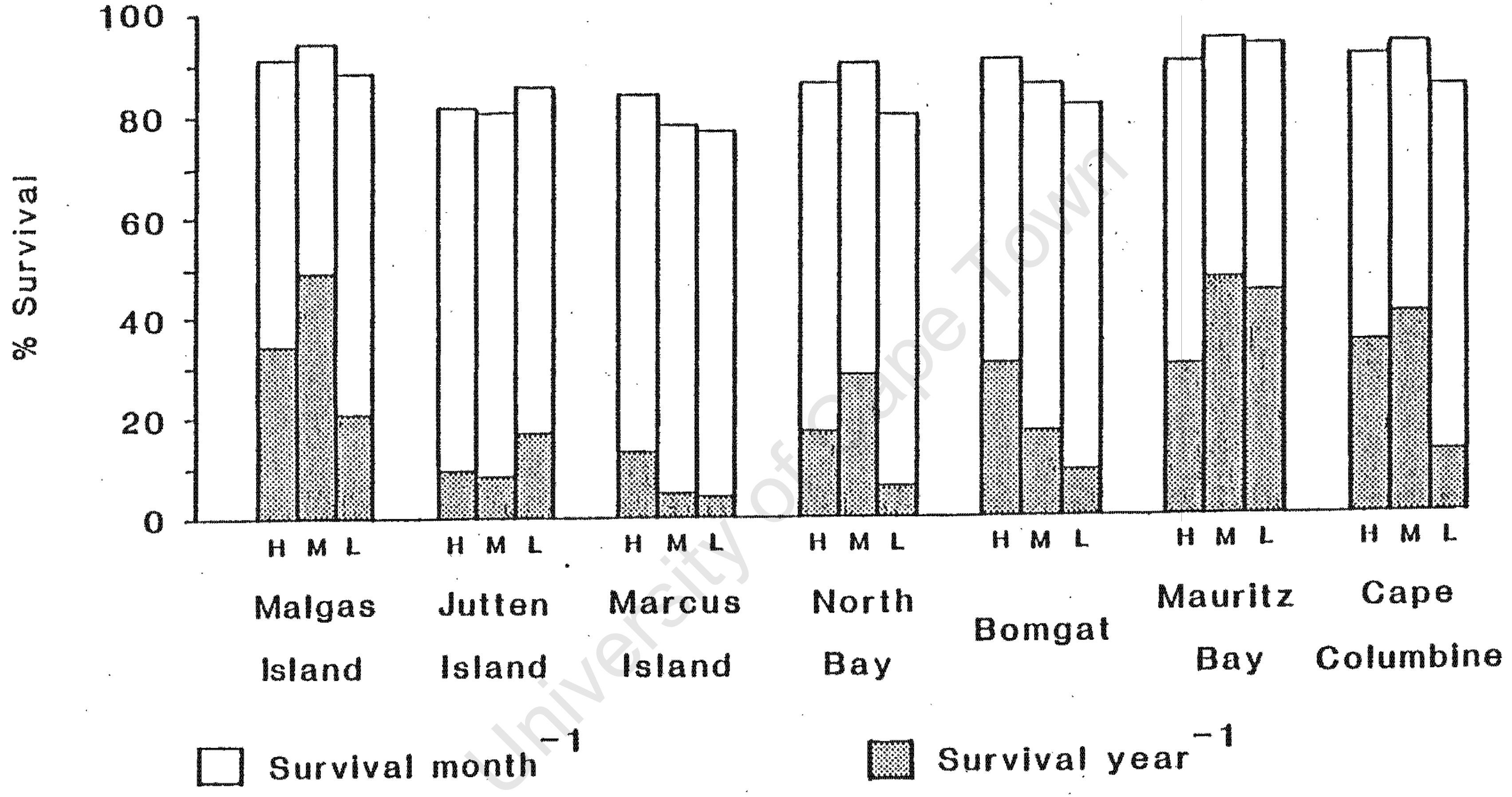

Fig. 3.6. Survival rates of *P. granularis* in the high- (H), mid- (M) and low-shore (L) regions at study sites in the Saldanha Bay area. Rates are calculated using mark/recapture techniques applied monthly over 12 months

the Bay (Fig. 3.6). Limpet survival rates recorded on the shores of Malgas Island are unexpectedly high.

Influence of limpet size and accessibility

The generalized linear model best explaining variations in limpet survival rates ($X^2_{28} = 38.62$, $P > 0.10$) incorporated the independent variables study site, shore region, limpet size and accessibility, as well as factors which accounted for interactions between site and region, and between site and limpet size (Table 3.6). The most significant correlate of limpet survival rate is limpet size (d.f. = 54, $t = 5.52$, $P < 0.005$ - Table 3.6), indicating that limpets measuring 50 mm or more in length have an enhanced probability of survival. The survival of inaccessible limpets is also enhanced (positive co-efficient), but this relationship is not significant. The shore region in which a limpet occurs also influences its probability of survival. Limpets in the mid-shore region have significantly enhanced predicted survival rates (d.f. = 56, $t = 2.99$, $P < 0.002$) when compared with those in the low-shore region. In contrast, predicted limpet survival in the high-shore region is significantly reduced (d.f. = 56, $t = -1.91$, $P < 0.05$) when compared with survival in both other regions.

Although the relationships described above are applicable to all the study sites considered, the patterns may be modified by the unique influence of each study site. For example (see Table 3.6), the predicted probabilities of survival of limpets at the 3 island sites (Malgas Island co-efficient is

Table 3.6. Estimated co-efficients, standard errors and significance levels generated when a generalized linear model is fitted to limpet survival rate data obtained from accessible and inaccessible limpets of 2 size classes: large are > 50 mm and small are < 50 mm in length

INDEPENDENT VARIABLE	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	1.01	0.161	6.84	<0.0005
SITE				
Jutten Island	0.627	0.217	2.89	<0.005
Marcus Island	-0.225	0.225	-1.00	
North Bay	0.928	0.264	3.77	<0.0005
Bomgat	0.667	0.227	2.94	<0.002
Mauritz Bay	1.243	0.270	4.60	<0.0005
Cape Columbine	1.449	0.305	4.75	<0.0005
SHORE-REGION				
Mid-shore	0.771	0.258	2.99	<0.002
High-shore	-0.402	0.211	-1.91	<0.05
LIMPET SIZE AND ACCESSIBILITY				
Large limpets (>50 mm)	1.112	0.201	5.52	<0.0005
Inaccessible limpets	0.137	0.171	0.80	
INTERACTIVE				
Jutten mid-shore	-1.116	0.334	-3.34	<0.001
high-shore	-0.788	0.280	-2.81	<0.005
Marcus mid-shore	0.030	0.339	0.09	
high-shore	0.899	0.295	3.04	<0.002
North Bay mid-shore	-0.208	0.435	-0.48	
high-shore	0.109	0.321	0.34	
Bomgat mid-shore	-0.507	0.352	-1.44	
high-shore	1.266	0.344	3.68	<0.0005
Mauritz mid-shore	-0.563	0.397	-1.42	
high-shore	0.578	0.354	1.63	
Columbine mid-shore	-2.188	0.451	-4.85	<0.0005
high-shore	0.011	0.398	0.03	
Jutten large limpets	-1.017	0.277	-3.68	<0.0005
Marcus large limpets	-1.027	0.297	-3.46	<0.0001
North Bay large limpets	-1.928	0.414	-4.65	<0.0005
Bomgat large limpets	-1.942	0.351	-5.51	<0.0005
Mauritz large limpets	-1.753	0.386	-4.54	<0.0005

0.00) are lower than at any other site, irrespective of the shore region involved or the sizes of the limpets concerned. Consequently, the predicted survival of limpets in different shore regions will be affected by the site at which they occur. Similarly, although larger limpets are predicted to have a higher probability of survival, this relationship will be tempered by the unique influence of the site. This accounts for the importance of the interactive factors.

The benefit afforded a larger limpet, in terms of enhanced survival, decreases (co-efficient becomes more negative) from island to mainland sites (Table 3.6). This is demonstrated clearly when the influences of all variables are taken into account and the survival rates (as predicted by the model) of limpets at island and mainland sites are compared (Table 3.7). Large limpets at island sites have consistently higher predicted probabilities of survival than do small limpets, whereas at mainland sites large limpets have reduced probabilities of survival. No limpets measuring more than 50 mm in length were recorded at the Cape Columbine site.

Influence of algal cover

On the shores of islands in Saldanha Bay the proportion of small, accessible limpets which are more than 50% covered by foliose algae peaks in the summer months, particularly between November and January (Fig. 3.7). During the winter months most limpets are free of algal cover, although there are generally a few individuals that support foliose algae

Table 3.7. Monthly limpet survival rates predicted by the generalized linear model fitted to survival rate data from accessible and inaccessible limpets in 2 size categories (small are < 50 mm, large are > 50 mm) in 3 regions of the shore (H = high-shore, M = mid-shore, L = low-shore)

SITE	SHORE REGION	ACCESSIBLE SMALL	ACCESSIBLE LARGE	INACCESSIBLE SMALL	INACCESSIBLE LARGE
Malgas Island	H	0.67	0.86	0.70	0.88
	M	0.87	0.95	0.88	0.96
	L	0.75	0.90	0.78	0.91
Jutten Island	H	0.63	0.65	0.66	0.68
	M	0.80	0.81	0.82	0.83
	L	0.85	0.86	0.87	0.88
Marcus Island	H	0.80	0.81	0.82	0.83
	M	0.84	0.85	0.86	0.87
	L	0.71	0.72	0.73	0.75
North Bay	H	0.85	0.72	0.87	0.74
	M	0.93	0.86	0.94	0.87
	L	0.88	0.77	0.90	0.79
Bomgat	H	0.93	0.86	0.94	0.87
	M	0.88	0.77	0.90	0.79
	L	0.85	0.72	0.87	0.75
Mauritz Bay	H	0.93	0.87	0.93	0.88
	M	0.93	0.87	0.94	0.89
	L	0.91	0.85	0.92	0.86
Cape Columbine	H	0.90	*	0.91	*
	M	0.76		0.78	
	L	0.93		0.94	

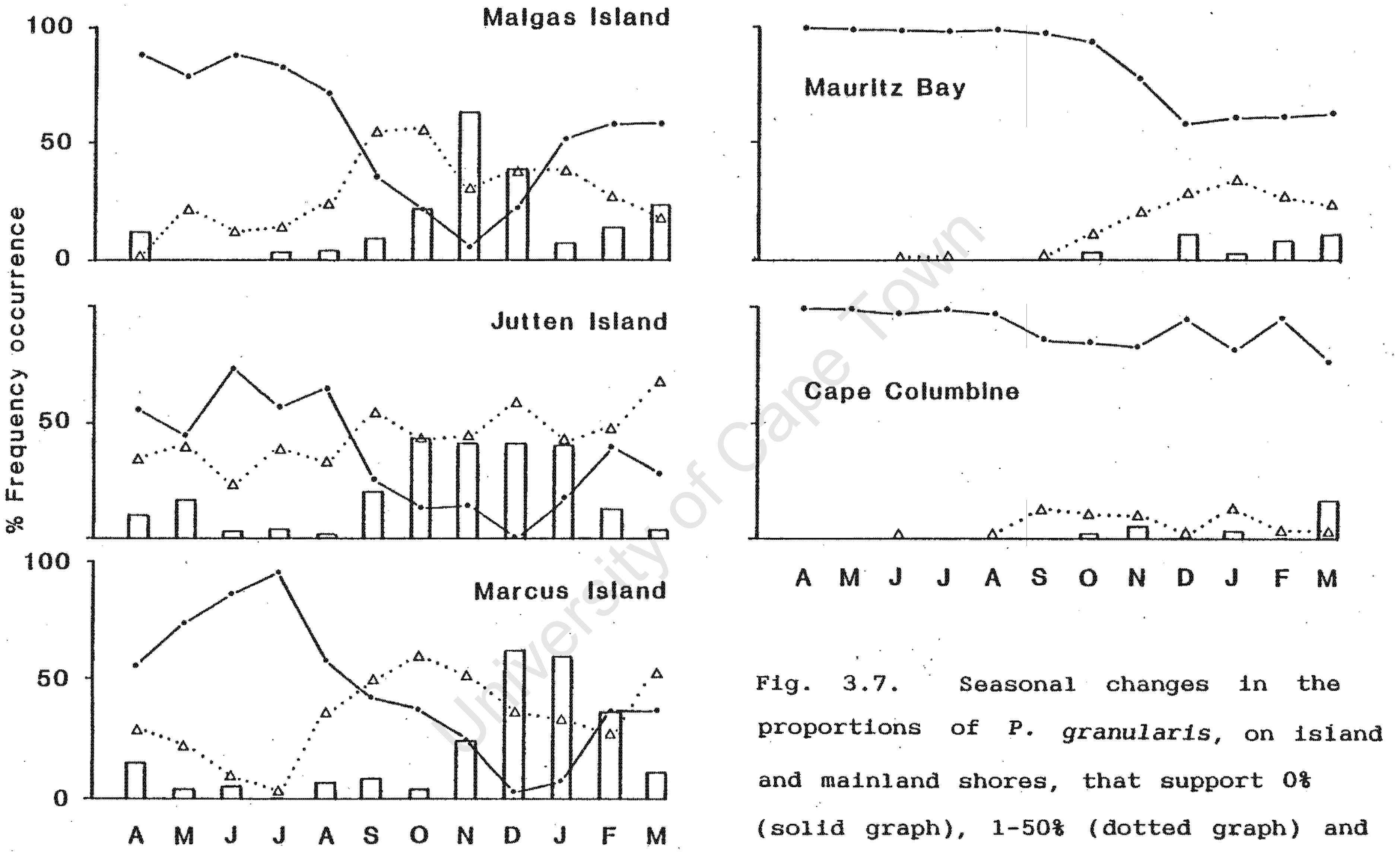

Fig. 3.7. Seasonal changes in the proportions of *P. granularis*, on island and mainland shores, that support 0% (solid graph), 1-50% (dotted graph) and >50% (histograms) algal cover on their shells

in all months of the year. In contrast, limpets on mainland shores outside the Bay seldom support any foliose algae on their shells.

The generalized linear model initially used to explain variations in the survival rates of small, accessible limpets included the independent variable percentage algal cover, which was divided into 3 categories, viz 0%, 1-50% and >50% cover. This model predicted no significant difference in the probability of survival of category 0 and 1 limpets (co-efficient = -0.002, d.f. = 56, t = -0.02) and consequently the data for these 2 categories were combined. The generalized linear model best fitting the data (X^2_{36} = 41.04, P > 0.20) incorporated the independent variables study site, shore level and percentage algal cover (0-50% or >50%) as well as a factor representing the interaction between site and shore region (Table 3.8).

Limpets which are more than 50% covered by foliose algae have a significantly enhanced monthly survival rate in comparison with limpets supporting less or no foliose algae (d.f. = 56, t = 1.67, P = 0.05). In addition, survival rate is highest in the mid-shore region (d.f. = 56, t = 2.47, P < 0.01) and lowest in the high-shore region (d.f. = 56, t = -1.77, P < 0.05), as was found in the previous model. Differences in attributes of study sites explained the largest amount of variation in survival rates (Table 3.8), with the predicted probability of survival being lowest at Malgas (co-efficient = 0.00) and Marcus Islands, and highest

Table 3.8. Estimated co-efficients, standard errors and significance levels generated when a generalized linear model is fitted to limpet survival rate data obtained from small (<50 mm), accessible limpets with variable amounts of foliose algae on their shells

INDEPENDENT VARIABLE	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	0.990	0.173	5.72	<0.0005
SITE				
Jutten Island	0.804	0.232	3.47	<0.0005
Marcus Island	-0.365	0.238	-1.53	
North Bay	0.975	0.251	3.88	<0.0005
Bomgat	0.717	0.236	3.03	<0.002
Mauritz Bay	1.446	0.290	4.99	<0.0005
Cape Columbine	0.245	0.325	0.78	
SHORE-REGION				
Mid-shore	0.978	0.395	2.47	<0.01
High-shore	-0.495	0.280	-1.77	<0.05
ALGAL COVER				
>50% cover	0.231	0.138	1.67	=0.05
INTERACTIVE				
Jutten mid-shore	-1.564	0.466	-3.35	<0.001
high-shore	-0.858	0.344	-2.49	<0.01
Marcus mid-shore	0.114	0.464	0.25	
high-shore	1.258	0.365	3.45	<0.001
North Bay				
mid-shore	-0.587	0.517	-1.13	
high-shore	0.273	0.374	0.73	
Bomgat mid-shore	-0.632	0.468	-1.35	
high-shore	0.511	0.548	0.93	
Mauritz Bay				
mid-shore	-0.793	0.514	-1.54	
high-shore	0.524	0.417	1.26	
Cape Columbine				
mid-shore	0.318	0.547	0.58	
high-shore	1.510	0.461	3.28	<0.001

at Mauritz Bay. Limpets at Cape Columbine have an unexpectedly low probability of survival, but when all independent variables are taken into account the interaction between site and shore region compensates for this (Fig. 3.8). Limpet survival rate, as predicted by this model for each shore region at each site, is enhanced in the case of limpets which are more than 50% covered by foliose algae (Fig 3.8). The predicted benefit to algal-covered limpets, in terms of enhanced survival, is greater at island sites than at mainland sites (Fig. 3.8), with the benefit being least (a predicted increase in monthly survival rate of 1%) in the high- and mid-shore regions at the Cape Columbine site.

Discussion

Limpet survival rates

African Black Oystercatchers are the major predator of adult *Patella granularis* on the west coast of southern Africa. Other potential predators of *P. granularis* include Kelp Gulls *Larus dominicanus* and the Giant Clingfish *Chorisochismus dentex*, but limpets only occasionally form dietary items in these species (Stobbs 1980; Armstrong 1984). The density of African Black Oystercatchers on islands in Saldanha Bay ranges from 25 (winter count on Malgas Island) to 78 birds per km coast (summer count on Jutten Island - Hockey 1983). In comparison, the mainland coast in the area of the North Bay and Bomgat sites supports

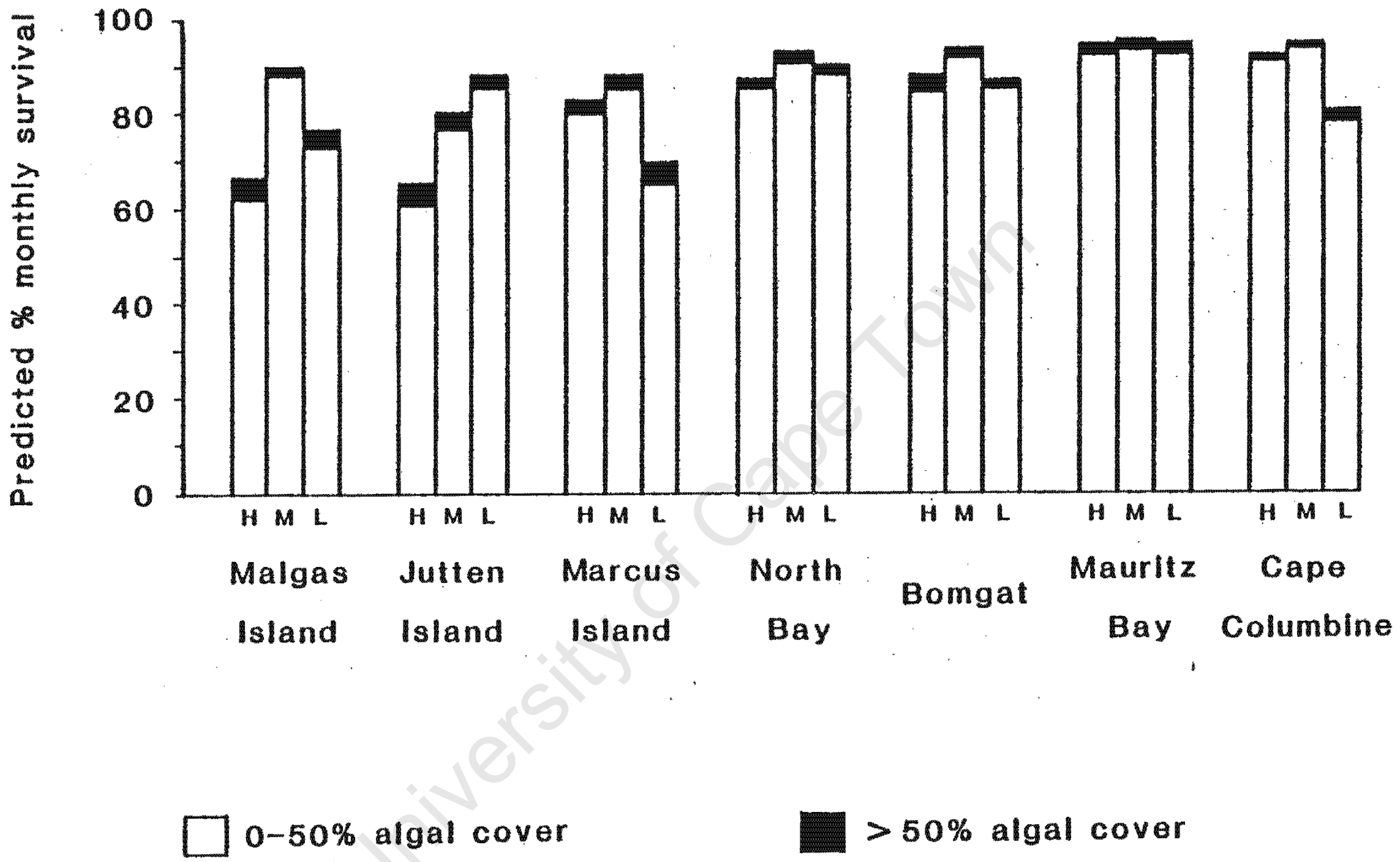

Fig 3.8. Predicted survival rates of small (<50 mm), accessible *P. granularis* in the high- (H), mid- (M) and low-shore regions at intertidal study sites. Shaded areas represent the predicted enhancement in survival afforded by a >50% covering of foliose algae

between 2 and 16 birds per km coast, and mean density of oystercatchers recorded on mainland shores outside the Bay is 2.6 birds per km coast (Hockey 1983).

Limpet mortality rates measured in the Saldanha Bay area (Fig. 3.6) are highest on the shores of Jutten and Marcus Islands, although these rates are not as high as the mortality rate of *Patella vulgata* Linnaeus (90% month^{-1}) in the presence of European Oystercatchers *Haematopus ostralegus* Linnaeus reported by Lewis and Bowman (1975). In their study however, large numbers of oystercatchers were present on rocky shores in Yorkshire on a seasonal and transient basis, whereas African Black Oystercatchers are resident on the shores of islands in Saldanha Bay. Recorded limpet mortality rates were lowest on the mainland shores at Mauritz Bay and Cape Columbine, and intermediate at the North Bay and Bomgat sites (Fig. 3.6). Variations in the survival rates of *P. granularis* at different study sites may be attributed largely to variations in the density of oystercatchers, and consequently, in predatory pressure.

Within each study site predicted limpet survival is lowest in the high-shore region, possibly reflecting the more stressful physical conditions prevalent in that region (Jernakoff 1983). Limpets in the low-shore region do not have to contend with high temperatures or desiccation as they are submerged for a large proportion of the tidal cycle. However, oystercatchers show a peak in foraging activity at the time of low-tide (Hockey 1984) and tend to forage at the water's edge (Hockey 1981), rendering low-shore limpets more likely to be removed than mid-shore limpets.

Influence of limpet size

The most significant correlate of limpet survival rate is limpet size. African Black Oystercatchers select limpets of between 20 and 40 mm in length, and are unlikely to be successful in removing individuals of more than 60 mm in length (Hockey and Underhill 1984). Consequently, larger limpets have a refuge in size. This is particularly important on the shores of seabird-breeding islands in Saldanha Bay where limpet growth rate is rapid (Part 3.1) and individuals soon reach a size at which they are free from oystercatcher predation. At these sites larger limpets are predicted to have enhanced survival rates (Table 3.7). In particular, limpets on the Malgas Island shores are affected by this relationship as the population at this site is dominated by very small and very large individuals (5.8% are greater than 60 mm in length, cf. Cape Columbine where no limpet grows larger than 50 mm - Part 3.1). Small individuals (<15 mm in length) are not suitable for labelling and consequently, although limpets larger than 50 mm were labelled in proportion to their occurrence in the population at the Jutten and Marcus Island sites (14% and 13% respectively), the larger limpets constitute 33% of the individuals labelled on the shore of Malgas Island. The survival rates recorded for Malgas Island limpets are thus artificially high.

In contrast, limpets on mainland shores do not benefit by being large, and the predicted probabilities of survival are lower for large individuals than for small ones at the same site (Table 3.7). Limpets have slower growth rates on mainland shores than on islands (Part 3.1) and, since maximum adult size attainable by an individual is a function of its growth rate (Branch 1974; Balaparameswara Rao 1976), limpets on unenriched mainland shores never attain sizes comparable with those on islands. Large limpets on an unenriched mainland shore are thus older than similarly-sized individuals on an island shore, and may experience higher mortality due to senescence.

Influence of accessibility and crypticity

Limpets inaccessible to oystercatchers automatically achieve a refuge from predation by birds, irrespective of their growth rate and size. *Patella granularis* exhibits homing behaviour and will return to a home scar during periods of inactivity and environmental stress, e.g. during the day-time low-tide period (Branch 1971). In this study limpets which were recorded as being inaccessible in a month, and which survived at least 3 subsequent months, had an 89% probability of being recorded as inaccessible on all 4 visits, yet the model used predicted no advantage (in terms of limpet survival) to this behaviour (Table 3.6). *Patella granularis* forages at night (Branch 1971) and those individuals recorded as inaccessible during day-time visits to a study site may have become accessible during the night (particularly those on the walls of crevices in the rock). Oystercatchers also forage at night, and Hockey and Underhill (1984) showed that on Jutten Island limpets formed a higher proportion of oystercatcher prey items during the night than they did during the day. Under such conditions, few limpets in this study were truly inaccessible to oystercatchers.

Oystercatchers forage using visual cues and have been shown to discriminate between the anterior and posterior shell margins when attacking limpets (Hockey 1981; Hockey and Branch 1983). Foliose algae which develop on the shell of a limpet and which obscure 50% or more of the individual render it less likely to be recognised as a prey item and significantly enhance its probability of survival. The probabilities of survival of limpets without algae and those with 1-50% cover are not different, indicating that it is the escape from predation afforded by the algal cover, rather than the amelioration of temperature and desiccation stresses, that gives rise to enhanced survival rates.

The development of algae on the shells of marine and intertidal organisms has been documented in several instances (Sinclair 1963; Bouxin 1964; Branch 1971) but no advantages have been demonstrated to accrue to affected individuals. In the Saldanha Bay area foliose algae develop on *P. granularis* shells during the months when rates of algal production are fastest (Part 2), and the development of algal covering is most profuse and widespread on island shores (Fig. 3.7). The effect of an algal covering on limpet survival rate is apparent (albeit very slight) on mainland shores, but is more pronounced on the shores of islands, where oystercatcher predatory pressure is intense (Fig. 3.8), once again indicating that the primary advantage of an algal covering is the camouflage it provides.

Differential survival rates: their impact on prey population dynamics

The selective removal of certain prey size classes by avian predators may have a significant impact on the demography and dynamics of the prey population. Howard and Lowe (1984) found that selection by Royal Spoonbills *Platalea regia* Gould of the largest and slowest-moving caridean shrimps in seagrass beds leads to a disproportionately high mortality of adult females. Females attain larger body sizes than males, and may be hampered, when attempting to escape, by the mass of the large clutch of eggs. There is a resultant skewed sex ratio in the population, and female longevity and life-time reproductive output are reduced. On the rocky shores of islands in Saldanha Bay predation by oystercatchers results in high mortality of medium-sized limpets. However, the rapid growth rates of limpets on island shores, and the inability of oystercatchers to handle large limpets ensure that a certain proportion of individuals attain a refuge from predation by virtue of their size.

Limpet gamete production increases exponentially with respect to an increase in shell length (Part 3.1), and Hockey and Branch (1984) estimate that as much as 86% of the female gametic material released by limpets on the shores of Jutten Island is derived from limpets which have a refuge in size. The reproductive effort of these individuals probably is vital in the continued functioning of this intertidal system, particularly with reference to the system's ability to support dense populations of oystercatchers. Oystercatchers are uncommon on mainland shores (particularly outside the Bay) where the rate of limpet growth is slow and even the largest and most fecund limpets would be available to the birds.

The demography and reproductive output of limpet populations on the shores of seabird-breeding islands are modified by the effects of oystercatcher predation. The size structure of prey populations is altered (Part 3.1), and the survival rates and life-time reproductive outputs of individuals are reduced. The reproductive output of the prey population may be maintained by virtue of a refuge in size for large individuals and, to a much lesser extent, by the crypticity resulting from the development of foliose algae on the shell of the prey. However, fundamental to the potential stability of this predator-prey relationship is the entry of nutrients from the dissolved guano of seabirds into the intertidal and nearshore waters. Enhanced rates of algal production stimulate limpet production, and are a direct consequence of nutrient enrichment.

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Section (3): Life-history patterns of populations of the limpet *Patella granularis*: the dominant roles of food supply and mortality rate

Summary. Rates of algal production were measured at 6 rocky intertidal sites on the southwestern Cape coast, South Africa, where populations of the limpet *Patella granularis* occur. Different rates of algal production and limpet mortality were recorded at each site and both factors affected limpet reproductive fitness. Limpet growth rates and biomass at different sites were significantly correlated with rates of algal production, and limpet mortality was related to the density of African Black Oystercatchers, important predators of *P. granularis*. Life-time gametic output of a hypothetical cohort of limpets at each site was modelled using the measurements of growth, reproduction and mortality made at each site. Limpet cohorts at sites with rapid rates of algal production were predicted to have a larger life-time production of gametic material than cohorts at sites with slow algal production rates, except in instances of acute predatory pressure. In the light of the overriding influence of food supply on the expression of limpet life-history parameters, it is imperative that researchers consider food availability before assuming that local, population-specific differences in life-history patterns are due to genetic differences.

Introduction

The 'fitness' of an individual organism generally is considered in terms of the number of its offspring which themselves survive to reproduce (Horn 1978; Grahame and Branch 1985). When applying this term to marine or intertidal invertebrates with external fertilization of gametes, the success of the individual is equated with the biomass of gametic material released during the organism's life-time (Fletcher 1984b). The expressions of life-history parameters of an organism - such as growth rate, age and size at maturity, reproductive effort and longevity - represent a combination of solutions to particular ecological problems (Stearns 1980), each solution being the optimal outcome of conflicting demands placed on the organism by its environment. Life-history patterns combine to maximize the individual's life-time reproductive success, given the constraints placed on the organism by the abiotic and biotic conditions prevailing (Grahame and Branch 1985), and are therefore adaptive.

Life-history patterns of intertidal invertebrates vary inter- and intra-specifically, as a result both of genetic differences and environmental influences. Although inter-specific comparisons have been more common, many studies have compared the life-history patterns of related and unrelated intertidal invertebrate species and populations

(Giesel 1969; Paine 1969; Sutherland 1970, 1972; Lewis and Bowman 1975; Thompson 1980; Workman 1983; Fletcher 1984a, b; Moran et al. 1984; Grahame and Branch 1985) However, few of these studies consider the implications of different population life-history patterns in terms of either differential life-time reproductive success or the ecology of the species as a whole. In addition, studies dealing with the growth and reproduction of intertidal limpets seldom have attempted to measure food availability at the study site and consequently, the influence of differences in food supply on the expression of life-history parameters, such as growth rate, could only be suggested (exceptions are Creese 1980; Underwood 1984b).

In the present study the growth rates, gonadial production and mortality rates of populations of the limpet *Patella granularis* were measured. By virtue of heterogeneity in the intertidal environment, each population was subject to a unique combination of physical and biological influences, such as substratum slope. In addition, since the major predator of *P. granularis* (viz African Black Oystercatchers *Haematopus moquini*) is unable to remove limpets on steep slopes (Hockey and Branch 1984), predatory pressure also varied between sites. Differences in these environmental parameters were quantified as far as was possible. The survival, growth and reproductive output of a hypothetical cohort of limpets at each site were modelled using actual measurements of these processes made in the field. The implications of different life-history patterns for the ecology of the species on an offshore island are discussed.

Methods and materials

Study sites

In December 1982, 5 study sites were established on the shores of Marcus Island (33°02'S, 17°58'E), a granitic seabird-breeding island in Saldanha Bay on the southwestern coast of South Africa. The sites were on smooth, rocky slopes inclined at 80°, 60°, 45°, 20° and 0° to the horizontal, respectively, and were positioned at intervals along a 100 m stretch of coastline. All sites were at approximately the same height above the mean spring low-tide level. An additional 0° (level) site was established at Cape Columbine (32°49'S, 17°51'E), on the mainland approximately 40 km north of Saldanha Bay (Fig. 1.1). Both study areas are in the Benguela Current system and, at times, are washed by nutrient-rich, upwelled water, but the nearshore and intertidal waters around Marcus Island are further enriched by nutrients from the dissolved guano of seabirds (Part 1). The rate of algal production on the shores of Marcus Island is enhanced as a consequence of increased nutrient availability (Part 2).

At all the sites where macro-algal settlement occurred, the species represented were *Enteromorpha* sp. and *Porphyra capensis* Kutz. and at all sites the only herbivorous invertebrate species present in large numbers was the limpet *Patella granularis* L. At the Marcus Island 0° site, where shallow, permanent rockpools occurred, the pulmonate limpet *Siphonaria capensis* Quoy & Gaimard was present in addition to *P. granularis*, but was less numerous and largely confined to shallow pools (see Stephenson and Stephenson 1972 for general shore descriptions).

Marcus Island supports ca. 120 resident African Black Oystercatchers (*Haematopus moquini* Bonaparte), large, territorial shorebirds that forage primarily on intertidal mussels and limpets, particularly on *P. granularis* (Hockey 1983; Hockey and Underhill 1984). This is one of the highest densities of African Black Oystercatchers recorded (67 birds per km coastline - Hockey op. cit.). The mean density of oystercatchers on the mainland between Cape Columbine and Saldanha Bay is 3.6 per km coastline (Hockey op. cit.).

Algal production

A herbivore exclusion plot was established at each site, by enclosing a 0.1 m^2 rectangular area with a strip of copper-based marine anti-fouling paint. The paint was renewed whenever it became worn. Each month for 15 months, after the rock had been scraped clean and burned with a blowtorch to kill existing algal spores, 4 high-intensity polystyrene settlement strips (each 30 x 50 x 2 mm) were glued to the rock inside the exclusion plot, using rapidly setting epoxy. After a month in position the strips were lifted, wrapped in aluminium foil to exclude light, and frozen for subsequent analysis.

Chlorophylls *a*, *b* and *c* were extracted from the algae that had growth on each strip, using the method of Strickland and Parsons (1972), and were quantified using a Beckman model 25 spectrophotometer and the equations of Jeffrey and Humphrey (1975) (see also Underwood 1984a and Part 2 for details of method). The values obtained were corrected for the exact area of each strip, and the number of days in position, so that the final index of algal production was expressed in ug chlorophyll cm^{-2} $month^{-1}$. The mean of the 4 monthly samples was used in analysis.

Limpet growth and mortality

Adjacent to each limpet exclusion plot, between 30 and 50 *P. granularis* were labelled individually with punched plastic labels and rapidly setting epoxy. Each month for 15 months, maximum shell length of recovered individuals was recorded. Predation and other factors caused the mortality of limpets, and supplementary individuals were labelled when numbers fell below 10. For each site, in each month, a linear regression of limpet length in the current month (L_{t+1}) on limpet length in the previous month (L_t) (Ford-Walford plot) was calculated using the measured values. If the parameters were not significantly linearly related the data for that month were considered of no predictive value and were discarded. The regression line was described by the equation:

$$L_{t+1} = mL_t + i$$

where m = rate of increase in length and i = growth in the first month (Balaparameswara Rao 1976; Branch 1981).

The predicted monthly growth of a 'standard' 30 mm limpet was calculated from each regression. Limpets of ca. 30 mm in length were common at all sites, and the monthly increment of a limpet this size was deemed a useful index of overall rate of limpet growth, considering that absolute growth rate is dependent on limpet size (Branch 1981). No true replication of study sites was obtained using this experimental design, and thus the statistical testing of mean predicted limpet growth is inappropriate (Hurlbert 1984). Multiple linear regression analysis (Sokal and Rohlf 1981) was employed to regress the dependent variable (predicted monthly increment in shell length of a 30 mm limpet) on the independent variables algal production rate, month and site. In addition, the predicted increment of a limpet which measured 30 mm in January 1983 and which grew, according to the predictions of monthly Ford-Walford plots, until December 1983, was calculated for each site. When the line described by the equation $L_{t+1} = L_t$ (i.e. no growth) is superimposed on each Ford-Walford plot, the intercept of the two lines indicates the predicted maximum length of a limpet growing at that site (L_∞) (Balaparameswara Rao 1976). Mean L_∞ values were calculated for each site.

Limpet mortality rates were calculated from the actual number of labelled individuals present monthly at each site, used in conjunction with the equation for the calculation of finite rate of mortality (Caughley 1977). When individuals were not found in a month, but were found subsequently, they were recorded as present in all previous months. In instances where an unusually high mortality was recorded in the first few (1 - 3) months after labelling, the data from these months were discarded, on the assumption that labelling may have caused the increased mortality.

Limpet biomass and gonadial production

Samples of 30 limpets were collected bi-monthly from areas adjacent to 0° (level) sites, and the wet mass of gonad was determined for individuals of both sexes. The supply of limpets at the angled sites was not large enough to permit this intensity of sampling, but it was considered that, for fertilization to be effected, times of spawning should be similar for all limpets in the same area (as Branch 1974a has demonstrated in other areas), and the spawning time at the Marcus 0° site was therefore taken as representative of all the sites on Marcus Island. For each sample gonadial wet mass was regressed on shell length (males and females being considered separately), the 2 parameters having a power relationship. For both study areas the months in which maximum and minimum gonadial material was present were determined, and the mass of gametic material released by a limpet of given length was considered to be equal to the difference between its annual maximum and minimum gonadial masses. From more detailed studies of the reproductive cycle of *P. granularis* (Branch 1974a) it was assumed that *P.*

granularis releases 75% of its gametes during June, and 25% during July each year.

A dry somatic and gonadial mass/length regression for *P. granularis* was calculated using 100 individuals of varying sizes, collected from an area near to the Marcus Island 0° site in June 1983. The biomass of limpets supported (per m^2 of rocky substratum) at each site was calculated by measuring all the limpets present (in the case of angled sites), or all the limpets in 10 randomly-placed 1 m^2 quadrats (at the 2 0° sites) during June. Length measurements were subsequently converted to biomass using the equation from the above regression analysis (viz dry somatic and gonadial mass = 1.9×10^{-6} $(\text{length})^{3.5}$, with n = 100, $r^2 = 0.98$, $P < 0.001$).

Model

Assuming a hypothetical settlement of a single cohort of 10 000 *P. granularis*, each 2 mm in length, at each site in August, 1 month after gonadial release is completed, I calculated the survival of cohort members using monthly mortality rates measured at each site. For simplicity I assumed a sex ratio of 1:1 and a constant rate of mortality for all limpet size classes. Although it has been shown that small individuals have a higher mortality rate (Part 3.2), the relevant analysis did not include individuals of less than 10 mm in length - the size class that might be expected to have the highest rate of mortality. The predicted size of cohort members still surviving in June and July each year was calculated using monthly growth rates measured at the sites. I also assumed that the conditions of monthly algal settlement and growth, limpet mortality and limpet growth recorded at each site would remain constant in all subsequent years of the cohort's existence. The annual output of gametic material by the cohort was calculated using measured release of gametic material by a limpet of given size, and assuming that 75% of gametic material was released in June of each year, and 25% in July (Branch 1974a).

The total biomass of each cohort at the time of spawning was calculated from the predicted number and length of limpets present. Since the biomass of limpets supported (g m^{-2}) in June at each site was known, the area occupied by each cohort at the time of spawning could be estimated, and the mass of gametic material released annually by each cohort was corrected for the area occupied. Reproductive output was expressed as the wet mass of gametic material released during the life-time of the cohort (g m^{-2}). In instances, towards the end of the hypothetical cohort's life-time, when the cohort occupied less than 1 m^2 of shore, the production of gametic material was not corrected for the area occupied by the cohort.

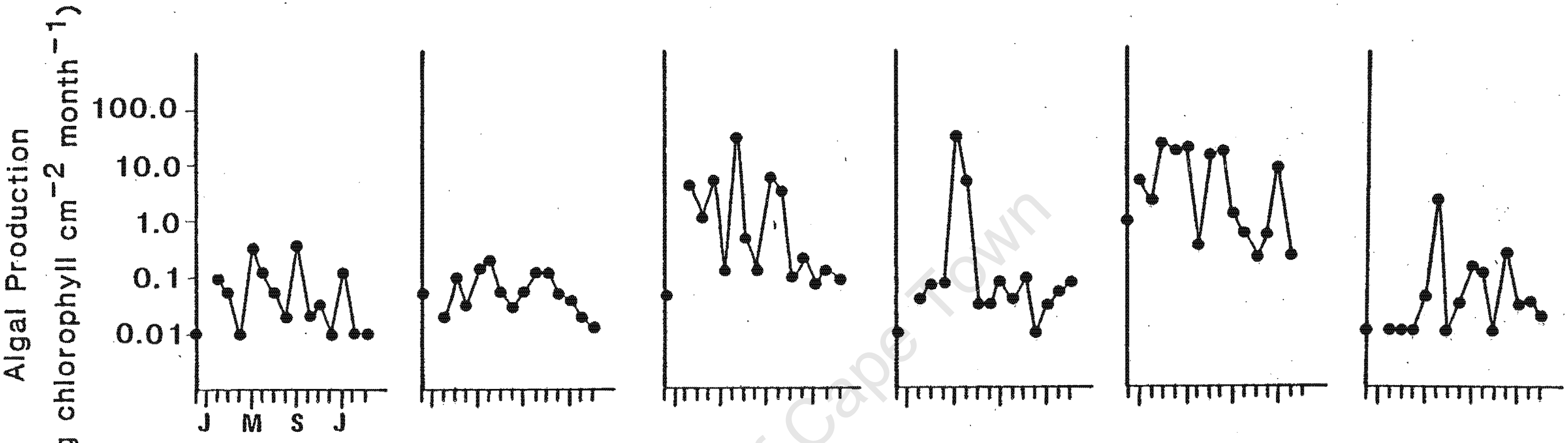
Results

Algal production

Although the measurement of algal production rate in this experiment is based on the use of pseudoreplicates, and the use of inferential statistics is thus inappropriate, the settlement and growth of intertidal macro-algae on the artificial surfaces is not similar at all sites. Production rate is particularly rapid at the 45° and Marcus 0° sites and is slowest at the 80° and Columbine 0° sites (Fig. 3.9 and Appendix 1).

Limpet growth

The predicted monthly increment of a 30 mm limpet at each site is linearly related to the mean algal production measured during that month at that site: shell increment = 0.09 (algal production) + 1.42 ($n = 78$, $r^2 = 0.11$, $P < 0.01$). Since the measurement of algal production rate was based on pseudoreplicated samples, the results of this analysis are of little predictive value, although the relationship is also evident using multiple linear regression analysis which shows a significant positive co-efficient for the independent variable algal production (d.f. = 76, $t = 2.78$, $P < 0.01$ - Table 3.9). In this analysis monthly limpet growth rate is slowest at the 80° (co-efficient = 0.00), 60° and Columbine 0° sites and is significantly faster at the 45°, 20° and Marcus 0° sites. Limpets at the 20° site show the most rapid growth (Table 3.9). Limpet growth rates measured (rather than predicted)



SITE	80°	60°	45°	20°	0° MARCUS	0° COLUMBINE
$\bar{x}$	0.09	0.09	2.89	2.49	6.83	0.16
SD	0.16	0.20	5.86	8.76	8.96	0.62

Fig. 3.9. Monthly mean algal production (ug chlorophyll cm^{-2} month^{-1}) on settlement strips (*n* = 4 for each month) at intertidal study sites (see Appendix 1 for standard deviations)

Table 3.9. Estimated co-efficients, standard errors and significance levels resulting from the multiple linear regression analysis of limpet growth rate at 6 intertidal study sites at Marcus Island and Cape Columbine

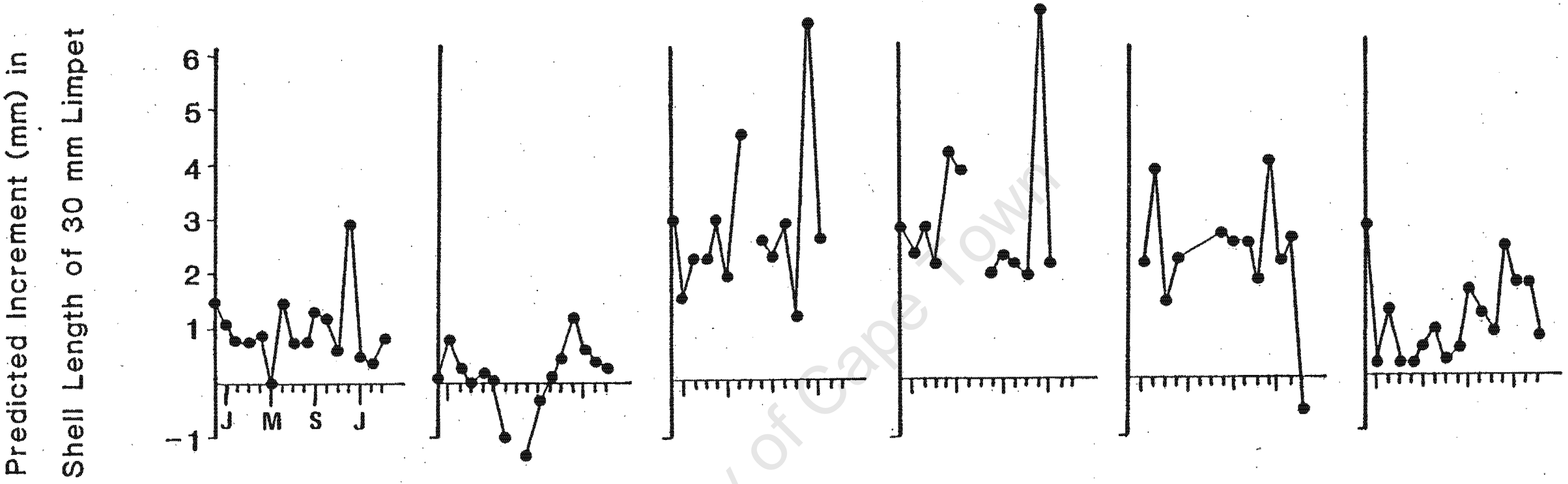
VARIABLE	CO-EFFICIENT	S.E.	*t*	*P* (2-tailed)
Constant	1.49	0.38	3.92	<0.001
SITES				
Marcus Island 60°	-0.94	0.28	-3.33	<0.002
Marcus Island 45°	1.60	0.30	5.28	<0.001
Marcus Island 20°	1.70	0.31	5.48	<0.001
Marcus Island 0°	0.91	0.33	2.75	<0.01
Cape Columbine 0°	0.09	0.27	0.33	
MONTHS				
February	-0.28	0.46	-0.61	
March	-0.96	0.46	-2.11	<0.05
April	-0.56	0.46	-1.22	
May	-1.08	0.49	-2.20	<0.05
June	-0.56	0.52	-1.08	
July	-0.99	0.64	-1.55	
August	-0.98	0.46	-2.14	<0.05
September	-0.65	0.46	-1.42	
October	-0.46	0.46	-1.01	
November	-0.94	0.46	-2.06	<0.05
December	1.90	0.46	4.16	<0.001
January	-0.47	0.46	-1.04	
February	-0.37	0.51	-0.71	
March	-1.21	0.51	-2.37	<0.02
ALGAL GROWTH	0.05	0.02	2.78	<0.01

at intertidal study sites show the same patterns (Fig. 3.10). In addition, limpet growth is not the same in all months, the highest rates of growth at all sites being predicted in December 1982 (co-efficient = 0.00) and December 1983, and the lowest in May 1983 and March 1984 (Table 3.9).

The predicted annual increment in length of a 30 mm limpet is greatest at the 45° site where an increment of nearly 20 mm is predicted (Table 3.10). Mean monthly L_∞ values were highest where algal production and limpet growth were fastest (Table 3.10). The mortality rate of labelled limpets was highest at the Marcus level site and lowest at the 80° and 45° sites (Fig. 3.11). Mortality rates at the 80°, 60°, 45° and Columbine level sites are comparable (Fig. 3.11).

Limpet biomass and gonadial production

The relationship between gonadial wet mass and shell length is best described by a power curve. The predicted bi-monthly gonadial wet masses for male and female limpets of 30 mm in length show a peak in June. Contrary to the finding of Branch (1974a), not all gametic material had been shed by August (Fig. 3.12). The biomass of limpets supported at each site is significantly correlated with the logarithm of mean algal production ($n = 6$, $r = 0.92$, $P < 0.01$).



SITE	80°	60°	45°	20°	0° MARCUS	0° COLUMBINE
$\bar{x}$	1.1	0.2	2.7	2.8	2.5	1.0
SD	0.7	0.7	1.5	1.5	0.8	0.7

Fig. 3.10. Predicted monthly increment in shell length of a 30 mm *P. granularis* at intertidal study sites. (Data omitted where monthly Ford-Walford plots are not statistically significant)

Table 3.10 Parameters (relating to limpet growth and mortality rates) which were used to model cohort reproductive fitness, and the modelled lifetime gametic output of the hypothetical cohort at each study site. Standard deviations are presented except where values represent single measurements or calculations. Asterisks indicate sites where total limpet biomass was measured, i.e. no standard deviation is presented

	80°	60°	45°	20°	0° MARCUS	0° COLUMBINE
Mean monthly algal production (ug chlorophyll cm^{-2})	0.09 ±0.16	0.09 ±0.20	2.89 ±5.86	2.49 ±8.76	6.83 ±8.96	0.16 ±0.62
Limpet biomass (g m^{-2}) supported at site	11.4 *	5.5 *	53.9 *	47.5 *	69.7 ±20.8	42.3 ±14.4
Predicted mean monthly increment (mm) of a 30 mm limpet	1.1 ±0.7	0.2 ±0.7	2.7 ±1.5	2.8 ±1.5	2.5 ±0.8	1.0 ±0.7
Mean predicted L_∞ (mm)	48.4 ±10.3	35.5 ±18.5	58.2 ±8.1	56.7 ±12.3	58.5 ±16.3	45.6 ±6.5
Monthly % mortality	6	8	6	10	27	7
Cohort survival (years)	13	9	13	7	3	10
Total gametic material released by cohort (g)	2629	298	12810	4465	86	1168
Gametic material released (g m^{-2})	77.6	16.5	446.5	199.5	57.8	187.4
Gametic material released per m^2 per year of cohort survival (g m^{-2} $year^{-1}$)	6.0	1.8	34.3	28.5	19.3	18.7

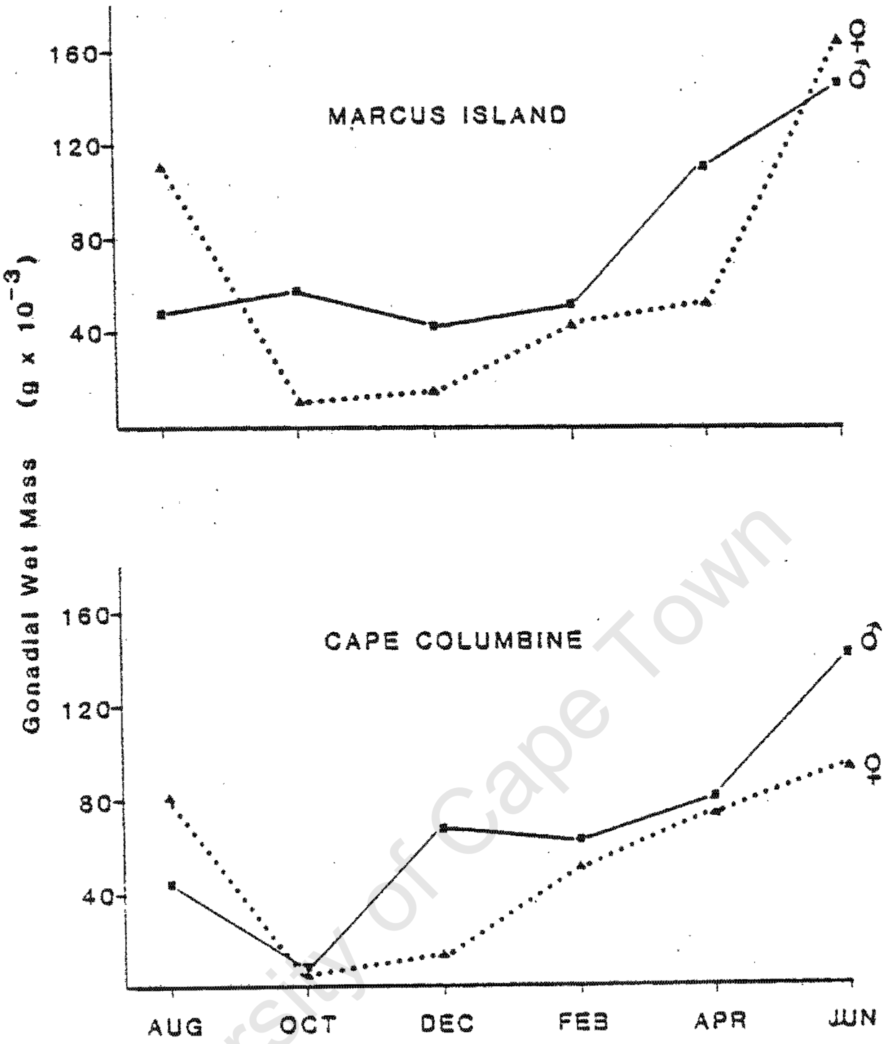


Fig. 3.12. Predicted bi-monthly gonadial masses in 30 mm male and female *P. granularis* at 2 sites on the west coast of South Africa. Calculations were made from bi-monthly measurements of shell length and gonadial mass at each site

Model

Cohort survival time, calculated from monthly mortality rates, ranges from 3 years at the Marcus level site to 13 years at the 80° and 45° sites (Table 3.10). The predicted wet mass of gametic material released over the life-time of each cohort ranges more than 2 orders of magnitude between the least productive (Marcus 0°) and the most productive (45°) sites, but when corrections are made for the area occupied by the cohort at the time of spawning, and the life-time of the cohort, the predicted release of gametic material (g m^{-2} $year^{-1}$) is more comparable. Cohorts occupying the steeper slopes produce least gametic material (Table 3.10), and the cohort at the Marcus level site (although the site has the most rapid rate of algal production and supports a larger biomass of limpets than any other site) was predicted to release an amount of gametic material comparable with that of the Columbine level cohort. The most productive cohort was that at the 45° site where limpets experienced the lowest rate of mortality, and had a high growth rate.

Discussion

Allusions are commonly made to the 'large genetic variability' and 'plastic biology' of intertidal invertebrate species that have a dispersive larval stage (Scheltema 1971, 1975; Crisp 1974a, b; Fletcher 1984b; Grahame and Branch 1985). These attributes apparently aid the survival of larvae that cannot select the exact position of their settlement. They are also thought to be manifest in populations of adults which live in a range of microhabitats within the intertidal region, and are subject to differing biotic and abiotic influences. Since life-history patterns are strongly linked to fitness, and are under selective pressure (Grahame and Branch 1985), research on populations of invertebrate species has raised the question of whether genetically determined intra-specific differences in life-history patterns exist (Stearns 1980), or whether observed differences are due primarily to environmental factors (Sutherland 1970; Bertness 1981). In some instances inter-specific differences in life-history patterns have been assumed to be 'strategies' without full exploration of the range of intra-specific variation which might swamp any inter-specific comparisons (Fletcher 1984a).

Algal production

In the present study the primary differences between sites are environmental, being the nutrient status of intertdial waters and the slope of the rocky substratum. Both these factors influence the rate of primary production. Differences between nutrient availability at Cape Columbine and Marcus Island, due to guano run-off from seabird colonies on Marcus Island, have been shown to influence the rate of primary production at these sites (Part 2). This is also evident from results presented in this study, which show that algal production at Cape Columbine is low when compared with production at the Marcus Island 0° site, despite the similarity in substratum slope between the 2 sites.

However, when sites are comparable in terms of intertidal nutrient status (as is the case with the Marcus Island sites), substratum slope becomes an important factor influencing the rate of primary production. Excluding the low-nutrient site (viz Columbine 0°), the rate of algal production is slowest at the sites with steeper slopes, where the forces of drag experienced by organisms as waves wash over them, are augmented by forces of pressure as waves crash against the rock face (Jones and Demetropoulos 1968; Denny et al. 1985). In addition to experiencing increased mechanical stress, algae on steep slopes may receive less incident light. The rate of algal production increases as the slope of the study site decreases, with the exception of the 20° site which, by virtue of its position, may have been submerged for a shorter period each tidal cycle than the other sites. Mean rates of algal production measured at all sites, except the Marcus level site, are comparable with measurements made by Underwood (1984b) in the mid-shore region of a rocky shore in New South Wales, Australia. Production rate at the Marcus level site is double the maxium recorded by Underwood (op. cit.)

Limpet growth

Patella granularis is a generalist forager and consumes any available micro-algae, algal sporelings and prostrate or creeping algae (Branch 1971). In this study *P. granularis* growth rate is related to the rate of algal production (see also Part 3.1), indicating that algal production is an index of food availability. Limpet growth is fastest at the sites which have the most rapid rates of algal production, viz the 45°, 20° and Marcus 0° sites. However, it appears that, at the 45° and 20° sites, limpet growth rates are near the maximum possible, since the enhanced rate of algal production at the Marcus 0° site is not associated with a concommitant increase in limpet growth rate. This indicates perhaps that the relationship between the rates of algal production and limpet growth ultimately is logarithmic (there being a maximum rate at which limpets can forage in the time available during a tidal cycle), although for the range of algal production rates considered in this study the relationship is better described by a linear curve.

Limpet mortality

African Black Oystercatchers are common on the shores of Marcus Island and they are important predators of *P. granularis* (Hockey and Underhill 1984; Part 3.2). They are estimated to remove 2.8 million limpets annually from the shores of Jutten Island, a slightly larger seabird-breeding island (with a coastline of 2.5 km) in Saldanha Bay (Hockey and Branch 1984). Limpets at the 20° and Marcus 0° sites are more accessible to oystercatchers than limpets occupying steeper substrata (Hockey and Branch op. cit.), and would thus be expected to have higher rates of mortality. However, even the rate of mortality measured at the Marcus Island site does not compare with that reported for *Patella* *vulgata* L. preyed upon by European Oystercatchers (*Haematopus ostralegus* L.) (Lewis and Bowman 1975), viz 90% month^{-1}. Mortality rates of limpets are much lower at the 80°, 60° and 45° sites, where limpets are less accessible to oystercatchers, and at the Columbine site where oystercatchers occur only at low densities (3.6 birds per km coast - Hockey 1983).

Limpet gonadial production

Since the quantity of gonadial material produced annually by a limpet is size-dependent, limpets with fast growth rates and high longevity would be expected to produce most gametes during their life-time. The parameters of growth and mortality at the 45° site exemplify this situation, and the modelled gametic output of a hypothetical cohort of limpets at this site is greater, in absolute terms and in terms of g m^{-2} year^{-1}, than at any other site. The 45° angle is not too steep to inhibit algal production, but is steep enough to prevent oystercatchers from foraging. Although the rate of algal production is faster at the Marcus 0° site than at the 45° site, annual limpet mortality at the Marcus site is 98% (cf. 51% at the 45° site) and so few individuals survive to reproduce that the modelled cohort gametic output (g m^{-2} year^{-1}) is comparable with that at Cape Columbine (Table 3.10).

There are certain refinements that must be made to this model, should future applications require accurate estimates of absolute, rather than relative, quantities of gametic material released. In this study, populations of *P. granularis* had not necessarily released all gametic material by July (as found by Branch 1974a), and mortality during the additional time taken to spawn would affect the amount of gametic material released. It is likely that small, newly-settled limpets experience much higher rates of mortality than do established adults, and in addition, limpets which grow to more than 50 mm in length subsequently have a refuge in size from predation by oystercatchers (Hockey and Underhill 1984; Part 3.2). Allowance must also be made for possible differences in sex ratios between study sites. However, even with these limitations, the present model allows an overview of the relative life-time gametic output of limpet cohorts.

Two important factors emerge from these results of modelled life-time gametic output at different sites. First, the observed differences in life-history parameters of populations of *P. granularis* are attributable largely to differences in food supply at the various sites. It is possible that genetic variation exists between *P. granularis* populations (Part 3.1), but the effect of this is small in comparison with the influence of local differences in the rate of primary production. One is forced to be cautious about existing evidence of intra-specific differences in limpet life-history patterns derived from studies in which food availability has not been measured (e.g. Giesel 1969). Stearns (1980) questions the existence of intra-specific life-history 'tactics' at all, and shows that within certain families of reptiles and mammals patterns of co-variation in life-history patterns are strongly influenced by adult size (Stearns 1984). What has been interpreted as variation in life-history 'strategies' in many limpet species could be simply a reflection of differing food supplies for populations which consequently show different growth rates, sizes at first reproduction and thus, gametic output. Such a situation has been demonstrated clearly by Moran et al. (1984) for predatory intertidal whelks feeding on a variety of prey species.

Secondly, it is clear that, although the chance settlement of a limpet on a steeply sloping rock-face renders it inaccessible to avian predators, its slow growth, small size and consequent small annual production of gametic material are not compensated by enhanced survival. At the other extreme, in areas with very high rates of algal production, enhanced limpet growth rate, larger size and gonadial release do not outweigh the effects of a high mortality rate. I hypothesize that the low production and reproduction rates of limpets at Cape Columbine could not support (in the long term) the intense predatory pressure that is associated with high densities of oystercatchers. Considering that hypothetical cohorts of limpets at the Marcus and Columbine level sites produce comparable mean annual quantities of gonadial material (when corrected for the area occupied by the cohort), it is possible that the persistence of *P. granularis*, and thus of oystercatchers, on Marcus Island as a whole, is dependent upon the supply of gametes and settling larvae from reproductively fitter segments of the population of *P. granularis* in productive areas of the Island which are inaccessible to predators.

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Appendix 1. Mean (± S.D.) monthly algal production (ug chlorophyll cm^{-2} month^{-1}) at intertidal study sites in the Saldanha Bay area. Means are from monthly algal production on 4 replicate settlement strips

SITE	80°		60°		45°		20°		MARCUS 0°		COLUMBINE 0°	
December	0.00	(0.00)	0.06	(0.06)	0.05	(0.04)	0.00	(0.00)	0.90	(0.52)	0.00	(0.00)
January 83												
February	0.10	(0.08)	0.02	(0.01)	4.34	(2.12)	0.04	(0.02)	4.32	(1.81)	0.01	(0.01)
March	0.06	(0.03)	0.09	(0.14)	1.11	(0.28)	0.07	(0.05)	2.16	(1.74)	0.01	(0.00)
April	0.01	(0.02)	0.03	(0.02)	5.81	(3.11)	0.08	(0.02)	23.43	(13.57)	0.00	(0.00)
May	0.33	(0.12)	0.15	(0.08)	0.14	(0.04)	32.67	(13.43)	17.48	(7.59)	0.04	(0.03)
June	0.12	(0.06)	0.19	(0.12)	20.91	(10.21)	4.10	(2.60)	18.79	(3.75)	1.86	(1.76)
July	0.06	(0.03)	0.05	(0.03)	0.61	(0.15)	0.03	(0.03)	0.33	(0.06)	0.01	(0.01)
August	0.02	(0.01)	0.03	(0.02)	0.11	(0.06)	0.03	(0.01)	10.14	(9.05)	0.03	(0.02)
September	0.38	(0.20)	0.60	(0.75)	5.18	(2.44)	0.08	(0.02)	12.45	(4.61)	0.15	(0.15)
October	0.02	(0.02)	0.13	(0.16)	3.48	(2.34)	0.04	(0.03)	1.24	(0.35)	0.11	(0.07)
November	0.03	(0.04)	0.12	(0.14)	0.09	(0.02)	0.09	(0.03)	0.65	(0.14)	0.01	(0.02)
December	0.00	(0.00)	0.03	(0.02)	0.23	(0.34)	0.00	(0.00)	0.23	(0.14)	0.02	(0.01)
January 84	0.12	(0.05)	0.06	(0.03)	0.07	(0.07)	0.03	(0.02)	0.69	(0.95)	0.03	(0.01)
February	0.01	(0.00)	0.03	(0.01)	1.12	(1.44)	0.06	(0.04)	8.21	(5.04)	0.04	(0.02)
March	0.01	(0.01)	0.02	(0.01)	0.09	(0.07)	0.07	(0.03)	0.22	(0.12)	0.02	(0.01)

PART 4

THE DYNAMICS OF ALGAL MATS

Section (1): The creation and persistence of algal mats on rocky shores: consequences of nutrient enrichment by seabirds and predation by shorebirds

Summary. The rocky shores of islands in Saldanha Bay, South Africa, are characterized by the presence of extensive, permanent mats of foliose algae. In the high-shore region algal cover reaches 100% in some months of the year. The dominant herbivore, *Patella granularis*, is most abundant in the low-shore region, where physical conditions are relatively benign. Limpet activity is concentrated in the low- and mid-shore regions, where grazing keeps the percentage algal cover low, despite the enhanced rate of algal production in these regions. High-shore algal mats remain ungrazed, although limpets caged in the algal mat habitat survive and grow, and denude the substratum of foliose algae as a consequence of their presence.

The origin and persistence of high-shore algal mats are attributed primarily to the presence of seabirds which breed on the islands. Their guano, when dissolved, enriches the intertidal waters with nutrients and stimulates the rate of primary production such that algae rapidly become foliose and thus immune to grazing by *P. granularis*. In addition, African Black Oystercatchers prey upon *P. granularis* and the consequent reduction in limpet density and in herbivore

activity may enable more algae to reach the foliose stage. On adjacent mainland shores, where intertidal waters are not enriched with nutrients from guano, and oystercatchers are uncommon, foliose algae seldom develop.

Introduction

The distribution of algae on rocky shores is determined largely by the interaction between the rate of primary production and the rate of removal of algae, usually by herbivores (Lubchenco and Gaines 1981). Grazing by herbivores may affect the abundance, distribution and species composition of algae growing on rocky shores (Paine and Vadas 1969; Dayton 1975; Sousa 1979; Lubchenco and Cubit 1980; Jara and Moreno 1984; Underwood and Jernakoff 1984). The foraging activity of limpets has been shown to limit the upward spread of algae on the shore (Underwood 1980) and to render areas of rocky shore completely devoid of foliose algae (Underwood and Jernakoff 1984). However, herbivores are involved in other processes operative in the intertidal community: they compete for space and food with conspecifics and with individuals of other species, and are preyed upon by predators. Changes in the nature of these interactions will have repercussions for herbivore population dynamics and might be expected to enhance or limit the impact of herbivores in modifying algal species composition, distribution and abundance. For example, algae on the rocky shores in New England compete with mussels for settlement space, and algal abundance and distribution reflect the activity of mussel predators. Algae are abundant where predatory pressure on mussels is intense (Menge 1976; Lubchenco 1980; Lubchenco and Menge 1978).

The rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, support large numbers of African Black Oystercatchers *Haematopus moquini* Bonaparte. Densities range between 25 and 78 birds per km coast on these islands, and are among the highest recorded (Hockey 1983). Oystercatchers prey on intertidal limpets, among them *Patella granularis* L. (Hockey and Underhill 1984), which is the dominant intertidal herbivore in this region (Stephenson and Stephenson 1972). *Patella granularis* is a generalist grazer, foraging mainly on algal spores and sporelings (Branch 1971), and the removal of large numbers of *P. granularis* (Hockey and Underhill op. cit.) probably results in a reduction in the intensity of herbivory.

In addition, the rate of algal production on island shores is enhanced by the presence, in intertidal waters, of nutrients from the dissolved guano of seabirds (Part 2). Underwood and Jernakoff (1984) state that the impact of grazing by intertidal herbivores is likely to be more severe where environmental conditions which influence the rate of primary production are harsh. Any environmental factor which modifies the rate of algal growth such that sporelings become foliose more rapidly and thus escape herbivory, will reduce the impact of grazers in modifying algal abundance and distribuion (Underwood and Jernakoff op. cit.). Thus algae on island shores not only are subject to reduced herbivory as a consequence of predation by oystercatchers, but also rapidly become immune to herbivory due to the presence of seabirds and their excrement. Extensive, permanent mats of algae (predominantly *Enteromorpha* sp.and *Porphyra capensis* Kutz) occur on island shores, whereas on nearby mainland shores, which are not enriched with nutrients and support few shorebirds, foliose algae are uncommon.

In this study the relationships between algal cover, shore-level and *P. granularis* densities on island and mainland shores are investigated. Limpets are translocated to areas in dense algal mats to establish their ability to survive in this habitat, and their growth rates and impact on the algae are recorded.

Methods and materials

Study sites

Intertidal sites on the rocky shores of Malgas, Jutten and Marcus Islands in Saldanha Bay (Fig. 1.1) were visited monthly for 13 (in some cases 14) months. Similarly the shores of nearby mainland sites at Mauritz Bay and Cape Columbine (Fig. 1.1) were visited, and at each site the density of *P. granularis* and the percentage foliose algal cover in 1 m^2 quadrats in a single fixed transect down the shore were recorded. Percentage algal cover was assessed visually, using 0.5 m^2 quadrats with 0.05 m^2 gradations affixed within the quadrats. Transects varied in length between sites, but in all cases the area between the low-shore mussel bed and the upper limit of the occurrence of foliose algae was surveyed. Data on limpet and algal abundances were subjected to a contouring program (SGP - Diedricks 1979) which fits a surface to the data, using a least squares polynomial analysis. Visual representation is thus in 3 dimensions.

Cage experiment

In May 1984 a galvanized steel cage measuring 1.0 x 1.0 m was positioned in a mat of foliose algae in the high-shore region on Marcus Island. The roof and walls of the cage were of galvanized steel mesh (2 x 2 cm) and the cage stood 10 cm above the surface of the substratum. The legs of the cage were inserted into holes drilled 30 cm into the granite. Four separate compartments (each 0.5 x 0.5 m) were constructed within the cage and access to each compartment was possible through a small, moveable door in the roof of the cage.

The 4 compartments (A, B, C and D) were stocked with 11 *P. granularis* each, representing limpet biomasses of 24.9, 19.9, 18.1 and 17.6 g respectively, calculated using the equation: *P. granularis* dry somatic and gonadial mass = $(1.9 \times 10^{-6})(\text{length})^{3.5}$, with $n = 100$, $r^2 = 0.98$, $P < 0.001$. In compartments A and B, small patches in the algal mat were scraped clean to enable limpets to attach to the substratum. Before the limpets were introduced into compartments C and D, the substratum was scraped clean of all foliose algae and then burned with a blow-torch to remove remaining spores and sporelings. During the following 10 weeks the limpets were counted and measured and the percentage algal cover in each compartment was assessed. After 6 weeks all limpets were labelled individually using punched plastic tape and rapidly setting glue, and the increment in length of individual limpets was monitored during the following month. The growth rates of limpets in compartments A and B combined, and in compartments C and D combined, were calculated by regressing the length of each limpet at the end of the month on its initial length (Ford-Walford plot) (Balaparameswara Rao 1976; Branch 1981).

In a second experiment, commencing in July 1984, compartments C and D were cleared and burned, and restocked with labelled limpets. In compartment C, 8 limpets, representing a dry biomass of 14.1 g, were introduced, whereas in compartment D, 5 limpets were introduced, representing a dry biomass of 4.0 g. Limpets were counted and measured during the following 10 weeks, and the percentage algal cover in each compartment was assessed. Ford-Walford plots were calculated for limpets in each compartment separately, but the relationships were not statistically significant and thus limpet growth rate could not be calculated.

MAINLAND SA.

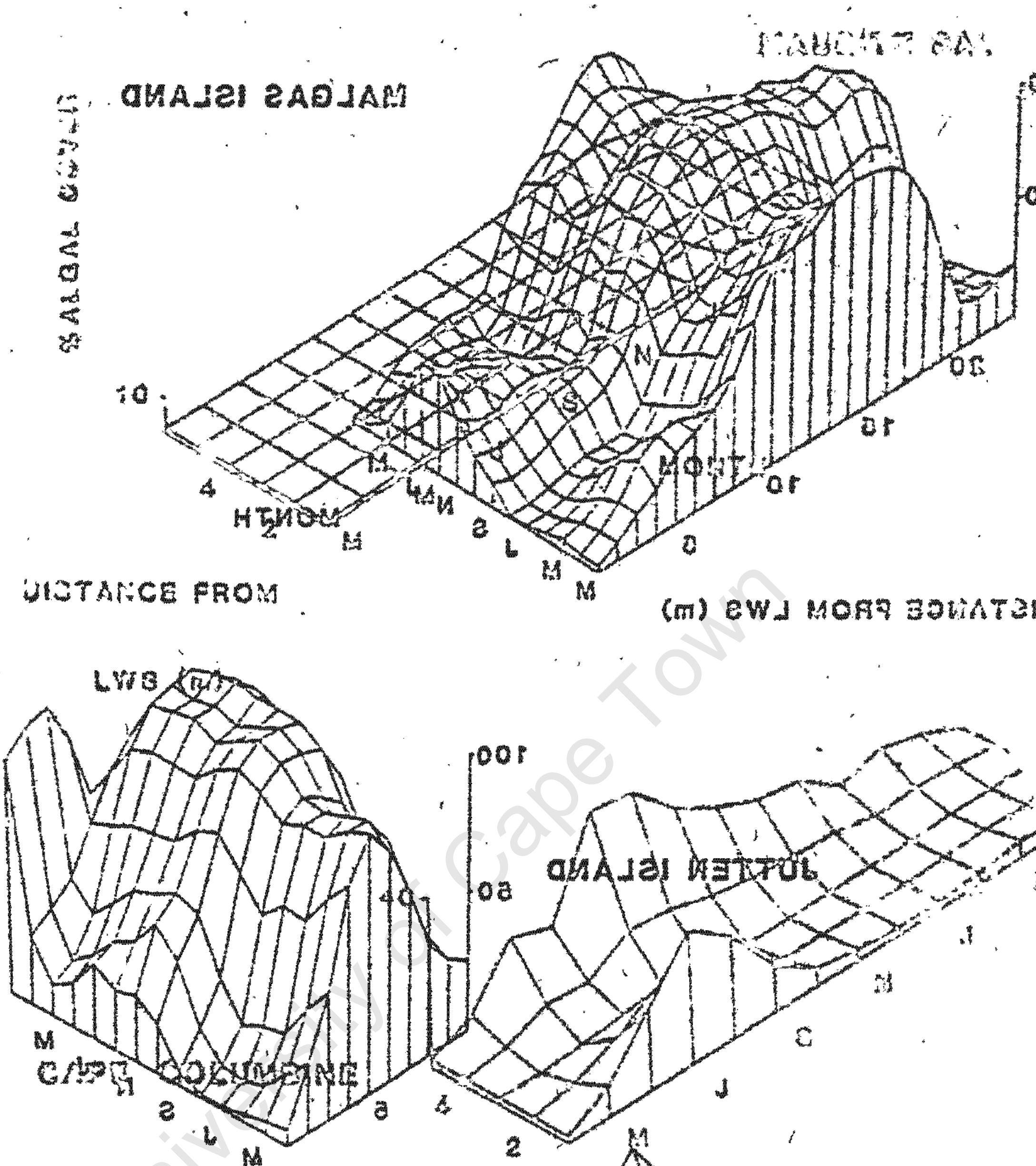
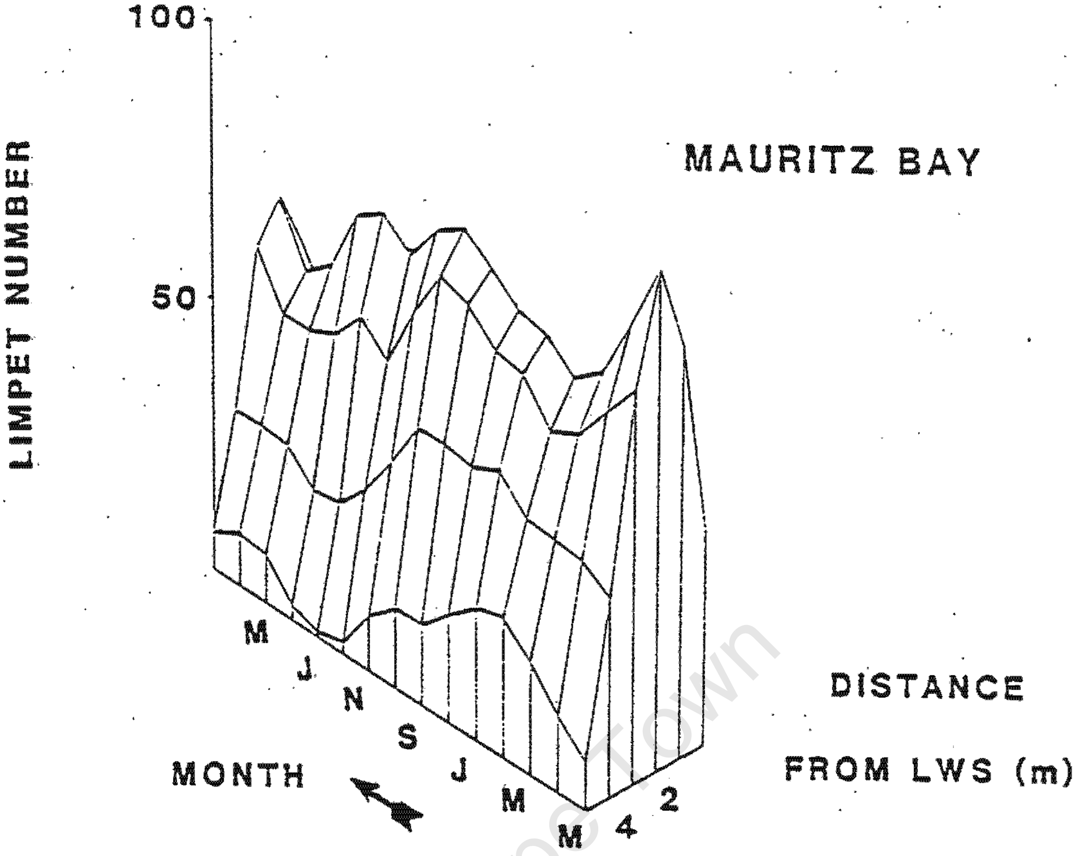


Fig 4.2. Extent of algal cover in 1 m² quadrats in fixed (1 m wide) transects on the shores at mainland sites north of Saldanha Bay. Figures are drawn as if viewed from the low-shore region



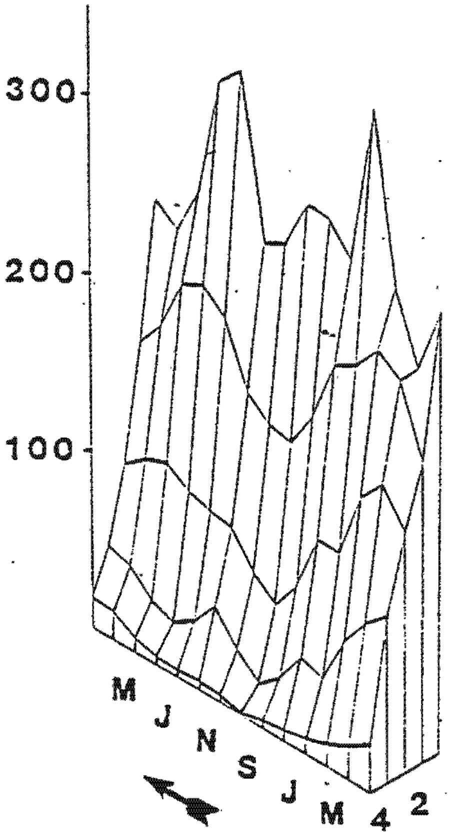


Fig 4.4. Numbers of limpets in 1 m^2 quadrats in fixed (1 m wide) transects on the shores of mainland sites north of Saldanha Bay. Figures are drawn as if viewed from the high-shore region

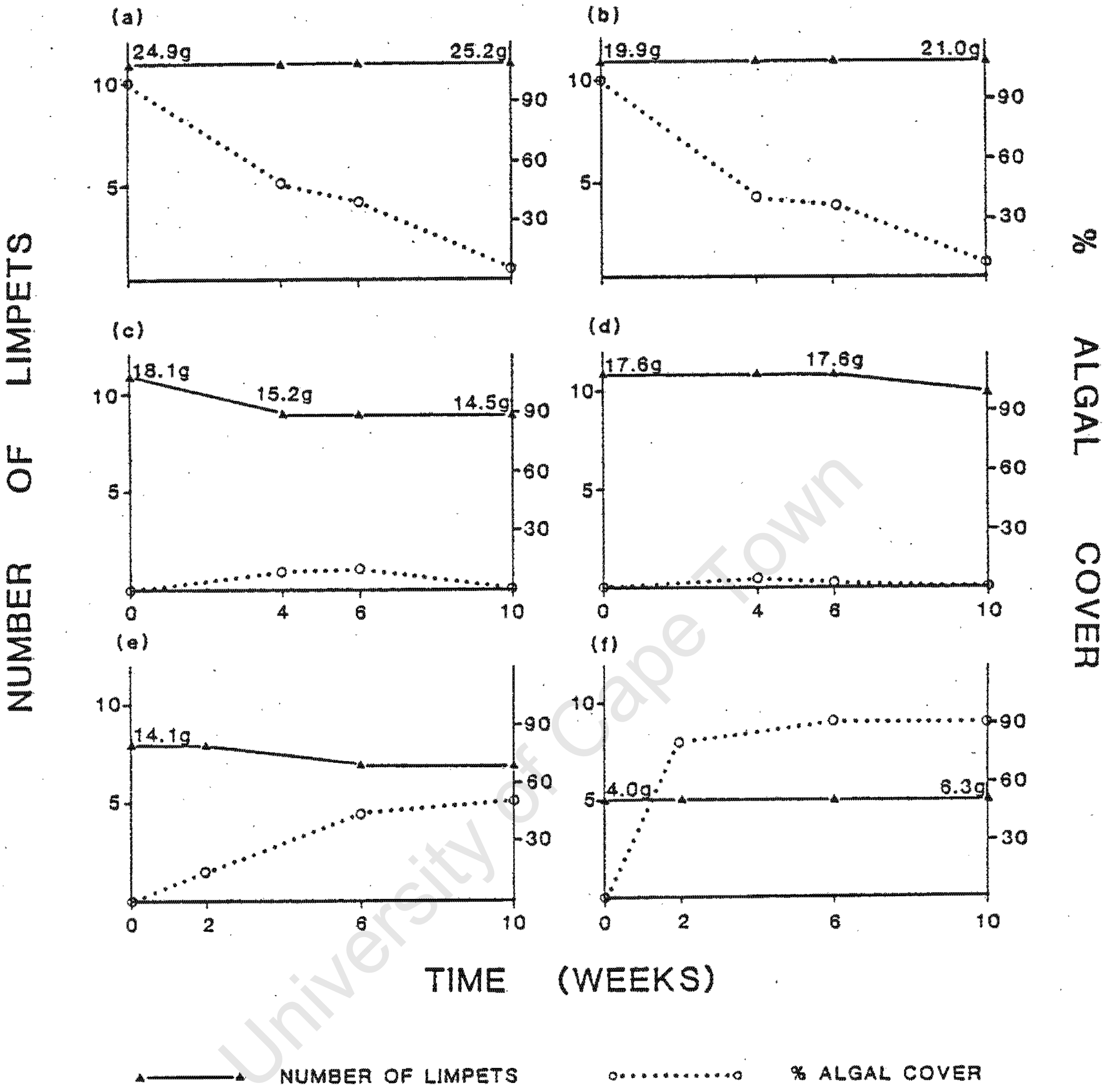


Fig 4.5. Limpet number, biomass and % algal cover in the compartments of a cage placed in a high-shore algal mat on Marcus Island. In figures (a) and (b) the substratum was not cleared of foliose algae before limpets were introduced, whereas in figures (c) and (d) the substratum was scraped and burned clean. These 4 experiments ran between early May and mid-July. In figures (e) and (f) the substratum was again cleared before the introduction of limpets, and these experiments ran between late July and early October.

$$\text{length}_{t+1} = 0.94\,(\text{length}_t) + 3.08$$

with $n = 18$, $r^2 = 0.92$, $P < 0.001$. In this instance a limpet of 30.0 mm is predicted to grow to 31.3 mm in length during the 4-week period, but any individual with an initial length of more than 51 mm is predicted to show negative growth. The development of foliose algae in these two compartments is severely restricted by the activity of the limpets, although a small amount does develop, particularly where two of the limpets initially introduced are subsequently lost.

In the second cage experiment, where lower biomasses of limpets are introduced into compartments, foliose algae develop rapidly (Figs 4.5e and f). In the compartment where 4.0 g (dry mass) of limpets are introduced, algal cover reaches 80% in 2 weeks. Algal cover is not as extensive in the other compartment, where a larger biomass of limpets is present.

Discussion

The ability of intertidal herbivores to influence the abundance and distribution of foliose algae has been demonstrated in many parts of the world, by the experimental removal of limpets. In the absence of herbivores dense settlements of algae develop where previously none had been visible (Lodge 1948; Hay 1979; Underwood 1980; Jernakoff 1983; Cubit 1984; Jara and Moreno 1984; Branch 1985a).

However, the impact of herbivores in modifying algal distribution and abundance may be tempered by the influence both of physical and biological factors (Connell 1972; Underwood 1979; Lubchenco 1980). Physical factors (e.g. temperature and desiccation stresses) act not only on the survival potential of the herbivores, but also on the potential for algal production and growth (Underwood and Jernakoff 1984). Where physical stresses cause slow algal production rates, the impact of grazing by herbivores may be heightened.

In many instances vertebrate predators have been shown to modify the demography and population dynamics of intertidal herbivores (Giesel 1970; Cook 1981; Hartwick 1981; Parry 1982b, Part 3.2), but in few cases have the consequences for algal abundance and distribution been investigated. Frank (1982) and Branch (1985b) suggest that the distribution of algae in intertidal regions is a result of the removal of limpets by avian predators, but no data are presented on algal abundances to substantiate their conclusions.

The role of physical factors

On the shores of seabird-breeding islands in Saldanha Bay limpet activity is concentrated in the low- and mid-shore regions of the intertidal zone. Limpet densities are highest just above the low-tide level, where environmental conditions are most benign (Underwood and Jernakoff 1984). In this region the effect of grazing is striking, algal cover being almost eliminated in places, while dense mats of foliose algae in the high-shore region remain ungrazed. Environmental stresses are most severe in the high-shore region and the risks of desiccation and exposure to high temperatures may make this region unsuitable for colonization by *P. granularis*. In this study limpets were caged in this region during late autumn and winter, and were not subjected to high temperatures.

Physical conditions prevalent in the high-shore region on islands also affect algal survival and growth. Although foliose algae are common, the rate of algal production is lower in this region than elsewhere on the shore (Castenholz 1961; Nicotri 1977; Jernakoff 1983; Underwood 1984; Part 2). Consequently the rate of food replacement, deemed important for the survival of herbivores (Underwood 1978; Part 3.1), is low in comparison with rates in the mid- and low-shore regions.

Unlike *Cellana tramoserica* (Sowerby), which starves when translocated into low-shore algal beds (Underwood and Jernakoff 1981), *P. granularis* is able to survive and grow in the algal beds on island shores. However, since the diet of *P. granularis* consists mainly of the spores and sporelings of prostrate and creeping algae (Branch 1971), it is unlikely that foliose algae are grazed when limpets are introduced experimentally into algal mats. The thalli of foliose algae may be severed from the substratum by the edge of a limpet's shell as the limpet moves about foraging, or by the limpet's grazing the base of the holdfast.

Whether or not *P. granularis* derives food from foliose algae, it remains that within a short time (10 weeks) limpets introduced into high-shore algal mats denude the substratum of foliose algae. Thereafter their nutritional requirements must be met by the macro-algal spores and sporelings, which have a slow rate of production (Part 2). It is possible that limpets might starve under these conditions. Parry (1978, 1982b) attributes the summer mortality of *Cellana tramoserica* and *Patelloida alticostata* (Angas) caged in different intertidal regions to starvation, and in the present study limpets introduced into the high-shore region in areas scraped and burned clean of algae suffered mortality. In addition, those remaining did not grow, possibly indicating a shortage of food (Parry 1982a, b; Part 3.1).

Limpets, in conjunction with the physical demands of the environment, modify the distribution of algae on island shores. Their activity is concentrated in certain shore regions only, and algal cover in these regions is severely reduced, despite the enhanced rates of algal production (Part 2). In the high-shore region limpets are absent or rare, but are able to survive and forage at this level, albeit for short periods only.

The role of biological factors - nutrient enrichment

Although the distribution of limpets on island and mainland shores is similar, foliose algae seldom develop on mainland shores. The combination of biotic and abiotic factors prevalent on mainland shores does not allow algae to reach the foliose stage. Since the density and biomass of limpets at island and mainland sites are similar (Figs 4.3 and 4.4; Part 3.1), it is likely that differences in the rate of algal production between sites lead to the observed differences in algal distribution.

Any factor that modifies the rate of survival and growth of algal sporelings so that they become foliose and thus escape herbivory may affect the impact of grazing by limpets (Underwood and Jernakoff 1984). On island shores the intertidal waters are enriched with nutrients from the dissolved guano of seabirds (Part 1). The rate of algal production is more rapid on these shores as a result of increased nutrient availability (Part 2), and thus foliose algae develop. On unenriched, mainland shores algal growth is slow and algae are consumed as fast as they settle; they seldom escape herbivory for long enough to become foliose.

Predation by oystercatchers

Although the removal of limpets by oystercatchers on the shores of seabird-breeding islands in Saldanha Bay was not quantified during this study, Hockey and Branch (1984) estimate that oystercatchers remove 2.8 million limpets from the shores of Jutten Island each year (1.1 million per km of shore), and Frank (1982) recorded a mean consumption rate of 0.35 limpets per oystercatcher per minute in foraging flocks of *Haematopus bachmani* Audubon on rocky shores in Oregon, USA. The densities of limpets on island and mainland shores in the Saldanha Bay area are similar, despite the enhanced rate of algal production on island shores. In addition it is unusual, particularly in intertidal systems, to find a source of primary production (such as high-shore algal mats) which is not utilized by herbivores able to survive, at least temporarily, in the habitat.

Patella granularis usually is active at night (Branch 1971) and its mobility would enable short feeding forays into the high-shore region when conditions were favourable. The persistence of the high-shore algal mats may indicate that the removal by oystercatchers of limpets from island shores results in the decrease of limpet biomass below the potential carrying capacity of the shore. Reduction in herbivory, in addition to the enrichment of intertidal waters with nutrients from seabird guano, may result in the escape of many algae from grazing, and the development of mats of foliose algae. This same response is apparent when limpet biomass is manipulated experimentally in compartments of the cage on Marcus Island. Where the biomass of limpets introduced is low, extensive foliose algal cover becomes established within a few weeks (Figs 4.5e and f). Similar results were observed by Hartnoll and Hawkins (1985) when they stocked intertidal cages with *Patella vulgata* L. at one-third of the normal density. In the presence of reduced herbivory a canopy of fucoid algae, covering 85% of the rocky substratum, became established in 4 months (Hartnoll and Hawkins op. cit.).

Algal mats - foraging habitat for small waders

Small waders (Charadrii), many of them migratory, occur in unusually high densities on the shores of islands in Saldanha Bay. On the shores of Marcus Island the small waders forage actively in the high-shore algal mats (Ryan 1983) - a habitat which has been created as a result of the activities both of African Black Oystercatchers and of seabirds which breed and deposit guano on the islands but which are otherwise in no way involved in the functioning of the intertidal community.

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Section (2): The impact of predation by small shorebirds on the species composition and abundance of rocky intertidal prey

Summary. Small shorebirds (Charadrii), which forage on the shores of Marcus Island, southwestern Cape, South Africa, were excluded from a region of high-shore algal mat by means of a cage. Samples of algal mat were removed from within the cage and from an adjacent control area both when shorebirds were present and after most individuals had departed on migration. Analysis of invertebrate densities inside and outside the cage showed that prey numbers were reduced outside the cage when shorebirds were present. Prey densities were most severely affected during the period just prior to migration, when predatory pressure is most intense and, after the departure of the birds, prey densities outside the cage increased. Shorebirds also influenced the species composition of the intertidal fauna by removing mussels and preventing the establishment of mussel beds and their associated biota. It is hypothesized that predation by shorebirds on Marcus Island affects not only the density and species composition of intertidal invertebrates, but also the natural succession of biotic assemblages on the rocky shore. It is proposed that predation by shorebirds contributes to the maintenance of the algal mat habitat.

Introduction

The impact of birds as predators of intertidal invertebrates has received attention recently, in association both with commercial interests (Davidson 1967; Norton-Griffiths 1967; Horwood and Goss-Custard 1977; Goss-Custard et al. 1980; Hulscher 1982), and with ornithologists' interest in the selective pressures which control the timing of migration (Duffy et al. 1981; Goss-Custard 1981; Schneider and Harrington 1981; Schneider 1985). It has been found that predation by shorebirds may lead to severe prey depletion (Lewis and Bowman 1975; O'Connor and Brown 1977; Evans et al. 1979; Puttick 1980; Quammen 1981; Schneider and Harrington 1981; Frank 1982), although most of these studies have been concerned with foraging in mud- or sand-flat habitat, and not on rocky shores. The role that birds play in the functioning of rocky shore communities has seldom been investigated (Feare and Summers 1985), although the few studies done indicate that small shorebirds in particular, may remove very large numbers of prey and cause local depletion of prey populations (Feare 1966, 1969).

Shorebird assemblages on rocky shores generally are depauperate in terms of numbers and species richness (Recher 1966), the numbers of migrant waders (Charadrii) that utilize rocky shore foraging habitats in no way comparing with the huge flocks that arrive seasonally in sheltered lagoons and estuaries. However, shorebirds are abundant on the islands in Saldanha Bay, South Africa, their densities being comparable on the islands and in the adjacent estuarine and lagoon habitats (Summers 1977). On the shores of Marcus Island in Saldanha Bay (Fig. 1.1) small shorebirds, most of them migratory, forage in the high-shore algal mats, where they obtain prey in the form of polychaetes, chironomid larvae (Diptera), isopods, amphipods and molluscs (Ryan 1983). It is estimated (Ryan op. cit.) that, during the austral summer, the small shorebirds consume 37% of the annual standing stock biomass of invertebrate prey on the shores of Marcus Island.

Reduction of prey density and biomass is only one aspect of an avian predator's potential impact on the rocky intertidal community. The preference of avian predators for certain prey size classes and morphotypes may modify prey population demography and reproductive output (Giesel 1970; Hartwick 1981; Hockey and Branch 1983, 1984; Branch 1985; Part 3.2), and predation on a competitively dominant, space-occupying species may result in the establishment of competitively inferior species and a consequent increase in species diversity. Marsh (1986) found that shorebird predation on mussels prevented the establishment of clumps of mussels on smooth, exposed surfaces in the high-shore region, while clumps in crevices survived. This was interpreted as causing an increase in spatial patchiness.

In this study an exclusion cage is used to prevent the access of small shorebirds to a region of high-shore algal mat on Marcus Island. Samples of algal mat infauna are taken both when the migrant shorebirds are present and after their departure. The invertebrate biomasses present in the cage are compared with those in an adjacent, uncaged area. The implications of shorebird predation on intertidal mussels are discussed.

Methods and materials

Shorebird densities

Small, wading shorebirds (Charadrii) present on the 1.6 km coast of Marcus Island were counted monthly during a low-tide period for 21 months. Mean summer densities of shorebirds were compared with densities recorded during a mid-summer count on the mainland rocky shore between Saldanha Bay and Cape Columbine (33.8 km) (Fig. 1.1) made by Underhill and Cooper (1984).

Impact of shorebird predation on algal mat infauna

In June 1983, 2 adjacent 1 m^2 areas of rocky shore on Marcus Island were cleared completely of foliose algae and intertidal organisms, and then burned with a blowtorch to kill algal spores and sporelings. When the surfaces were cool, the edges were painted with copper-based marine anti-fouling paint to discourage herbivores from entering. Replicate 10 x 10 cm settlement strips of high-intensity polystyrene were glued to the rock using rapidly setting epoxy. One set of strips was then covered with a 1 x 1 m galvanized steel cage which stood 10 cm high and was covered, on the top and sides, with 2 x 2 cm galvanized steel mesh. The rods supporting the cage were embedded in holes drilled 30 cm into the granite substratum. Rolls of wire mesh placed around the bottom edges of the cage prevented grazers from entering through gaps between the cage and the substratum. The adjacent control area was left uncovered.

Within 6 months a thick, even mat of foliose algae had developed over the settlement strips inside and outside the cage. During subsequent months (although not in every month) settlement strips were removed in groups of 4 or 5, without disturbing the cage. The subsample of algal bed was scraped from each strip, and the invertebrate infauna removed and identified. The algae from each strip were dried and ashed in a muffle furnace at 450°C.

Results

Shorebird densities

The species of small shorebirds most commonly recorded on Marcus Island are Turnstones *Arenaria interpres* (L.), Curlew Sandpipers *Calidris ferruginea* (Pallas), Sanderlings *C. alba* (Pallas), Grey Plovers *Pluvialis squatarola* (L.) and Whitefronted Plovers *Charadrius marginatus* Vieillot. All these species except Whitefronted Plovers are migratory, although young birds frequently overwinter in the southern hemisphere. Migratory shorebirds arrive on Marcus Island in

September each year (Fig. 4.6) and depart in March. The mean number (± S.D.) of Turnstones counted (per km of coast) during these months on Marcus Island (*n* = 12) is 63.3 ± 23.4, whereas on the mainland rocky shore between Cape Columbine and Saldanha Bay a mean of 26.8 birds per km was obtained by Underhill and Cooper (1984). Other species of migrant shorebirds are less numerous on Marcus Island, their mean summer density being 21.9 ± 11.1 birds per km coast. The mean number of migratory shorebirds (excluding Turnstones) counted on adjacent mainland shores by Underhill and Cooper (op. cit.) was 10.1 per km. Whitefronted Plovers are present on the shores of Marcus Island in all months of the year (Fig. 4.6).

Algal mat infauna

Foliose algae, predominantly *Enteromorpha* sp. and *Porphyra capensis* Kutz, generally grew more profusely on strips outside the cage than on those within, perhaps as a result of altered water-flow patterns inside the cage. Consequently, the numbers of invertebrate fauna in algal mat samples are expressed per 2 g ash-free dry algae. A total of 35 different invertebrate species was recorded from algal samples within the cage, and 27 species from outside. The mean number (± S.D.) of species per sample is greater inside the cage (8.8 ± 4.3) than outside (6.3 ± 2.9).

Species are grouped into 7 major categories and the mean numbers of individuals (per 2 g AFD algae) in samples from inside and outside the cage are compared (Fig. 4.7). With

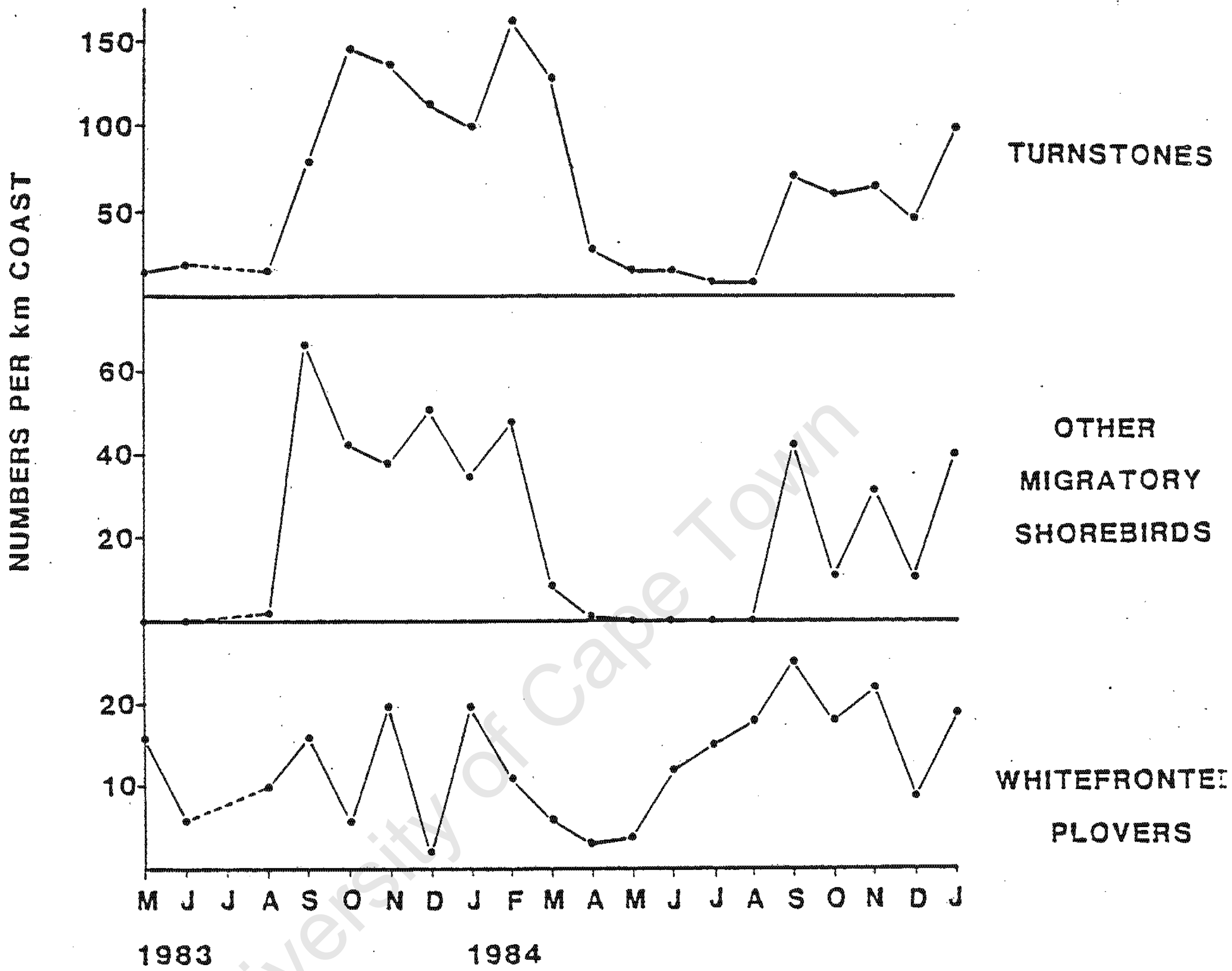
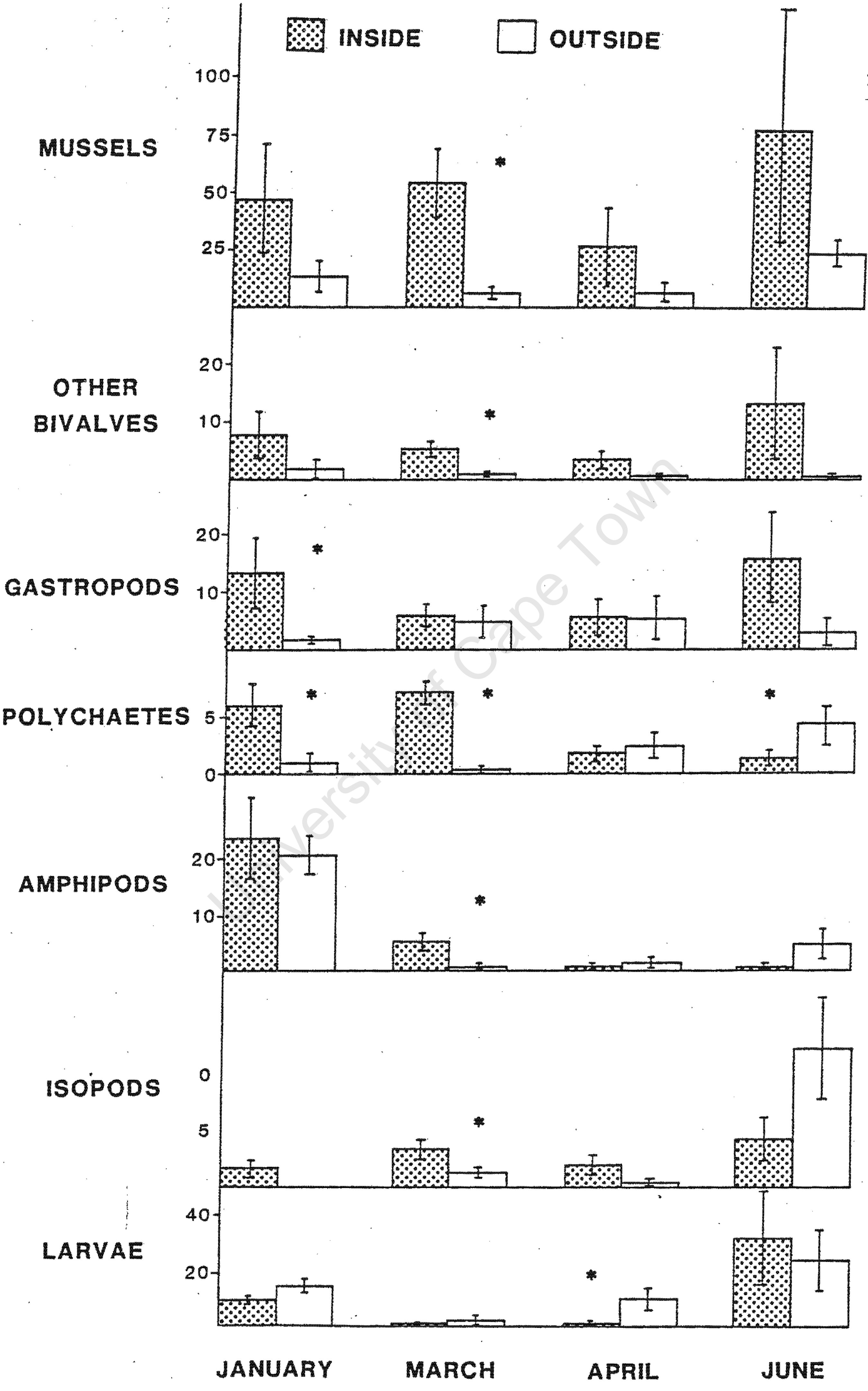


Fig. 4.6. Numbers of small shorebirds counted on the shore of Marcus Island during a single spring low-tide period each month


▨ INSIDE
☐ OUTSIDE
MUSSELS
100
75
50
25
OTHER BIVALVES
20
10
GASTROPODS
20
10
POLYCHAETES
5
0
AMPHIPODS
20
10
ISOPODS
0
5
LARVAE
40
20
*
JANUARY
MARCH
APRIL
JUNE

the exception of chironomid larvae, algal mat invertebrates are more numerous inside the cage than outside when migratory shorebirds are present (January and March). In March, when birds are feeding voraciously before their departure, and predatory pressure might be expected to be most intense, differences between mean densities of invertebrates inside and outside the cage are significant in 5 of the invertebrate categories (Fig. 4.7). (Although this experimental design does not make use of true replicates, thus making the use of inferential statistics inappropriate, the results of Mann-Whitney *U* tests are presented for interest in Fig. 4.7.)

After the departure of the majority of migratory waders from the shore of Marcus Island, invertebrate densities inside and outside the cage may equilibrate rapidly, and in the case of the more mobile invertebrates such as amphipods, isopods and polychaetes, the densities may become greater outside the cage than inside (Fig. 4.7). The pattern of changes in densities of chironomid larvae is opposite to that in all other categories. Mean density is higher outside the cage in the presence of migratory shorebirds, and becomes higher inside the cage several months after the shorebirds have left.

The mussels *Mytilus galloprovincialis* Lamarck, *Aulacomya ater* (Molina) and *Choromytilus meridionalis* (Krauss) are numerically dominant in many of the samples. The density of mussel-associated species (per 2 g AFD algae) in each sample is positively correlated with the number of mussels present (n = 39, r = 0.87, P < 0.001), indicating the importance of mussel beds in creating habitats for other organisms.

Discussion

Shorebird diets

Small shorebirds on Marcus Island have considerable dietary overlap, and consume prey from all the invertebrate categories considered (Ryan 1983). From stomach analysis it has been determined that polychaetes are the most important source of energy for Turnstones and Curlew Sandpipers, whereas Sanderlings and Whitefronted Plovers derive the majority of their energy from chironomid larvae. Mussels are found commonly in the stomachs of all shorebird species considered except Whitefronted Plovers (Ryan op. cit.). In addition, the species considered have all been shown to utilize the high-shore algal mats for foraging, some species spending more than 40% of their foraging time in this habitat (Ryan op. cit.).

Impact of predation on invertebrate densities

Exclusion cages have been used in several studies to determine the impact of avian predators on prey populations (Hancock and Urquhart 1967; Bengston et al. 1976; Goss-Custard 1977; Schneider 1978). More recently, rigorous exclusion experiments by Quammen (1981, 1984) and Marsh (1986) have separated the effects of predation by birds and by other predators, using cages which ostensibly allow access to non-avian predators. High-shore algal mats on Marcus Island often are subject to high wave action during the short time that they are submerged and it is unlikely that predatory fish would be able to use this habitat regularly. In addition, species of predatory invertebrates present outside the cage (nereid and syllid worms) were all recorded inside the cage as well. Patches of mussel bed which develop inside the cage also support predators, such as other polychaetes and the whelk *Nucella squamosa* (Lamarck), which are not present outside the cage. Thus, although the design of the cage did not enable separation of the effects of predation by birds and by other predators, the absence of other obvious predators and the inaccessibility of the habitat to marine predators indicate that the effects observed are attributable to predation by birds.

The densities of invertebrates in algal mats are reduced as a result of foraging activity by small shorebirds. In particular, invertebrate populations are severely depleted just prior to the departure of the migrant waders (Fig. 4.7). It is during this time that migrant shorebirds may lay down reserves of fat at the rate of over 2% of their body mass per day (Summers and Waltner 1979). This increases the daily energy requirements of the migrants and thus the amount of prey they consume. After the departure of the migrant shorebirds certain types of prey, in particular those species of polychaetes, isopods and amphipods not necessarily associated with mussel bed habitat, may become more abundant outside the cage than inside. This increase in density of certain invertebrate species outside the cage indicates that the cage does not form a preferred habitat and that the high densities recorded inside the cage when small shorebirds are present are not an artefact of the caging technique.

Chironomid larvae are an important prey (in terms of numbers) for Turnstones, Curlew Sandpipers, Sanderlings and Whitefronted Plovers (Ryan 1983) and are found among the fronds of foliose algae. Since Whitefronted Plovers are resident and chironomid larvae form approximately 65% of their diet (by numbers) (Ryan op. cit.), there is likely to be less of a seasonal trend in the relative densities inside and outside the cage (Fig. 4.7). In addition, it is possible that the mesh covering the cage acts as a barrier to adult chironomid midges, *Telmatogeton* sp. (Hesse 1934), which do not readily enter the cage to lay their eggs.

Impact of predation on the natural succession of intertidal biotic assemblages

Beds of foliose algae may form a settlement substratum for mussel spat (Suchanek 1978; Petersen 1984a, b), a phenomenon which is considered part of the natural succession of biotic assemblagess on southern African rocky shores (Brokenham and Stephenson 1938). On Marcus Island the foraging activity of small shorebirds leads to a reduction in mussel densities and inhibits the establishment of mussel beds (Fig. 4.7).

Mats of foliose algae persist in the high-shore region (Part 4.1) and subsequent successional assemblages do not become established, even though the algal species involved (*Enteromorpha* sp. and *Porphyra capensis*) are pioneers and usually of a transient nature (Brokenham and Stephenson 1938).

Where small shorebirds are excluded from areas of high-shore algal mat mussels are more numerous (a maximum of 373 per 2 g AFD algae was recorded inside the cage in June). The small mussels trap sediment and form a structurally complex matrix which provides shelter and habitat for a wide diversity of invertebrates (Suchanek 1985). Thus, the presence of a mussel bed influences not only the densities of associated species, but also the species composition of the community. The higher mean number of species in samples from inside the cage can be attributed largely to the presence of species associated with mussel beds.

Marsh (1986) attributes the absence of mussel patches in exposed, high-shore areas to predation by surfbirds, oystercatchers and gulls, although he neglects to consider environmental differences between the exposed areas and adjacent moist crevices where mussels do become established. In his study predation by birds is seen to increase spatial heterogeneity, whereas on Marcus Island avian predation results in habitat homogeneity. In addition, the temporal persistence of high-shore algal mats (Part 4.1) is due, in part, to the predatory activity of shorebirds, which remove mussels and prevent the establishment of mussel beds in this region of the shore. In this manner predation by shorebirds not only influences the natural succession of biotic assemblages on the rocky shore, but also contributes to the maintenance of the algal mat foraging habitat in the high-shore region.

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PART 5

COMPARATIVE STUDIES

Section (1): The influence of seabird guano on the biological structure of rocky intertidal communities on islands off the west coast of southern Africa

Summary. On the rocky west coast of southern Africa the growth rate of intertidal algae is limited by the availability of inorganic nutrients. On offshore islands, where colonies of seabirds breed and roost, intertidal waters are enriched with nutrients from dissolved guano, and the growth rate of algae is enhanced. Comparison of the mid-intertidal communities from island and nearby mainland shores showed that mainland communities were characterized by the absence of foliose algae and sessile filter-feeders, and the presence of large areas of vacant rocky surface. On island shores, mats of foliose algae dominated mid-intertidal communities and herbivorous limpets grew more rapidly and attained larger sizes. Dense populations of African Black Oystercatchers, which feed on limpets, occurred on island shores, but were absent from mainland shores. The effects of nutrient enrichment were evident, not only in the rate of primary production, but also in interactions between organisms at higher trophic levels and in the structure and functioning of the intertidal community as a whole.

Introduction

The importance of nutrient availability in modifying the production rates and species composition of plant assemblages has long been recognized (Tilman 1982). In terrestrial, marine and fresh-water environments enrichment of growth media with inorganic nutrients (particularly nitrogen and phosphorus) has led not only to increased plant biomass through enhanced growth rates, but also to changes in plant species composition (Willis 1963; Thurston 1969; Zelickman and Golovkin 1972; Schindler 1977; Tilman 1977). Bradshaw (1969) concluded that the requirements of all plants for mineral nutrients, the stimulation of plant growth by nutrient addition in the field, and the changes observed in species composition after fertilization strongly suggest that competition for nutrients is the major factor determining the nature of natural plant assemblages.

In any system the plant species composition and the rate of primary production may influence feeding interactions between organisms at all trophic levels (Tilman 1982), and changes in nutrient availability might be expected to influence relationships at higher trophic levels as well. On the Isle of Rhum in Scotland enrichment of soil nitrogen and phosphorus by the guano of Herring Gulls (*Larus argentatus* Pontoppidan) leads to improved forage for Red Deer (*Cervus elephas* L.). Furthermore, hinds which graze regularly in enriched pasture have an increased life-time reproductive success (Iason et al. 1986). In the rocky intertidal system, where the plants and animals form a community of interacting species, maintenance of a balance between space-occupying and space-creating organisms is essential to the persistence of the community (Lubchenco and Menge 1978; Paine et al. 1985; Hockey and Bosman 1986). In this system enhanced rates of primary production which may result from nutrient enrichment may alter the representation by space-creating and space-occupying elements, giving rise to an intertidal community which is functionally different.

Rocky islands off the west coast of southern Africa support large breeding colonies of seabirds, mainly Jackass Penguins *Spheniscus demersus* (L.), Cape Cormorants *Phalacrocorax capensis* (Sparrman) and Cape Gannets *Sula capensis* (Licht.) (Cooper et al. 1982; Crawford et al. 1983; Shelton et al. 1984). Historically, seabird guano was collected from almost all of the offshore islands, and it was sold as fertilizer (Hutchinson 1950; Rand 1963a, b). Until 1986 guano was still collected on an annual basis from Malgas Island in Saldanha Bay. On the rocky shores of the seabird-breeding islands in Saldanha Bay, nutrient enrichment of intertidal waters by the dissolved guano of seabirds leads to enhanced rates of primary production (Part 2). Since intertidal herbivorous limpets grow more rapidly where algal food is abundant (Parts 3.1 and 3.3), limpet population dynamics are also modified as a result of guano run-off from islands. The rapid growth of algae to the foliose stage on island shores, and the activity of larger limpets in grazing the rocky substratum clean of algae and settling organisms may alter totally the appearance of the intertidal community when compared to nearby unenriched shores. In addition, nutrient enrichment may lead to modifications in intertidal community structure, particularly in terms of the abundances, distributions, demographies and population size structures of component species.

In this study the functional structures (i.e. no attention given to species composition or diversity, but only to the functional relationships between guilds of species) of rocky mid-intertidal communities on seabird-breeding islands and on adjacent mainland shores are compared to determine whether the process of nutrient enrichment by seabird guano results in changes to intertidal community structure which are common to, and characteristic of, the shores of seabird-breeding islands.

Methods and materials

Study sites

The structures (in terms of representation of functional guilds of organisms) of mid-shore communities at 5 island and 6 mainland sites were analysed. The islands support permanent aggregations of breeding or roosting seabirds, and have all, at times, been used as a source of commercially exploitable guano. Study sites were chosen on the shores of Malgas, Jutten and Marcus Islands in Saldanha Bay, and on Ichaboe and Penguin Islands off the coast of South West

Africa/Namibia (Fig. 5.1). Sites on mainland shores (where aggregations of seabirds are absent) comprised Mauritz Bay, Cape Columbine, North Bay and Bomgat in the Saldanha Bay area (Fig. 1.1), and Grossebucht and Essy Bay in SWA/Namibia (Fig. 5.1). Although North Bay and Bomgat are mainland sites without colonies of seabirds, they are within Saldanha Bay and may be influenced by guano run-off from the shores of nearby seabird-breeding islands. All the study sites fall in the Benguela upwelling region, and are washed by nutrient-rich waters at times of coastal upwelling (Nelson and Hutchings 1983). Sites on the islands and at North Bay, receive supplementary nutrient enrichment from dissolved guano (Part 1).

Intertidal community structure on the west coast of southern Africa has been studied in detail by Stephenson and Stephenson (1972), and all the study sites chosen support species typical of the region. The dominant algal species are *Enteromorpha* sp. and *Porphyra capensis* Kutz., and *Patella granularis* (L.) is the dominant herbivore in terms of numbers and biomass. All shores considered are granitic and are exposed to heavy wave action.

Community analysis

All sites were visited between November 1984 and March 1985 (i.e. during the austral summer) and at each one the structure of the intertidal community in replicate 0.5 m^2 quadrats in the mid-shore region was determined. All macrofauna in the randomly-positioned quadrats were identified

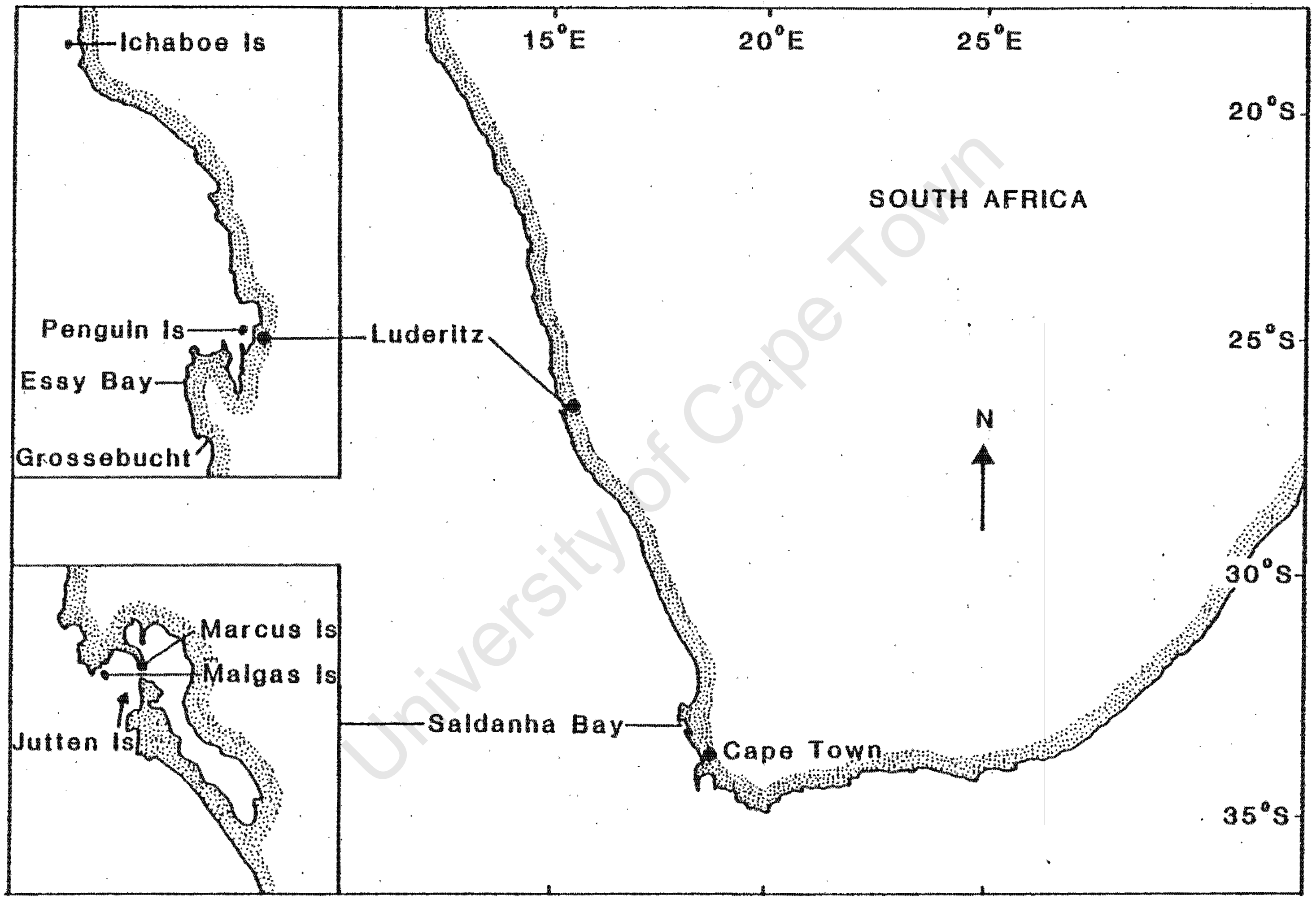

Fig. 5.1. Map of the southern African west coast showing the study areas and selected study sites

and counted, and the percentage area covered by algae and by sessile filter-feeders was determined visually. Between 9 and 15 replicates were obtained, depending on the width of the mid-shore region. All species recorded were classed into functional groups, based on whether they were sessile and occupied ground-space or whether they were mobile and created space within the system. Space-creators were further divided into limpets and other herbivores, and space-occupiers were divided into algae and sessile filter-feeders. The amount of 'vacant' rocky surface available in each community was also deemed an important attribute of community structure. Limpets and other herbivores were not considered to occupy ground-space, and thus the sum of ground-cover by algae, sessile filter-feeders and vacant space is 100% in each quadrat.

Limpet biomass was considered a more accurate index of the impact of these herbivores than limpet number, as the amount of algae grazed is more closely related to the biomass of limpets present than to the number (Branch 1971). At each site the size distribution of a sample of 100 *Patella granularis* was determined. The median limpet length and the number of individuals counted were used to calculate the biomass (g) of *P. granularis* in each quadrat, according to the following mass/length regression equation:

$$\text{Dry somatic and gonadial mass} = 1.9 \times 10^{-6}\ (\text{length})^{3.5}$$

$$n = 100,\ r^2 = 0.98,\ P < 0.001$$

Correspondence analysis (Greenacre 1984; Underhill and Peisach 1985) was used to analyse community structure in terms of the similarity of contributions by each functional group to the pattern of organization observed in each quadrat. This method displays graphically both the objects (quadrat samples) and the variables (functional groups) simultaneously. The extent of similarity between objects or variables is related to their separation in the two-dimensional graphical display; objects which are plotted close together are similar, and variables plotted close together are (using the term loosely) correlated. Variables plotted close to the origin are most typical of the greatest number of objects. Tables which accompany the analysis determine the distortion in the display as a whole, and show how accurately the multi-dimensional cloud of data points is projected into two dimensions.

In this analysis the variables (functional groups) may be weighted according to a subjective assessment of their importance in influencing community structure and functioning. The analysis was conducted first with the data matrix unaltered and then with all the variables weighted equally. In both these instances the analysis was dominated by variations in the percentage cover of sessile filter-feeders and in the number of herbivores other than limpets. Both these variables have low values generally, and the single, or few, sites with unusually high values are identified by the analysis as being the major source of between-site variation. Consequently, the functional groups were weighted for the purpose of de-emphasising between-site differences due to the local abundance of uncommon species. In the analysis presented the functional groups of % space, % algal cover and biomass of limpets were given weightings of 20, % sessile filter-feeders and limpet number received weightings of 10, and the number of other herbivores was given a weighting of 5.

Results

Algal and invertebrate species composition is similar at all sites (Table 5.1) although the patterns of organization of intertidal communities at island and mainland sites differ considerably. Intertidal communities on island shores are characterized by the presence of mats of foliose algae which cover substantial areas of the rocky substratum (Fig. 5.2). Mean percentage cover by algae is significantly higher on island shores than on mainland shores (Mann-Whitney U test: $n_1 = 39$, $n_2 = 61$, $U = 2357.5$, $P < 0.0001$), while the mean percentage of vacant rocky surface is significantly higher on mainland shores ($n_1 = 39$, $n_2 = 61$, $U = 0.00$, $P < 0.0001$). The mean cover by sessile filter-feeders is less than 5% at all sites and, since no sessile filter-feeders were recorded at any of the mainland sites (S.D. = 0.00), statistical testing would be meaningless. Communities at North Bay and Bomgat have values intermediate between the values for island and mainland communities in all three ground-cover categories (Fig. 5.2).

Table 5.1. Invertebrate and algal species recorded in mid-intertidal sample quadrats, and their separation into the functional groups used in correspondence analysis

	ISLAND SHORES	NORTH BAY AND BOMGAT SHORES	MAINLAND SHORES
SESSILE FILTER-FEEDERS	*Tetraclita serrata* *Octomeris angulosa* *Notomegabalanus algicola* *Chthamalus dentatus* *Mytilus galloprovincialis*	*Octomeris angulosa* *Chthamalus dentatus* *Mytilus galloprovincialis*	*Chthamalus dentatus*
LIMPETS	*Patella granularis* *Patella granatina*	*Patella granularis* *Patella granatina*	*Patella granularis*
OTHER HERBIVORES	*Siphonaria capensis* *Littorina knysnaensis*	*Siphonaria capensis* *Littorina knysnaensis*	*Siphonaria capensis* *Chaetopleura papilio*
ALGAE	*Enteromorpha sp.* *Porphyra capensis*	*Enteromorpha sp.* *Porphyra capensis*	*Enteromorpha sp.* *Porphyra capensis*

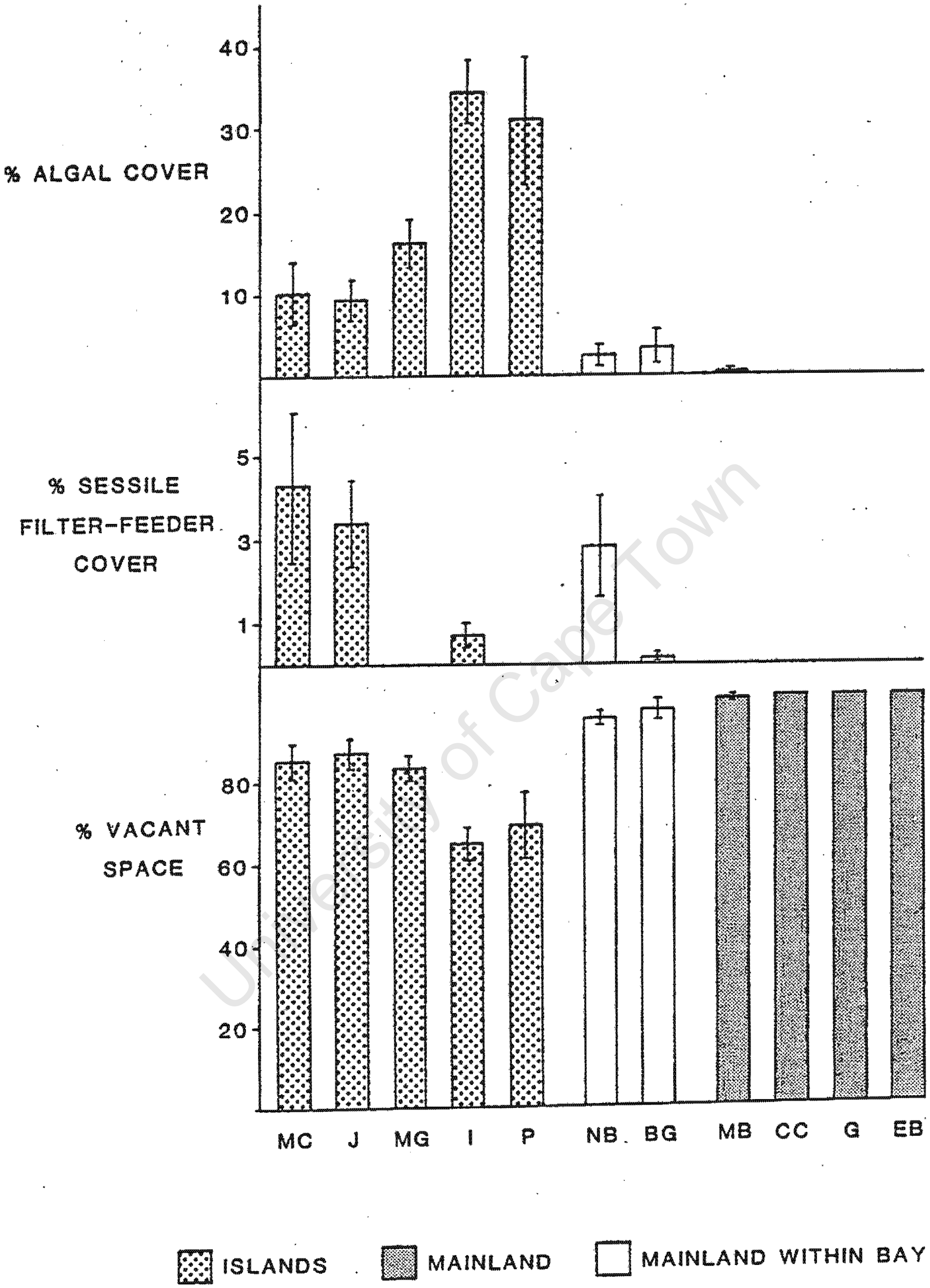

Fig. 5.2. Mean values and standard deviations recorded for ground-cover categories in the mid-intertidal regions at study sites on the west coast of southern Africa. Sites are Marcus Island (MC), Jutten Island (J), Malgas Island (MG), Ichaboe Island (I), Penguin Island (P), North Bay (NB), Bomgat (BG), Mauritz Bay (MB), Cape Columbine (CC), Grossebucht (G) and Essy Bay (EB).

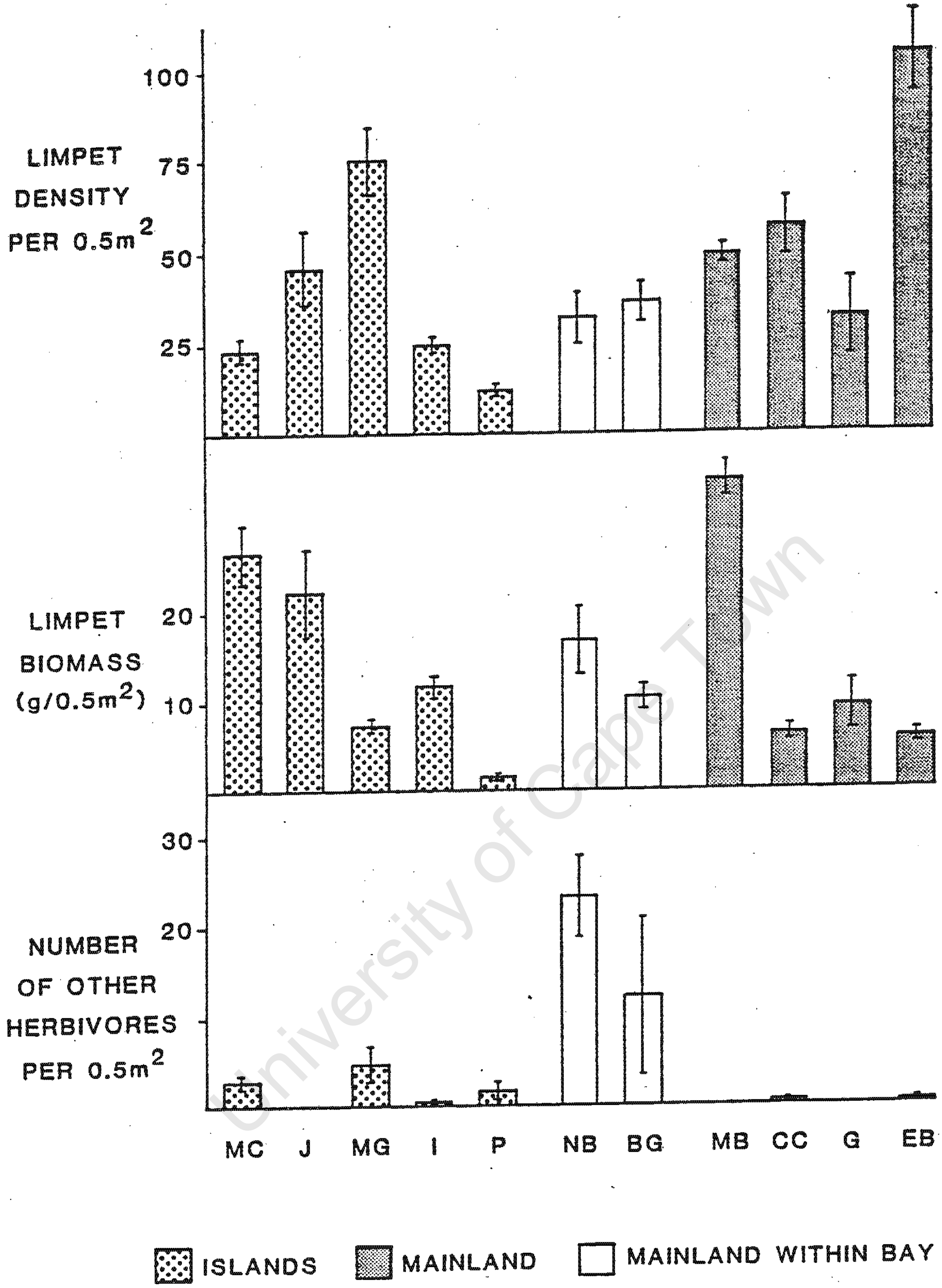

Fig. 5.3. Mean values and standard deviations recorded for attributes of mid-intertidal community structure at island and mainland study sites on the west coast of southern Africa. Sites are Marcus (M), Jutten (J), Malgas (M), Ichaboe (I) and Penguin (P) Islands, North Bay (NB), Bomgat (BG), Mauritz Bay (MB), Cape Columbine (CC), Grossebucht (G) and Essy Bay (EB)

Table 5.2. The median sizes and size ranges of *Patella granularis* at study sites ($n = 100$ in all instances)

SITE	MEDIAN (mm)	SIZE RANGE (mm)
Marcus Island	45	13 - 64
Jutten Island	35	7 - 62
Malgas Island	22	9 - 46
Ichaboe Island	35	9 - 59
Penguin Island	24	5 - 60
North Bay	36	12 - 62
Bomgat	30	10 - 50
Mauritz Bay	39	10 - 57
Cape Columbine	23	6 - 41
Grossebucht	30	7 - 44
Essy Bay	19	7 - 31

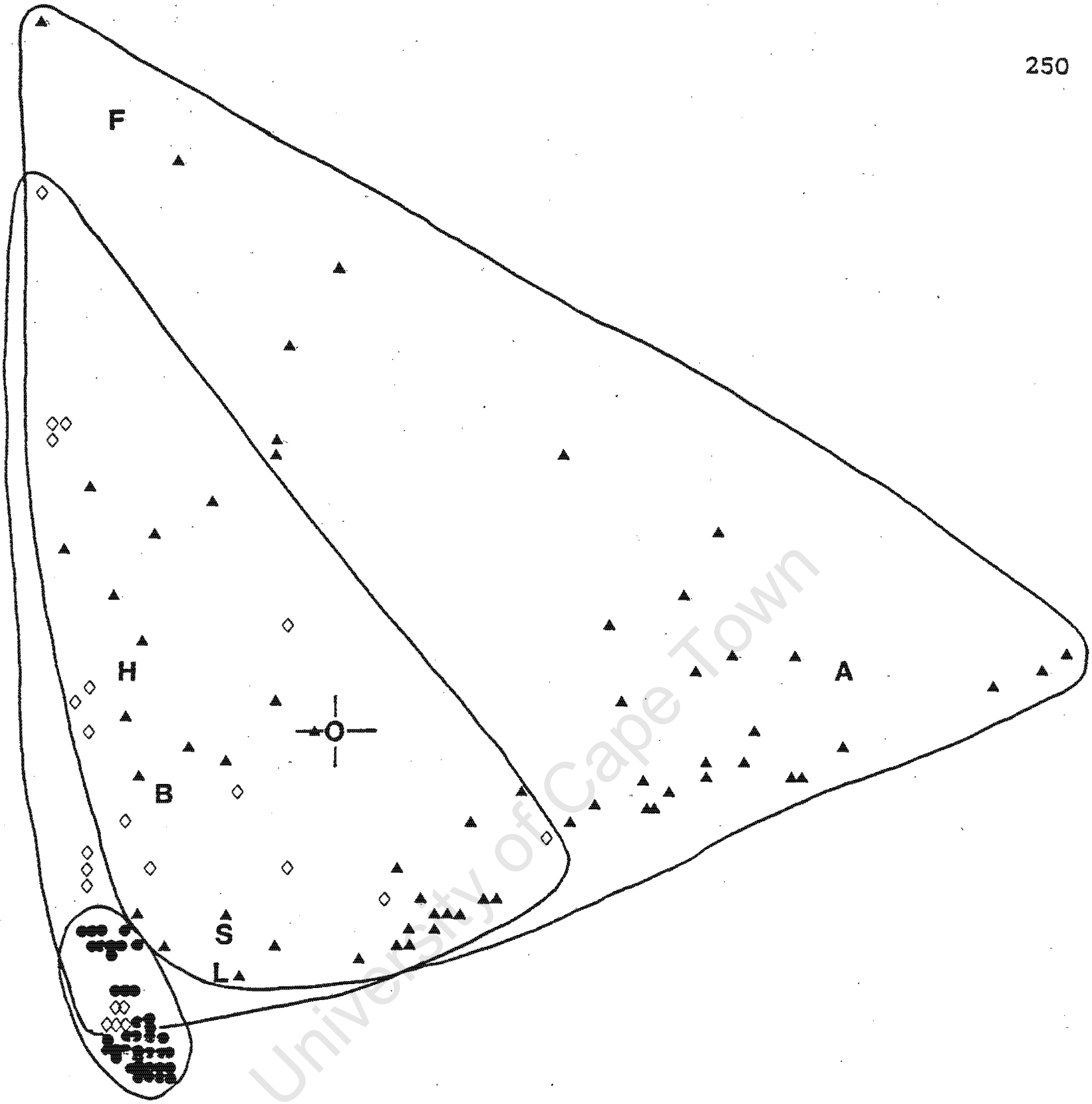

Fig. 5.4. Correspondence analysis of mid-intertidal community structure at island and mainland sites on the west coast of southern Africa. Key to variables: mainland sites = ● , island sites = ▲ and intermediate sites (North Bay and Bomgat) = ◇ ; A = % algal cover, F = % cover by sessile filter-feeders, S = % vacant space, L = limpet number, B = limpet biomass, H = number of herbivores besides limpets, O = origin

being characterized by low limpet density and biomass, little vacant space and the presence of foliose algae (particularly at sites on Malgas, Ichaboe and Penguin Islands) and sessile filter-feeders (particularly on Marcus and Jutten Islands).

No variable appears close to the origin in Figure 5.4, indicating that no functional group is equally represented at all sites. Variation in the amount of algal cover accounts for the largest percentage of total inertia in the analysis (26.8%) and separation along the horizontal axis (factor 1) is due to the contributions of algal cover and cover by sessile filter-feeders. Along the vertical axis (factor 2) variations in limpet density and cover by sessile filter-feeders account for most inertia, and factor 3 identifies variations in the number of other herbivores as being the principal cause of separation. Factor 4 identifies variations in limpet number and biomass as important in separating sites. The first 2 factors account for 63.8% of the total inertia of the analysis, while the first 4 factors account for 95.6%.

Mid-shore communities at North Bay and Bomgat, the mainland sites adjacent to seabird-breeding islands, show characteristics of both mainland and nutrient-rich island communities (Fig. 5.4). Sample quadrats from North Bay and Bomgat do not form a discrete group, but overlap with both island and mainland quadrats. The North Bay mid-shore community is characterized by the presence of sessile filter-feeders, and the Bomgat community by the absence of filter-feeders and the presence of foliose algae (Figs 5.2 and 5.4), mimicking the divergence between island sites.

Discussion

Primary effects of nutrient enrichment

The aspect of mid-shore community structure which can most readily be used to discriminate between the communities of nutrient-rich and unenriched shores on the west coast of southern Africa is the amount of algal cover. Foliose algae invariably are absent from the mid-shore region on mainland shores, while they may be the dominant space-occupiers on island shores. Marine algae which are provided experimentally with excess inorganic nutrients respond by growing and reproducing more rapidly (Prince 1974; Chapman and Craigie 1977; DeBoer 1978; Morgan and Simpson 1981), and the experimental supply of seabird guano to intertidal algae leads to an enhanced algal production rate (Part 2). The enrichment of intertidal and nearshore waters around seabird-breeding islands results in rapid algal growth to the foliose stage, after which algae form dense, permanent mats on the shore (Part 4.1). On mainland shores, where the rates of algal production are slower, most sporelings are grazed before they become foliose, and vacant rocky surface predominates (Fig. 5.2).

At the North Bay and Bomgat sites foliose algae are present and occupy more ground-space than do algae at the mainland sites. North Bay and Bomgat are adjacent to seabird-breeding islands in Saldanha Bay, and are within the possible zone of influence of guano run-off from the islands. Intertidal waters at the North Bay site have been shown to be enriched with nutrients from dissolved guano carried by water movement from Malgas Island (Part 1). Although this has not been demonstrated for Bomgat it is possible that occasional storms and winds cause abnormal water movement which may bring nutrient-rich water to the Bomgat shore.

Secondary effects of nutrient enrichment

Several species of intertidal herbivores have been shown to grow more rapidly where micro-algal food is more abundant (Creese 1980; Underwood 1984) or where the rate of algal production is enhanced (Parts 3.1 and 3.3). Limpets on the shores of islands attain larger sizes than those on mainland shores (Table 5.2), indicating that their growth rates are more rapid (Branch 1974; Balaparameswara Rao 1976). Since the reproductive output of limpets increases exponentially with shell length (Part 3.1), the reproductive potential of populations of limpets on island shores is greater than that of mainland populations, despite the fact that the biomass of limpets supported on island and mainland shores is similar.

The consequences of grazing by limpets are two-fold: first, limpets create and maintain ground-space by grazing algal spores and sporelings, and secondly, while foraging they may inhibit the settlement of sessile organisms such as mussels and barnacles by 'bulldozing' spat from the rocky surface. Limpets on mainland shore appear to keep the rocky substratum free of sessile filter-feeders. The effect of this activity possibly is enhanced by the density of limpets and by the relative shortage of algal food. On island shores however, where one would expect the larger limpets to function similarly, there are settlements of sessile filter-feeders and algae. Those island sites with the highest limpet biomass (viz Marcus and Jutten Islands) do have the lowest cover by algae, but even this is substantial in comparison with algal cover at mainland sites.

Many islands off the west coast of southern Africa support dense populations of African Black Oystercatchers *Haematopus moquini* Bonaparte (Hockey 1983) which prey on limpets. Oystercatcher densities on islands in Saldanha Bay range from 25 to 78 birds per km coast, with the highest densities occurring on the shores of Marcus and Jutten Islands (Hockey op. cit.). On mainland shores in the area (Mauritz Bay - Cape Columbine) the mean density is 2.6 birds per km coast (Hockey op. cit.). On island shores oystercatchers remove large numbers of limpets (Parts 3.2 and 3.3), selecting particularly individuals from the middle size classes (Hockey and Underhill 1984). Thus the densities and size structures of island limpet populations may be altered. It is possible that the removal of limpets by oystercatchers, in addition to the enhanced rate of algal growth on island shores (particularly on the shores of Marcus and Jutten Islands), enables algae and sessile filter-feeders to become established. On Ichaboe Island, however, where approximately 30 000 Cape Gannets (Crawford et al. 1983) and 90 000 Cape Cormorants (Cooper et al. 1982) breed, the mean density of oystercatchers is 1 per km coast, the shorebirds being excluded by densely-packed seabirds (Rand 1963a; Hockey 1983). Here limpet predation by oystercatchers is negligible and both algae and sessile filter-feeders do become established, indicating the dominant role of enhanced primary production rate in modifying island intertidal communities.

The enrichment of waters around seabird-breeding islands with nutrients from dissolved guano results in a modification of the functional structure of the intertidal community. Although the composition of intertidal species is similar at all sites, enhanced primary production rate on island shores results in an alteration in the representation by space-occupying and space-creating organisms. Limpets on island shores have modified size distributions, and their rapid growth rate, as well as the enhanced fecundity of the large individuals, may enable dense populations of African Black Oystercatchers to be supported on island shores. The removal of limpets by oystercatchers, together with the rapid growth of algae to the foliose stage, lead to the formation of persistent mats of algae on island shores. The effects of nutrient enrichment of intertidal waters by the dissolved guano of seabirds are apparent not only in the production rate of algae, but in interactions between organisms at higher trophic levels, and in the structure and functioning of the intertidal community as a whole.

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Section (2): The influence of coastal upwelling on the functional structure of rocky intertidal communities

Summary. Relationships between organisms at all trophic levels are influenced by the rate of primary production in the ecosystem, and factors which enhance rates of primary production may modify trophic relationships and community structure. Nutrient enrichment of intertidal and nearshore waters leads to enhanced production by intertidal algae, and it was hypothesized that where rocky shores are washed by nutrient-rich upwelled waters the intertidal communities should show a characteristic functional structure, based on the consequences of enhanced primary production. Study sites were chosen on rocky shores in southern Africa, central Chile and the Canary Islands, in areas with and without coastal upwelling, and mid-shore community structure at these sites was analysed in terms of the abundance of certain functional groups of organisms.

It was found that algal cover and the biomass of herbivorous limpets supported per unit area on rocky shores were significantly greater in regions of coastal upwelling than in regions where upwelling did not occur. Ground-cover by sessile filter-feeding organisms was significantly greater on shores in non-upwelled areas. However, correspondence analysis showed no functional aspect of intertidal community

structure that was characteristic of coasts washed by upwelled waters. Primary reasons for this are probably the large variations in the nature of nutrient enrichment that accompanies upwelling, and in the nutrient status of non-upwelled areas. Other factors are man's exploitation of intertidal organisms and differences in the genetic origins of the intertidal species involved.

Introduction

The intertidal zone has become a fertile study area for ecologists seeking universal truths about the functional structure, succession and stability of natural communities (Paine 1969, 1974, 1981; Dayton 1971; Connell 1972, 1975; Menge 1976; Connell and Slatyer 1977; Grossman 1982; Jara and Moreno 1984; Lubchenco et al. 1984; Castilla and Rozbaczylo 1985; Paine et al. 1985). The rocky intertidal zone is narrow and discrete, and its biota lend themselves to manipulative experimentation aimed at understanding the causes of differences in community structure and functioning. In this context, the opposing roles of sessile, 'space-occupying' and mobile, 'space-creating' organisms have been emphasized in several studies (Lubchenco and Menge 1978; Paine et al. 1985; Hockey and Bosman 1986; Part 4.1). Within any intertidal system the balance between these functional groups of organisms may be altered as a result of ecological processes such as competition, predation and disturbance (Menge 1972, 1973; Connell 1975;

Goodman 1975; Paine 1976; Lewis 1977; Lubchenco and Menge 1978).

The nutrient enrichment of intertidal and nearshore waters by the dissolved guano of seabirds leads to the modification of community structure on the shores of seabird-breeding islands (Parts 1 and 2). Intertidal algae respond to nutrient enrichment and both the enhanced algal production and the increased biomass of herbivorous limpets supported (Part 3.3) represent shifts in the balance between space-occupying and space-creating organisms. The densities of avian predators which forage intertidally are also modified when compared with controls (Parts 2 and 4.2).

Nutrient enrichment of surface waters as a result of the upwelling of deeper, oceanic water is well documented for several shores around the world (Robinson 1981, Whitledge 1981). It has been found that areas of upwelling in the world's oceans are typified by enhanced primary (phytoplankton) production (Wooster 1981). Where rocky shores are washed by nutrient-rich upwelled water, it might be expected that intertidal algae would show enhanced production and abundance, leading in turn to a change in the representation of sessile, space-occupying organisms and in the functional structure of the intertidal community as a whole.

In this study I assess community structure on rocky shores in terms of the quantitative representation of certain functional groups of organisms. I compare rocky shore communities in areas with and without coastal upwelling, in Chile, southern Africa and the Canary Islands, in order to determine whether the process of nutrient enrichment through upwelling leads to modification of their functional structure, in a way which is common to, and characteristic of, shores washed by upwelled waters.

Methods and materials

Study sites

The rocky intertidal communities at 12 sites were analysed, 6 sites being in areas of coastal upwelling. The shores at Cape Columbine (32°49'S, 17°51'E), Essy Bay (26°42'S, 15°05'E) and Grossebucht (26°44'S, 15°06'E) on the west coast of southern Africa, are washed by upwelled waters from the Benguela Current system (Nelson and Hutchings 1983). Two sites in central Chile, Los Molles (32°15'S, 71°33'W) and Punta Lagunillas (30°05'S, 71°24'W), were chosen from areas of coastal upwelling in the Humboldt Current system (Espinoza et al. 1983), and a single site, Playa de las Salinas (28°18'N, 14°12'W), was selected in an area of local upwelling on the west coast of Fuerteventura, Canary Islands. At all sites the rocky shore was unbroken, sloped gently into the sea and was exposed to wave action.

Study sites in areas without upwelling were Dwesa (32°16'S, 28°50'E), Hluleka (31°49'S, 29°18'E) and Isi Laka (31°39'S, 29°30'E) in Transkei, southern Africa, and Punta el Lacho (41°52'S, 71°39'W), Mehuin (39°24'S, 73°13'W) and Ancud (41°52'S, 73°50'W) in Chile. The Transkeian coast is washed by the warm surface waters of the Agulhas Current and the Chilean sites are in areas of the Humboldt Current system where upwelling does not occur. The site at Ancud was altogether different from other sites, being in a sheltered bay with no upwelling, but also being adjacent to the local town's sewage-outflow pipe. Nutrient enrichment from this source, and from upwelling, were hypothesized to affect mid-intertidal community functioning in a similar manner (via the response of intertidal algae to enhanced nutrient supply) and to lead to convergence in community structure. Although there were intertidal areas without coastal upwelling in the Canary Islands, none was accorded protection from intensive exploitation by man and consequently none was suitable for this study.

Most of the study areas and their intertidal communities have been described elsewhere (see Stephenson and Stephenson 1972; Viviani 1975; Castilla 1981; Moreno et al. 1984; Hockey and Bosman 1986; Hockey 1987). Although many different intertidal invertebrate and algal species have been recorded for each area, the major species can all be separated into functional groups based on their classification as space-occupiers and space-creators (sensu Paine et al. 1985; Hockey and Bosman 1986).

Community analysis

At each site the intertidal region was divided into a high-, mid- and low-shore zone on the basis of the dominant species present and the superficial community structure. In the mid-shore zone at each site, all macro-fauna within a number of randomly-positioned quadrats of 0.5 m^2 were identified and counted. Between 8 and 20 replicates were taken at each site, depending on the width of the mid-shore zone and its homogeneity. The abundance of organisms that were numerous and covered much ground-space was expressed in terms of percentage cover and, although this was determined subjectively, quadrats were divided into several equal segments to aid assessment. At each site 100 individuals of the dominant limpet species were measured to obtain size distributions and medians.

All species recorded were classed into functional groups (Table 5.3), based on whether they were sessile and occupied ground-space, or whether they were mobile and created space within the system. Space-creators were further divided according to their size and relative potential impact, and space-occupiers were divided into algae and invertebrates. The percentage of 'vacant' ground-space was deemed an important attribute of community structure and was assessed in each quadrat and recorded in a separate category. Limpets, other herbivores, carnivores and anemones were not considered to occupy ground-space in the system and consequently the sum of ground-cover by algae and by sessile

Table 5.3. Invertebrate species recorded in mid-intertidal sample quadrats, and their separation into the functional groups used in correspondence analysis

	SOUTHERN AFRICA	TRANSKEI	CHILE	CANARY ISLANDS
SESSILE FILTER-FEEDERS	*Chthamalus dentatus*	*Chthamalus dentatus* *Octomeris angulosa* *Tetraclita serrata*	*Chthamalus scabrosus* *Chthamalus cirratus*	*Chthamalus stellatus*
		Perna perna	*Perumytilus purpuratus*	*Perna picta*
LIMPETS	*Patella granularis*	*Cellana capensis* *Fissurella natalensis* *Patella barbara* *Patella concolor* *Patella granularis* *Patella granatina* *Patella oculus*	*Scurria variabilis*	*Patella candei* *Patella pipperata*
OTHER HERBIVORES	*Siphonaria capensis*	*Siphonaria aspera* *Siphonaria capensis*	*Siphonaria lessoni*	*Siphonaria sp.*
	Chaetopleura papilio		*Chiton granosus*	
		Oxystele tigrina *Oxystele variegata*		
CARNIVORES		*Thais capensis*		*Thais haemastoma*
ANEMONES			*Anthothoe chilensis* *Phymactis clematis*	
LITTORINA		*Littorina africana*	*Littorina araucana* *Littorina peruviana*	

filter-feeders, and of vacant space was 100% in each quadrat.

Limpets were the most important grazers of settled micro- and macro-algae at all sites, but their numbers were not an accurate index of their functional impact since the amount of algae consumed is more closely related to limpet biomass (Branch 1971). Biomass was calculated for each sample using the median limpet length for the site and an appropriate mass/length regression. Mass/length conversions were determined for the following southern African limpet species:

Patella granularis L.: Dry mass = (1.9×10^{-6}) length $^{3.5}$

$n = 100$, $r^2 = 0.98$, $P < 0.001$

Patella granatina L.: Dry mass = (4.9×10^{-6}) length $^{3.1}$

$n = 40$, $r^2 = 0.94$, $P < 0.001$

Patella concolor Krauss: Dry mass = (3.2×10^{-6}) length $^{3.1}$

$n = 40$, $r^2 = 0.94$, $P < 0.001$

P. argenvillei Krauss: Dry mass = (8.7×10^{-7}) length $^{3.5}$

$n = 27$, $r^2 = 0.94$, $P < 0.001$

Cellana capensis (Gme.): Dry mass = (4.2×10^{-8}) length $^{4.5}$

$n = 40$, $r^2 = 0.92$, $P < 0.001$

Mass/length conversion equations were not available for *Scurria variabilis*, *Collisella zebrina* (central Chile), *Patella pipperata*, *P. candei* (Canary Islands), *Fissurella natalensis* or *Patella oculus* (Transkei). In these instances equations for limpets with similar body morphology were substituted. *Scurria variabilis*, *Collisella zebrina* and *Patella pipperata* were considered most like *P. granularis* in morphology, *P. candei* and *P. oculus* were most like *P. granatina*, and *Fissurella natalensis* was most like *P. argenvillei*.

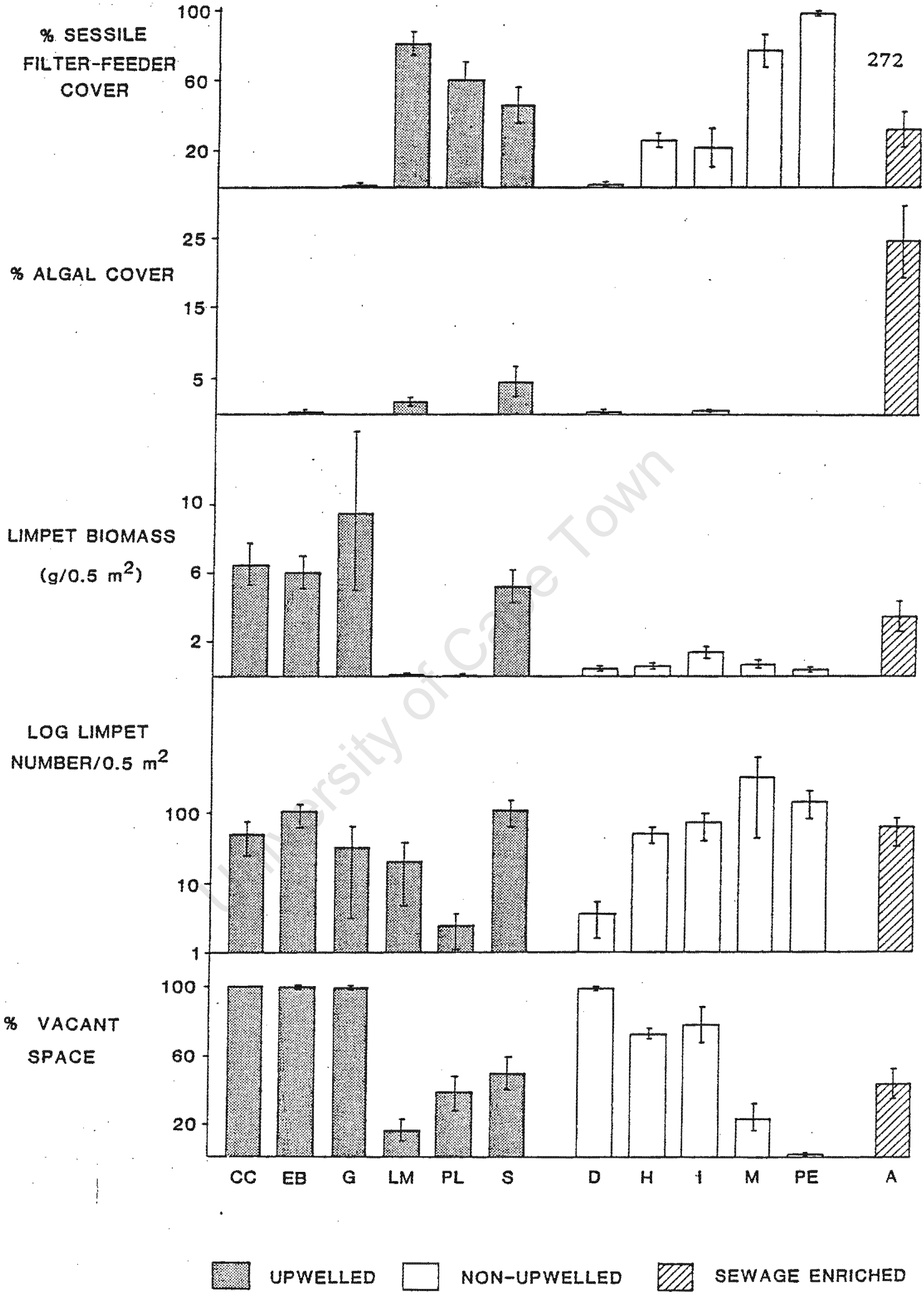
Correspondence analysis (Greenacre 1984; Underhill and Peisach 1985) was used to analyse community structure in terms of the similarity of contributions by each functional group to the pattern of organization observed in each quadrat. This method displays graphically both the objects (quadrat samples) and the variables (functional groups) simultaneously. The extent of similarity between objects or variables is related to their separation in the two-dimensional graphical display; objects which are plotted close together are similar, and variables plotted close together are (using the term loosely) correlated. Variables plotted close to the origin are most typical of the greatest number of objects. Tables which accompany the analysis determine the distortion in the display as a whole, and show how accurately the multi-dimensional cloud of data points is projected into 2 dimensions.

In this analysis the variables (functional groups) may be weighted according to a subjective assessment of their importance in determining community structure. The analysis was conducted first with the data matrix unaltered, then with all the variables weighted equally, and lastly with variables weighted according to an intuitive assessment of their role in determining community structure. In this last analysis the 4 key groups (viz cover by algae, cover by sessile filter-feeders, amount of vacant ground-space and the biomass of herbivorous limpets) received weightings of 20, while limpet number received a weighting of 10. Organisms in the remaining 4 groups were considered to have little influence on the functioning of the community because they were rare, very small, or occurred at 1 or 2 sites only. By giving these groups weightings of 1 (carnivores, other herbivores excluding *Littorina*), 0.5 (anemones) and 0.1 (*Littorina*) the between-site differences due to the local abundance of uncommon species were de-emphasised, thereby highlighting similarities in the functional nature of community structure.

Results

Intertidal sites in areas of coastal upwelling have a significantly greater mean algal cover than do sites in non-upwelled areas, excluding the Ancud site in Chile (Mann-Whitney U test; $n_1 = 42$, $n_2 = 69$, $U = 2079.5$, $P < 0.001$). Mean algal cover (± S.D.) at upwelled and non-upwelled sites is very low (viz 1.6 ± 3.0% and 0.1 ± 0.4% respectively), in comparison with the cover recorded on the shores at Ancud (24.7 ± 10.4%). The mean algal cover is significantly higher at the Ancud site than at sites on upwelled shores ($n_1 = 12$, $n_2 = 69$, $U = 2.0$, $P < 0.0001$ - Fig. 5.5).

Although no group of sites (upwelled, non-upwelled or Ancud) has a significantly different mean density of limpets, mean


% SESSILE FILTER-FEEDER COVER
100
60
20
% ALGAL COVER
25
15
5
LIMPET BIOMASS (g/0.5 m^2)
10
6
2
LOG LIMPET NUMBER/0.5 m^2
100
10
1
% VACANT SPACE
100
60
20
CC
EB
G
LM
PL
S
D
H
I
M
PE
A
UPWELLED
NON-UPWELLED
SEWAGE ENRICHED

limpet biomass is significantly greater at upwelled sites than at non-upwelled sites ($n_1 = 42$, $n_2 = 69$, $U = 2064.5$, $P < 0.001$ - Fig. 5.5). Mean limpet biomass per 0.5 m^2 is significantly higher at Ancud than at non-upwelled sites ($n_1 = 12$, $n_2 = 42$, $U = 8.00$, $P < 0.0001$), but is not significantly different between Ancud and the shores at upwelled sites. Combining the data from all sites, limpet biomass and percentage vacant ground-space are significantly positively correlated ($n = 123$, $r = 0.36$, $P < 0.0001$).

Since percentage algal cover generally is low, the relationship between cover of sessile filter-feeders and amount of vacant ground-space is complementary (Fig. 5.5). Mean percentage cover of sessile filter-feeders is significantly higher at non-upwelled than at upwelled sites ($n_1 = 42$, $n_2 = 69$, $U = 1174.0$, $P < 0.02$), and mean percentage ground-space is significantly higher on the shores of upwelled sites ($n_1 = 42$, $n_2 = 69$, $U = 1979.5$, $P < 0.05$). In both instances the values recorded at the Ancud site fall within the range of values recorded for the other groups of sites, and thus in these aspects the Ancud site does not differ statistically from either upwelled or non-upwelled shores.

Correspondence analysis

Within groups of upwelled and non-upwelled sites, results for each analysis of a community-structure attribute ranged widely. The use of mean values, although indicating trends, certainly masks within-group variability in community structure (Fig. 5.5). Correspondence analysis does not show any clear and consistent difference between the communities of upwelled and non-upwelled shores, irrespective of the manner in which variables are weighted. When unweighted data are used, as well as when all variables are given equal weight, differences in the density of *Littorina* account for most of the variation between sites (22.1% and 20.6% respectively). This is an artefact of the range of *Littorina* densities recorded - high mean densities (± S.D.) were recorded at Punta Lagunillas (3225 ± 645 per m^2) and at Hluleka (180 ± 118 per 0.5 m^2), while *Littorina* were absent from all other sites.

Although the use of weightings produces a clear separation of sites (Fig. 5.6), it shows no differences between the communities of upwelled and non-upwelled shores in particular. Upwelled sites on the southern African west coast (viz Grossebucht, Cape Columbine and Essy Bay) are closely grouped with Dwesa, a Transkeian non-upwelled site, and all are characterized by high limpet biomass and much vacant ground-space. The Chilean upwelled (Punta Lagunillas and Los Molles) and non-upwelled (Punta el Lacho and Mehuin) sites are grouped, and are characterized by high sessile filter-feeder cover. The non-upwelled Ancud site is discrete and removed from all other Chilean sites.

Although there is a tendency for geographically proximate sites to be grouped together (Fig. 5.6), variation in algal cover between sites is the aspect of community structure

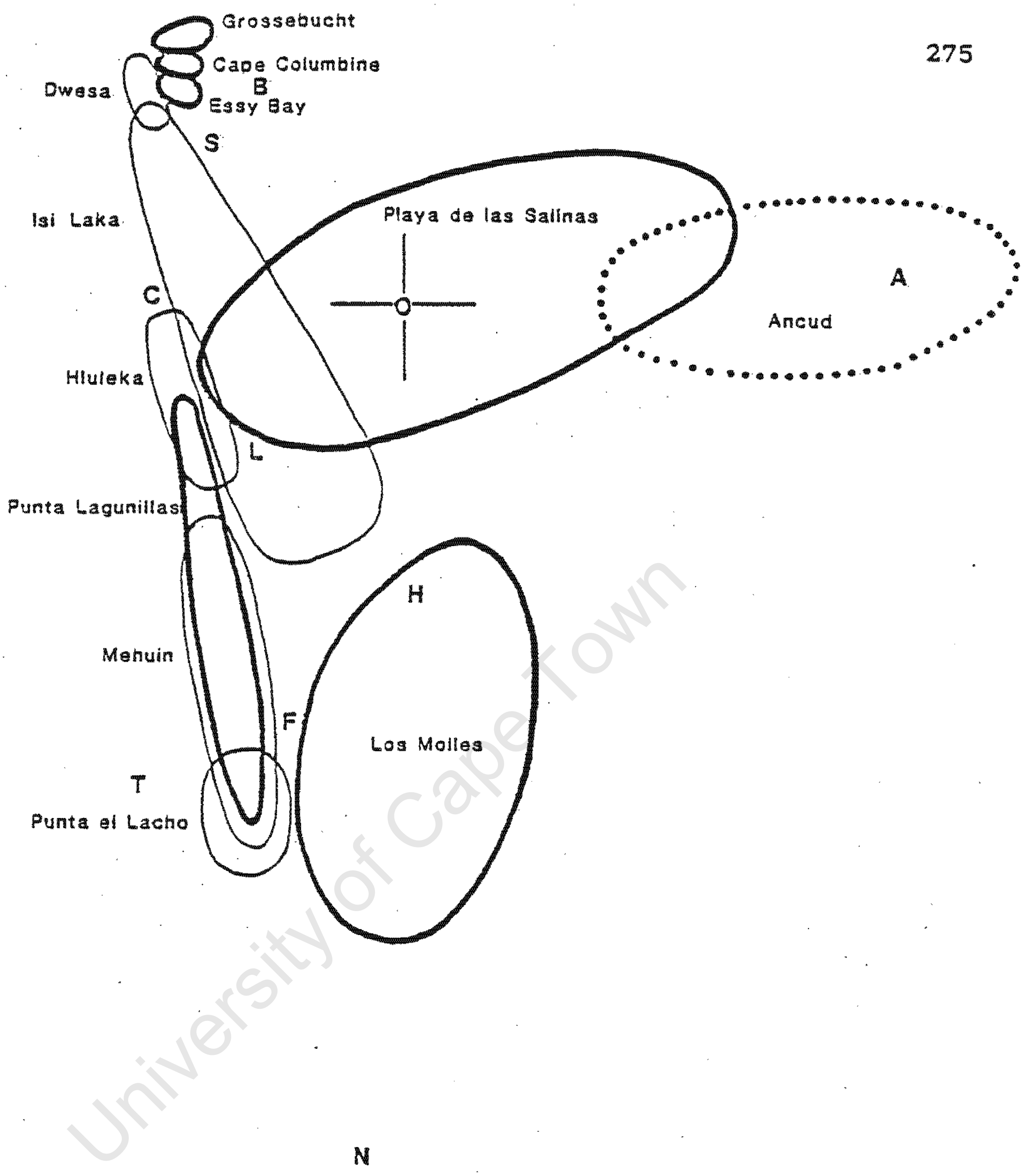


Fig. 5.6 Correspondence analysis of mid-intertidal community structure at upwelled and non-upwelled sites. Bold lines = upwelled sites, thin lines = non-upwelled sites, dotted line = Ancud. Key to variables: A = % algal cover, B = limpet biomass, F = % sessile filter-feeder cover, S = % vacant space, L = limpet number, C = carnivore number, H = number of other herbivores, N = anemone number, T = *Littorina* number, O = origin

responsible for the overriding separation of sites. The first factor of the correspondence analysis (horizontal separation along axis 1) identifies algal cover and vacant ground-space as the variables accounting for most of the inertia of this factor (76.5% and 10.9% respectively), and principal separation along the vertical axis (factor 2) is due to contributions by sessile filter-feeder cover (56.4% of inertia in factor 2) and limpet biomass (20.0%). Abundance of anemones and limpet number together account for 80.3% of the inertia in factor 3, while variations in the abundance of carnivores account for 22.0% of the inertia in factor 4.

Sixty-one per cent of the total inertia is explained by the first 2 factors, while the first 4 factors account for 85% of the inertia of the analysis. Variations in algal cover account for the largest percentage of total inertia in the analysis (25.3%), and variations in *Littorina* density account for the least inertia (0.2%). No variable appears close to the origin in Fig. 5.6, indicating that no functional group is equally represented at all sites.

Discussion

Effects of nutrient enrichment

The hypothesis that rocky intertidal community structure and functioning may be influenced by the nutrient status of waters washing this zone has not been tested before. The growth and reproduction rates of almost all plants are nutrient-limited (Tilman 1982), and an enhanced supply of essential nutrients has been shown to stimulate plant production in terrestrial, aquatic and marine environments (Golovkin 1967; Ganning and Wulff 1969; Zelickman and Golovkin 1972; Smith 1976; Chapman and Craigie 1977; Gillham 1977; Part 2). Differences in rates of primary production between intertidal habitats are known to affect the growth rates and life-history parameters of certain herbivorous species (Creese 1980; Underwood 1984; Part 3.3), but the implications of differences in algal production rates have not been considered in terms of the functioning of intertidal communities.

In the present study I found that intertidal algal cover on rocky shores is significantly higher in areas of coastal upwelling than in non-upwelled areas (excluding Ancud). Although mean algal cover at upwelled sites nowhere exceeds 5%, the large mean biomass of limpets supported at upwelled sites indicates enhanced algal production as a factor contributing to the higher levels of algal cover. In non-upwelled areas which support a low limpet biomass and thus experience reduced grazing pressure, the percentage algal cover remains very low. Since mean number of limpets per 0.5 m^2 is not significantly different between shores in areas of upwelling and non-upwelling, higher limpet biomass on shores with upwelling is attributable to faster limpet growth rate and to the attainment of larger individual size by limpets in these areas with enhanced algal production.

This is illustrated at the Chilean non-upwelled sites, Mehuin and Punta el Lacho, where mean algal cover is 0%, mean limpet numbers are 344 and 146 per 0.5 m^2 respectively, and median limpet length is 7 mm. At Ancud, however, where mean algal cover is 24.7% and limpets of the same species average 61 per 0.5 m^2 (Fig. 5.5), median limpet length is 18 mm.

Intertidal limpets graze primarily algal spores and sporelings (Branch 1981) and their grazing activity, together with the 'bulldozing' effect of their movements, can keep the intertidal substratum free of settling organisms (Dayton 1971). Consequently, the amount of vacant ground-space present in samples from the mid-intertidal communities considered is significantly correlated with the limpet biomass present. The southern African upwelled sites are characterized by having large limpet biomasses and no settlement of sessile, space-occupying filter-feeders (i.e. 100% vacant ground-space). At sites where limpet biomass is lower, sessile organisms are able to settle in ungrazed areas and become established. This phenomenon characterizes community structure at all the Chilean sites except Ancud.

Variations in the extent of nutrient enrichment

The range of responses in community structure to upwelling is very wide and, in addition, for each type of community structure represented in the group of upwelled sites (i.e. dominated by ground-space, or by sessile organisms, or comprising a mixture of components), a site with similar community structure can be recognized from the group of non-upwelled sites. Certainly, detailed community analysis (Fig. 5.6) shows no division into upwelled and non-upwelled sites. Although sites in areas of coastal upwelling are washed by nutrient-rich waters at times, the extent, duration and timing of upwelling events varies greatly. Upwelling usually occurs in response to wind movement, which may vary seasonally (Codispoti 1981), and the duration and intensity of upwelling are unpredictable from year to year, let alone for different current systems and continents. In addition, the sites were visited at different times of year which may have confounded comparisons between sites of seasonally variable parameters, such as algal cover.

It is likely that nutrient regimes vary substantially within the groups of selected upwelled and non-upwelled sites, and that categorization of sites into 'nutrient-rich' and 'nutrient-poor' would be more informative. For example, the Dwesa site, although not in a region of coastal upwelling, is positioned between the mouths of 2 major rivers, the Nqabara and the Mbashe, both with catchments in agriculturally developed areas. Nutrient enrichment of the Dwesa shores from this source may be considerable. Intertidal community structure at Dwesa is most similar to that at the southern African upwelled sites (Fig. 5.6). At Ancud, Chile, where nutrient enrichment from sewage occurs, algal production is enhanced significantly. Although a relatively high limpet biomass is present at this site (Fig. 5.5), it appears that grazing by limpets cannot control the profuse algal growth, and mats of foliose algae have formed on the shore. At this site the rate of algal production probably exceeds the rate at which limpets can graze, given the restrictions of tidal cycles and radula size. In addition, it is possible that the removal, by man, of limpets from these shores may exacerbate this situation.

Effects of exploitation by man

It has been assumed that the intertidal communities at each site are in a state of equilibrium (sensu Connell and Sousa 1983), and that a community dominated by limpets and vacant ground-space, and one dominated by sessile filter-feeders are two stable communities which emerge in response mainly to differences in intertidal nutrient levels and consequent rates of primary production. However, some sites show a community structure which is intermediate, comprising moderate representation by both components, e.g. Playa de las Salinas, Fuerteventura. Access by man to this area has been restricted for approximately 10 years, but limited exploitation of intertidal organisms, particularly of *Patella candei* and *Perna picta* probably occurs (Hockey 1987), with the result that the intertidal community may have been prevented from reaching a stable state.

The high percentage algal cover (up to 15%) on the shores at Playa de las Salinas indicates that limpet activity is supressed and is not sufficient to keep the rocky substratum clear of developing algal sporelings or settling sessile animals (cf. Hockey and Branch 1984). The sites at Dwesa, Hluleka and Isi Laka also have been protected for up to 10 years and, although it has been suggested that the recovery of exploited intertidal communities in this area is rapid (Hockey and Bosman 1986), it is possible that communities at these sites have not yet reached a stable state. At higher latitudes recovery from severe environmental disturbance (e.g. an oil spill) may take up to 20 years (Hawkins et al. 1983).

In Chile intertidal and subtidal populations of the 'loco' *Concholepas concholepas* have been heavily exploited for many years (Guisado and Castilla 1983). This predator forages on, amongst other things, sessile filter-feeders such as mussels and barnacles and its exploitation, together with the exploitation of large fissurellid limpets (Oliva and Castilla in press) may result in the removal of space-creating organisms, and the consequent establishment of sessile elements in the community. Although the sites chosen in this study were, with the exception of Ancud, in marine reserves and protected areas, it is possible that these communities have not been protected for long enough to be representative of undisturbed communities, and that some of the community attributes recorded are due to the effects of exploitation by man (Moreno et al. 1984).

Effects of genetic differences

Individuals of the dominant limpet species on the central Chilean coast (*Scurria variabilis*) are small in size and even at Ancud, where food is abundant, their median size reached only 18 mm, while the largest individual recorded at this site measured 24 mm. At Grossebucht on the west coast of southern Africa, median length of *Patella granularis* was 30 mm and the largest individual measured 44 mm. Although limpet growth rate is dependent on food availability (Fletcher 1984, Parts 3.1 and 3.3), inter-specific differences in the maximum limpet size attainable are genetically determined (Branch 1974), and it is possible that genetic differences between these limpet species prevent individuals from functioning in the same manner within the intertidal system. At a density of up to 680 per 0.5 m^2, as recorded at Mehuin, Chile, it is possible that these limpets (which have a calculated total dry biomass of only 1.6 g) are not limited by food supply, but by space.

Alternate community structures: a response to nutrient enrichment?

The intertidal communities considered in this study cannot be separated into 2 clear groups, characteristic of shores with and without coastal upwelling respectively. However, 2 very different types of intertidal community are evident. The first is based on a system of space creation by numerous large limpets, and is characterized by the predominance of vacant rocky surface (e.g. Grossebucht, Essy Bay and Cape Columbine). The second is characterized by the occurrence of extensive beds of sessile, space-occupying organisms which are competitively dominant, and by the absence of large grazers (e.g. Mehuin, Punta el Lacho and Los Molles).

Limpets are herbivorous, and therefore the biomass of limpets supported on the shore is dependent on the rate of algal production (Part 3.3). An intertidal system dominated by large limpets may indicate enhanced algal production due to nutrient enrichment of nearshore waters. Differences in the extent of algal cover at the study sites accounted for the largest amount of variation in community structure, and although the relationship between algal production rate and algal cover has not been investigated here, it has been shown that profuse algal cover on the rocky shores of seabird-breeding islands reflects enhanced algal production and nutrient-enriched intertidal waters (Parts 1 and 2). Thus intertidal and nearshore nutrient concentrations may play an important role in determining the functional structure of rocky intertidal communities. Upwelled waters may convey excess nutrients into the intertidal region, but because the nutrient status of upwelled waters is very variable, upwelling per se does not modify intertidal community structure in a characteristic manner.

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SYNTHESIS

In this section the essential findings of this study are summarized, and placed in context against the background of the search for a general theory of the processes influencing biological structure in rocky intertidal communities. Some of the findings are summarized in Table 6.1.

Summary of findings

1. Nutrient concentrations in intertidal rockpools are consistently higher on islands in Saldanha Bay than on nearby mainland shores. Seabirds breed and roost on the islands, and their guano washes from the shores into the sea, enriching intertidal waters with nutrients. A zone of enrichment surrounds each island and extends to nearby mainland shores under the influence of prevailing winds and currents.

2. The production rates of intertidal algae are more rapid on most nutrient-rich shores than on unenriched shores. In addition, the rate of algal production on unenriched shores is enhanced by the experimental introduction of seabird guano in solution. On nutrient-rich shores, where the growth rate is rapid, algae become foliose and form extensive mats. On unenriched mainland shores foliose algae are rare or absent.

3. The growth rate of the dominant herbivorous limpet *Patella granularis* is correlated with the rate of intertidal

algal production, indicating that algal production rate is an index of limpet food availability. On nutrient-rich shores the rapid limpet growth rate leads to the presence, in the population, of large, fecund individuals. On unenriched shores limpets generally are small. Limpets translocated from nutrient-rich to unenriched shores (and vice versa) show growth rates comparable with those of the local limpets, indicating that differences in growth rates between limpet populations are not genetically fixed.

4. African Black Oystercatchers *Haematopus moquini* prey on *P. granularis*, and limpet mortality is highest on island shores where oystercatchers are most abundant. Limpet survival is enhanced in individuals hidden by a covering of foliose algae on their shells, and in individuals measuring more than 50 mm in length (oystercatchers preferentially remove limpets of between 20 and 40 mm in length). Large limpets thus have a refuge from predation by oystercatchers, and their contribution of gametes becomes significant in terms of the population reproductive output.

5. Life-history patterns of populations of *P. granularis* at different sites are influenced by the rate of algal production at each site. Limpet growth rate, size and age at first reproduction, and life-time reproductive output are all modified by the rate of algal production. Limpet populations on unenriched mainland shores are predicted to have low life-time reproductive outputs. Conditions of limpet production and reproduction on these shores are

hypothesised to be insufficient to support the predatory pressure of large densities of oystercatchers for long periods.

6. The grazing activity of limpets on unenriched mainland shores prevents the development of foliose algae. On nutrient-rich shores, however, where the rate of algal production is enhanced and the extent of herbivory is reduced as a consequence of oystercatcher predation on limpets, extensive mats of foliose algae develop. These mats form a foraging habitat for small shorebirds, which modify both the species composition and abundances of the algal mat infauna.

7. Comparisons of the intertidal communities on other southern African seabird-breeding islands with the communities on adjacent mainland shores confirm the importance of nutrient availability in modifying community structure. In particular, the features explaining most of the variation in community structure between island and mainland sites are the extent of foliose algal cover, and the biomass and density of limpets supported.

8. The extent of foliose algal cover, and the biomass and density of limpets supported, are also important in differentiating between intertidal communities in geographically disparate regions of coastal upwelling and in regions where upwelling does not occur. However, these trends are not clear-cut, due possibly to variations in the

nature of the nutrient enrichment associated with different upwelling systems.

Nutrient status and primary production - neglected factors in the search for generalizations

Ecologists, in their quest to identify and understand the factors which influence intertidal community structure on the world's rocky shores, have tended to use an inductive approach. From the results of numerous, discrete analyses of patterns of community organization, and the mechanisms accounting for them, have arisen hypotheses of wider scope and even generalizations about the structure of rocky intertidal communities. 'Generalized' models currently espoused in the literature concern the roles of physical factors, predation and competition (Paine 1966, 1977; Dayton 1971; Connell 1972, 1975; Levin and Paine 1974; Menge 1976; Menge and Sutherland 1976; Lubchenco 1978). However, there are many instances in which currently accepted generalizations do not explain observed structure, and Underwood and Denley (1984) propose alternative hypotheses which might explain the results of several studies used to generate these models. It is surprising, considering the lack of applicability of these generalizations (if they can be considered generalizations at all), that intertidal ecologists have seldom considered the possible role of differing rates of primary production in influencing intertidal community structure.

Most of the experimental studies used as a basis for generating models explaining intertidal community structure (e.g. Levin and Paine 1974; Paine 1974; Connell 1975; Menge and Sutherland 1976) have been conducted on shores with obvious, competitively dominant species, or with large, voracious predators. Not surprisingly, these elements have attracted attention, while less obvious elements (such as the supply of algal food for herbivores) have been ignored. In a few studies differences in the rate of primary production have been shown to influence the life-history patterns of intertidal herbivores (Fletcher 1984a, b), but the consequences for other elements of the community have not been considered. Furthermore, the origin of differences in primary productivity between sites (e.g. variations in the availability of inorganic nutrients in intertidal waters) has never received attention as an environmental variable in intertidal systems.

Biological communities on island and mainland rocky shores in the Saldanha Bay area are composed of similar suites of species, particularly of numerically dominant species. However, the patterns of organization of these organisms differ considerably between the sites. Communities on mainland shores outside the Bay are characterized by the absence of foliose algae and the presence of high densities of limpets (*Patella granularis*). On nutrient-rich shores, communities are dominated by mats of foliose algae and the limpets occur at lower densites. In addition, limpet growth rates on nutrient-rich shores are enhanced, and the limpets attain larger sizes, when compared with limpets on unenriched mainland shores outside the Bay. Shorebirds are abundant in the intertidal regions of islands, and are scarce, or absent, on mainland shores.

Differences in community structure on island and mainland shores in the Saldanha Bay area are explicable largely in terms of differences in the levels of nutrients in the intertidal waters, and the consequences for plants and animals in the community. An ecologist viewing the intertidal community at Cape Columbine might conclude that the observed pattern of organization on this shore is a result primarily of competition between limpets (Branch 1984). Grazing by limpets keeps the shore free of foliose algae. On the shore of Marcus Island, approximately 40 km away, the ecologist might identify predation by oystercatchers as being of primary importance in explaining the structure of the intertidal community (Hockey and Branch 1984). Here, the removal by oystercatchers of limpets reduces the extent of herbivory. Many algae are not grazed and become foliose and, in addition, competition for food between limpets is less intense. This might be considered another case in which the relative importances of processes influencing community structure differ from site to site, with no apparent explanation.

This study suffers from the limitation that experimental sites could not be replicated in their entirety. The rigorous statistical testing of mean values was thus not possible (Hurlbert 1984). However, an experimental design incorporating more than one study site at each locality would not necessarily suffer less from this problem, spatial patchiness of intertidal organisms being, at times, as great within as between geographical areas. Despite this drawback, the potential of birds in modifying intertidal community structure in the Saldanha Bay ares is clear. The impact of predatory shorebirds on the densities and population dynamics of intertidal prey on islands in Saldanha Bay is comparable with the impact of avian predators in other rocky intertidal systems (Lewis and Bowman 1975; Frank 1982; Marsh 1986). However, in this study the impact of predation is modified by the presence of seabirds, which are not themselves components of the intertidal community, and which have not previously been considered important in the functioning of intertidal communities.

However, a major, if inconspicuous, difference between the study sites is the concentration of nutrients in the intertidal waters. Viewed in this light, these sites represent points on a continuum of nutrient availability. Differences in the nutrient status of intertidal waters certainly influence the rates of primary production in all intertidal systems, and it is possible that the impacts of processes such as competition, predation and physical disturbance on intertidal communities are mediated by the productivity of the system. The categorization of all

Table 6.1. Summary of data relating to intertidal community structure in the mid-shore region at sites in the Saldanha Bay area

	MALGAS ISLAND	JUTTEN ISLAND	MARCUS ISLAND	NORTH BAY	BOMGAT	MAURITZ BAY	CAPE COLUMBINE
Mean NO_3-N ± S.D. (ug at l^{-1}) in rockpools	11.8 7.2	12.6 6.8	10.5 9.0	9.7 9.3	4.9 4.3	7.4 3.2	5.4 2.7
Mean PO_4-P ± S.D. (ug at l^{-1}) in rockpools	5.2 3.9	10.0 18.1	16.9 50.8	2.5 1.5	1.6 1.0	1.4 0.7	1.6 0.5
Mean mid-shore primary production ± S.D. (ug chlorophyll cm^{-2} mo^{-1}	0.66 1.22	7.51 11.44	6.75 7.91	1.27 1.56	0.05 0.04	3.37 4.24	0.16 0.47
Mean mid-shore limpet density (± S.D.) per 0.5 m^2 vacant rock	18.0 12.1	25.3 18.5	43.1 13.9	79.4 13.6	33.0 13.7	32.9 6.0	124.8 21.3
Mean density oystercatchers per km - 1981 (Hockey 1983)	41.3	78.4	58.3	6.9	2.2	3.6	3.6

shores, according to their nutrient status and rates of primary production, may lead to an understanding of differences in the importance of processes influencing intertidal communtiy structure in each system. Thus I propose that ecologists seeking universal truths about the structure of rocky intertidal communities should consider the productivity of systems used in comparisons, and should assess particularly the availability of nutrients to the primary producers in each system.

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